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# THE GENUS *TROCHULUS* CHEMNITZ, 1786 (GASTROPODA: PULMONATA: HYGROMIIDAE) – A TAXONOMIC REVISION

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ABSTRACT: The revision of the genus *Trochulus* Chemnitz, 1786 is based on conchological and anatomical characters of 4,377 adult specimens (3,190 dry shells and 1,187 alcohol-preserved snails) from 303 localities. Shell descriptions with the variation ranges, based on morphometric analysis, reproductive system descriptions with figures, identification key, synonymy, and distribution maps are provided. The most significant diagnostic characters are: shell shape and colour, umbilicus shape and size, durability of hairs, penis/epiphallus length ratio, flagellum/epiphallus length ratio, number and arrangement of mucous glands, length and location of dart sacs. Three names are synonymised: *T. plebeius, T. concinnus* and *T. hispidus*. Phylogenetic analysis yielded 96 equally parsimonious trees; the strict consensus procedure resulted in an incompletely resolved cladogram, with two distinct monophyletic groups of species: the *villosus* group including *villosus*, *czarnohoricus*, *unidentatus* and *bielzi*, and the *striolatus* group, with *striolatus*, *graminicolus*, *montanus, caelatus*, *hispidus*, *suberectus, edentulus*, *bakowskii, luridus*, *filicinus* and *leucozonus*. These two groups and *erjaveci, biconicus, villosulus, clandestinus, lubomirskii* and *piccardi*, form a phylogenetic bush. The monophyletic groups appearing in the cladogram are not compatible with any of the earlier proposed divisions. Most members of *Trochulus* inhabit the Alps and the Carpathians. The only widely distributed species is *T. hispidus*. The second most widespread species is *T. striolatus*. The remaining species are endemics with limited ranges. The number of species within particular parts of the range points to the Alpine-Carpathian area as the diversity centre of the genus.

KEY WORDS: terrestrial snails, Hygromiidae, *Trochulus*, revision, phylogeny

## INTRODUCTION

The genus *Trochulus* is commonly known as *Trichia*, but the ruling by ICZN, Opinion 2079 (BZN 61 (3) Sep 2004) resulted in replacing *Trichia* Hartmann, 1840, which turned out to be a junior homonym of *Trichia* de Haan, 1839 (Crustacea: Brachyura), with *Trochulus* Chemnitz, 1786.

Prior to this study the genus *Trichia* included 20 nominal species (KERNEY et al. 1983) inhabiting Europe, especially the Alps and the Carpathians, some of them with many subspecies and forms (WAGNER 1915, KLOETI-HAUSER 1920, POLIŃSKI 1928, FORCART 1965, SHILEYKO 1978a). Recently, a new species *Trochulus piccardi* Pfenninger et Pfenninger, 2005 was described from the Swiss Alps. Moreover, some species from northern Africa were included in the genus: *Trichia roseotincta* (Forbes), *T. faidherbiana* (Bourguignat), *T. baccueti* (Bourguignat), *T. mongrandiana* (Bourguignat) and *T. zonitomaea* (Letourneux). The anatomical data provided by SZIGETHYI (1976) who analysed only the penial papilla of these species, do not solve the problem of their generic status. The conchological features of the specimens deposited in the collection of the Museum and Institute of Zoology, Polish Academy of Science (Warsaw) and habitat preferences of some species suggest that in all likelihood they represent another genus and, consequently, they are excluded from this publication.

None of the numerous previous papers dealt with all the members of the genus (WAGNER 1915, KLOETI-HAUSER 1920, POLIŃSKI 1928, FORCART 1965, SHILEYKO 1978a, BANK 1995), their classification and phylogenetic relationships among them were ob-

scure, and there were no data on their conchological and anatomical variation; likewise there was no information on the anatomy of some species.

Most species of *Trochulus* show a wide conchological variation, resulting in identification problems. A conspicuous example is the fact that LOCARD (1895–1896) – a representative of the French Nouvelle École – distinguished 55 species of the genus in France alone. As a result of the synonimisation done by GERMAIN (1929) their number decreased to three! An additional impediment is the fact that most of the original descriptions are very laconic and it is unclear which species they refer to, besides, the type specimens of most species have not been preserved.

Considering the identification difficulties, the lack of data on the shell and genital variation ranges of most species (except shell variation in *T. hispidus*, see NAGGS 1985, PROĆKÓW 1997, and some morphometric data on *T. leucozonus*, see BANK 1995) and incompleteness of the distribution data, a revision of *Trochulus* seemed to be necessary.

## HISTORICAL ACCOUNT

The *Trochulus* research history starts with LINNAEUS's (1758) description – as *Helix hispida* – of the first and most common member of the genus. Subsequent species, like other members of the family Hygromiidae, were for a long time placed in the genus *Helix* Linnaeus, 1758.

Two trends, resulting in two groups of papers, can be distinguished in the previous studies on *Trochulus:* some authors tried to solve classification problems within the genus, while others focused on detailed investigations of lower rank taxa, describing new species, subspecies and forms, or providing detailed data on distribution, ecology and anatomy of some members of the genus.

The first attempts at revisions were made by CLESSIN (1874) and LOCARD (1888) at the end of the 19th c. Both studies were based only on conchological characters and the latter author in his subsequent papers (LOCARD 1895–1896), like RISSO (1826), GRAS (1840), BOURGUIGNAT (1864), MABILLE (1868, 1877), LETOURNEUX (1869), RAMBUR (1869), SERVAIN (1880) and CAZIOT (1910), introduced an excessive number of specific names, having no justification in reality.

WAGNER (1915) published a revision of the Balkan members of the genus, based on both conchological and anatomical characters. He included the investigated species in the genus *Fruticicola* sensu WAGNER (1915), in which he distiguished two subgenera: *Fruticicola* sensu stricto and *Perforatella* Schlüter, 1838. However, in his study he did not specify the subgeneric characters. *Fruticicola* was characterised as inhabiting "Westliche Balkanländer von der Save bis nach Mazedonien" (WAGNER 1915: 51 [479]), and *Perforatella* as snails with a narrow shell and partly or entirely covered umbilicus, 5.5–7 slowly increasing whorls, a well developed lip where a basal tooth may be present, shell surface with fine growth lines and dense, short setae. He described their radulae and reproductive systems as typical (WAGNER 1915: 58 [486]).

KLOETI-HAUSER (1920) published a revision of seven Swiss species of *Trichia*, describing their genital characters. However, the author neither described the shells nor preserved the specimens; he only gave exact data on his collecting localities.

POLIŃSKI (1928) carried out a critical conchological and anatomical revision of the Alpine and Carpathian species. He placed them within three sections of the genus *Fruticicola* Held, 1837: *Petasina* Beck, 1847, *Filicinella* Poliński, 1928 and *Edentiella* Poliński, 1928, giving shell and reproductive system characters, and type species as well. He also analysed the distribution of the included species.

In 1965 FORCART clarified the taxonomic status of some problematic species, based on conchological and anatomical studies of materials collected, among other localities, in the sites listed by KLOETI-HAUSER (1920).

SHILEYKO (1978a, b) provided shell and reproductive system descriptions of *Trichia* species inhabiting the area of the former Soviet Union and proposed their cassification. *Trichia* sensu auct. (WAGNER 1915, POLIŃSKI 1928, FORCART 1965) and closely related genera were treated as "*Trichia* sensu lato" and divided into several genera. The members of *Trichia/Trochulus* in its traditional sense were included in three of them, i.e. *Plicuteria* Shileyko, 1978, *Trichia* Hartmann, 1840, with subgenera *Petasina* Beck, 1847 and *Trichia* s. str., and *Edentiella* Poliński, 1924.

FALKNER (1985) accepted POLIŃSKI's (1928) "groupe *Perforatella* auct." as "eine echte monophyletische Einheit und lassen sich – ebenfalls unter der Einschränkung des jetzigen Kenntnisstands – mit keiner anderen Gattung der Trichiinae zu einer gesichert monophyletischen Gruppe vereinigen" and thereby elevated the subgenus *Petasina* Beck, 1847 to the generic rank, retaining its contents and system as proposed by POLIŃSKI (1928).

Later NORDSIECK (1993), in his proposed classification system of Palaearctic Hygromiidae, distinguished three genera within *Trichia* sensu KERNEY et al. (1983), i.e. *Trichia* Hartmann, 1840, *Petasina* Beck, 1847 (+*Edentiella* Poliński, 1928) and *Plicuteria* Shileyko, 1978. *Petasina* was divided in two subgenera: *Petasina* s. str. and *Edentiella*.

Recently, three molecular analyses of helicoid phylogeny have been published (STEINKE et al. 2004, KOENE & SCHULENBURG 2005, MANGANELLI et al. 2005). However, they deal only with some species and focus on phylogenetic analysis at the level of family or selected genera.

Among the researchers dealing with the systematics of *Trochulus* at the specific or subspecific level it is necessary to mention WAGNER (1915) and POLIŃSKI (1928), both of whom described a large number of subspecies, and FORCART (1965), who tried to unravel the systematic complexity among *Trichia hispida* sensu lato. Only few studies dealt with morphometric analysis of *Trichia* from Great Britain (NAGGS 1985) and shell variation of *T. hispida* from Poland (PROĆKÓW 1997). KRAUSP's (1952), MAHLER's (1952), HUDEC's (1964, 1965, 1972) and KAISER's (1966) papers all contributed to the knowledge of the genus, as well as later FALKNER's (1985) and BANK's (1995) articles aiming to solve the systematic position of some subspecies in the genus *Petasina*.

*Trochulus plebeius* and *T. hispidus* in the Czech Republic have been subject to karyological analysis. All the studied populations have identical numbers of chromosomes (n=23) of a similar morphology. Sequence analysis of 16S rDNA and COl genes showed two divergent groups of *T. hispidus* populations, differing in their geographic distribution (north-western versus eastern) but with overlapping morphology (HRABAKOVA et al. 2007).

The recent Fauna Europea project (BANK 2006) lists 49 taxa of *Trochulus* and *Petasina*. They belong to two (*Trochulus* with 26 taxa and *Plicuteria* with 1 taxon), and three (*Petasina* with 6 taxa, *Edentiella* with 7 taxa and *Filicinella* with 9 taxa) subgenera, respectively. The high number of subspecies (20) is striking. Some of them seem to be dubious entities requiring further studies.

## MATERIAL AND METHODS

The material used in the study was obtained from the following collections: BMNH – The Natural History Museum, London, England, MIZW – Museum and Institute of Zoology, Polish Academy of Science, Warsaw, MPW – Natural History Museum, Wrocław University, NHMB – Naturhistorisches Museum, Bern, NHMW – Naturhistorisches Museum, Wien, UAM – Department of General Zoology, Adam Mickiewicz University, Poznań, UŁ – Department of Invertebrate Zoology and Hydrobiology, University of Łódź, ZW – specimens collected especially for the purpose of this study, now deposited at MPW.

A total of 4,377 adult specimens, including 3,190 dry shells and 1,187 alcohol-preserved snails were examined. In the list of samples "alc." denotes alcohol-preserved material and "s." – dry shells. The shells were measured with the accuracy of 0.1 mm. The measurements are shown in Fig. 1. Besides, the following coefficients of shell proportions were calculated: height/width ratio (H/W), relative height of body whorl = body whorl height/shell height ratio (bwH/H), umbilicus relative diameter = umbilicus major diameter/shell diameter ratio (U/D), ratio of umbilicus major to its minor diameter (u/U). Whorls were counted according to EHRMANN's (1933) method. Morphometric data were statistically analysed with respect to the significance of differences between populations (Duncan test). Statistical analysis was performed with Statistica 5. The specimens for anatomical examination were drowned in water and preserved in 70–75% ethyl alcohol. Prior to dissection their shells were dissolved in 1N (10%) HCl (5–10 min), and the remaining periostracum removed.

All figures were drawn using the stereomicroscope equipped with an eyepiece grid. Photographs of the respective type specimens were obtained from the Naturhistorisches Museum in Vienna. SEM photos of gold-coated shells were taken at the laboratory of the Institute of Materials Science and Applied Mechanics,

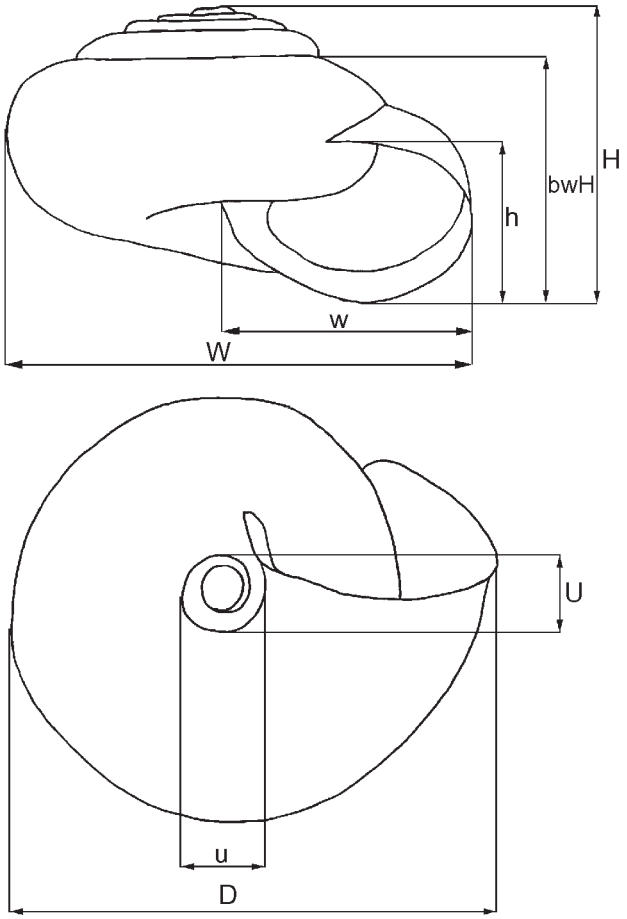



Fig. 1. Shell measurements: H – shell height, W – shell width, D – shell diameter, bwH – body whorl height, h – aperture height, w – aperture width, U – umbilicus major diameter, u – umbilicus minor diameter

Wrocław University of Technology, using the microscope Jeol JSM–5800 LV.

The members of the Nouvelle École (such as LOCARD 1880, 1881, 1882, 1884–1889, 1888, 1894) described many species of the genus *Trochulus*, which were later synonymised. In cases when references and/or specimens of nominal species are not available, the synonyms are marked with an asterisk and cited after GERMAIN (1929).

## GENERAL CHARACTERISTICS OF THE GENUS

### Diagnosis

Shell from conical to flattened; shell diameter 3.5–14.3 mm; whorls 4.5–7.0; lip developed to various extent; shell surface with radial striae and hairs at least in juveniles. On internal vaginal walls longitudinal plicae; four groups of two mucous glands each, or glands not grouped.

### Shell

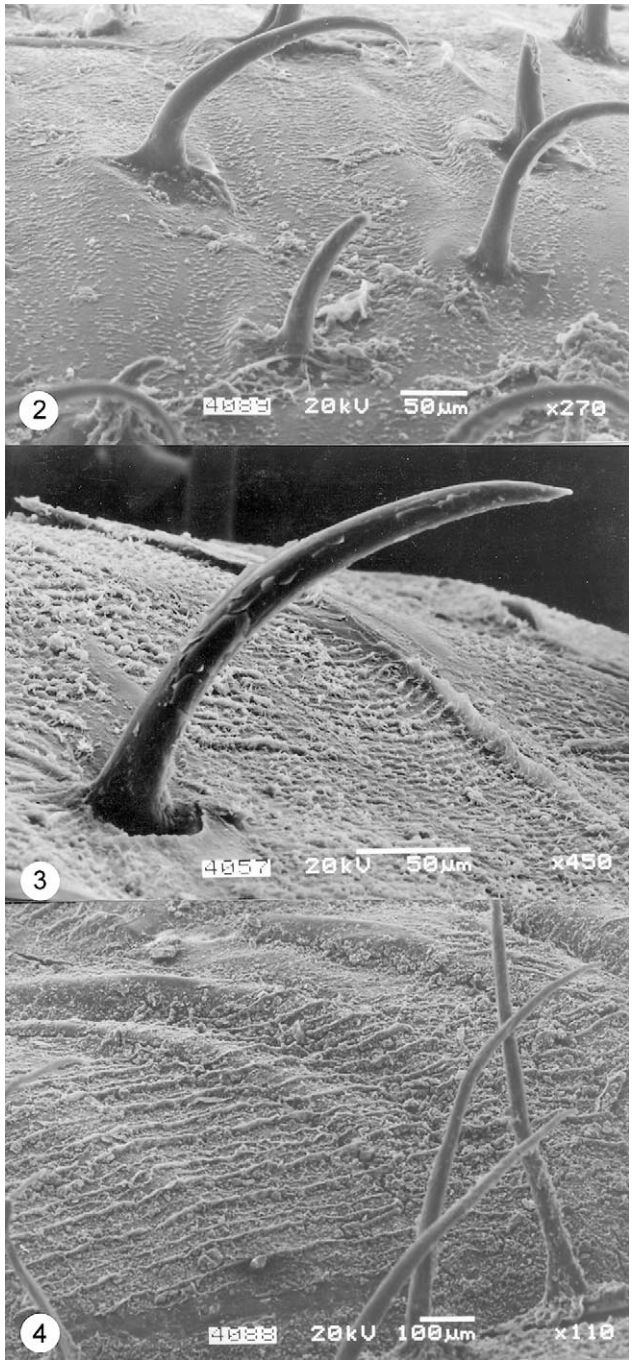
Shells of all members of *Trochulus* are dextral. Their shape varies. Most of them are depressed conical, roundish-conical (*T. striolatus*) or strongly flattened *(T. villosus*, *T. caelatus*). Shells of some species vary widely in shape, for example *T. hispidus* varies from much elevated to quite flattened. The variation is mainly of interpopulation, but to some extent also individual character.

The number of whorls in adult specimens ranges from 4.7–5.0 in *T. lubomirskii* to 7.0 in *T. unidentatus*. The individual variation is small: differences within populations reach 0.5–1 whorl. The number of whorls appears to show no or only slight differences among the species. Most interspecific differences are usually not greater than the interpopulation variation. Convexity of whorls varies greatly between species: from very flat, especially in species with flattened shells, to pretty convex in some species with conical shells. In some members of the genus (*T. hispidus*, *T. striolatus*) this character varies individually and between populations.

The umbilicus, depending on the species, is round or oval, open and wide so that the earlier whorls are visible, and its major diameter is then up to 0.24 shell diameter (*T. erjaveci*), partly covered by the columellar aperture margin, or entirely covered (some specimens of *T. bielzi*). In species with open, wide umbilicus the character is constant, whereas in those with partly covered umbilicus it varies inividually.

In all species the aperture is elliptical or crescentic, its margin usually regularly curved. It is not much variable. In the majority of species it is equipped with a white lip, sometimes weakly developed *(T. lubomirskii*, *T. villosulus*). The lip may be situated right on the aperture margin (*T. luridus, T. leucozonus*) or slightly removed from it (*T. hispidus*). In *T. unidentatus* there is a white tooth on the basal aperture margin, sometimes poorly visible. The remaining species do not have any apertural barriers.

The greatest dimension of adult specimens in *Trochulus* (shell width) ranges from 3.5–5.5 mm (the smallest specimens of *T. edentulus*) to 7.8–14.3 mm (the largest specimens of *T. erjaveci*). The aperture size ranges from 1.7 × 2.8 mm (*T. edentulus*) to 4.2 × 7.2 (big specimens of *T. erjaveci*). The intrapopulation variation of shell size is wide.

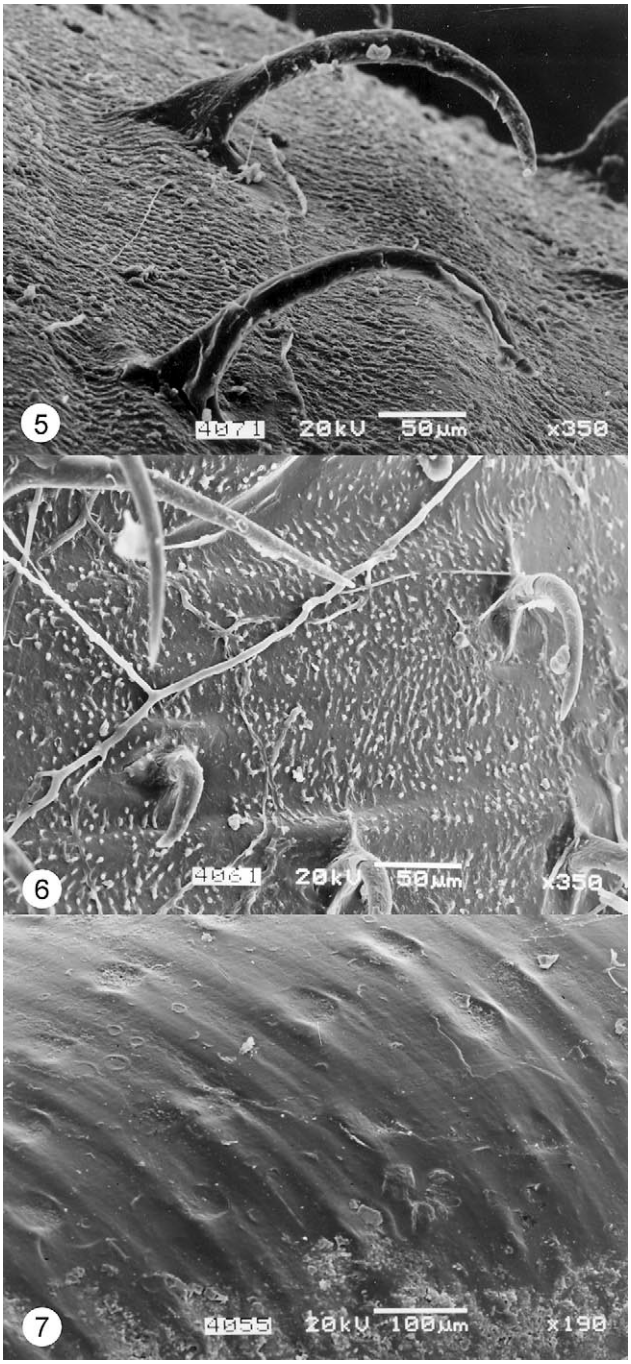



Figs 2–4. Shell surface sculpture. Undamaged shells of: 2 – *T. luridus*, 3 – *T. bakowskii*, 4 – *T. villosus*

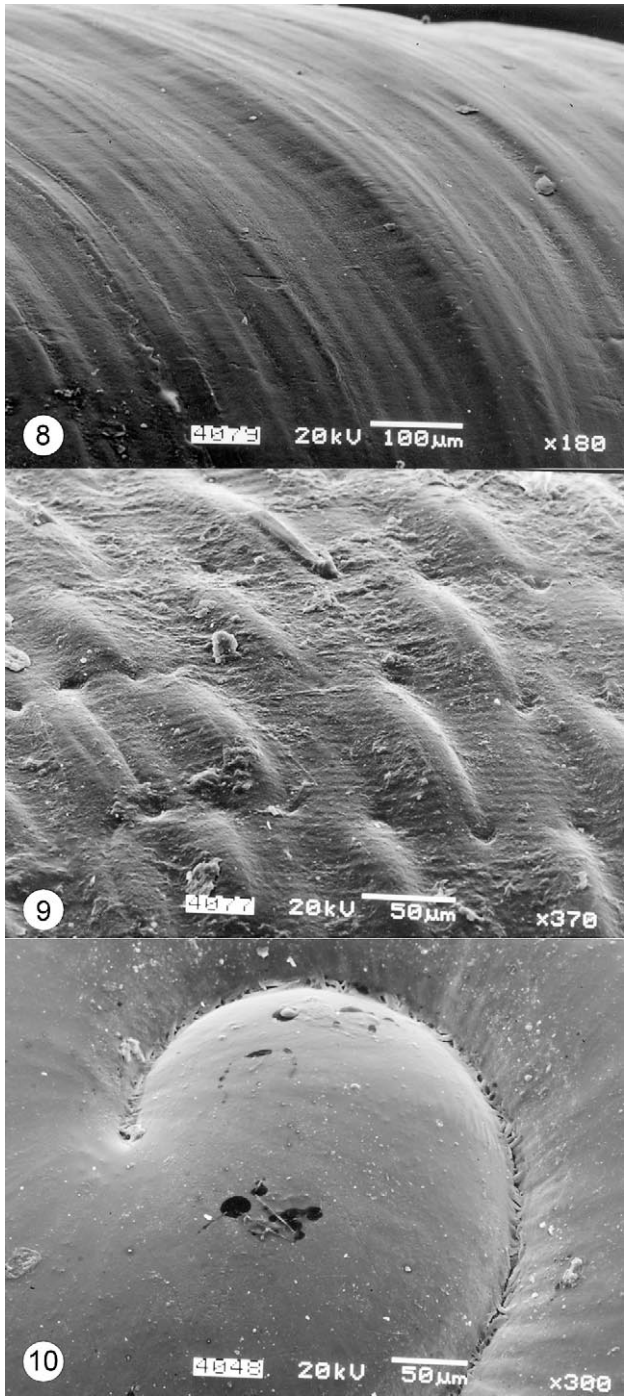
In all species juvenile shells and younger whorls of adult specimens, except the protoconch, are covered with hairs (Figs 2–6). Their length, thickness and density vary between species but shows also some individual variation. In some species (*T. villosus, T. villosulus*) the hairs are rather permanent, while in others, soon after forming each shell increment, they are lost partly *(T. bakowskii, T. hispidus*) or entirely (*T. lubomirskii, T. erjaveci*), leaving characterisic scars on the shell surface (Fig. 7).

The shell sculpture between the hairs (Figs 2–6) consists of periostracal convexities which form a network of different density, with most components often arranged radially. On shells devoid of periostracum only slightly irregular growth lines are visible (Fig. 8). Only the shell surface of *T. lubomirskii* is covered with regular radial rows of elongated convexities (Fig. 9).

In all the studied species the surface of embryonic whorls is entirely smooth (Fig. 10).




Figs 5–7. Shell surface sculpture. Undamaged shells of: 5 – *T. bielzi,* 6 – *T. unidentatus,* 7 – scars left by lost hairs on a shell of *T. hispidus* devoid of periostracum




Figs 8–10. Shell surface sculpture. Shells of: 8 – *T. clandestinus,* 9 – *T. lubomirskii* devoid of periostracum, 10 – surface of embryonic shell of *T. caelatus*

The shell colour varies among species: from very light, nearly transparent, horny-yellow, through light brown, to dark brown or reddish-brown. There is also some individual variation. In a part of individuals of some species (*T. hispidus*, *T. suberectus*, *T. striolatus*, *T. montanus*, *T. caelatus*, *T. clandestinus*, *T. graminicolus*, *T. erjaveci*, *T. unidentatus*, *T. edentulus*, *T. filicinus*, *T. leucozonus*, *T. luridus*, *T. bakowskii*, *T. bielzi*) a light, spiral band runs along the body whorl, at approximately half of its height. Shells of albino specimens are white and almost completely transparent.

Reproductive system

The structure of the reproductive organs follows the hygromiid pattern and their nomenclature is shown in Figure 11. The gonad (glandula hermaphroditica) consists of varied number (6–12) of light lobes embedded in the digestive gland. Their collecting ducts merge to form the hermaphrodite duct (ductus hermaphroditicus), which in its initial section is thin and straight, the remaining section, closer to the albumen gland, being thicker and coiled. Just next to the albumen gland the hermaphrodite duct

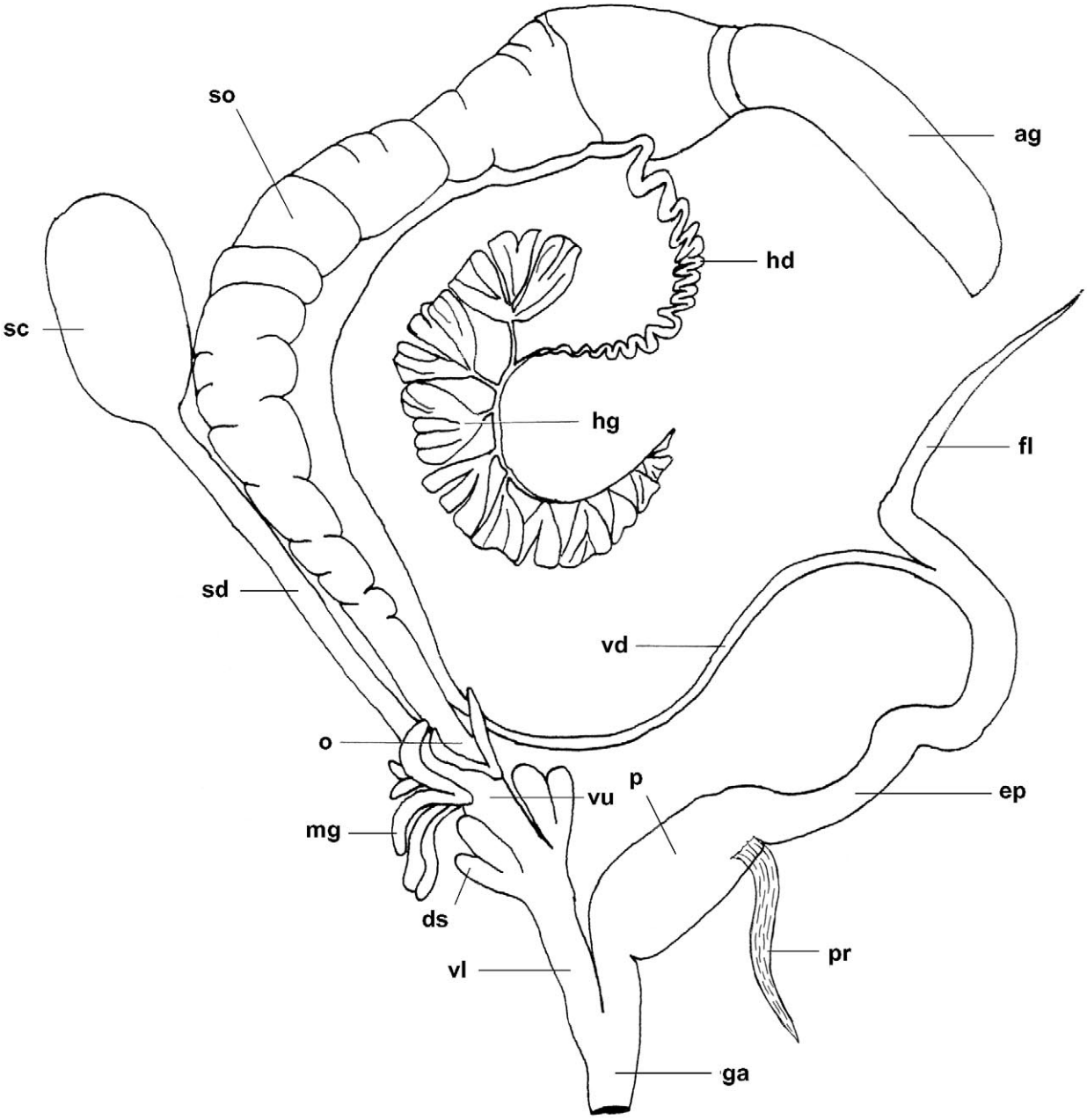



Fig. 11. Reproductive system: ag – albumen gland, ds – dart sacs, ep – epiphallus, fl – flagellum, ga – genital atrium, hd – hermaphroditic duct, hg – hermaphroditic gland, mg – mucous glands, o – oviduct, p – penis, pr – penial retractor, sc – spermatheca, sd – spermatheca duct, so – spermoviduct, vd – vas deferens, vl – lower vagina, vu – upper vagina

forms a characteristic bend, called the fertilisation chamber. The albumen gland (glandula albuminalis) is large and elongate, whitish or cream-coloured. Its size depends on the phase of reproductive activity: in male-phase individuals it is considerably smaller than in individuals producing and lying eggs. The spermoviduct (spermoviductus) is incompletely divided into female and male sections.

The free oviduct section (oviductus) is very short and passes into the vagina, consisting of the upper vagina (from the outlet of the mucous glands to the tips of the inner dart sacs) and the lower vagina (from the base of the dart sacs to the genital atrium). In a great majority of species there are four pairs of mucous glands (glandulae mucosae), but some reductions or secondary branches are also possible, and then the total number may vary from four to ten. The only species with constantly lower number of the mucous glands are *T. suberectus* – six and *T. biconicus* – four. The length and position of the glands vary: from very long (2.5 mm) and situated just above the tips of the dart sacs (*T. edentulus*), through equally long, but located in the upper section of the vagina (*T. luridus, T. leucozonus*) to short and situated just above the dart sacs (*T. villosus*).

The dart sacs are placed symmetrically in pairs, on both sides of the vagina. The sacs lying near the vagina – internal – may be as long as the outer sacs (*T. hispidus, T. suberectus, T. bakowskii, T. edentulus, T. luridus*), slightly longer (*T. villosulus, T. striolatus, T. montanus, T. bielzi, T. villosus, T. biconicus, T. erjaveci, T. caelatus, T. graminicolus, T. leucozonus, T. filicinus*) or cosiderably longer, reaching the outlet of the mucous glands *(T. unidentatus*). The exception is *T. piccardi*, in which no accessory dart sacs are visible. However, since the main dart sacs are unusually wide, a fusion of the sacs is possible (PFENNINGER & PFENNINGER 2005). In all species (no data on *T. piccardi*) only the outer dart sacs contain darts, one each. The spermathecal duct (ductus spermathecae) opens to the vagina. The spermathecal duct may be thin and very long, like in *T. villosulus, T. bakowskii, T. edentulus*, in which the spermatheca (receptaculum seminis) reaches the albumen gland, or thick, straight and short (*T. lubomirskii*), or else coiled (*T. unidentatus*), reaching approximately 1/2 spermoviduct length (*T. hispidus, T. suberectus, T. villosus*). The shape of the spermatheca varies among species: from roundish (*T. striolatus*) or oval (*T. montanus, T caelatus, T. villosulus*) to irregularly club-like (*T. lubomirskii*) or hammer-like (*T. unidentatus*). The lower vagina (below the dart sacs) can be long and narrowing toward the genital atrium (*T. bielzi, T. luridus, T. villosus*) or long and cylindrical (*T. edentulus, T. bakowskii*). On the internal walls of the vagina there are four to six longitudinal folds, depending on the species.

The spermiduct (vas deferens) passes into the epiphallus which terminates with the flagellum. The latter is as long as the epiphallus or slightly longer (*T. hispidus*). The flagellum is always longer than the epiphallus in *T. bakowskii, T. bielzi, T. leucozonus, T. filicinus,* only slightly longer in *T. hispidus, T. suberectus*, but considerably shorter in *T. lubomirskii*, *T. clandestinus*, and in *T. unidentatus* the flagellum reaches about 2/3 epiphallus length. Folds are visible on the cross-section of the epiphallus, their size depending on the species. The penis is massive and conical (*T. bakowskii*), cylindrical (*T. bielzi, T. villosus, T. filicinus*) or fusiform (*T. edentulus, T. villosulus*). Inside the penis, in its section closer to the genital atrium, there is a papilla with an apically situated pore. On its cross-section, three or more cavities are visible developed to various extent, depending on the species. The insertion of the penial retractor muscle (musculus retractor penis) is situated at the epiphallus/penis junction. The genital atrium (atrium genitale) is short.

## Ecology and bionomics

A great majority of *Trochulus* species inhabit humid and shaded habitats in forests or scrub along streams. Some are found in montane (*T. edentulus, T. villosus, T. suberectus, T. unidentatus, T. bakowskii, T. villosulus*) or submontane forests (*T. bielzi*). Even species which are widely distributed and regarded as euryoecious (*T. hispidus, T. striolatus*) prefer not very dry places. All the species like to spend humid summer days among or on plants (*Urtica dioica, Petasites* sp., *Caltha palustris, Cirsium oleraceum*), in other weather conditions and seasons they are found on the ground, in leaf-litter, under rotting timber, in moss and under stones. The exceptions are three species. *T. biconicus* inhabiting grassy limestone screes, *T. graminicolus* – known only from the type locality – found in grassy screes in sparse forests on steep mountain slopes, with pines, spruces and junipers, and *T. piccardi* living in extensively used pastures on south-facing slopes. Except *T. clandestinus*, which lives in both natural and synanthropic habitats (gardens, parks and road margins) of canton Bern (Switzerland), *T. striolatus* – a synanthrope of northern France and the British Isles, and *T. hispidus* found in anthropogenic sites in its entire distribution area, the remaining members of the genus are limited to natural or nearly-natural habitats.

The reproductive biology of *Trochulus* is completely obscure. It is only known that eggs of *T. hispidus* are calcified, white and spherical, their diameter is about 1.5 mm. Considering the fact that upon dissection no eggs were found in the female ducts, probably all species are strictly oviparous i.e. the eggs are laid immediately after they have been formed.

## Distribution

Disregarding the north African species with their very doubtful placement in the genus *Trochulus* (see Introduction), the majority of species inhabit the Alps

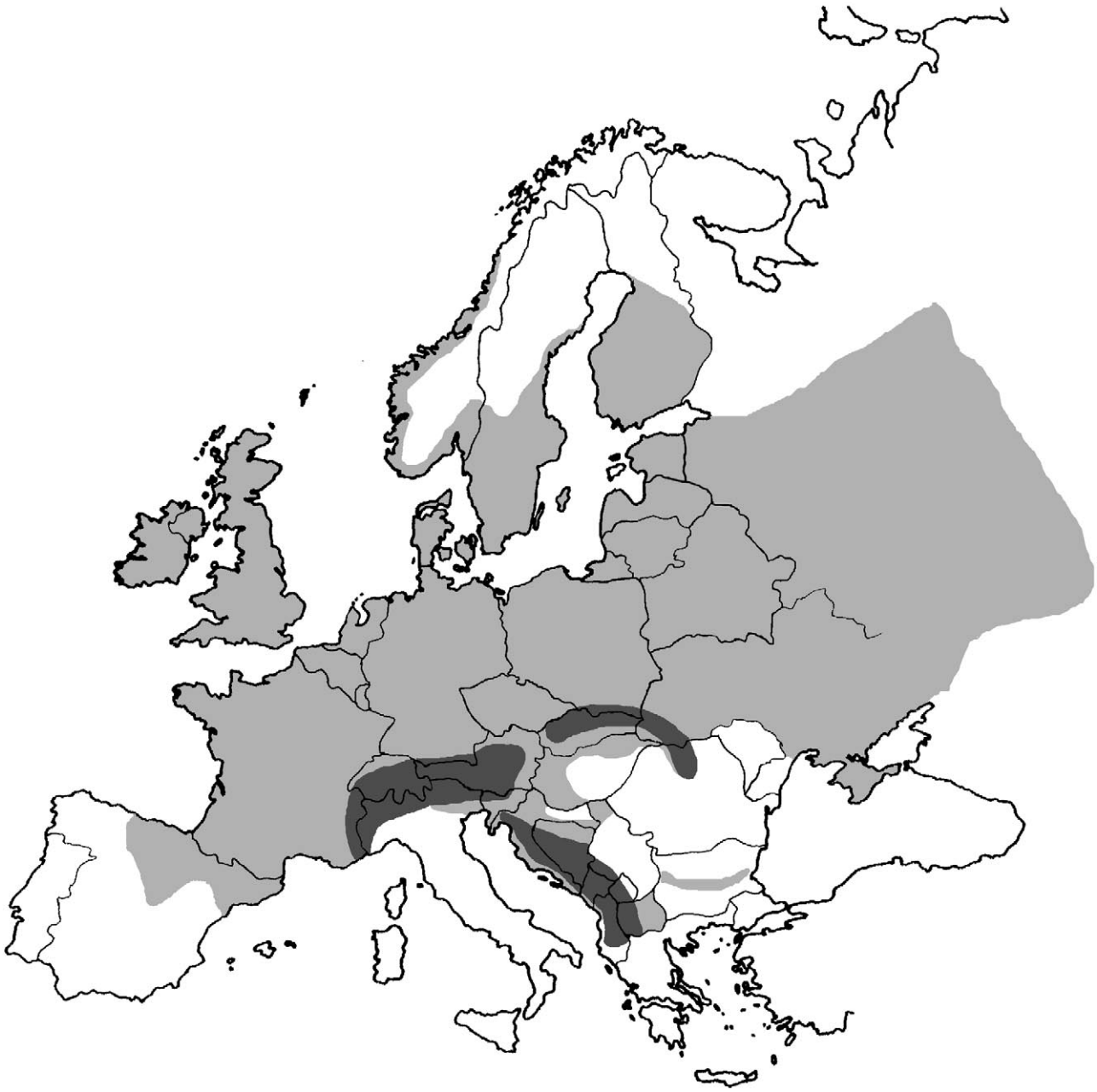


Fig. 12. Distribution of *Trochulus* (diversification centres indicated in dark)

and the Carpathians (Fig. 12). The only widely distributed species is *T. hispidus*, occuring in western, central and eastern Europe, and a part of northern Europe. The second largest distribution area is that of *T. striolatus* which inhabits the British Isles, northern France, Switzerland and Austria, the Netherlands, southern Germany and south-western Slovakia. The remaining species are endemics of limited range. Thus, four groups may be distiguished: 1. Alpine group, limited to the whole Alps or their small parts – 9 species (*T. suberectus, T. villosus, T. biconicus, T. caelatus, T. edentulus, T. clandestinus, T. graminicolus, T. montanus, T. piccardi*), 2. Carpathian group, distributed in the Carpathians or their parts – 5 species *(T. villosulus, T. bakowskii, T. bielzi, T. lubomirskii, T. czarnohoricus*), 3. Alpine-Carpathian group – 1 species (*T. unidentatus*) and 4. East-Alpine-Dinaric group, limited to the Eastern Alps and/or the Dinaric Mts – 4 species *(T. erjaveci, T. filicinus, T. leucozonus, T. luridus*).

## SYSTEMATIC INDEX OF SPECIES

Genus: *Trochulus* Chemnitz, 1786

1. *Trochulus bakowskii* (Poliński, 1924)
2. *Trochulus biconicus* (Eder, 1917)
3. *Trochulus bielzi* (A. E. Bielz, 1860)
4. *Trochulus caelatus* (Studer, 1820)
5. *Trochulus clandestinus* (Hartmann, 1821)

6. *Trochulus czarnohoricus* (Poliński, 1924)
7. *Trochulus edentulus* (Draparnaud, 1805)
8. *Trochulus erjaveci* (Brusina, 1870)
9. *Trochulus filicinus* (L. Pfeiffer, 1841)
10. *Trochulus graminicolus* (Falkner, 1973)
11. *Trochulus hispidus* (Linnaeus, 1758)
12. *Trochulus leucozonus* (C. Pfeiffer, 1828)
13. *Trochulus lubomirskii* (Ślósarski, 1881)
14. *Trochulus luridus* (C. Pfeiffer, 1828)
15. *Trochulus montanus* (Studer, 1820)
16. *Trochulus piccardi* Pfenninger et Pfenninger, 2005
17. *Trochulus striolatus* (C. Pfeiffer, 1828)
18. *Trochulus suberectus* (Clessin, 1878)
19. *Trochulus unidentatus* (Draparnaud, 1805)
20. *Trochulus villosulus* (Rossmässler, 1838)
21. *Trochulus villosus* (Draparnaud, 1805)
22. *Trochulus waldemari* (Wagner, 1912) nomen dubium

KEY FOR SPECIES IDENTIFICATION

Note! The key serves to determine adults of all the taxa listed above, except *T. czarnohoricus* with no current anatomical data and *T. waldemari*, specimens of which were unavailable.

1. Umbilicus entirely open and wide, previous whorls always visible. Umbilicus major diameter/shell diameter ratio 0.1–0.3 . . . . . 2
– Umbilicus narrow, sometimes punctured, partly or entirely covered by columellar aperture margin. Umbilicus major diameter/shell diameter ratio 0.02–0.13 . . . . . 13
2. Shell roundish-conical or nearly flattened; no hairs or hairs short and easily lost in adults. Aperture with white lip inside . . . . . 3
– Shell flattened, low spire with blunt apex; no hairs or hairs long, curved and rather durable but not dense. Aperture with white lip, sometimes lip poorly developed . . . . . 7
3. Shell width 5–10 mm (not more than 10 mm), with short, thin hairs, easily lost in adults. Inner and outer dart sacs approximately equal in length . . . . . 4
– Shell width usually more than 10 mm (9–14 mm), no hairs in adults. Inner dart sacs reach slightly beyond outer ones . . . . . 5
4. Four pairs of mucous glands. Shell width 5.5–10 mm, shell height 3–6.7 mm, shape variable: from roundish-conical to nearly flattened, sometimes with light band body whorl . . . *T. hispidus*, p. 128
– Six mucous glands. Similar to the preceding species. Shell width 5–7.5 mm, shell height 4–5.6 mm, roundish-conical. . . . . *T. suberectus,* p. 153
5. Flagellum longer than epiphallus. Shell width 8–14 mm, shell height 4.5–9 mm. Aperture with distinct lip inside . . . . . 6
– Flagellum shorter than epiphallus. Shell width 9–12.5 mm, shell height 5.5–7 mm. Body whorl inflated. Aperture with weakly developed lip inside . . . . . *T. clandestinus,* p. 118
6. Flagellum slightly longer than epiphallus; epiphallus as long as penis or longer. Inner dart sacs reach only slightly beyond outer ones, considerably more massive. Spermatheca roundish . . . . . *T. striolatus,* p. 146
– Flagellum considerably longer than epiphallus; epiphallus shorter than penis. Inner dart sacs reach far beyond outer ones. Spermatheca oval . . . . . *T. montanus,* p. 143
7. Shell height up to 6 mm, shell width up to 10 mm. Umbilicus diameter 0.8–3 mm. . . . . 8
– Shell height more than 6 mm (6–8.5 mm), shell width more than 10 mm (10–14.7 mm). Umbilicus diameter 1.9–3.5 mm . . . . . 12
8. Shell covered with long and sparse hairs in both juveniles and adults . . . . . *T. villosulus*, p. 162
– Shell devoid of hairs in adults . . . . . 9
9. Shell width up to 9.5 mm, shell height up to 5 mm. Mucous glands inserting directly above tips of inner dart sacs . . . . . 10
– Shell width more than 9.5 mm, shell height usually more than 5 mm. Outlet of mucous glands removed from tips of inner dart sacs . . . . . *T. graminicolus,* p. 127
10. Aperture narrow, crescentic. Inner and outer dart sacs distinctly visible. Shell flattened or nearly disc-like with low spire . . . . . 11
– Aperture elliptical. No inner dart sacs visible. Shell depressed but with elevated apex . . . . . *T. piccardi,* p. 146
11. Shell small: width up to 7 mm, height up to 3.5 mm. Whorls tightly coiled.Four long mucous glands (ca. 2.5 mm) . . . . . *T. biconicus,* p. 112
– Shell larger: width more than 7 mm, height more than 3.5 mm. Whorls moderately coiled. Eight short mucous glands grouped in pairs . . . . . *T. caelatus*, p. 116

12. Shell covered with long, up to 1 mm, hairs in both juveniles and adults. Lip poorly developed. No light band on body whorl . . . . . *T. villosus,* p. 164
– Shell devoid of hairs in adults. Lip distinct. Sometimes light band on body whorl . . . *T. erjaveci,* p. 124
13. Aperture simple . . . . . 14
– Aperture with prominent white tooth on basal margin. Inner dart sacs up to 2× longer than outer ones . . . . . *T. unidentatus,* p. 155
14. Shell translucent, whitish-yellow to greenish-yellow. Aperture rounded with very weakly developed lip. Flagellum conical, very short, considerably shorter than epiphallus . . . . . *T. lubomirskii,* p. 140
– Shell horny-brown to reddish-brown, often with light band on body whorl. Aperture with distinct lip inside. Flagellum and epiphallus approximately equal in length . . . . . 15
15. Dart sacs situated just below outlet of mucous glands. Vagina long and cylindrical. Shell small: width 5–8.5 mm, height 2.8–5.5 mm; roundish-conical with tightly coiled whorls . . . . . 16
– Outlet of mucous glands and tips of inner dart sacs ca. 1.5–4 mm apart. Vagina expands at dart sacs region and narrows toward genital atrium. Shell larger: width 7.5–12.6 mm, height 4.5–8.3 mm; roundish with moderately tightly coiled whorls . . . . . 17
16. Flagellum 1.5–2 × longer than epiphallus which is shorter than conical penis. Shell roundish-conical. Hairs fine, easily lost in adults, scars hardly visible . . . . . *T. bakowskii,* p. 110
– Flagellum slightly shorter than epiphallus or approximately as long; epiphallus as long as fusiform penis or slightly longer. Shell very similar to *T. bakowskii*, shape variable from conical to flat. Juveniles with dense hairs, often lost in adults, then shell slightly shiny and finely striated . . . *T. edentulus,* p. 121
17. Flagellum 1.5–2 × as long as epiphallus; penis cylindrical . . . . . 18
– Flagellum only slightly longer than epiphallus; penis fusiform . . . . . 19
18. Spermatheca does not reach albumen gland. Umbilicus very narrow, most often entirely covered by columellar aperture margin. Hairs short, curved and easily lost, leaving pronounced scars . . . . . *T. bielzi,* p. 114
– Spermatheca reaches albumen gland. Umbilicus very narrow, sometimes partly or nearly entirely covered by columellar aperture margin; when open, most often round. Both juveniles and adults with short and dense hairs . . . . . *T. filicinus,* p. 125
19. Shell devoid of hairs in adults. Flagellum considerably longer than epiphallus. Inner dart sacs slightly longer and narrower than outer ones . . . . . *T. leucozonus,* p. 138
– Shell with short, fine and sparse hairs. Flagellum as long as epiphallus or slightly longer. Inner and outer dart sacs approximately equal in size . . . . . *T. luridus,* p. 141

## SYSTEMATIC REVIEW

### *Trochulus bakowskii* (Poliński, 1924)

*Fruticicola bielzi bąkowskii* POLIŃSKI 1924: 196, pl. 13, fig. 72–74. Locus typicus: Ukraine [formerly Poland]: upper Prut valley: Dora and Tatarów; and East Carpathians: E slopes of Czarnohora. Syntypes: Museum of Natural History, Kraków.

#### Material examined

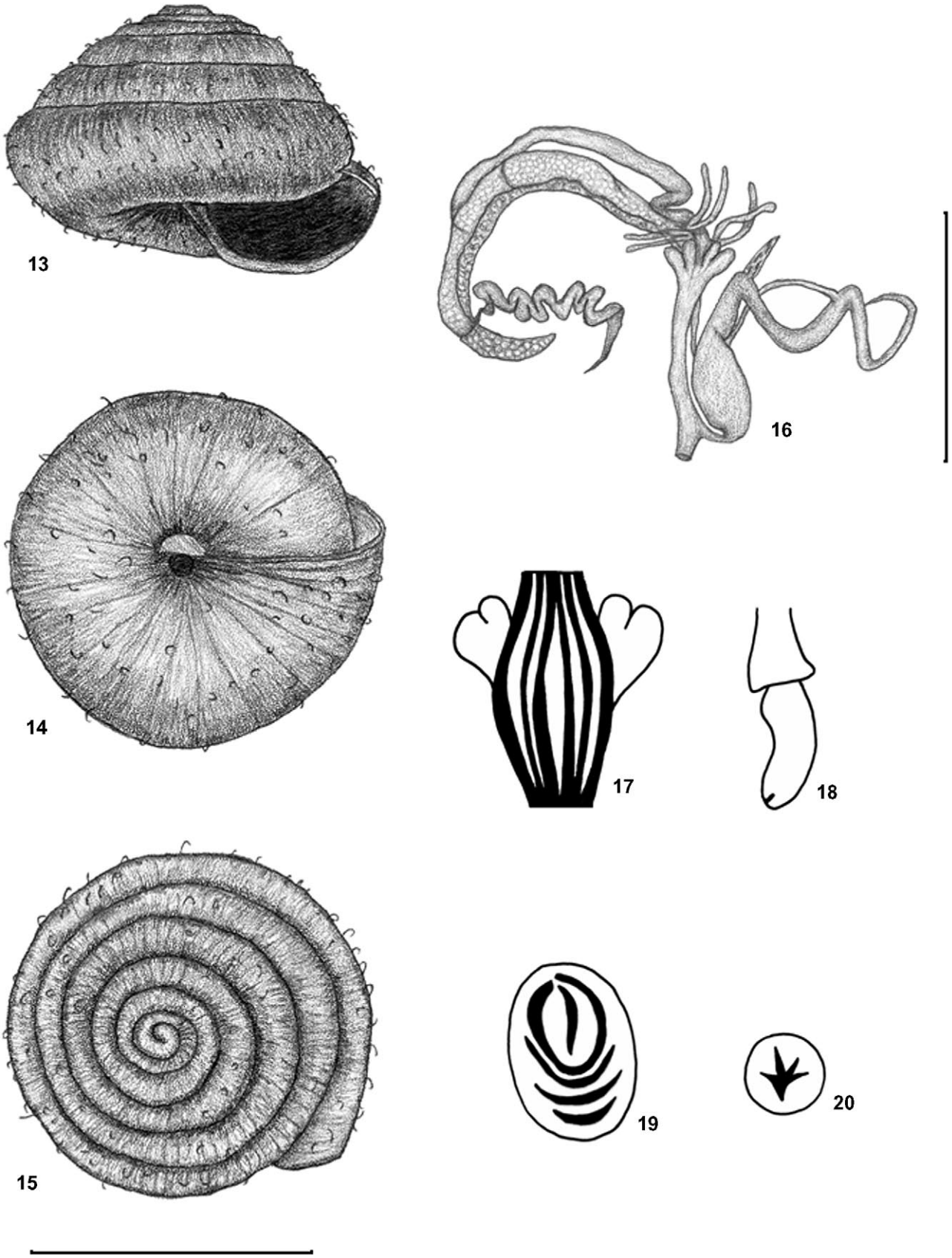
Poland: Bieszczady Mts: Bereżki near Ustrzyki Górne, 10.08.1972, leg. Studenckie Koło Biologów Wrocław, 1788, MPW, 5 alc.; Terebowiec Valley, 6.08.1972, leg. Studenckie Koło Biologów Wrocław, 1787, MPW, 32 alc.; Bystry Stream Valley, 6.08.1972 leg. Studenckie Koło Biologów Wrocław, 1876, MPW, 19 alc.; Ustrzyki Górne, 21.08.1996, ZW, 5 s.+38 alc.; Cisna, 24.08.1996, ZW, 28 alc.; Wetlina, 25.08.1996, ZW, 24 alc.; Moczarne, 25.08.1996, ZW, 49 alc.; s. prec. loc., Bieszczady, 10.08.1972, leg. Studenckie Koło Biologów Wrocław, 1790, MPW, 40 alc.

#### Shell (Figs 13–15)

Shell roundish-conical with 5.1–6.6 regularly and slowly increasing whorls. Shell height 2.8–5.1 mm, shell width 5.2–7.3 mm, height/width ratio 0.57–0.76, body whorl height 2.5–3.6 mm, relative height of body whorl 0.63–0.81, aperture height 1.6–2.6 mm, aperture width 2.6–3.7 mm, umbilicus major diameter 0.2–0.7 mm, umbilicus minor diameter 0.2–0.6 mm, umbilicus major diameter/shell diameter ratio 0.03–0.1. Aperture transversely crescentic (wider than high) with distinct white lip inside. Umbilicus narrow, punctured, always open and most often round. Hairs fine, easily lost in adults, scars hardly visible. Shell horny-brown to reddish-brown, shiny with light band on body whorl.

#### Reproductive system (Figs 16–20)

Most often four pairs of rather long mucous glands; sometimes glands reduced to three pairs, in other specimens with secondary branches. Inner dart sacs as large as outer ones, well separated. Vagina very




Figs 13–20. *T. bakowskii*. Specimen from Moczarne, Bieszczady, Poland, ZW. 13–15 – shell: 13 – apertural view, 14 – umbilical view, 15 – apical view; 16–20 – reproductive system: 16 – general view, 17 – longitudinal section of vagina, 18 – penial papilla, 19 – cross-section of penial papilla, 20 – cross-section of epiphallus. Scale bar 5 mm

long (ca. 5 mm) and cylindrical. Flagellum 1.5–2× longer than epiphallus which is shorter than conical penis. Spermatheca duct long and bent. Spermatheca oval, reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 17–20.

Ecology

*T. bakowskii* lives in very damp places in the herb layer of montane forests between 700 and 1,500 m a.s.l.; it is found in tussocks of vegetation (*Petasites* sp., *Caltha palustris*, *Cirsium oleraceum*) or leaf-litter. It prefers beech-fir forests (*Fageto-Abietum*) with *Alnus incana* and *Petasites albus*; in spruce forests (*Piceetum altiherbosum*) it is found in tussucks of *Adenostyle* sp., *Doronicum* sp. and *Mulgedium* sp. (HUDEC 1965).

Distribution (Fig. 21)

A North-East-Carpathian species; it occurs in Slovakia (Muransky-Kras, Pol'ana, eastern part of the Low Tatra Mts) (HUDEC 1965) Poland (Bieszczady and an isolated locality on the Ropa River near Uście Gorlickie) (RIEDEL 1988) Ukraine (Svidovec; Gorgany; in the east to Czarnohora) (POLIŃSKI 1924, KERNEY et al. 1983) and Hungary (FALKNER et al. 2001).

Remarks

According to SHILEYKO (1978b), there are 6–8 not grouped mucous glands. All the adult specimens anatomically examined had eight or six mucous glands, always grouped in pairs.

HUDEC (1965) noted that the flagellum was approximately as long as the epiphallus but most often shorter, which was not confirmed by my studies. In all the dissected adults the flagellum was considerably longer than the epiphallus (see also POLIŃSKI 1928 and SHILEYKO 1978b). Moreover, in the figured specimen (HUDEC 1965) the outlet of the mucous glands was situated at a distance from the upper tips of the inner dart sacs, while in the examined specimens they were at the same level.

### *Trochulus biconicus* (Eder, 1917)

*Fruticicola biconica* EDER 1917: 119, figs 1–4. Locus typicus: Switzerland: Canton Nidwalden: Bannalpass, steep SW-facing screes slope, 2,000 m a.s.l.

Material examined

Switzerland: Bannalppass, 2,100–2,200 m, 3.09.1967, coll. M. Wüthrich, Nr 1918, NHMB, 6 s.+2 alc.; Bannalppass, 2,150 m, leg. Böckel, coll. Klemm 50496, NHMW, 5 s.

Shell (Figs 22–24)

Shell flattened, with low spire. Whorls 5–6.5 tightly coiled, slowly but regularly increasing, body whorl only ca. twice wider than the first one. Shell height 2.5–3.5 mm, shell width 5.0–7.0 mm, height/width ratio 0.48–0.57, body whorl height 2.5–2.8 mm, relative height of body whorl 0.78–0.9, aperture height 1.7–2.2 mm, aperture width 2.5–3.1 mm, umbilicus major diameter 0.9–1.3 mm, umbilicus minor diameter 0.8–1.1 mm, umbilicus major diameter/shell diameter ratio 0.16–0.19. Aperture narrow, crescentic, with whitish lip. Basal and palatal aperture margins slightly reflexed. Umbilicus deep and always open. Adults hairless. Shell pale brown with irregular growth lines distinct above, much weaker below.

Reproductive system (Figs 25–29)

Four long mucous glands. Inner dart sacs slightly longer than outer ones. Vagina long and cylindrical.

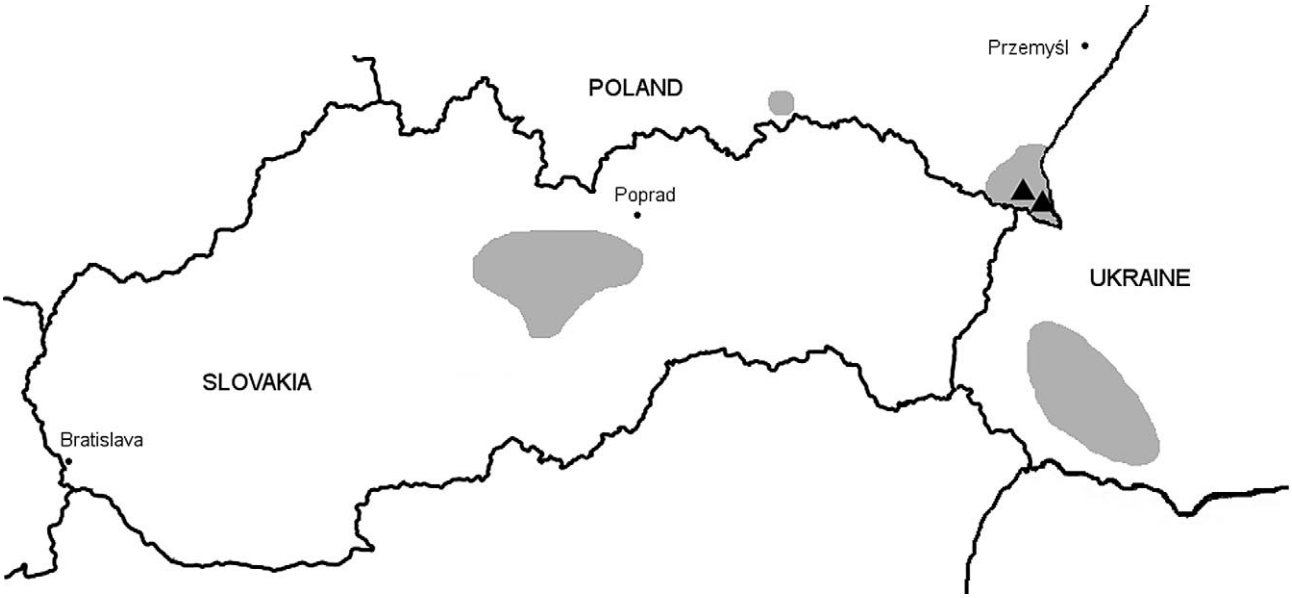
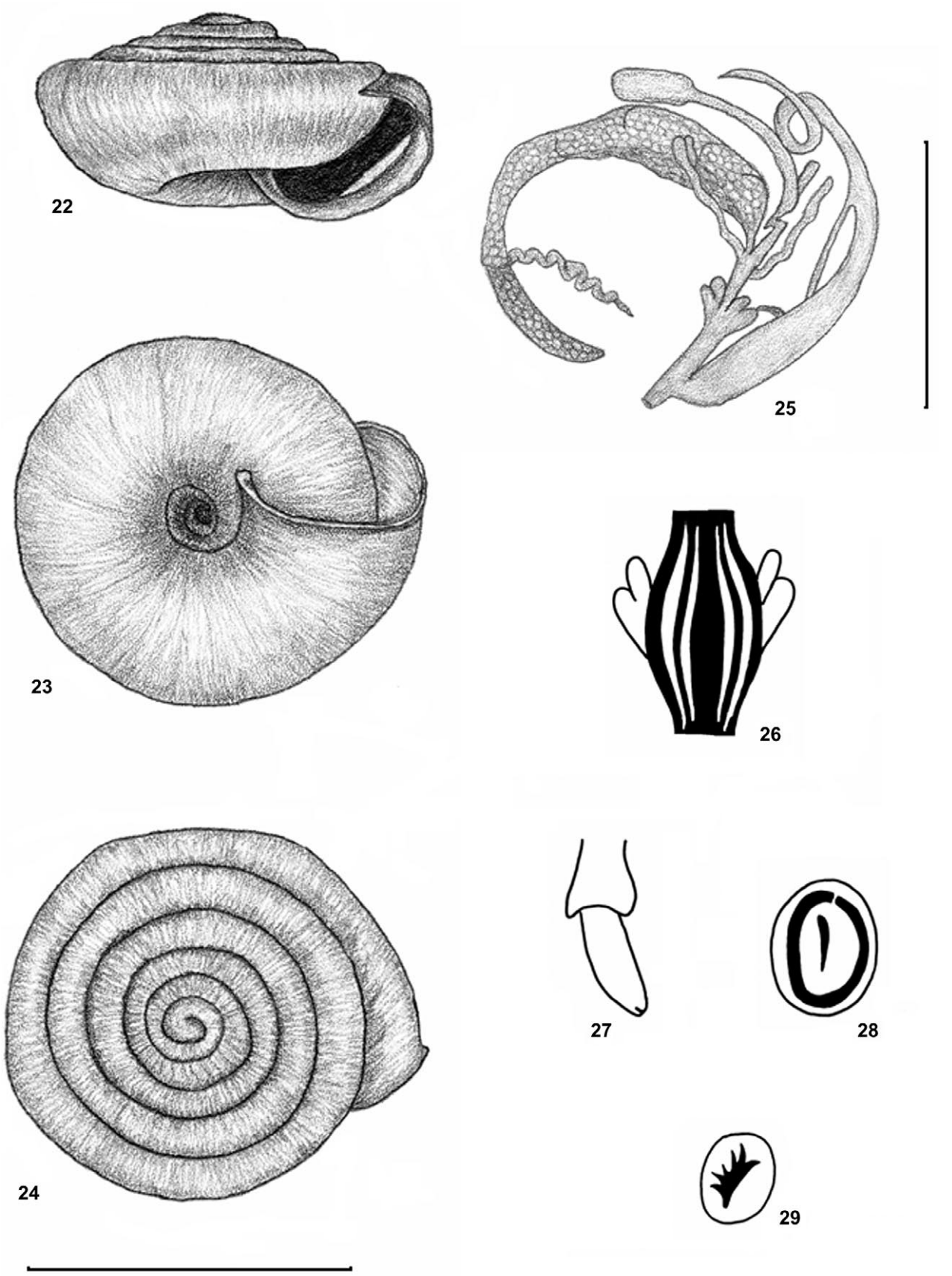



Fig. 21. Distribution of *T. bakowskii*. Black triangles – localities of origin of the examined material




Figs 22–29. *T. biconicus*. Specimen from Bannalppass (type locality), Switzerland, coll. M. Wüthrich, Nr 1918, NHMB. 22–24 – shell: 22 – apertural view, 23 – umbilical view, 24 – apical view; 25–29 – reproductive system: 25 – general view, 26 – longitudinal section of vagina, 27 – penial papilla, 28 – cross-section of penial papilla, 29 – cross-section of epiphallus. Scale bar 5 mm

Flagellum longer than epiphallus, which is longer than fusiform penis. Spermatheca duct straight. Spermatheca oval, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 26–29.

Ecology

*T. biconicus* lives in grassy limestone screes, on mountain slopes with rock outcrops and sparse vegetation, ca. 2,000 m a.s.l. and higher.

Distribution (Fig. 30)

A microendemic species; earlier known only from its type locality in Bannalppass (canton Nidwalden) in Switzerland. However, since 2005 it has been regularly found in other localities: Isenthal (canton Uri); Kerns, Engelberg, Ruchstock (canton Obwalden); Wolfenschiessen, Beckenried (canton Nidwalden) (BAGGENSTOS 2006).

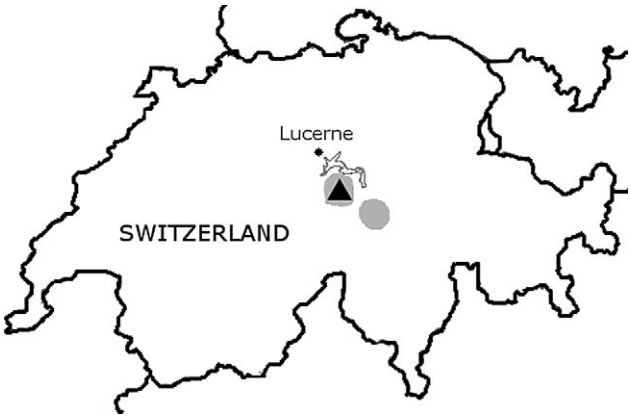



Fig. 30. Distribution of *T. biconicus*. Black triangle – locality of origin of the examined material

***Trochulus bielzi* (A. E. Bielz, 1860)**

*Helix bielzi* A. E. BIELZ 1859: 216. [nomen nudum] [see also FALKNER 1995: 100]

*Helix bielzi* A. E. BIELZ 1860: 151. Terra typica: Romania: Transylvania.

*Helix euconus* WESTERLUND 1890: 121. Locus typicus: Poland: near Przemyśl.

*Fruticicola bielzi euconus* var. *globulina* POLIŃSKI 1928: 187, pl. XXVIII, fig. 38. Locus typicus: Ukraine: south of Kołomyja: "Czarny Las" near Wierbiąż.

Material examined

Poland: Bieszczady Mts: Wetlina, Wierch Muchanin, 9.07.1962, leg. C. Dziadosz et W. Staręga, MIZW, 4 s.; Cisna, 24.08.1996, ZW, 16 s.+6 alc.; Wetlina, 25.08.1996, ZW, 7 alc.; Dwernik, 26.08.1996, ZW, 1 s.+3 alc.; Dwerniczek, 26.08.1996, ZW, 1 s.; s. prec. loc., Bieszczady, 10.08.1972, leg. Studenckie Koło Biologów Wrocław, Nr 1789, MPW, 14 alc.; Romania: Transylvania: Attelsloch near Schässburg [=Schäßburg=Sighişoara], 1918, coll. Poliński 228/37, MIZW, 9 s.; Mediasch [=Mediaş], coll. Poliński 228/37, MIZW, 2 s.

Shell (Figs 31–33)

Shell roundish-conical with 5.5–6.25 regularly increasing convex whorls. Shell height 5.2–7.3 mm, shell width 7.5–10.1 mm, height/width ratio 0.61–0.78, body whorl height 4.0–5.1 mm, relative height of body whorl 0.64–0.81, aperture height 2.7–3.6 mm, aperture width 4.1–5.3 mm, umbilicus major and minor diameter 0.2–0.4 mm, umbilicus major diameter/shell diameter ratio 0.02–0.13. Aperture transversely oval, with white lip inside. Umbilicus very narrow, most often entirely covered by columellar aperture margin. Hairs short, curved and easily lost leaving pronounced scars. Shell horny-yellow to reddish-brown, matt, often with light band on body whorl.

Reproductive system (Figs 34–38)

Four pairs of short mucous glands situated around upper vagina, ca. 1.5 mm from tips of inner dart sacs, which are slightly longer than outer ones. Vagina long (ca. 6.0 mm); its expanded dart sac region narrows toward genital atrium. Flagellum up to 1.5× longer than epiphallus, which is as long as cylindrical penis or slightly shorter. Spermatheca duct thick and long. Spermatheca oval, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 35–38.

Ecology

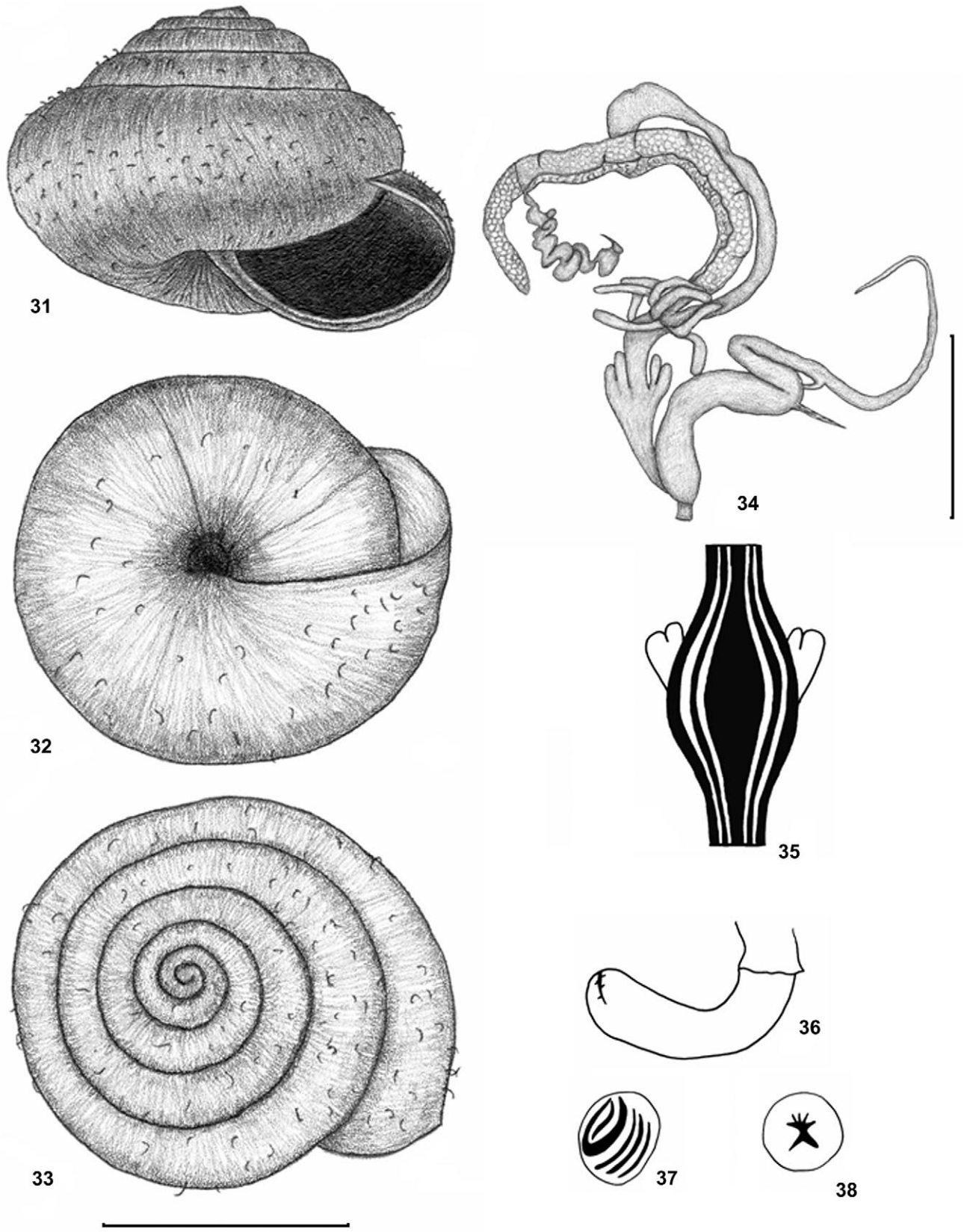
*T. bielzi* lives in damp herbal layer of forests; it shelters in leaf litter and rotting timber, but also often stays on the underside of leaves of e.g. *Petasites* sp., *Caltha palustris, Cirsium oleraceum*. It is found in the foothills and lower mountain altitudes, up to 600–700 m.

Distribution (Fig. 39)

An Eastern-Carpathian species; known from Slovakia (Carpathians), Poland (Bieszczady, eastern Beskid Niski Mts, Pogórze Dynowskie foothills; in the west to the Wisłok River) (RIEDEL 1988), Romania (Transylvania) (KERNEY et al. 1983) and Ukraine (Carpathians: Czeremosz-Tal) (POLIŃSKI 1924, 1928).

Remarks

Populations inhabiting the northern part of the range, including Poland, were identified as a subspecies *T. bielzi euconus* (Westerlund, 1890). Moreover, among the specimens of *euconus* POLIŃSKI (1928) distinguished smaller individuals with a very weakly developed lip, which he designated as *Fruticicola bielzi euconus* var. *globulina*. Besides the detailed shell description, he gave figures and descriptions of the reproductive system, but without specifying any differences between the two taxa.




Figs 31–38. *T. bielzi*. Specimen from Cisna, Bieszczady, Poland, ZW. 31–33 – shell: 31 – apertural view, 32 – umbilical view, 33 – apical view; 34– 38 – reproductive system: 34 – general view, 35 – longitudinal section of vagina, 36 – penial papilla, 37 – cross-section of penial papilla, 38 – cross-section of epiphallus. Scale bar 5 mm

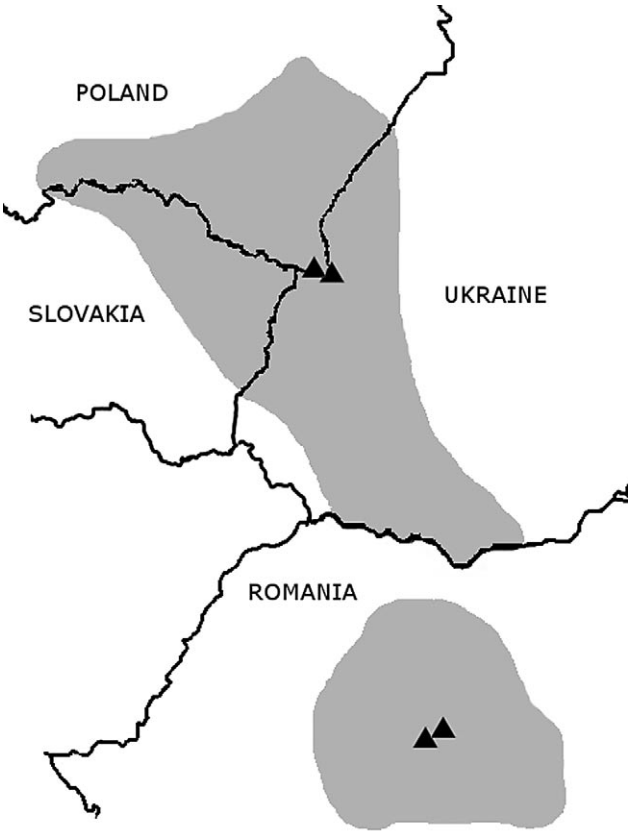



Fig. 39. Distribution of *T. bielzi*. Black triangles – localities of origin of the examined material

Comparison of shells of *T. bielzi* (HUDEC 1972) from the Slovak Carpathians and from various Romanian populations showed that specimens corresponding to the description of *euconus* and its forms, also occurred among Romanian populations. The variation is probably of individual and to some degree interpopulation characters and does not justify the taxonomic distinctions.

HUDEC (1972) remarked that juvenile *T. bielzi* had the flagellum approximately as long as the epiphallus. However, in his figure of the reproductive system, the flagellum seems to be longer than the epiphallus which may be caused by the fact that the figured flagellum is twisted, or the figure shows an adult specimen (which is not specified). In this study, in all the anatomically examined specimens, the flagellum was up to 1.5x longer than the epiphallus.

### *Trochulus caelatus* (Studer, 1820)

*Helix caelata* Vallot, 1801 [nomen oblitum – see FALKNER 1995: 99, TURNER et al. 1998: 343]

*Glischrus (Helix) caelata* STUDER 1820: 86 [12]. Terra typica**:** Switzerland: Jura, in forests, at humid rocks. Lectotype: NHMB.

*Helix corrugata* Var. $\gamma$ – *coelata* HARTMANN 1821: 236, pl II, fig. 12. Terra typica: Switzerland: mountains in Bernese Oberland; Jura.

*Helix glypta* LOCARD 1880–1881: 95. Locus typicus: France: dep. Rhône-Alpes: environs of Lyon; dep. Ain: Laumusse and Hauleville [according to FALKNER (1995: 99) this name is also nomenclatorically correct].

*Helix coelomphala* LOCARD 1888: 352. Locus typicus: Switzerland: Mt. Righi, Zurich, Lucerne and Jura neuchâtelois; Germany: Dillingen near Saarlouis, Günzburg, Dinkelsbühl; E France: dep. Savoie: environs of Annecy, Chambéry, Aix-les-Bains, Mouxy, Albertville; dep. Isère: vicinity of Genoble, Sassenage, Saint-Martin-le-Vinoux, Allevard-les-Bains, Grande-Chartreuse, Sappey, Voreppe; dep. Hautes-Alpes: Barcelonnette; dep. Rhône: environs of Lyon, alluvions of Rhône N Lyon, Brotteaux, Sathonay, Pape; dep. Ain: Laumusse, Bugey, alluvions of Suran; dep. Jura: Bief-du-Fourg, Saint-Claude, Poligny; dep. Côte-d'Or: Châtillon-sur-Seine; environs of Paris; Bionville near Metz; dep. Finistère: Brest.* [see FALKNER 1990: 202, FALKNER et al. 2001: 57, FALKNER & FALKNER 2008 – *Trochulus coelomphala* (Locard, 1888)]

*Helix coelata* CLESSIN 1874: 187, pl. VIII, fig. 5.

#### Material examined

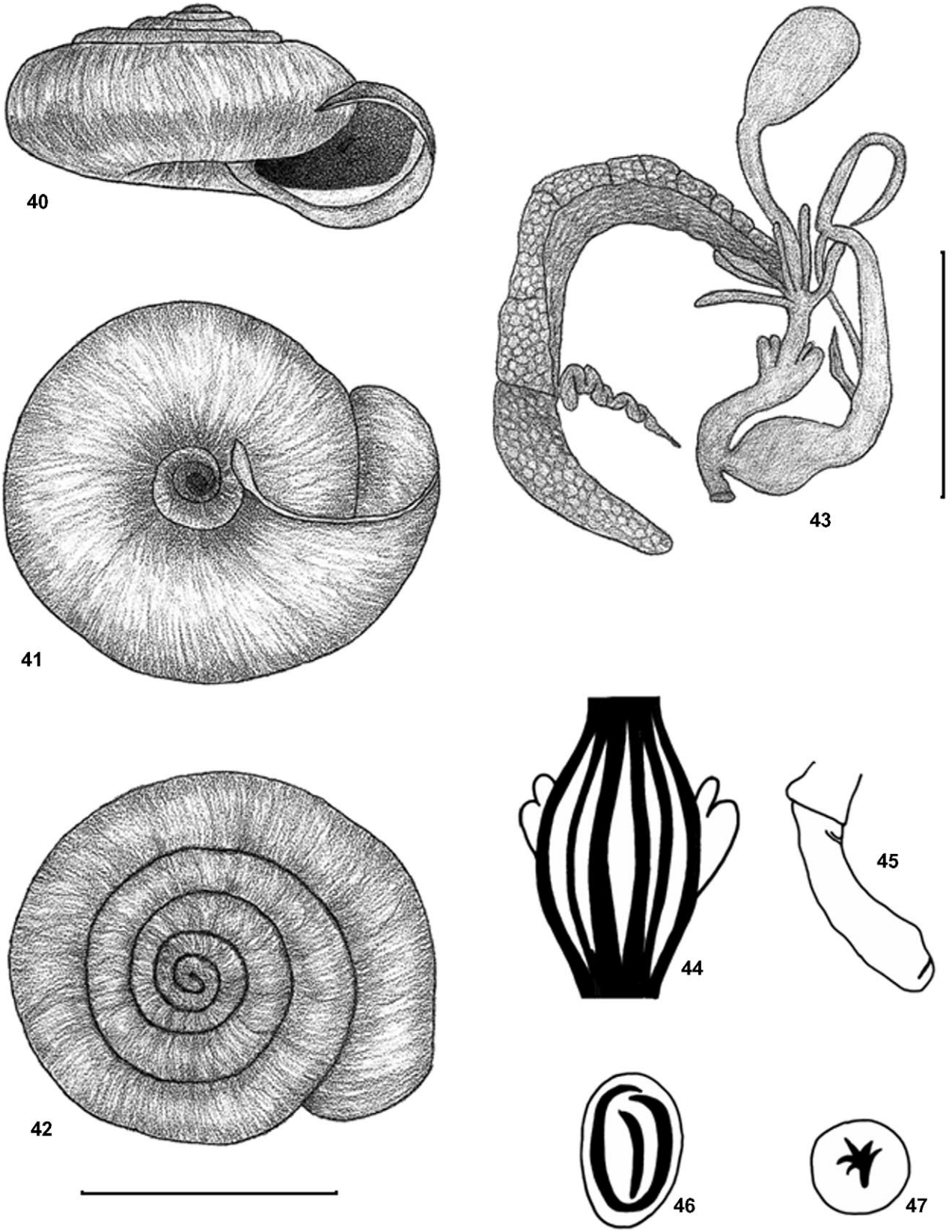
Switzerland: Mt. Wandfluh, Bettlach, Jura, 1,280 m, 11.06.1961, coll. M. Wüthrich Nr 2330, NHMB, 6 s.+2 alc.; Gorges de Moutier valley, Jura, 506 m, 27.06.1969, coll. M. Wüthrich Nr 228, NHMB, 6 s.+2 alc.; Gänsbrunnen, cant. Solothurn, MIZW, 5 s.

#### Shell (Figs 40–42)

Shell strongly flattened, nearly discoidal, convex underneath. Whorls flat, 5.0–5.7. Shell height 3.7–5.0 mm, shell width 8.0–9.5 mm, height/width ratio 0.47–0.59, body whorl height 3.3–4.2 mm, relative height of body whorl 0.84–0.95, aperture height 2.3–3.0 mm, aperture width 3.5–4.6 mm, umbilicus major diameter 1.5–2.4 mm, umbilicus minor diameter 1.2–1.9 mm, umbilicus major diameter/shell diameter ratio 0.17–0.2. Aperture with white lip. Umbilicus deep, open and wide. Hairs present only in very young juveniles. Shell reddish-brown, shiny, prominently striated, sometimes with light band on body whorl.

#### Reproductive system (Figs 43–47)

Four pairs of short mucous glands. Inner dart sacs narrower but slightly longer than outer ones. Vagina long and cylindrical. Flagellum longer than epiphallus which is shorter or as long as fusiform penis. Spermatheca duct short and straight. Spermatheca oval, reaching ca. 2/3 spermoviduct length. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 44–47.




Figs 40–47. *T. caelatus*. Specimen from Bettlach, Wandfluh, Switzerland, coll. M. Wüthrich, Nr 2330, NHMB. 40–42 – shell: 40 – apertural view, 41 – umbilical view, 42 – apical view; 43–47 – reproductive system: 43 – general view, 44 – longitudinal section of vagina, 45 – penial papilla, 46 – cross-section of penial papilla, 47 – cross-section of epiphallus. Scale bar 5 mm

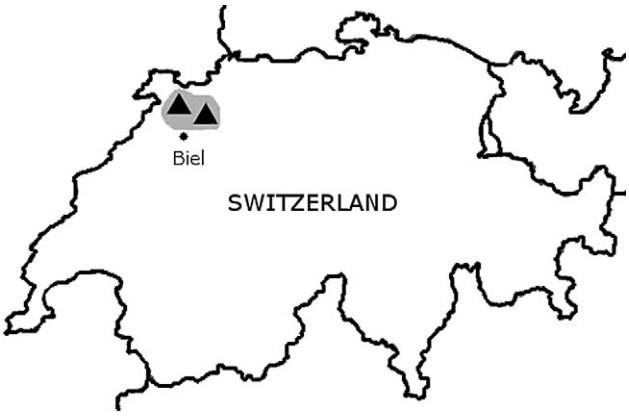



Fig. 48. Distribution of *T. caelatus*. Black triangles – localities of origin of the examined material

Ecology

*T. caelatus* lives in shaded limestone habitats, between 500 and 1,300 m a.s.l.

Distribution (Fig. 48)

An endemic species; known only from Switzerland: Jura, the middle Birs valley (TURNER et al. 1998).

Remark

The reproductive system is very similar to those of *T. striolatus* and *T. montanus*. It differs in its very short dart sacs.

### *Trochulus clandestinus* (Hartmann, 1821)

*Helix corrugata* Var. α *H. clandestina* HARTMANN 1821: 236. Locus typicus: Austria: Vienna and Switzerland: near Zürich.

*Helix Putonii* CLESSIN 1874: 314. Terra typica: Belgium and NE France: Vosges Mountains. [see FALKNER et al. 2001: 58 – *Trochulus clandestinus putonii* (Clessin, 1874)]

Material examined

Switzerland: Culm, cant. Aargau, 569a 44, MPW, 2 s.; Boll-Sinneringen, cant. Bern, 24.07.1977, coll. M. Wüthrich Nr 3842/50, NHMB, 6 s.+2 alc.; Wattenwil, Bellevue, cant. Bern, 27.05.1967, coll. M. Wüthrich Nr 3117/47, NHMB, 6 s.+2 alc.; Schleitheim, cant. Schaffhausen, coll. Sterki 31800, NHMW, 5 s.

Shell (Figs 49–51)

Shell roundish-conical with 5.3–6.0 whorls. Shell height 5.6–7.0 mm, shell width 9.3–12.3 mm, height/width ratio 0.55–0.78, body whorl height 4.5–6.0 mm, relative height of body whorl 0.79–0.88, aperture height 3.4–4.5 mm, aperture width 4.3–6.1 mm, umbilicus major diameter 1.3–2.2 mm, umbilicus minor diameter 1.0–1.7 mm, umbilicus major diameter/shell diameter ratio 0.15–0.22. Aperture with weakly developed lip. Umbilicus wide and open. Adults hairless. Shell light horny-brown to yellowish-grey, shiny, body whorl inflated, sometimes with light band.

Reproductive system (Figs 52–56)

Four pairs of short mucous glands situated around upper vagina, ca. 1 mm from tips of inner dart sacs, which are slightly longer than more massive outer ones. Vagina long and cylindrical. Flagellum considerably shorter than epiphallus, which is longer than conical penis. Spermatheca duct thin and straight. Spermatheca oval, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus, and shown in Figs 53–56.

Ecology

*T. clandestinus* is a montane species, inhabiting the herb layer in forests, scrubstreams, but is also found in cultivated land (as a synanthrope in parks, gardens, verges and in ruderal vegetation); between 400 and 1,000 m a.s.l., maximum up to 2,300 m a.s.l.

Distribution (Fig. 57)

Known from Switzerland (middle and northern Jura; the northern Alps; canton Bern; Vierwaldstätter See to the Thur valley), Liechtenstein and southern Germany (Hegau) (FORCART 1965, KERNEY et al. 1983, TURNER et al. 1998).

Remarks

The species is often confused with *T. striolatus* and *T. montanus*, but it differs from them in more rapidly increasing whorls, resulting in shells of the same size having fewer whorls. Likewise, the very short flagellum is distinctive (FORCART 1965).

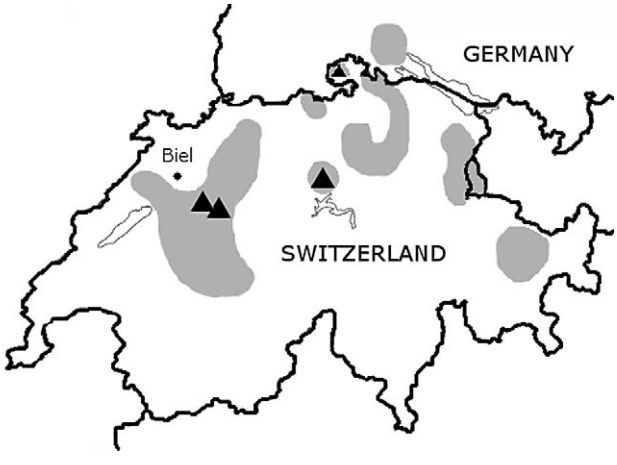
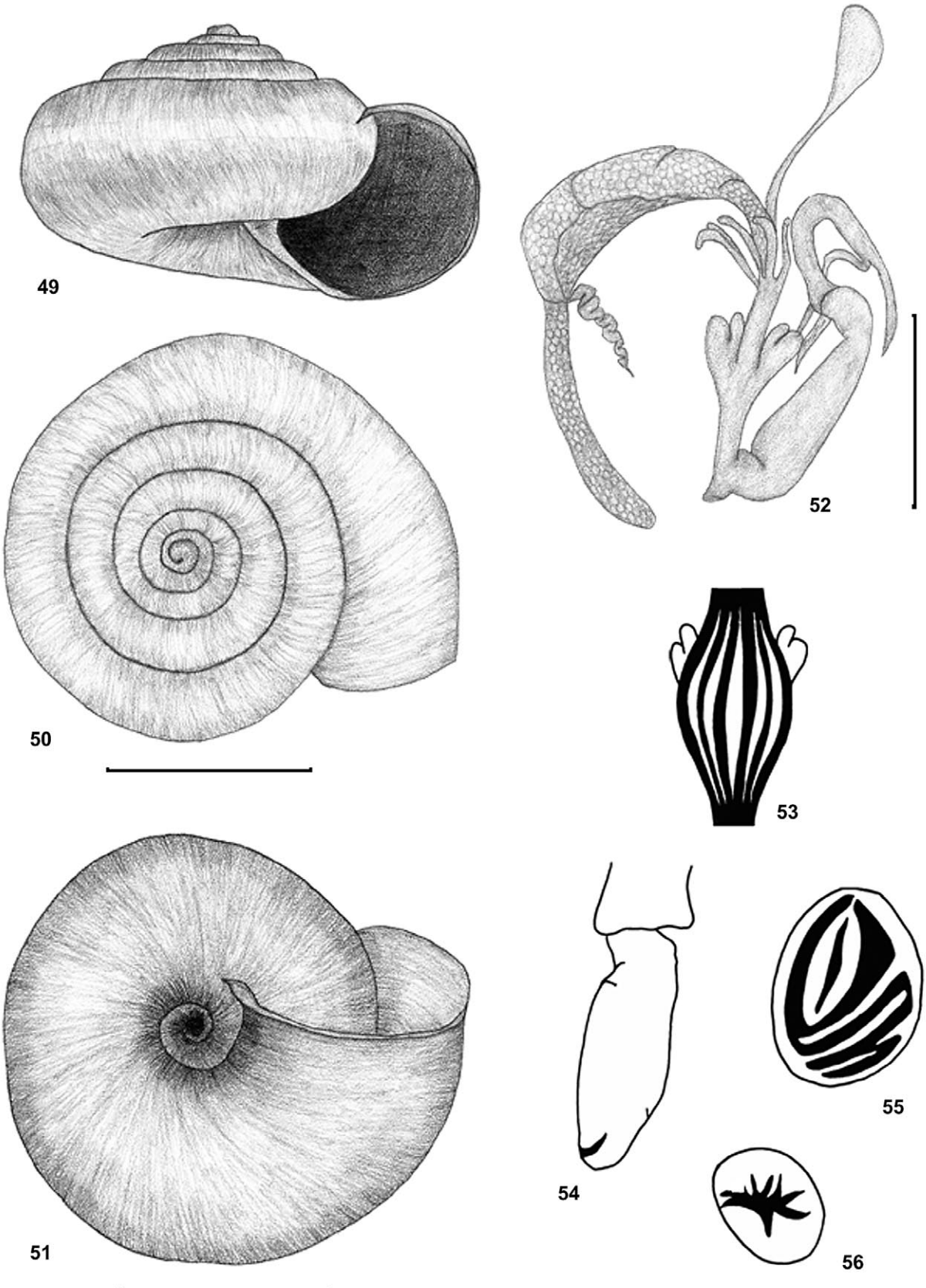



Fig. 57. Distribution of *T. clandestinus*. Black triangles – localities of origin of the examined material




Figs 49–56. *T. clandestinus*. Specimen from Boll-Sinneringen, Switzerland, coll. M. Wüthrich Nr 3842/50, NHMB. 49–51 – shell: 49 – apertural view, 50 – apical view, 51 – umbilical view; 52–56 – reproductive system: 52 – general view, 53 – longitudinal section of vagina, 54 – penial papilla, 55 – cross-section of penial papilla, 56 – cross-section of epiphallus. Scale bar 5 mm

### *Trochulus czarnohoricus* (Poliński, 1924)

*Fruticicola czarnohorica* POLIŃSKI 1924: 193–195, figs 75–77. Locus typicus: Ukraine: district Nadwórna: south of Worochta and west of Ardzheludza: in the valley between Kiczera and Kukul Ridges ("Kiczera--Kukul-Rücken").

Material examined

Ukraine: valley between Kiczera and Kukul Ridges, 12.04.1921, leg. Sz. Tenenbaum, MIZW, 16 s. [1 lectotype and 15 paralectotypes]

Shell (Figs 58–60)

Shell small, roundish with 4.5–4.75 whorls. Shell height 4.1–4.5 mm, shell width 4.9–5.6 mm, height/width ratio 0.73–0.89, body whorl height 3.0–3.2 mm, relative height of body whorl 0.66–0.78, aperture height 2.0–2.2 mm, aperture width 2.7–2.9 mm, umbilicus diameter 0.8–0.9 mm, umbilicus major diameter/shell diameter ratio 0.16–0.18. Aperture slightly broader than high, with very weakly developed lip. Body whorl approximately 1.5× wider than penultimate and not descending. Umbilicus narrow, partly covered by columellar aperture margin. Juveniles with fine hairs, which in adults are lost, leaving scars. Shell horny-brown, semi-translucent.

Ecology

The dry shells were found on a stream bank in a fir forest at ca. 1,300 m a.s.l. (POLIŃSKI 1924).

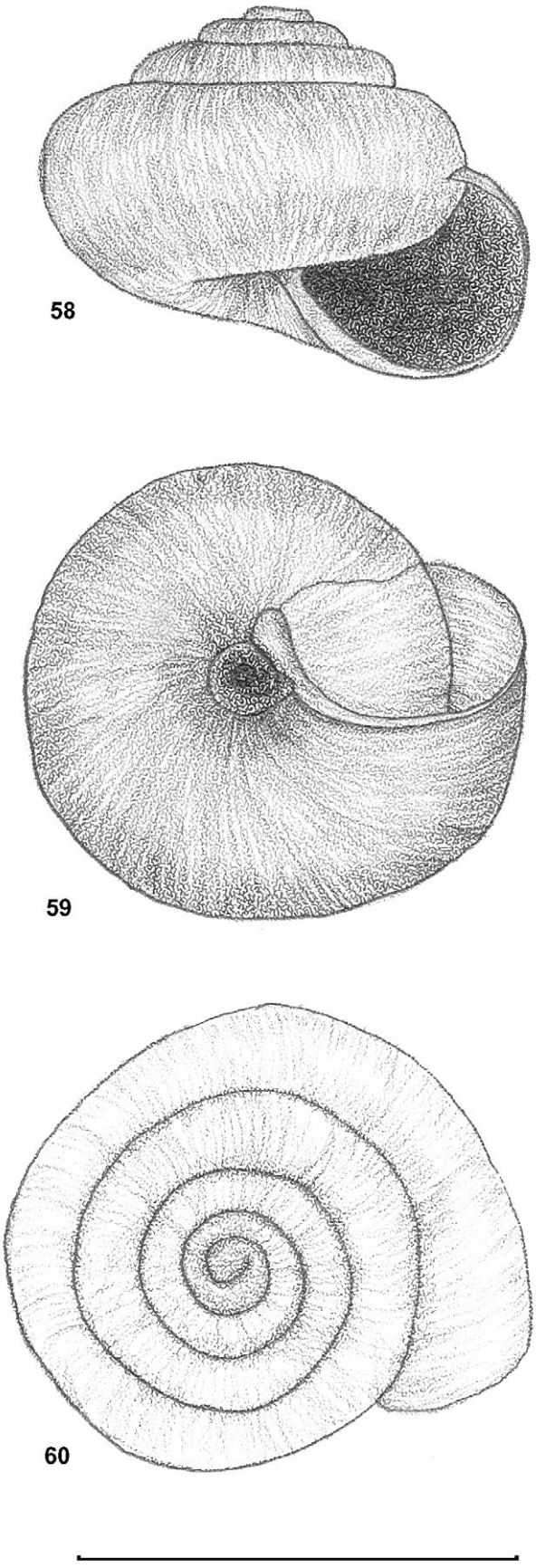
Distribution (Fig. 61)

A species known only from the type locality in the Ukrainian Eastern Carpathians.

Remarks

The species differs from its congeners in its smaller size, roundish shell (the height/width ratio is the highest in the genus: 0.73–0.89) as well as the relatively low body whorl (relative height 0.66–0.78), and consequently, rather high spire. Further studies are required to decide about its taxonomic status.


Fig. 61. Distribution of *T. czarnohoricus*. Black triangles – localities of origin of the examined material




Figs 58–60. *T. czarnohoricus*. Shell. Lectotype: 58 – apertural view, 59 – umbilical view, 60 – apical view. Scale bar 5 mm

### *Trochulus edentulus* (Draparnaud, 1805)

*Helix edentula* DRAPARNAUD 1805: 80, pl. VII, fig. 14. Terra typica: France: Bresse. Type specimen: NHMW.

*Helix depilata* DRAPARNAUD 1801: 72. Locus typicus: France: environs of Lyon: Mont Pilat. [non *Helix depilata* C. Pfeiffer] [see also FALKNER et al. 2002: 151]

*Helix limnifera* HELD 1836: 273. Terra typica: Germany: Bavaria. Locus typicus restrictus (according to FALKNER 1985): Berchtesgadener Alpen: Watzmann-Massiv.

*Helix Cobresiana* var. δ? L. PFEIFFER 1846: 190, pl. 99. figs 19–21. Locus typicus: Austria: Styria: Mürztal.

*Helix unidentata* var. *subleucozona* WESTERLUND 1889: 32, no 89. Locus typicus: Austria: Styria: Mürztal.

*Helix Lorteti* LOCARD 1894: 104. Terra typica: France: mountainous regions of Dauphiné and Savoie.*

*Fruticicola edentula helvetica* POLIŃSKI 1928: 195, pl. XXVIII, figs 42–43. Locus typicus: Switzerland: Füringen, Frutt, Zürich; Germany: Schwarzwald: Schramberg; Baden-Württemberg: Aichtal valley near Nürtingen.

*Fruticicola edentula helvetica* var. (natio) *suevica* POLIŃSKI 1928: 199 (shell), 152 (genitalia). Locus typicus: Germany: Schwäbische Alb: Seeburger Tal near Urach.

#### Material examined

Austria: Golling an der Salzach near Salzburg, 6.11.1997, leg. A. Riedel et F. Seidl 10/97, MIZW, 31 s.+11 alc.; Tiefbrunnau, Salzkammergut, 4.07.1998, ZW, 6 alc.; Vordersee, Salzkammergut, 4.07.1998, ZW, 2 alc.; Ostermiething, Upper Austria, 04.1926, coll. Poliński 228/37, MIZW, 4 s.; Rettengraben gorge, Mt. Floning, Styria, ex coll. Wagner, MIZW, 13 s. [*subleucozona*]; Thörlgraben gorge near Kapfenberg, Styria, ex coll. Wagner, MIZW, 20 s. [*subleucozona*]; Schafferweg near Admont, Styria, ex coll. Wagner, MIZW, 2 s.; Röthelstein castle near Admont, Styria, ex coll. Wagner, MIZW, 1 s.; s. prec. loc., Carynthia, ex coll. Gallenstein, MIZW, 1 s.; Germany: Urach, Württemberg, coll. Poliński 228/37, MIZW, 5 s.; Seeburger Tal valley near Urach, Württemberg, 28.04.1928, leg. D. Geyer, MIZW, 4 s. [*suevica*]; Schamberg, Schwarzwald, Württemberg, coll. Poliński 228/37, MIZW, 7 s.; Aichtal valley near Nürtingen, S Stuttgart, ± 300 m, coll. Poliński 228/37, MIZW, 6 s.; Moosburg, Bavaria, 30.06.1998, ZW, 2 s.; Wimbachklamm gorge near Reichenhall, Bavaria, coll. Poliński 228/37, MIZW, 6 s. [*subleucozona*]; Switzerland: Aiguebelle near Veyrier, S Geneva, 450 m, 04. 1929, coll. Poliński 228/37, MIZW, 13 s.; Pomier, Mt. Salève, S Geneva, ± 900 m, 04.1929, leg J. Favre, MIZW, 4 s.; Vaux forest, between Chasseron and Fleurier, Jura Vaudois, ± 1,200 m, 09.1928, coll. Poliński 228/37, MIZW, 4 s.; Zürich, coll. Poliński 228/37, MIZW, 3 s.; Frutt, cant. Obwalden, ± 1,700 m, coll. Poliński 228/37, MIZW, 6 s. [*helvetica*]; s. prec. loc., Swiss Jura, 1928, coll. Poliński 228/37, MIZW, 1 s.

#### Shell (Figs 62–67)

Shape variable, from conical to flat, with 5.25–7.0 tightly coiled whorls, body whorl angled at periphery. Shell height 3.5–5.3, shell width 5.5–8.2, height/width ratio 0.57–0.74, body whorl height 2.7–3.6 mm, relative height of body whorl 0.57–0.71, aperture height 1.7–2.5 mm, aperture width 2.8–4.4 mm, umbilicus major diameter 0.2–0.6 mm, umbilicus minor diameter 0.2–0.6 mm, umbilicus major diameter/shell diameter ratio 0.04–0.1. Aperture with white lip inside, its basal wall slightly thickened but without teeth; aperture margin slightly reflected. Umbilicus very narrow and often round, sometimes partly or entirely covered by columellar aperture margin. Juveniles with dense hairs often lost in adults, then shell slightly shiny and finely striated. Shell horny to reddish-brown with light band on body whorl.

#### Reproductive system (Figs 68–72)

Four pairs of rather long mucous glands. Both inner and outer dart sacs approximately equal in size, situated around upper vagina just below outlet of mucous glands. Vagina relatively long and cylindrical. Flagellum usually slightly shorter than epiphallus or approximately equal in length. Epiphallus as long as fusiform penis or somewhat longer. Spermatheca duct long. Spermatheca large and elongate, reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 69–72.

#### Ecology

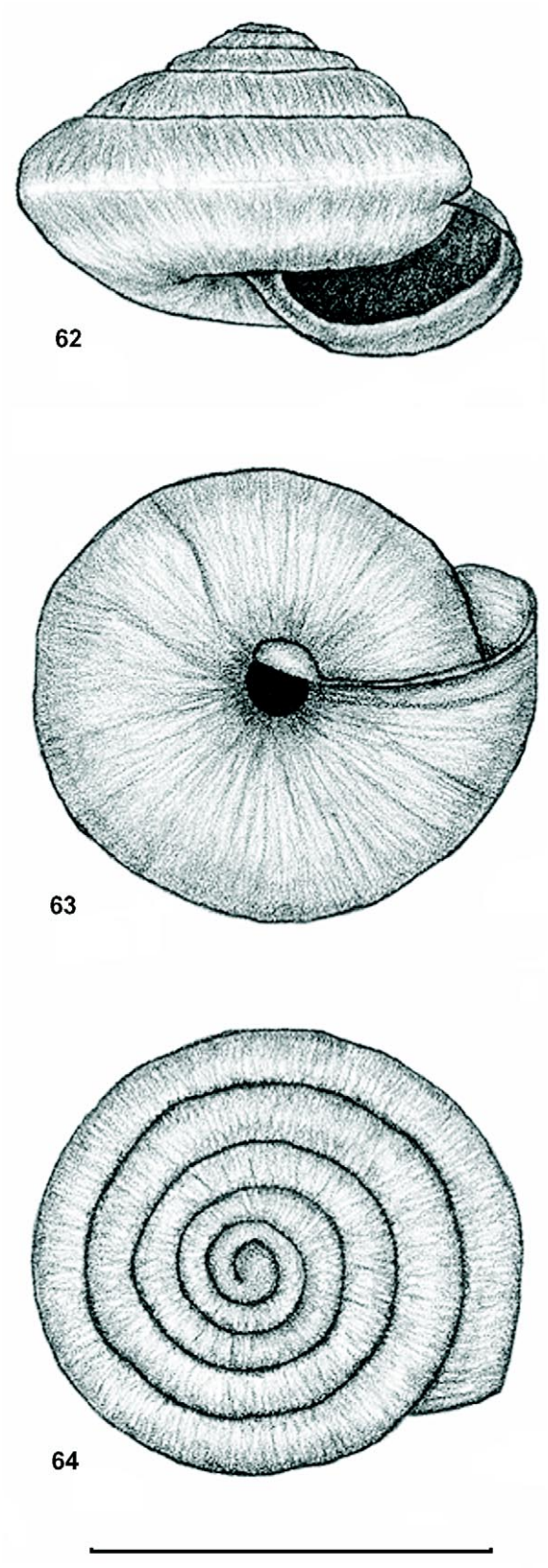
*T. edentulus* lives among herbaceous vegetation, in leaf litter and under stones in damp montane forests; between 300 and 2,000 m a.s.l. (usually not found above the timberline).

#### Distribution (Fig. 73)

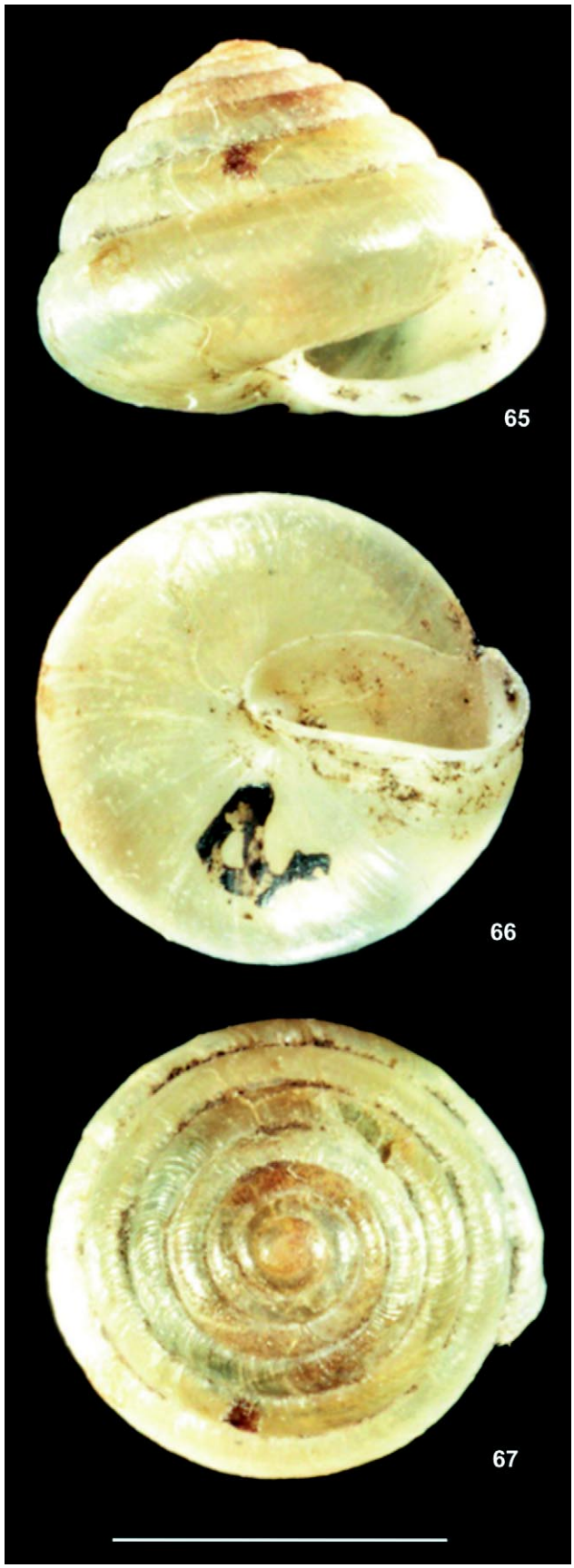
A West-Alpine species; known from France (Jura; southern Vosges; in the west to the Rhone River and the upper Loire River), Switzerland (Jura; from Genfersee to Bodensee; Alpenrheintal; northern part of reg. Waadt; Berner, Vierwaldstätter and Glarner Alps; western Walliser Alps; Nordbünden), Germany (pre-Alpine region in southern Bavaria: along the Salzach and Inn Rivers; Bavarian Alps; Bavarian Forest) and Austria (widely distributed except the eastern part) (POLIŃSKI 1928, KERNEY et al. 1983, TURNER et al. 1998).

#### Remarks

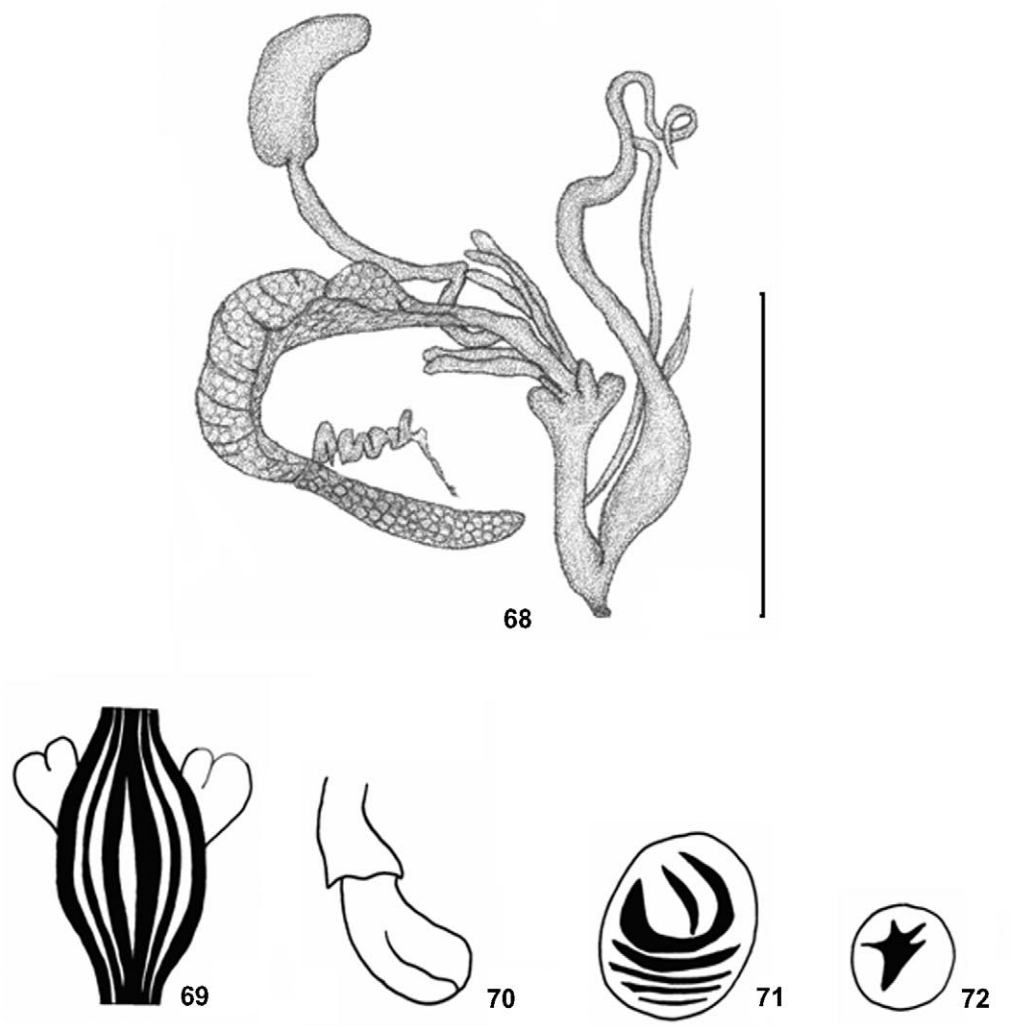
Some populations from Switzerland and Germany were described as *Fruticicola edentula helvetica* Poliński,




Figs 62–64. *T. edentulus*. Specimen from Golling, Salzburg, Austria, MIZW. Shell: 62 – apertural view, 63 – umbilical view, 64 – apical view. Scale bar 5 mm




Figs 65–67. *T. edentulus*. Specimen from Draparnaud's collection, NHMW. Shell: 65 – apertural view, 66 – umbilical view, 67 – apical view. Scale bar 5 mm




Figs 68–72. *T. edentulus*. Specimen from Golling, Salzburg, Austria, MIZW. Reproductive system: 68 – general view, 69 – longitudinal section of vagina, 70 – penial papilla, 71 – cross-section of penial papilla, 72 – cross-section of epiphallus. Scale bar 5 mm

1928. The subspecies differs from *edentulus* s. str. in its smaller size and narrower umbilicus, sometimes entirely covered. The upper and underside of the shell are similarly convex thus slightly resembling *T. biconicus*. Another form, described from Schwäbische Alb by POLIŃSKI (1928) – *Fruticicola edentula helvetica* var. (natio) *suevica* – was distinguished from the other froms of *edentulus* by its higher spire and much narrower aperture. Its reproductive system did not generally differ from the nominate species (POLIŃSKI 1928: 152). The shell material from the respective regions at my disposal was scanty and no alcohol-preserved specimens were available which made it impossible to solve the taxonomy of these entities.

The name *Fruticicola edentula helvetica* var. (natio) *suevica* Poliński, 1928 is infrasubspecific (Art. 45.6.4.1 ICZN), but was made available by JAECKEL jun. (1962: 182).

According to FALKNER (1985, 1990) two main-forms can be distiguished i.e. the western shells more conical, flattened on underside, with a very narrow, almost covered umbilicus and hairs present only in juveniles (including *T. edentula* s. str., *T. edentula helvetica* and *T. edentula suevica*); the eastern shells are more flattened, rounded underneath, with umbilicus open or half open, and stronger and more permanent hairs (including *T. edentula limnifera* and *T. edentula subleucozona*). He also pointed out the possible transi-

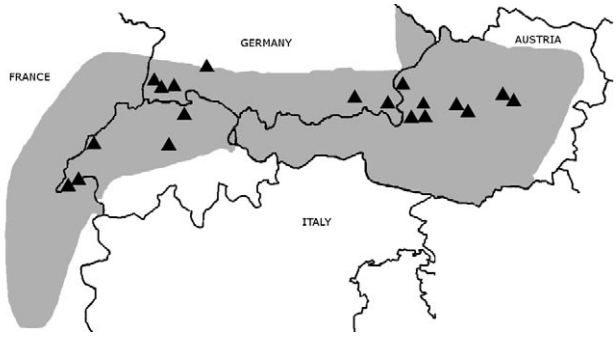



Fig. 73. Distribution of *T. edentulus*. Black triangles – localities of origin of the examined material

tion zone between *limnifera* and *subleucozona*, running along the Salzach River and the lower Inn River. The subspecies show no differences in the structure of their genitalia.

### *Trochulus erjaveci* (Brusina, 1870)

*Helix (Fruticicola) Erjaveci* BRUSINA 1870: 26. Locus typicus: Croatia: reg. Varaždinska: Vidovec; Agram [=Zagreb]; reg. Karlovačka: Ozalj and Slunj; reg. Ličko-senjska: Plitvice and Oštaria.

*Helix Hirci* CLESSIN 1883: 198. Locus typicus: Croatia: Schneeberg [=Snjeznik] and Veliki Risnjak.

*Helix osoria* BRANCSIK 1889: 69, pl. II, fig. 4. Locus typicus: Bosnia and Herzegovina: Miljacka valley.

*Helix haueri* BRANCSIK 1889: 69, pl. II, fig. 3. Locus typicus: Bosnia and Herzegovina: Mt. Trebević.

*Helix (Trichia) erjaveci blaui* KOBELT 1892: 6, pl. 122, fig. 727. Locus typicus: Bosnia and Herzegovina: near Sarajevo.

*Euomphalia (?) floerickei* KOBELT 1898: 162. Locus typicus: Montenegro: Moraca.

*Fruticicola erjaveci* var. *cincta* SOÓS 1904: 295. Locus typicus: Croatia: Lika-Krbava [historic county, now in south-western Croatia]: Goszpics [=Gospić].

*Fruticicola erjaveci* var. *syrmiensis* SOÓS 1904: 295. Locus typicus: Serbia: Krušedol.

*Fruticicola erjaveci leptolasia* WAGNER 1912: 250. Locus typicus: Bosnia and Herzegovina: Vlasič near Travnik and Jablanica.

*Fruticicola erjaveci osoria oreinos* WAGNER 1915: 481, pl. 18, figs. 154a-d (shell, genitalia). Locus typicus: Bosnia and Herzegovina: Ljubična and Radovina near Celebič.

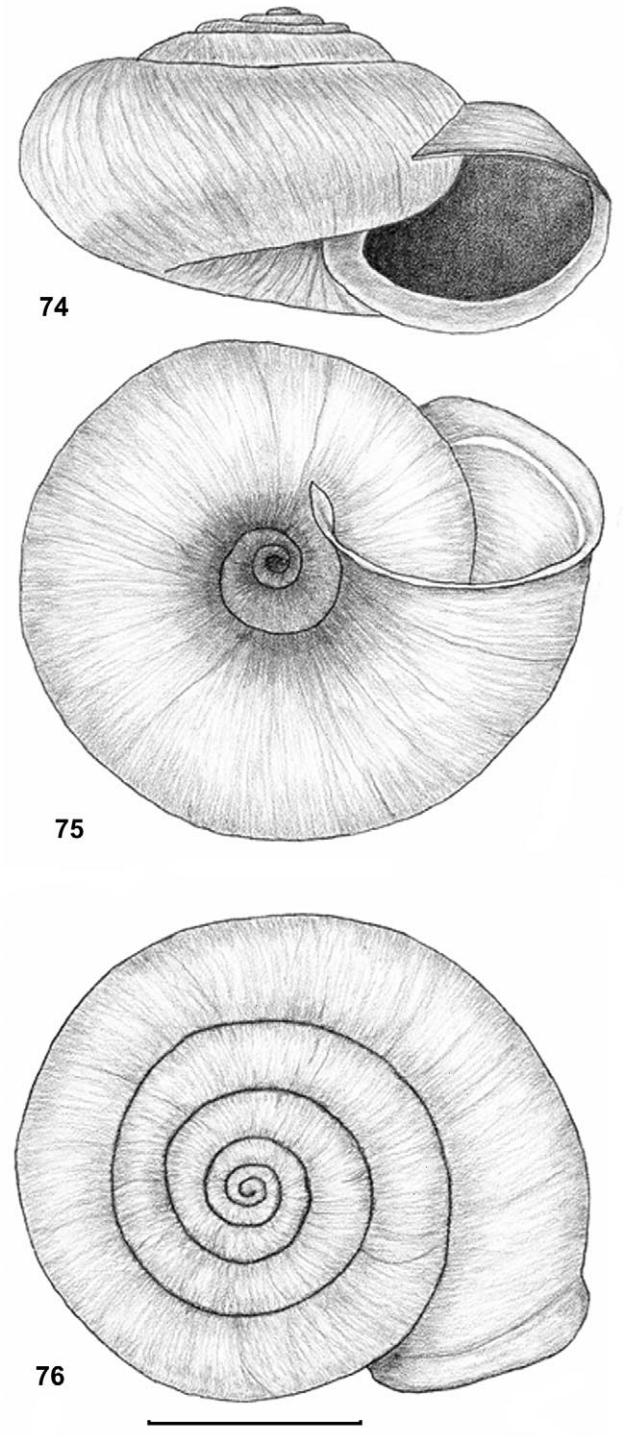
*Trichia erjaveci hajlensis* Jaeckel in JAECKEL & MEISE 1956: 29, pl. 1, fig. 4. Locus typicus: Serbia (Kosovo): Hajla Planina 1,900 m a.l.s.

Material examined

Bosnia and Herzegovina: Vlašičnear Travnik, MIZW, 5 s.; Croatia: Vorstadt Nova Ves near Agram [=Zagreb], MIZW, 6 s.; Agram Tramvag, MIZW, 24 s.; Agram, MIZW, 17 s.; Agram; leg. Častek 1912, coll. Poliński 228/37, MIZW, 3 s.; Zagreb, MIZW, 12 s.; Maksimir near Agram [now a part of Zagreb], MIZW, 10 s.; Brušane, reg. Ličko-senjska, MIZW, 1 s.; Kostajnica, reg. Sisačko-moslavačka, MIZW, 3 s.; Brodske gory, MIZW, 3 s.; Serbia: Krušedol [monastery], MIZW, 1 s.

Shell (Figs 74–76)

Shell cone-shaped, sometimes flattened, with 5.25–6.0 whorls. Shell height 5.6–8.5 mm, shell width 10.0–14.7 mm, height/width ratio 0.49–0.63, body whorl height 5.2–7.3 mm, relative height of body whorl 0,76–0,90, aperture height 3.0–4.3 mm, aperture width 5.4–7.0 mm, umbilicus major diameter 1.9–3.4 mm, umbilicus minor diameter 1.5–2.7 mm, umbilicus major diameter/shell diameter ratio 0.16–0.24. Aperture transversely oval with distinct white lip inside. Basal and palatal aperture margins slightly reflexed. Umbilicus open, earlier whorls visible. Adults hairless. Shell yellowish-white, sometimes with lighter band on body whorl, matt and smooth, sometimes translucent.




Figs 74–76. *T. erjaveci*. Specimen from Zagreb – Croatia, MIZW. Shell: 74 – apertural view, 75 – umbilical view, 76 – apical view. Scale bar 5 mm


Fig. 77. Distribution of *T. erjaveci*. Black triangles – localities of origin of the examined material

Reproductive system

The description below is given according to WAGNER (1915) because material for anatomical examination was unavailable.

Four pairs of short mucous glands, sometimes with secondary branches. Inner dart sacs slightly longer than outer ones. Vagina cylindrical. Flagellum shorter than epiphallus, which is longer than fusiform penis. Spermatheca duct short and thick. Spermatheca oval, reaching ca. 1/2 spermoviduct length.

Ecology

*T. erjaveci* lives in damp, shaded forests, rarely in open places; it is found on vegetation (preferably shrubs). In the area of Batak Village it was collected at 1,100 m a.s.l. (IRIKOV & MOLLOV 2006).

Distribution (Fig. 77)

A North-Western Balkan species; found in Croatia, Bosnia and Herzegovina, Montenegro to Macedonia, also in Hungary (environs of Budapest and south of the country: Mecsek mountain range) (WAGNER 1915, KERNEY et al. 1983), known from northern Albania (DHORA & WELTER-SCHULTES 1996) and Bulgaria (Ropotamo National Park, Stara Planina, west of Topolowgrad, southwest of Svilengrad, the Western Rhodopes: only in the area of Batak Village) (DAMJANOV & LIKHAREV 1975, IRIKOV & MOLLOV 2006).

### *Trochulus filicinus* (L. Pfeiffer, 1841)

*Helix filicina* L. PFEIFFER 1841: 39. Terra typica: Slovenia: "Carniolia" [=Carniola].

*Helix (Fruticicola) Bielzi* var. *bosnensis* MÖLLENDORFF 1873: 35. Terra typica: Bosnia: Igmangebirge.

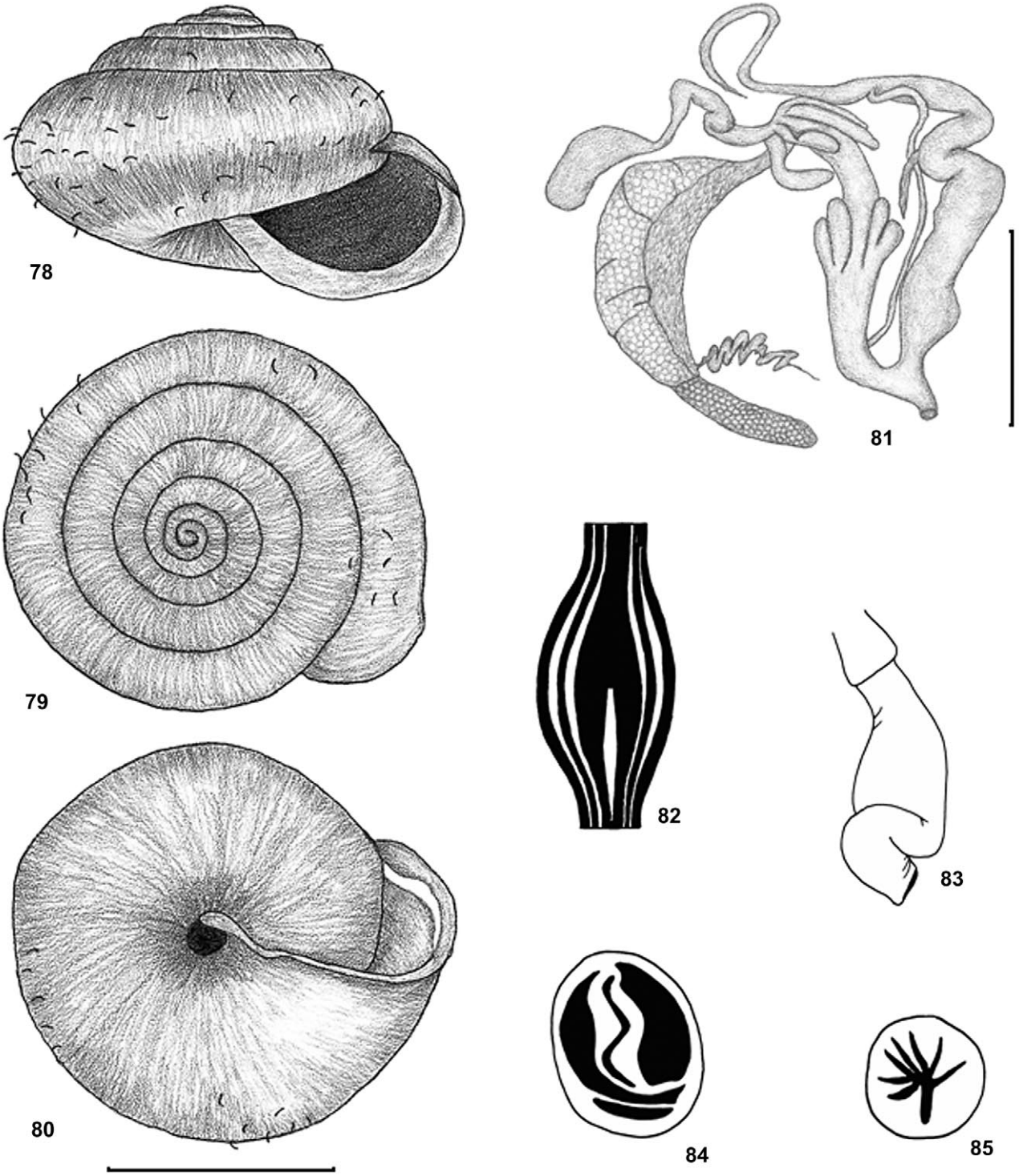
*Fruticicola filicina filicina* natio *styriaca* POLIŃSKI 1928: 181, pl. XXVII, fig. 32 [not 92]. Locus typicus: Austria: Styria: Graz.

Material examined

Austria: Styria: Bärenschützklamm, NHMW, 5 s.; Bärenschütz, Hochlantsch, MIZW, 1 s.; Hochlantsch, coll. Poliński 228/37, MIZW, 10 s.; Fronleiten, 1918, leg. A. J. Wagner, coll. Poliński 228/37, MIZW, 2 s.; Ruine Peggau, coll. Edlauer 27407, NHMW, 12 s.; Austria and Italy: Carnische Alpen [=Carnic Alps], coll. Gallenstein 53532, NHMW, 12 s.; Slovenia: Mt. Velika Gora, SW of Reifnitz (=Ribnica), Krain [=Carniola], coll. Edlauer 20807, NHMW, 8 s.; Isonzo [=Soča] valley, Woltschach [=Volče], W of Tolmin, coll. Wagner, MIZW, 2 alc.; Mt. Grintovec, Kamnik Alps, coll. Poliński 228/37, MIZW, 1 s.

Shell (Figs 78–80)

Shell roundish with 5.5–6.3 whorls. Shell height 5.3–7.6 mm, shell width 7.7–11.4 mm, height/width ratio 0.56–0.73, body whorl height 4.3–5.8 mm, relative height of body whorl 0.76–0.96, aperture height 2.7–4.1 mm, aperture width 4.3–6.2 mm, umbilicus major diameter 0.2–0.9 mm, umbilicus minor diameter 0.2–0.9 mm, umbilicus major diameter/shell diameter ratio 0.02–0.11. Aperture oblique, basal aperture margin horizontally expanded and slightly reflected, with distinct lip inside. Umbilicus very nar-




Figs 78–85. *T. filicinus*. Specimen from Hochlantsch, Styria, Austria, coll. Poliński 228/37, MIZW. 78–80 – shell: 78 – apertural view, 79 – apical view, 80 – umbilical view; 81–85 – reproductive system: 81 – general view, 82 – longitudinal section of vagina, 83 – penial papilla, 84 – cross-section of penial papilla, 85 – cross-section of epiphallus. Scale bar 5 mm

row, sometimes partly or nearly entirely covered by columellar aperture margin; when open, most often round. Both juveniles and adults with short and dense hairs. Shell horny-brown with prominent growth lines, light band on body whorl.

Reproductive system (Figs 81–85)

Four pairs of short mucous glands situated around upper vagina, ca. 3.5 mm from tips of inner dart sacs, which are slightly longer than outer ones. Vagina very long (ca. 9 mm); its expanded dart sac region narrows toward genital atrium. Flagellum almost twice as long as epiphallus, which is shorter than very long, cylindrical penis. Spermatheca duct long and bent. Spermatheca elongate, reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 82–85.

Ecology

*T. filicinus* lives in shaded, damp forests in the uplands and lower mountain altitudes; it is quite often found in river valleys.

Distribution (Fig. 86)

An East-Alpine and Carpathian species; known from Austria (Carynthia, Styria), western Slovakia (Inovec Mts), Hungary (Mecsek; Vértes; Örtilos; Zalamerenge), Slovenia (Julian Alps: in the south to Tolmin) and northern Italy (only in Alpi Giulie and Carso) (POLIŃSKI 1928, KERNEY et al. 1983, MANGANELLI et al. 1995, ČEJKA et al. 2007); the Dinaric Alps to southern Serbia (FALKNER 1990).


Fig. 86. Distribution of *T. filicinus*. Black triangles – localities of origin of the examined material

Remarks

The geographical "natio" *styriaca* is smaller and more roundish than the nominate species: it has rounded aperture, umbilicus almost covered, shorter and sparser hairs (POLIŃSKI 1928).

### *Trochulus graminicolus* (Falkner, 1973)

*Trichia (Trichia) graminicola* FALKNER 1973: 211, figs 1–4 (shell), fig. 6 (genitalia). Locus typicus: Germany: Bayern: region of Donaueschingen: Eichberg near Blumberg, W slopes at half distance between Achdorf and Eschach. Holotype: Senckenberg-Museum Frankfurt SMF 228814.

The description of the species is given according to FALKNER (1973) because I had neither dry shells nor alcohol-preserved material at my disposal, and failed to get access to the type material.

Shell

Shell strongly flattened, usually twice broader than high, with nearly flat spire and 5.6–6.2 whorls (usually 5.7). Body whorl ca. 1.5 × wider than penultimate. Suture deep, especially between the penultimate and body whorl. Shell height 4.7–5.3 mm, shell major diameter 9.6–10.7 mm, shell minor diameter 8.4–9.4 mm, aperture height 3.4–3.9 mm, aperture width 4.2–5.1 mm, umbilicus major diameter 2.1–3.0 mm, umbilicus minor diameter 1.6–2.4 mm., umbilicus major diameter/shell diameter ratio 0.22–0.29. Aperture oblique, aperture margin reflected, with white lip. Umbilicus wide. Adults hairless, in juveniles hairs short and weak (0.1–0.2 mm long, near umbilicus 0.03–0.06 mm). Shell dark horny to reddish-brown, irregularly prominently striated above and smooth, distinctly convex below; shiny, sometimes with light band on body whorl.

Reproductive system

Four pairs of short mucous glands, sometimes with secondary branches or reduced to four in total. Inner dart sacs slightly longer than club-shaped outer ones. Vagina very long and cylindrical (6.8–8.9 mm); distance between outlet of mucous glands and tips of inner dart sacs (called by FALKNER Vaginahals = vaginal neck, which I call upper vagina) equal to ca. 1/3 vagina length. Flagellum usually longer than epiphallus, which is longer than penis; but all these parts can be approximately equal in length. Spermatheca duct thin and long. Spermatheca elongatedly oval, not reaching albumen gland.

Ecology

*T. graminicolus* lives in grassy screes in sparse montane forests on steep slopes, with pine, spruce and juniper (*Calamagrostio variae-Pinetum* community). Both juveniles and adults stay firmly attached to


Fig. 87. Distribution of *T. graminicolus*

grass blades, especially to their underside. While feeding, they choose wider damaged blades. It is not found directly on the ground or higher vegetation (FALKNER 1973).

Distribution (Fig. 87)

An endemic species; known only from south-western Germany (Baden-Württemberg, Schwäbische Alb near Geislingen and Blumberg) (FALKNER 1973).

Remarks

It differs from *T. hispidus* in a flatter shell and a more oblique aperture. The vaginal neck is longer than in the other members of *Trochulus*.

### *Trochulus hispidus* (Linnaeus, 1758)

*Helix hispida* LINNAEUS 1758: 771. Terra typica: Sweden.

*Helix sericea*[1] DRAPARNAUD 1801: 85. Terra typica: not given in original description – probably France.

*Helix plebeium* DRAPARNAUD 1805: 105, pl. VII, fig. 5. Terra typica: not given in original description – probably France. **Syn. nov.**

*Helix depilata* C. PFEIFFER 1821: 35, pl. II, fig. 18. Locus typicus: Germany: near Cassel [=Kassel]: "Bellevuegarten" [Palais Bellevue] and on Kratzenberge, in grass and under fallen leaves.*

*Helicella Prevostina* RISSO 1826: 73. Terra typica: France: dep. Alpes-Maritimes.*

*Helix concinna* JEFFREYS 1830: 336. Locus typicus: Wales: vicinity of Swansea, "under stones & c. in dry places"; England: near Bristol, "among the rejectamenta of the Avon river" [non *Helix concinna* Dupuy, 1848]. **Syn nov.**

*Helix hispida* Var. *nana* JEFFREYS 1862: 199. Locus typicus: England: Isle of Wight (Metcalfe), freshwater.*

*Helix Vendeana* LETOURNEUX 1869: 60. Locus typicus: France: dep. Vendée: near Fontenay-le-Comte.*

*Helix Gratianopolitana* RAMBUR 1869: 267. Locus typicus: France: environs of Grenoble.*

*Helix liberta* WESTERLUND 1871: 54. Locus typicus: Sweden: prov. Skåne: near Lund, in garden.*

*Helix Bellovacina* MABILLE 1877: 305. Locus typicus: France: dep. Oise: "in humidis silvisque pagi Compendiaci Galiae" [=probably Compiègne].*

*Helix Steneligma* Bourguignat in MABILLE 1877: 305. Locus typicus: France: Pyrenees and dep. Oise: "in silvis pagi Compendiaci" [=probably Compiègne].*

*Helix Elaverana* Bourguignat in MABILLE 1877: 305. Locus typicus: France: Pyrenees and environs of Paris.*

*Helix saporosa* MABILLE 1877: 305. Locus typicus: France: dep. Aisne: "in silvis pagi Suessoniensis Galiae" [=Soissons].*

*Helix Axonana* MABILLE 1877: 306. Locus typicus: France: dep. Aisne: "in silvis ad Castrium-Theodorici Galiae" [=Château-Thierry].*

*Helix Matronica* MABILLE 1877: 306. Locus typicus: France: environs of Paris.*

*Helix Goossensi* MABILLE 1877: 306. Locus typicus: France: dep. Essone: "in locis limpsis ad Firmitatem Adelahidis Galiae" [=La Ferté-Alais].*

*Helix hispidosa* Letourneux in SERVAIN 1880: 60. Locus typicus: France: dep. Loire-Atlantique: Vertou near Nantes (coll. Letourneux); Spain: alluvions of Arta [=Arga] near Pampelune (coll. Servain). [non *Helix hispidosa* Bourguignat in Fagot, 1879]*

*Helix badiella* Ziegler in LOCARD 1881: 107, fig. on p. 107. Locus typicus: France: dep. Seine-et-Marne: banks of Marne River towards drains of Pomponne [lake], between Thorigny and Pomponne".*

*Helix urbana* Coutagne in LOCARD 1881: 107, fig. on p. 108. Locus typicus: France: dep. Seine-et-Marne: banks of Marne River, in environs of Lagny and Pomponne.*

*Helix Latiniacensis* LOCARD 1881: 108, fig. on p. 109. Locus typicus: France: dep. Seine-et-Marne: environs of Paris: Lagny, Thorigny, Pomponne, Carnetin; dep. Seine-et-Oise: Argenteuil, palace of Versailles; Seine: Vincennes and Charenton (coll. Locard); Saint-Mandè forest and Paris: Arsenal street near Bastille (coll. Coutagne).*

*Helix subbadiella* Bourguignat in LOCARD 1882: 74, 317. Locus typicus: France: environs of Paris; dep. Alpes-Maritimes: Monton (coll. Bourguignat).*

*Helix Vendoperanensis* Bourguignat in LOCARD 1882: 76, 317. Locus typicus: France: dep. Aube: Vendeuvre-sur Barse and Viélaines near Rosières; environs of Lyon (coll. Bourguignat).*

[1] As FALKNER et al. (2002) point out, the name *plebeius* has been wrongly applied to the taxon *Trochulus sericeus* (Draparnaud, 1801). FORCART (1965) originally proposed the replacement of the name *sericeus* by the younger name *plebeius* to sort out a difficult taxonomic problem relating to the validity of the name *sericeus* (Draparnaud, 1801) in contradistinction to *sericeus* (Müller, 1774). However, in so doing, he synonymised what have subsequently been regarded as two distinct species, one widespread in north-west Europe, the other confined to the alpine region (ANDERSON 2005).

*Helix Vocoutiana* Bourguignat in LOCARD 1882: 76, 317. Locus typicus: France: dep. Isère: La Salette near Corps (coll. Bourguignat).*

*Helix Hypsellina* Pons in LOCARD 1882: 78, 318. Locus typicus: France: dep. Aveyron: Estaing (coll. Bourguignat).*

*Helix microgyra* Bourguignat in LOCARD 1882: 79, 319. Locus typicus: France: dep. Basses-Pyrènèes [=Pyrénées-Atlantiques]: valley near Pic du Ger, above Eaux-Bonnes (coll. Bourguignat).*

*Helix Cularensis* Bourguignat in LOCARD 1882: 79, 319. Locus typicus: France: dep. Isère: Sassenage near Grenoble (coll. Bourguignat).*

*Helix hispidella* Bourguignat in LOCARD 1882: 79. Locus typicus: France: dep. Loire-Inférieure [=Loire-Atlantique]: Vertou near Nantes (coll. Letourneux); dep. Aube: Othe forest, vis-à-vis Montaigu near Bouilly (coll. Bourguignat).*

*Helix Ataxiaca* FAGOT 1883: 220. Locus typicus: France: dep. Aude: above Quillau, Fanges forest. [FALKNER et al. 2001: 58 – *Trochulus ataxiacus* (Fagot, 1884)].

*Helix Beaudouini* LOCARD 1887: 165. Locus typicus: France: dep. Côte-d'Or: environs of Châtillon-sur-Seine.*

*Helix Duesmensis* LOCARD 1887: 168. Locus typicus: France: dep. Côte-d'Or: environs of Châtillon-sur-Seine and Auxonne; dep. Aube: Courtenot and Troyes; dep. Marne: Châlons-sur-Marne; dep. Meurthe-et-Moselle: Bionville; dep. Moselle: Fouligny and environs of Metz.*

*Helix latiscensis* LOCARD 1887: 172. Locus typicus: France: dep. Côte-d'Or: environs of Châtillon-sur-Seine.*

*Helix Sarinica* LOCARD 1887: 174. Locus typicus: Switzerland: Sarine valley near Fribourg; France: alluvions of Rhone, Lyon; dep. Ain: Chartreuse-de-Portes and Dampierre; dep. Côte-d'Or: Châtillon-sur-Seine; dep. Aube: environs of Troyes.*

*Helix montigena* LOCARD 1894: 116. Locus typicus: France: Ste Foy lès Lyon; dep. Ain: Chevry and Hauteville; sources of the Doubs River.*

*Helix Segusiana* LOCARD 1894: 116. Terra typica: France: deps: Ain, Isère, Savoie and Haute-Saône.*

*Helix Alixae* Bourguignat in LOCARD 1894: 120. Locus typicus: France: dep. Hautes-Pyrènèes: Loudres.*

*Helix Drunasiana* LOCARD 1894: 121. Locus typicus: France: dep. Drôme: Die and Col du Rousset.*

*Helix Barcelonnettensis* Bourguignat in LOCARD 1894: 125. Locus typicus: France: dep. Ain: Hauteville; dep. Savoie: Albertville; dep. Hautes-Alpes: Barcelonnette.*

*Helix foeni* LOCARD 1894: 126. Terra typica: France.*

*Helix Pictavica* Bourguignat in LOCARD 1894: 127. Locus typicus: France: Clain valley; dep. Vienne: between Poitiers and Saint-Benolt.*

*Helix Niverniaca* LOCARD 1894: 127. Locus typicus: France: dep. Nièvre: environs of Nevers; dep. Charente: Flèac.*

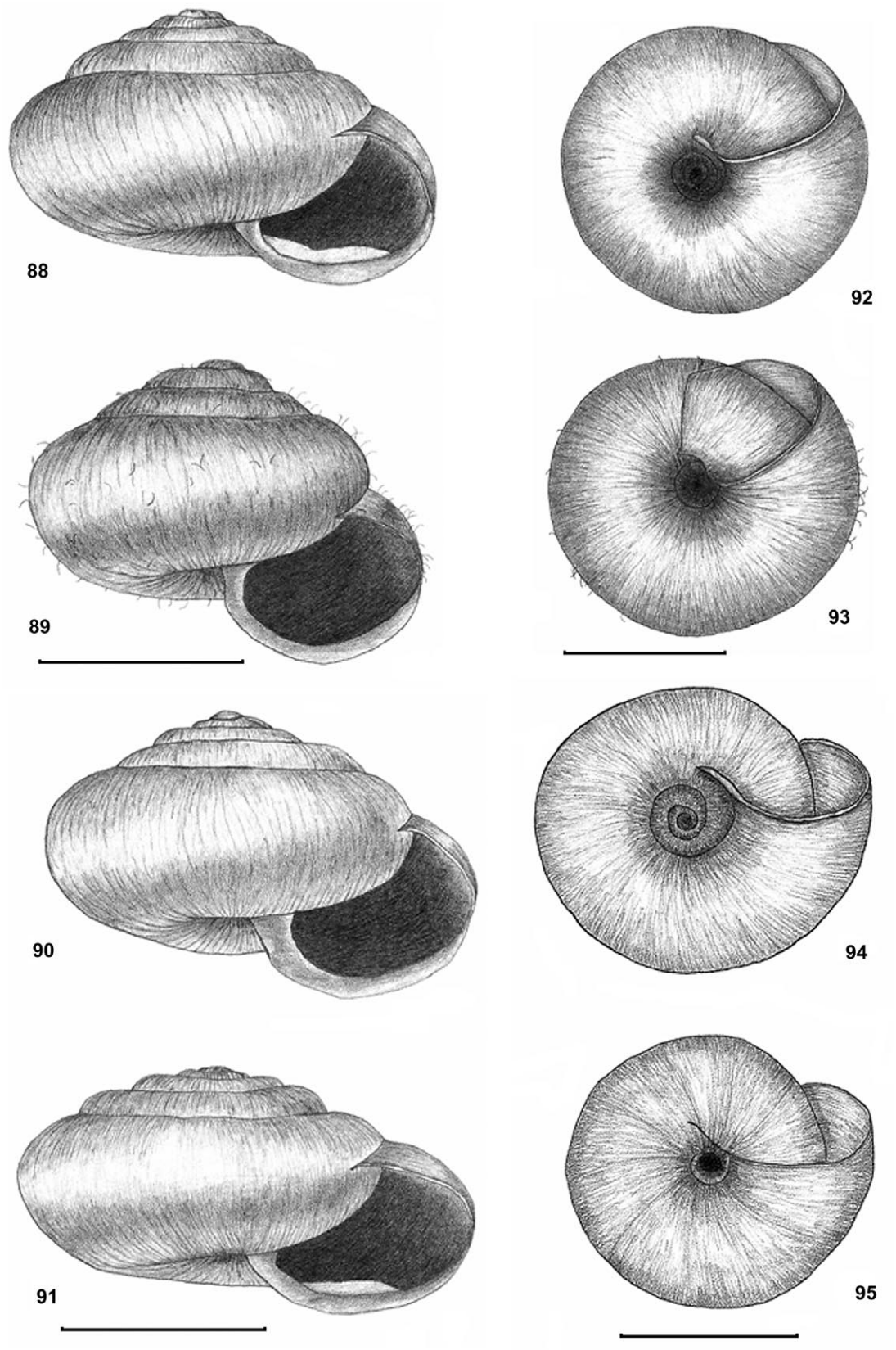
*Helix Salinae* Bourguignat in LOCARD 1894: 131. Locus typicus: France: dep. Jura: Salins.*

*Helix subniverniaca* CAZIOT 1910: 115. Terra typica: France: dep. Alpes-Maritimes.*

*Helix Orzeszkoi* CAZIOT 1910: 117, pl. VI, fig. 36. Terra typica: France: dep. Alpes-Maritimes.*

Material examined

Austria: Trins im Gschnitztal, Tyrol, MIZW, 2 s. [*plebeius*]; Strasse von norders nach Martinsbrück, 1,300 m, Tyrol, MIZW, 5 s. [*plebeius*]; St. Jodok, Tyrol; 2.07.1998, ZW, 30 alc.; between Zirl and Innsbruck, Tyrol, 2.07.1998, ZW, 15 alc.; Teichwiesen near Bruck an der Leitha, Lower Austria, coll. Oberwimmer, NHMW, 17 s.; loess Nußdorf ob der Traisen towards Neusiedl, Lower Austria; coll. Klemm 63023, NHMW, 18 s.; Fischamend, Lower Austria, coll. Sterki 1, NHMW, 21 s.; Schwöll near Pfongau, Upper Austria, 28.03.1946, coll. Klemm 23697, NHMW, 29 s. [*plebeius*]; s. prec. loc., Carinthia, coll. Gallenstein 53569, NHMW, 22 s.; Britain: Box Hill near Dorking, Surrey; 18–25.09.1963, leg. J. F. Peake & A. J. Knight, BMNH, 10 s; Portholme Meadow, Huntingdon; 1.08.1988, leg. D. T. Bilton, BMNH, 3 alc. [*plebeius*]; France: Lyon; Jickeli, MIZW, 1 s. [*plebeius*]; Mt. Ceindre near Lyon; coll. O. Retowski 41/39, MIZW, 3 s. [*plebeius*]; s. prec. loc. Frankreich; coll. Edlauer 48822, NHMW, 6 s. [*plebeius*]; Germany: Mauer an der Elsenz near Heidelberg, Baden-Württemberg; coll. Klemm 19416, NHMW, 11 s. [*concinnus*]; Freiburg, MPW, 4 s. [*concinnus*]; Bonn, Breslauer Promenade, MPW, 31 s.; Günzburg, Bavaria, coll. Edlauer 35288, NHMW, 26 s.; Dinkelscherben, Bavaria, MIZW, 4 s. [*plebeius*]; Netherlands: Amsterdam, NHMW, 15 s.; Poland: Ziemia Lubuska: Zielona Góra, 03.1964, leg. Łużna, UŁ, 20 s.; Wielkopolska: Stęszew, 24.07.1979, leg. E. Koralewska, UAM, 112 s.; Chyby, 18.06.1969, leg. M. Stachowiak, UAM, 56 s.; Poznań, 13.05.1991, leg. E. Koralewska, UAM, 58 alc.; Rąbczyn, leg. Strojkowska, UAM, 60 s.; Jarocin, 30.10.1976, 13.03.1977, leg. M. Michałkiewicz, UAM, 179 s.; Węgierki, 2.07.1973, leg. E. Koralewska, UAM, 101 s.; Lower Silesia: Zieleniec, Bystrzyca Dusznicka valley, 24.05.1997, ZW, 35 alc. [*plebeius*]; Wałbrzych, 07.1994, leg. T. Maltz, MPW, 8 s.+58 alc.; Lubawka, 9.09.1994, leg. M. Majkowska, MPW, 41 s.+27 alc.; Muszkowice, 26.08.1994, leg. M. Majkowska, E. Kuźnik, MPW, 12 s.+59 alc.; Oława, 30.07, 27.08.1973, leg. G. Notz, MPW, 41 s.+203 alc.; Arnoldsmühle [=Jarnołtów in Wrocław], MPW, 3 s. [*concinnus*]; Kapsdorf bei Breslau [=Czerńczyce near Wrocław], MPW, 1 s. [*concinnus*]; Greiffenstein [=Gryf castle in Proszówka], MPW, 5 s.; Pomorze: Gdynia, 17.08.1993, leg. T. Maltz, MPW, 51 s.; Miłosna near Kwidzyń, leg. B. & A. Piechoccy, UŁ, 9 s.; Warmia and Mazury:




Figs 88–95. *T. hispidus*. Shell. 88–91 – apertural view: 88 – specimen from Lubawka, Sudetes, Poland, ZW, 89 – specimen from Muszkowice, Sudetes, Poland, ZW, 90 – specimen from Parzynów, Poland, ZW, 91 – specimen from Gołdap, Poland, ZW; 92–95 – umbilical view: 92 – specimen from Lubawka, Sudetes, Poland, ZW, 93 – specimen from Muszkowice, Sudety Foothills, Poland, ZW, 94 – specimen from Günzburg, Germany, NHMW, 95 – specimen from Zieleniec, Sudetes, Poland, ZW. Scale bar 5 mm

Kudypy nature reserve, on the Pasłęka River, 5.09.1966, leg. A. Piechocki, UŁ, 3 s.; on the Pasłęka River near Wapnik, 8.09.1966, leg. A. Piechocki, UŁ, 6 s.; Gołdap, on lake Gołdap, 25.08.1994, leg. M. Majkowska, A. Leśniewska, MPW, 156 s.; Błądziszki, 26.08.1994, leg. T. Maltz, B. M. Pokryszko, MPW, 90 alc.; Mazowsze: Radom, 13–15.04.1919, leg. K. Gajl, MIZW, 118 s.; Ziemia Łódzka: Łódź, 17.11.1960, leg. A. Piechocki, UŁ, 2 s.; Świętokrzyskie Mts: Św. Krzyż, Polana Bielnik, 19, 24.06.1977, leg. A. Piechocki, UŁ, 3 s.; Św. Krzyż, near monastery, 20.06.1970, leg. A. Piechocki, UŁ, 4 s.; Św. Krzyż, slope, 20.09.1973, leg. A. Piechocki, UŁ, 10 s.; Kielce, Karczówka hill, 29.04.1978, leg. A. Piechocki, UŁ, 4 s.; Słowik near Kielce, 30.04.1978, leg. A. Piechocki, UŁ, 1 s.; Wyżyna Małopolska: Złoty Potok, Wały nature reserve, 7.07.1976, leg. E. Ruszkowska, UŁ, 2 s.; Biłgoraj, 17.07.1910, leg. Lorez, MIZW, 114 s.; Polesie: Chełm, 03.1923, leg. W. Wolberg, MIZW, 113 s.; Staw, 29.08.1994, leg. M. Majkowska, A. Leśniewska, MPW, 159 s.+46 alc.; Roztocze: Zwierzyniec, Roztoczański National Park, 23.07.1987, I. Kow. Jeziorko, UŁ, 14 s.; Żurawnica, 1.08.1988, leg. A. Piechocki, UŁ, 11 s.; Tartaczna Góra, 19.07.1989, leg. A. Piechocki, UŁ, 1 s.; Szewnia Dolna, 20.10.1989, leg. M. Puchyr, UŁ, 2 s.; Turzyniec, 10.05.1989, leg. A. Piechocki, UŁ, 9 s.; Ukraine: Taschlik [=Tashlyk], Podolien, 1873, coll. O. Retowski 41/39, MIZW, 13 s. [*plebeius*];

### Shell (Figs 88–95)

Shape variable: from roundish-conical to nearly flattened, with 5–6 moderately convex whorls. Shell height 3.0–6.7 mm, shell width 5.4–10.5 mm; height/width ratio 0.47–0.78, body whorl height 2.9–5.2 mm, relative height of body whorl 0.73–0.93, aperture height 1.9–3.8 mm, aperture width 2.6–5.0 mm, umbilicus major diameter 0.5–2.5 mm, umbilicus minor diameter 0.6–2.3 mm, umbilicus major diameter/shell diameter ratio 0.1–0.31. Aperture with thin white lip inside. Umbilicus entirely open and wide, earlier whorls always visible. Hairs thin, short and slightly curved, in adults often lost, leaving pronounced scars. Shell cream-coloured to dark brown, some specimens have light band on body whorl.

### Shell variation

Individual and inter-population variation of almost all the studied morphometric characters is very considerable (Figs 96–108). Each of the studied populations differs statistically significantly from the remaining ones in at least one character and the intra-population variation ranges of most parameters are very wide. Variation of some populations has been discussed in PROĆKÓW (1997); a few more populations are added here.

Almost every examined population differs statistically significantly from the remaining ones in at least one character. Most populations differ in their shell size (Figs 96–103), and proportions (Figs 105–108), and in the number of whorls (Fig. 104). Some pairs of populations differ in all or nearly all the parameters examined, e.g. those from Bonn, Muszkowice and Zieleniec. Likewise, populations from Fischamend, Jarocin and Gołdap differ from the remaining ones in such characters as shell width and height/width ratio. The least variable characters are relative height of body whorl and umbilicus relative diameter.

### Reproductive system (Figs 109–113)

Four pairs of short mucous glands, sometimes with additional branches or some branches may be reduced to 4–6 in total. Inner and outer dart sacs approximately equal in length. Vagina cylindrical. Flagellum as long as epiphallus or slightly longer. Epiphallus longer than massive, fusiform and slightly bent penis. Spermatheca duct straight. Spermatheca oval, reaching ca. 1/2 spermoviduct length. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 110–113.

### Ecology

*T. hispidus* lives in various damp habitats: in sparse forests, semi-open (shrubland) and open (meadows, cultivated areas) places, never in very dry sites; in summer it climbs plants, preferably stinging nettles (*Urtica dioica*). It is usually found below 1,600 m a.s.l., but in the Alps and the Pyrenees it occurs up to

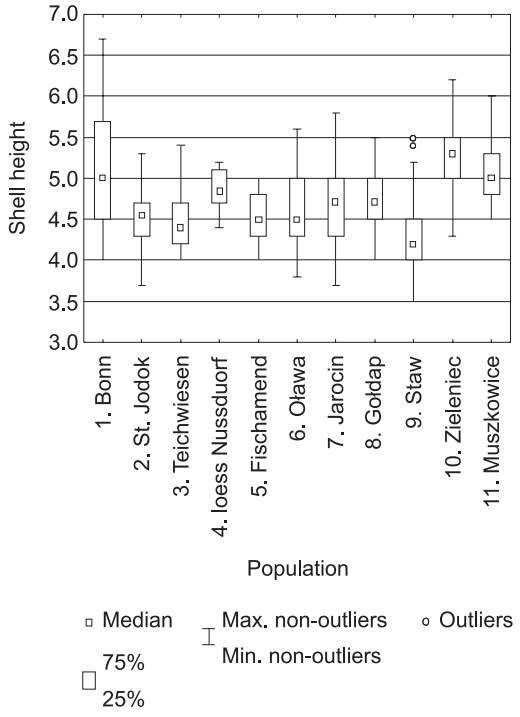



Fig. 96. Interpopulation variation of *T. hispidus*: shell height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–5, 1–6, 1–7, 1–8, 1–9, 2–9, 2–10, 2–11, 3–10, 3–11, 4–9, 4–10, 5–10, 5–11, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 8–11, 9–10, 9–11

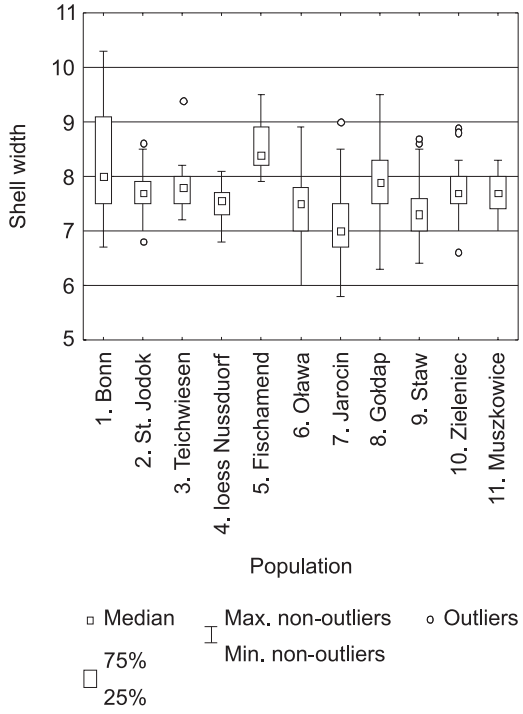



Fig. 97. Interpopulation variation of *T. hispidus*: shell width. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–7, 1–8, 1–9, 1–10, 1–11, 2–5, 2–7, 2–9, 3–5, 3–7, 4–5, 4–7, 5–10, 6–7, 6–8, 7–8, 7–9, 7–10, 7–11, 8–9, 9–10

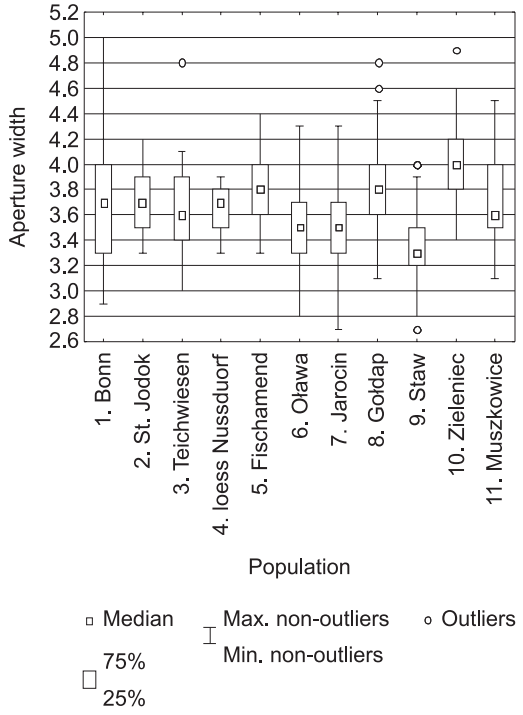



Fig. 99. Interpopulation variation of *T. hispidus*: aperture width. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–6, 1–7, 1–9, 2–6, 2–7, 2–9, 2–11, 3–9, 4–9, 5–7, 5–9, 6–8, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 9–10, 9–11

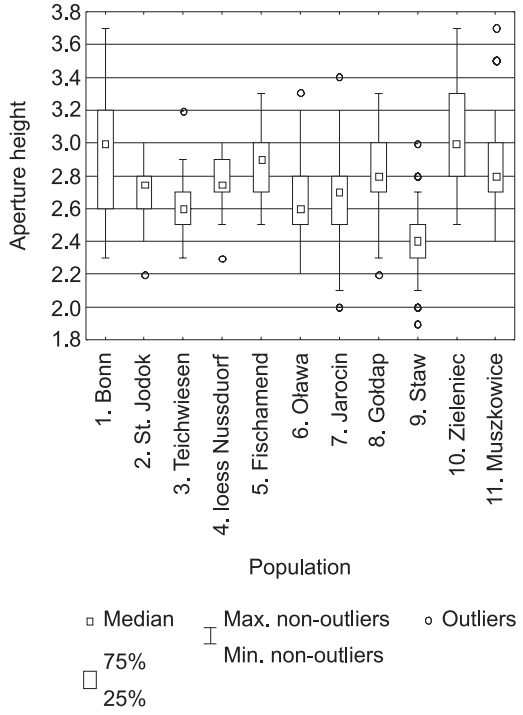



Fig. 98. Interpopulation variation of *T. hispidus*: aperture height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–6, 1–7, 1–9, 1–10, 2–9, 2–10, 3–9, 3–10, 4–9, 4–10, 5–6, 5–7, 5–9, 6–8, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 9–10, 9–11

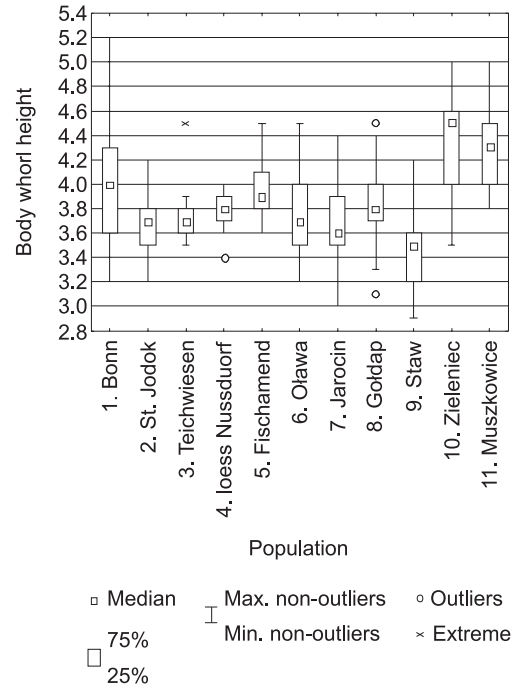



Fig. 100. Interpopulation variation of *T. hispidus*: body whorl height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–6, 1–7, 1–8, 1–9, 1–10, 1–11, 2–9, 2–10, 2–11, 3–9, 3–10, 3–11, 4–9, 4–10,. 4–11, 5–7, 5–9, 5–10, 5–11, 6–7, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 8–11, 9–10, 9–11

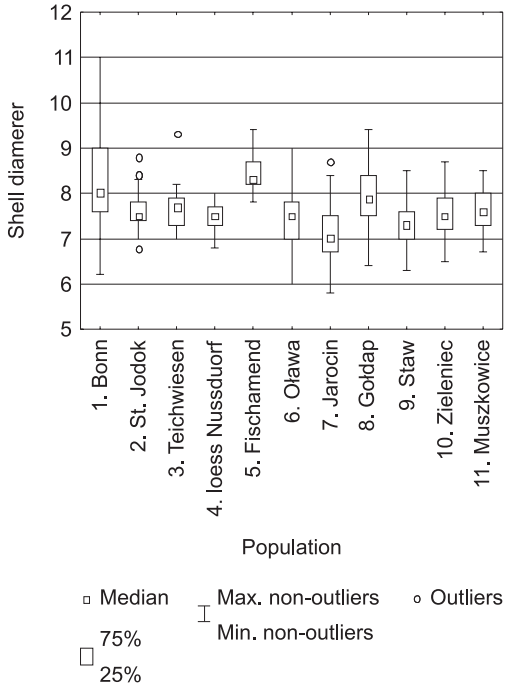



Fig. 101. Interpopulation variation of *T. hispidus*: shell diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–6, 1–7, 1–8, 1–9, 1–10, 1–11, 2–5, 2–7, 3–5, 3–7, 4–5, 4–7, 5–6, 5–7, 5–8, 5–9, 5–10, 5–11, 6–7, 6–8, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10

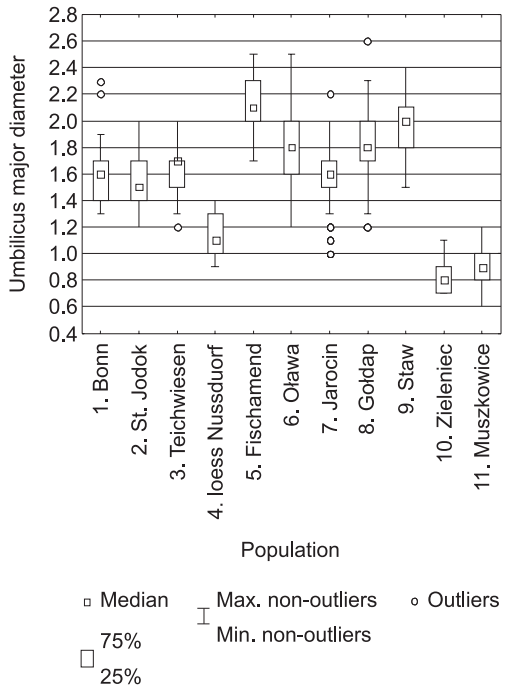



Fig. 102. Interpopulation variation of *T. hispidus*: umbilicus major diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–4, 1–5, 1–6, 1–8, 1–9, 1–10, 1–11, 2–4, 2–5, 2–6, 2–8, 2–9, 2–10, 2–11, 3–4, 3–5, 3–6, 3–8, 3–9, 3–10, 3–11, 4–5, 4–6, 4–7, 4–8, 4–9, 4–10, 4–11, 5–6, 5–7, 5–8, 5–9, 5–10, 5–11, 6–7, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 8–11, 9–10, 9–11

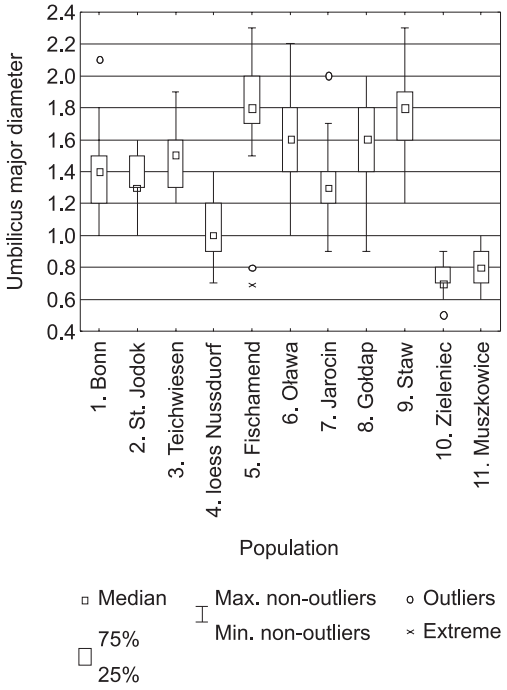



Fig. 103. Interpopulation variation of *T. hispidus*: umbilicus minor diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–4, 1–5, 1–6, 1–8, 1–9, 1–10, 1–11, 2–4, 2–5, 2–6, 2–8, 2–9, 2–10, 2–11, 3–4, 3–5, 3–8, 3–9, 3–10, 3–11, 4–5, 4–6, 4–7, 4–8, 4–9, 4–10, 4–11, 5–6, 5–7, 5–8, 5–10, 5–11, 6–7, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–9, 8–10, 8–11, 9–10, 9–11

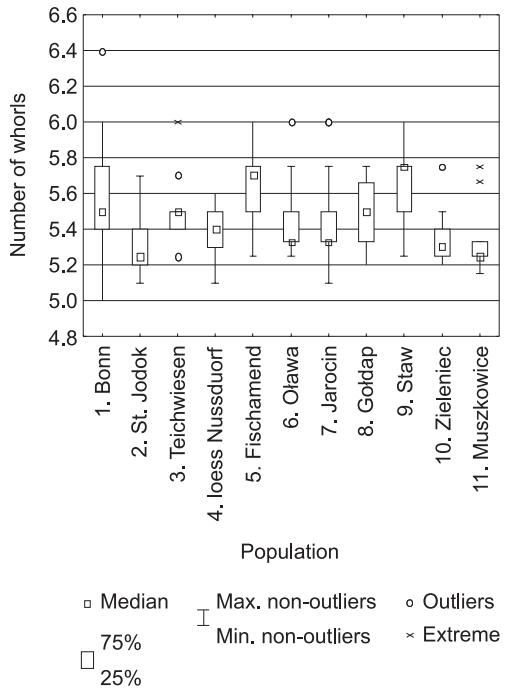



Fig. 104. Interpopulation variation of *T. hispidus*: number of whorls. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–4, 1–6, 1–7, 1–9, 1–10, 1–11, 2–3, 2–5, 2–8, 2–9, 3–9, 3–11, 4–5, 4–9, 5–6, 5–7, 5–8, 5–10, 5–11, 6–8, 6–9, 7–8, 7–9, 8–9, 8–10, 8–11, 9–10, 9–11

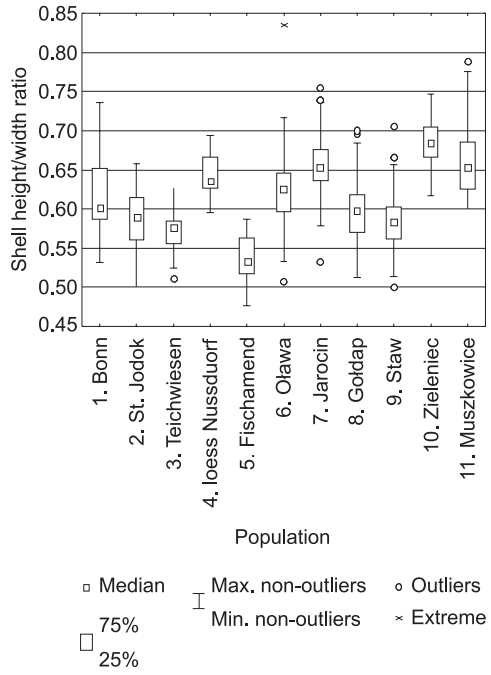



Fig. 105. Interpopulation variation of *T. hispidus*: shell height/width ratio. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–5, 1–7, 1–8, 1–9, 1–10, 1–11, 2–4, 2–5, 2–6, 2–7, 2–10, 2–11, 3–4, 3–5, 3–6, 3–7, 3–10, 3–11, 4–5, 4–8, 4–9, 4–10, 5–6, 5–7, 5–8, 5–9, 5–10, 5–11, 6–7, 6–8, 6–9, 6–10, 6–11, 7–8, 7–9, 7–10, 8–9, 8–10, 8–11, 9–10, 9–11, 10–11

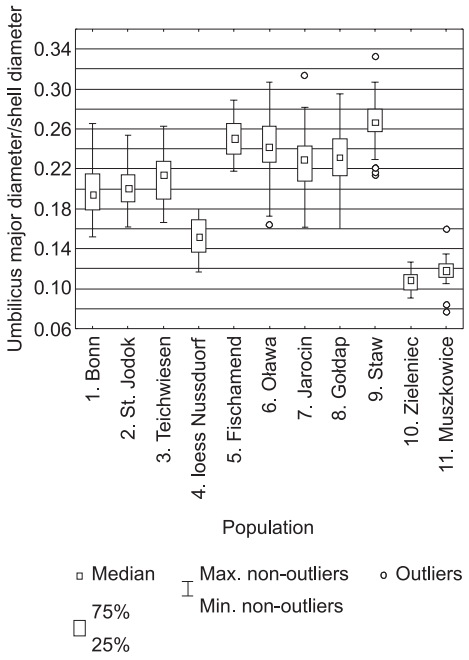



Fig. 106. Interpopulation variation of *T. hispidus*: umbilicus major diameter/shell diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–4, 1–5, 1–6, 1–7, 1–8, 1–9, 1–10, 1–11, 2–4, 2–5, 2–6, 2–7, 2–8, 2–9, 2–10, 2–11, 3–4, 3–5, 3–6, 3–8, 3–9, 3–10, 3–11, 4–5, 4–6, 4–7, 4–8, 4–9, 4–10, 4–11, 5–7, 5–8, 5–9, 5–10, 5–11, 6–8, 6–9, 6–10, 6–11, 7–9, 7–10, 7–11, 8–9, 8–10, 8–11, 9–10, 9–11

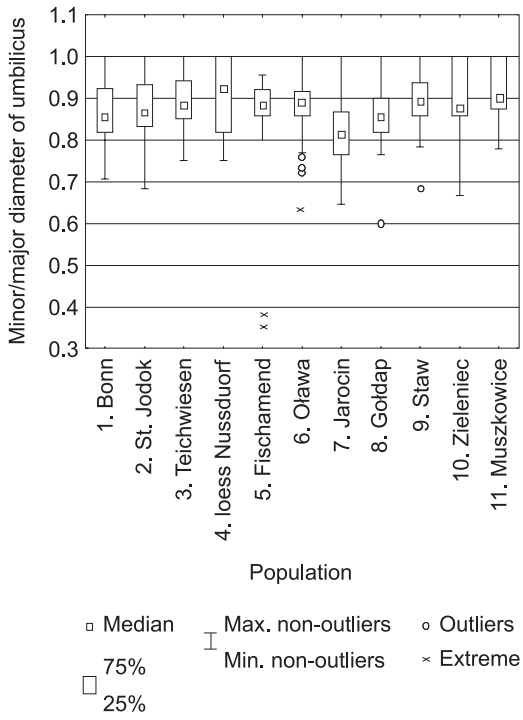



Fig. 107. Interpopulation variation of *T. hispidus*: minor/major diameter of umbilicus. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–7, 2–7, 3–7, 4–7, 6–7, 7–8, 7–9, 7–10, 7–11, 8–9

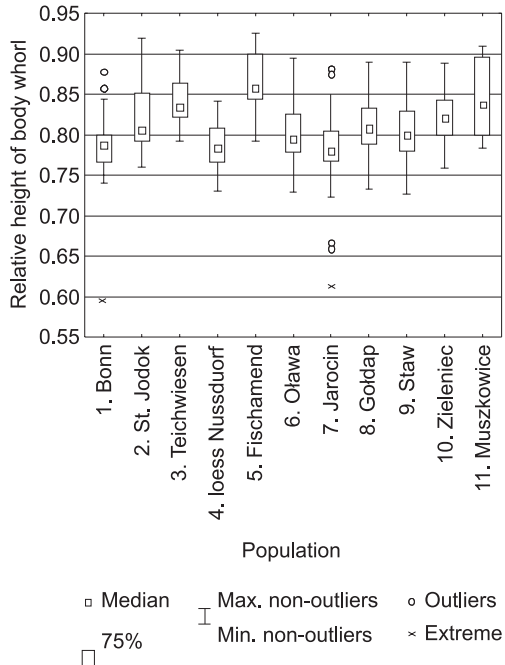
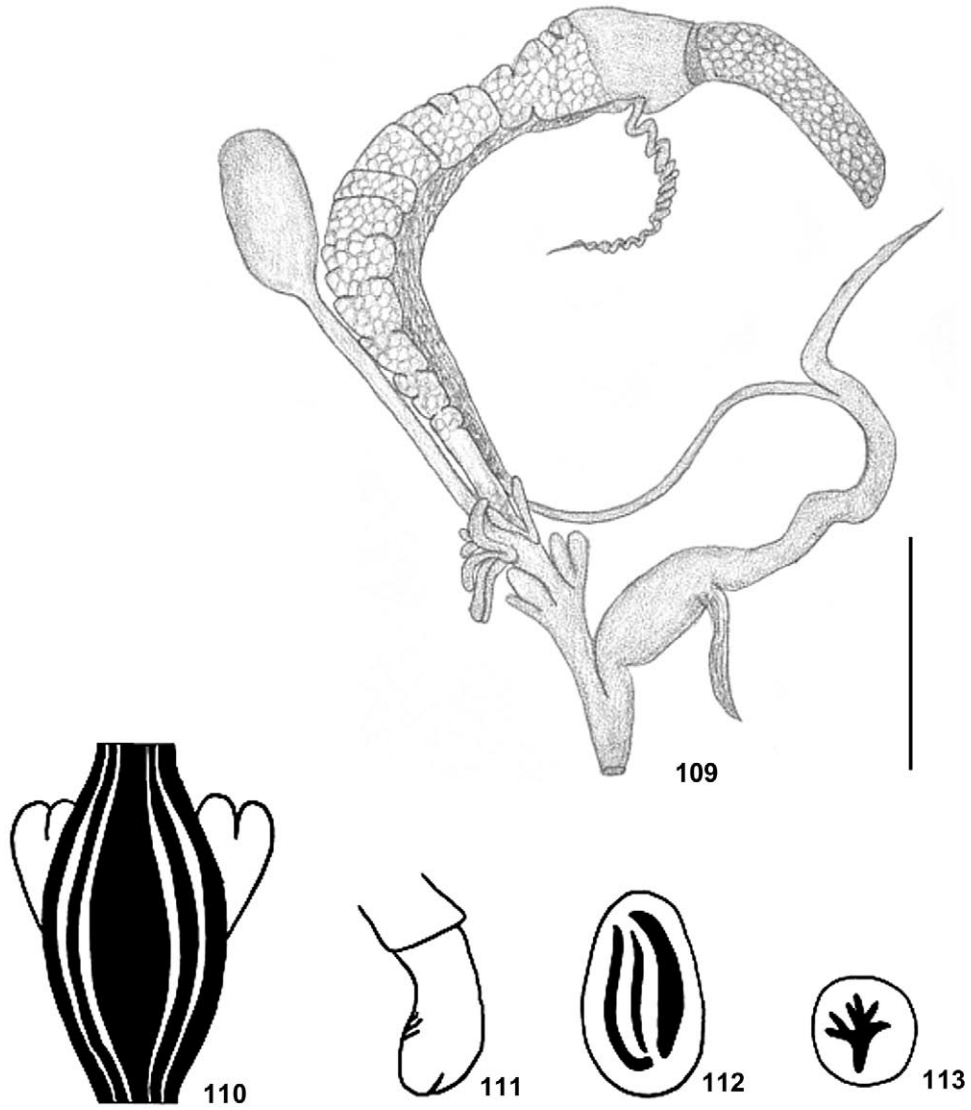



Fig. 108. Interpopulation variation of *T. hispidus*: relative height of body whorl. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–5, 1–8, 1–10, 1–11, 2–4, 2–5, 2–7, 3–4, 3–6, 3–7, 3–8, 3–9, 4–5, 4–10, 4–11, 5–6, 5–7, 5–8, 5–9, 5–10, 6–11, 7–8, 7–9, 7–10, 7–11, 8–11, 9–11




Figs 109–113. *T. hispidus*. Specimen from Lubawka, Sudetes, Poland, ZW. Reproductive system: 109 – general view, 110 – longitudinal section of vagina, 111 – penial papilla, 112 – cross-section of penial papilla, 113 – cross-section of epiphallus. Scale bar 5 mm

2,300 m a.s.l. In Spain it usually lives in dry places, only single sites are damp, e.g. stream banks, vicinity of springs (ALTONAGA et al. 1994).

Distribution (Fig. 114)

A widely distributed European species: in the north, along the Atlantic coast of Scandinava, it reaches the Arctic circle (SHILEYKO 1978a, RIEDEL 1988), in the east – southern Ukraine, the Urals and St. Petersburg (FORCART 1965), in the west – the British Isles (KERNEY et al. 1983). Its southern distribution border is not precisely known: it has been recorded from north-eastern Spain (from Catalonia to the Picos de Europa Mts; common in the Basque Country; in the south to province de Teruel in Aragon and Mt. Moncayo in Sistema Ibérico) (ALTONAGA et al. 1994), northern Italy (MANGANELLI et al. 1995); in western Bulgaria it has only few records (near Tran, not confirmed in the Western Rhodopes) (DAMJANOV & LIKHAREV 1975, IRIKOV & MOLLOV 2006, IRIKOV & ERÖSS 2008), northern Croatia (Bansko Brdo) (UHERKOVICH et al. 2008). In Poland *T. hispidus* is common in the whole country except the Carpathians, in the Sudetes recorded up to 800 m a.s.l. (WIKTOR & WIKTOR 1968).

Remarks

Till recently *T. hispidus* was regarded as distinct from the very similar *T. plebeius* (Draparnaud, 1805)/*sericeus* (Draparnaud, 1801) and *T. concinnus* (Jeffreys, 1830), descibed from western and central Europe (see synonyms). Delimitation of the three forms has always been regarded as problematic. Analysis of individual and inter-population shell variation of *T. hispidus* from Poland revealed a very wide variation range (PROĆKÓW 1997). With respect to shell propor-

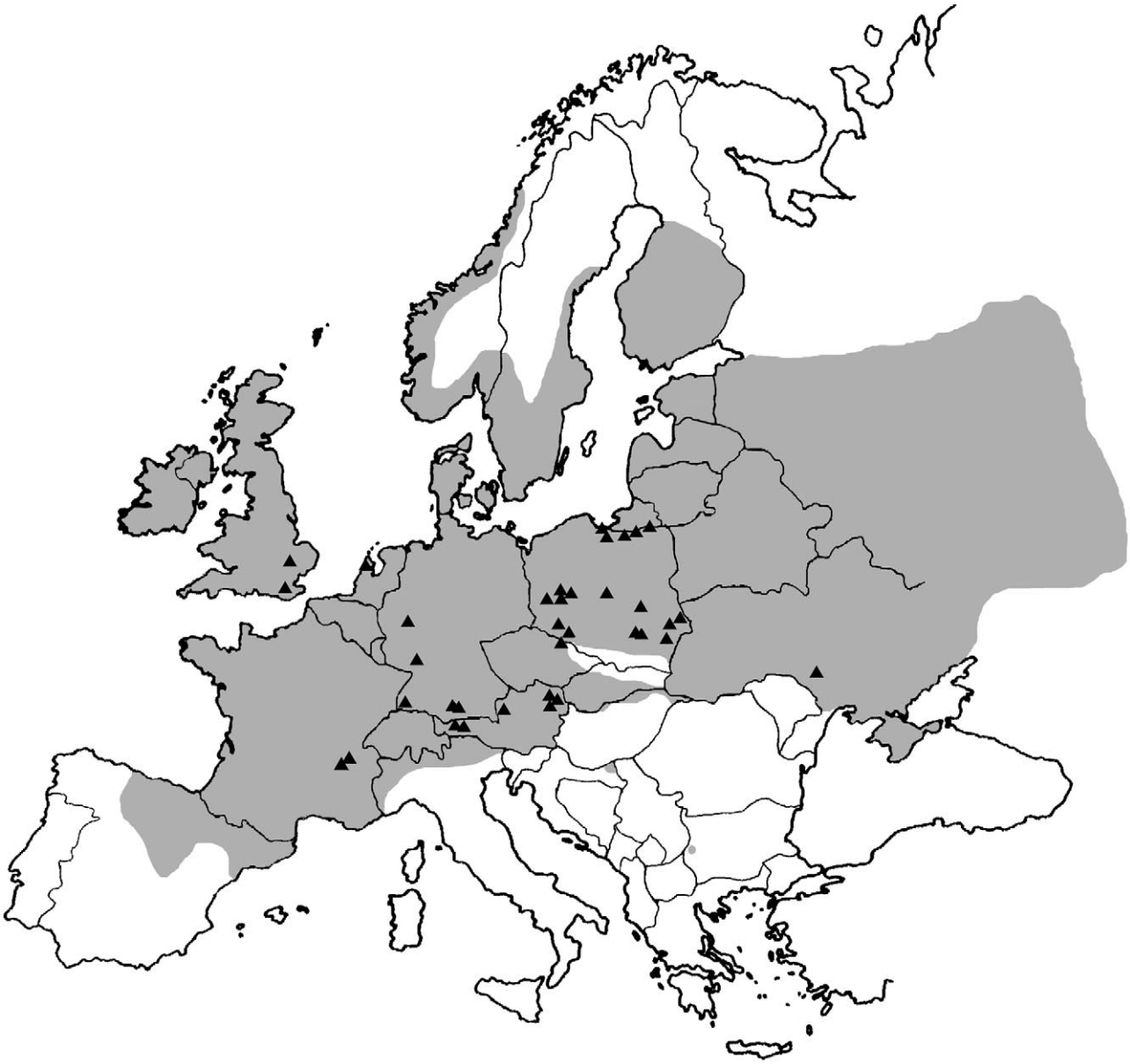


Fig. 114. Distribution of *T. hispidus*. Black triangles – localities of origin of the examined material

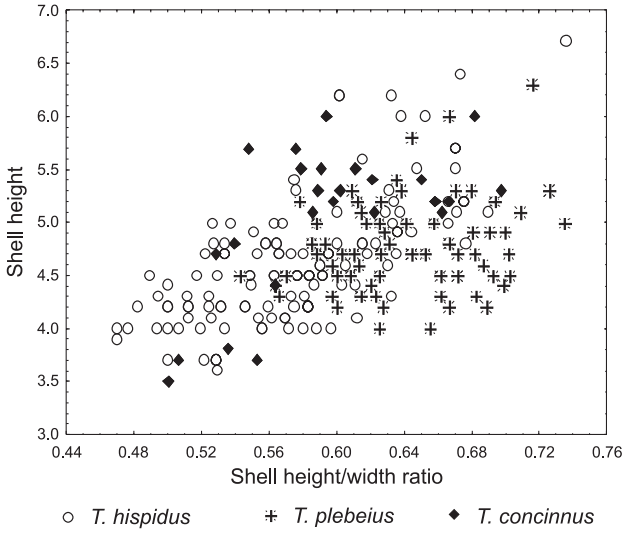



Fig. 115. Morphometric comparison of shells of *T. hispidus*, *T. plebeius* and *T. concinnus*. Shell height plotted against height/width ratio

tions, *T. hispidus* from Muszkowice and Zieleniec distinctly departs from the remaining Polish populations, thus resembling *T. plebeius*. Biometrical studies on an extensive material (a total of 2,339 specimens) (Figs 115–122) showed that the shell variation ranges of *T. plebeius*, *T. concinnus* and *T. hispidus* overlapped, and it was impossible to indicate any diagnostic characters of the three nominal taxa. Similar results, although based on a poorer material, were obtained by NAGGS (1985).

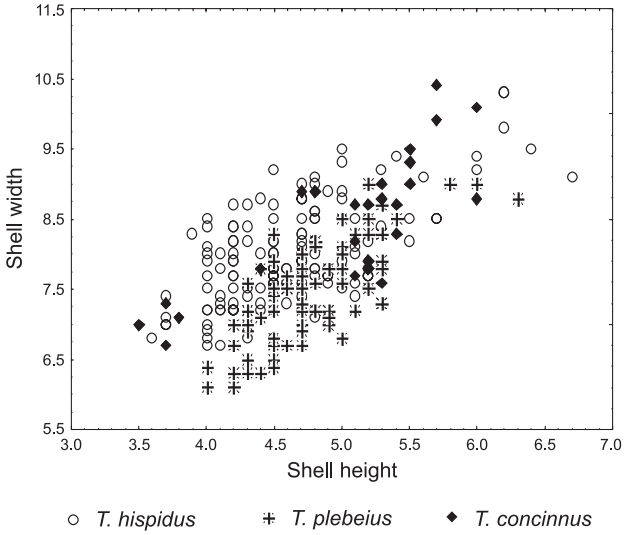



Fig. 116. Morphometric comparison of shells of *T. hispidus*, *T. plebeius* and *T. concinnus*. Shell width plotted against shell height

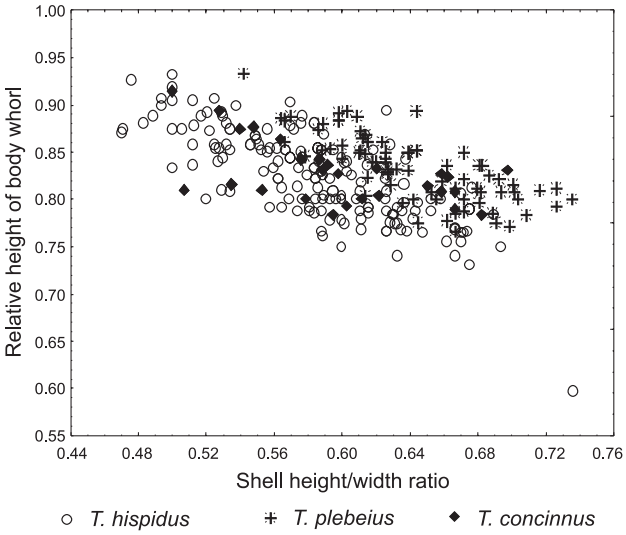



Fig. 117. Morphometric comparison of shells of *T. hispidus*, *T. plebeius* and *T. concinnus*. Relative height of body whorl plotted against hight/width ratio

Therefore, in spite of the very laconic descriptions of *T. plebeius* (DRAPARNAUD 1805: 105) and *T. concinnus* (JEFFREYS 1830: 336), it seems to be reasonable to synonymise *T. plebeius, T. concinnus* and *T. hispidus*. The single shell (subadult) labelled as a type of *T. plebeius,* deposited in DRAPARNAUD's collection in Vienna, actually is not a *Trochulus*, but a *Monachoides* species, and was no doubt mislaid (WINTER 1990), which was already remarked by LOCARD (1895).

Fig. 120. Morphometric comparison of shells of *T. hispidus* and *T. plebeius* with populations from Zieleniec and Muszkowice. Shell width plotted against shell height

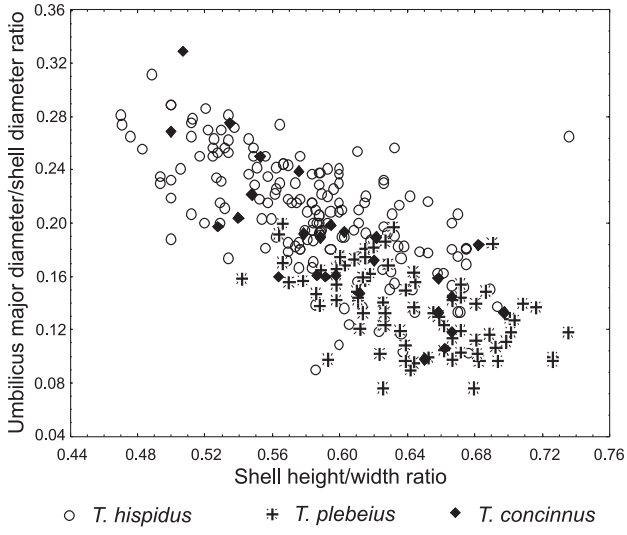



Fig. 118. Morphometric comparison of shells of *T. hispidus*, *T. plebeius* and *T. concinnus*. Ratio of umbilicus major to shell diameter plotted against height/width ratio

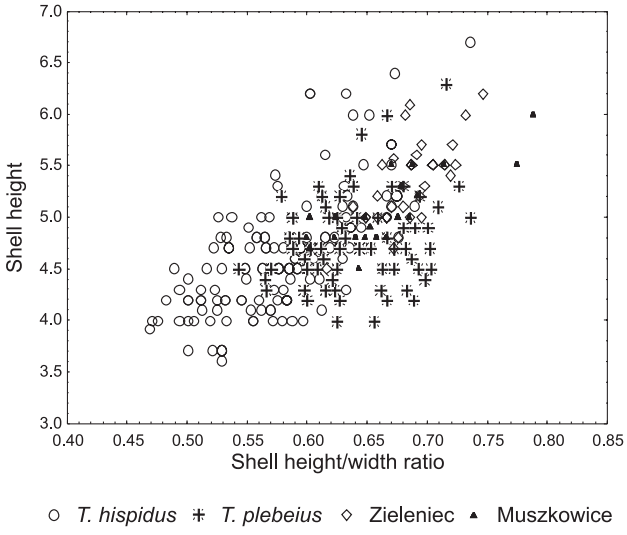
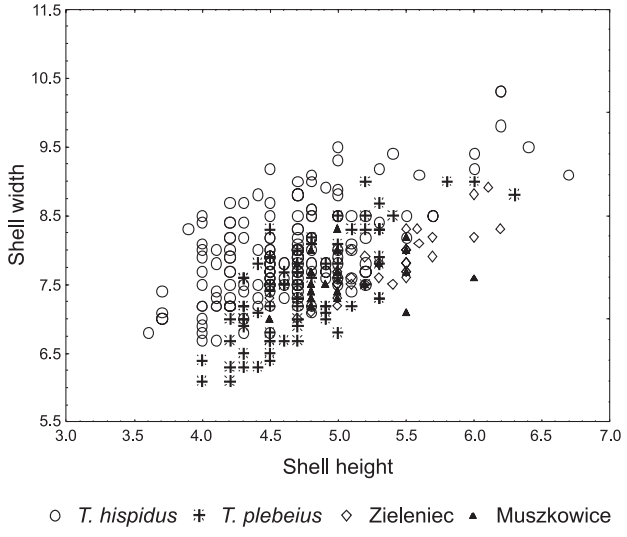



Fig. 119. Morphometric comparison of shells of *T. hispidus* and *T. plebeius* with populations from Zieleniec and Muszkowice. Shell height plotted against height/width ratio



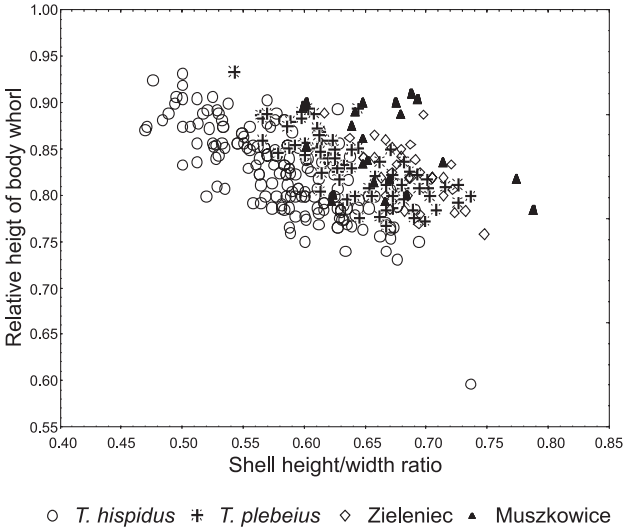



Fig. 121. Morphometric comparison of shells of *T. hispidus* and *T. plebeius* with populations from Zieleniec and Muszkowice. Relative height of body whorl plotted against hight/width ratio

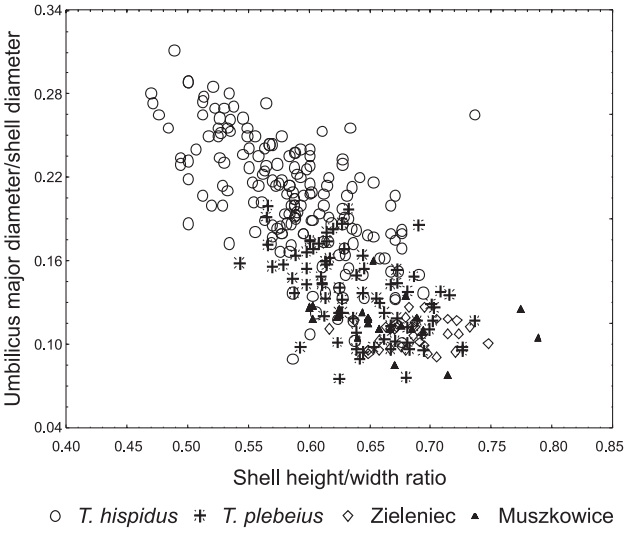



Fig. 122. Morphometric comparison of shells of *T. hispidus* and *T. plebeius* with populations from Zieleniec and Muszkowice. Ratio of umbilicus major diameter to shell diameter plotted against height/width ratio

## *Trochulus leucozonus* (C. Pfeiffer, 1828)

*Helix leucozona* C. PFEIFFER 1828: 34, pl. VI, figs 19–20. Terra typica: "Illyrien".

*Helix dolopida* CRISTOFORI & JAN 1832: 1. Terra typica: "Ital. bor." [probably North Italy]

*Helix leucozona* var. *ovirensis* ROSSMÄSSLER 1838: 4, pl. XXXI, fig. 434. Locus typicus: Austria: Carinthia: Ovir summit, under stones.

*Helix leucozona* var. *heteromorpha* WESTERLUND 1876–1878: 52. Terra typica: Austria: "Carinthia".

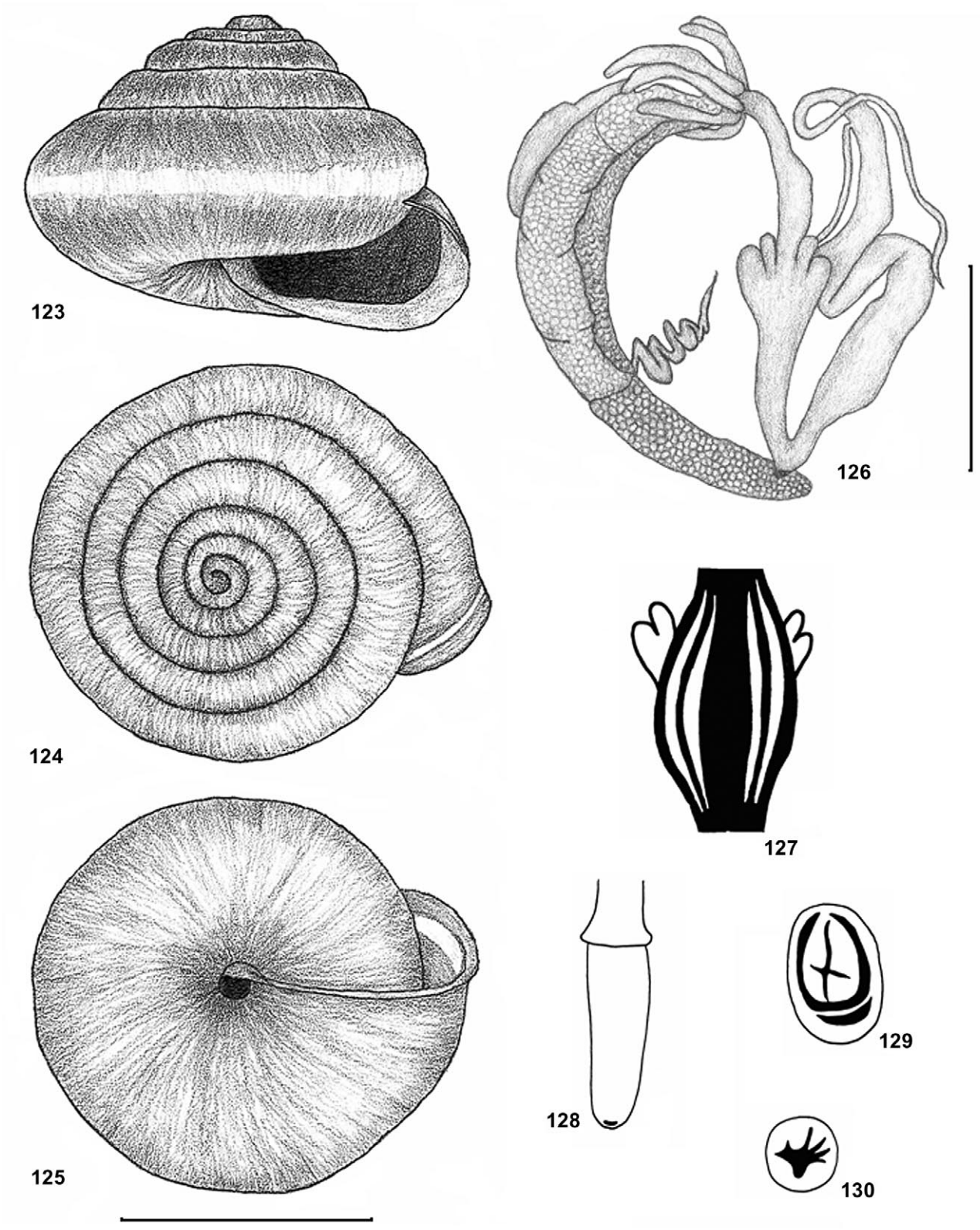
*Helix leucozona* var. *Erjaveci* CLESSIN 1887: 122. Locus typicus: Slovenia: "Im Friaul, Eingang zur Grotte Vodnik ober Tublje auf dem Karste". [according to BANK (1995) a synonym of *leucozona heteromorpha*]

### Material examined

Austria: Vellach near Eisenkappel, Karawanken, leg. V. Sturany, MIZW, 1 alc.; between Kozje [=Kossiach] and 'Ir', ± 1650 m, Karawanken, 09.1913, coll. Poliński 228/37, MIZW, 19 s.; Bärntal, Karawanken, MIZW, 1 s.; Velika Kotla (=Gerlouc=Gerloutz), Karawanken, 18.09.1913, leg. W. Poliński, MIZW, 3 s.; Loiblstrasse, Karawanken, 19.09.1913, coll. Poliński 228/37, MIZW, 1 s.; s. prec. loc., Karawanken, ex coll. H. Gallenstein, coll. Poliński 228/37, MIZW, 2 s.; Hochobir, 1,100–2,000 m, MIZW, 8 s. [*ovirensis*]; Mt. Dobratsch, Carynthia, MIZW, 11 s. [*ovirensis*]; Villach, Carynthia, 1918, MIZW, 3 s.; Croatia: between Rijeka and Opatija, 09.1913, leg. W. Poliński, coll. Poliński 228/37, MIZW, 2 s.: between Rann and Agram [=Zagreb], MIZW, 4 s. [*dolopida*]; Italy: Sette Comuni, prov. Veneto, MIZW, 5 alc.: Dosso dei Morti, Adamello Alps, 2,000 m, 27.07.1932, coll. Edlauer 10620, NHMW, 15 s.: Matajur, Julian Alps, 1,000 m, coll. Poliński 228/37, MIZW, 3 s.: Slovenia: Gonobitz [=Slovenske Konjice], Bachergebirge [=Pohorje], coll. Poliński 228/37, MIZW, 1 s.; Mt. Grintovec, Kamnik Alps, 1,800 m, coll. Edlauer 10635, NHMW, 7 s.; Mt. Ursula [= Uršlja Gora], Karawanken, coll. Oberwimmer, NHMW, 4 s. [*dolopida*]; Mt. Ursula [=Uršlja Gora], Karawanken, coll. Klemm 69381, NHMW, 15 ok. [*dolopida*]; Mt. Stol, Krain [=Carniola], 22.09.1923, leg. W. Poliński, coll. Poliński 228/37, MIZW, 8 s.; Mt. Razor, between Isonzo [=Soča] valley and Woheinersee [=Bohinjsko jezero], MIZW, 4 s.; Isonzo [=Soča] valley, environs of Tolmin, coll. Wagner, MIZW, 1 s.+2 alc.; Mt. Čaven, "Tarnovaner Wald", NW Haidenschaft [=Ajdovščina], MIZW, 3 s.

### Shell (Figs 123–125)

Shell conical to roundish with 5.5–6.5 regularly coiled, convex whorls and dome-shaped spire. Shell height 4.5–7.6 mm, shell width 7.7–11.4 mm, height/width ratio 0.54–0.76, body whorl height 4.0–4.9 mm (one specimen 5.2 mm), relative height of body whorl 0.7–0.79, aperture height 2.6–3.6 mm, aperture width 3.6–5.3 mm, umbilicus major diameter 0.2–0.8 mm, umbilicus minor diameter 0.2–0.8 mm, umbilicus major diameter/shell diameter ratio 0.06–0.1. Aperture slightly oblique, crescentic; aperture margin sharp, its short columellar wall passes into horizontal or almost horizontal basal wall with distinct shiny lip inside. Umbilicus narrow, usually open but sometimes partly or, very rarely, entirely covered by columellar aperture margin. Adults hairless. Shell pale to horny brown, with fine growth lines, light band on body whorl.




Figs 123–130. *T. leucozonus*. Specimen from Villach, Carynthia, Austria, 1918, MIZW. 123–125 – shell: 123 – apertural view, 124 – apical view, 125 – umbilical view; 126–130 – reproductive system: 126 – general view, 127 – longitudinal section of vagina, 128 – penial papilla, 129 – cross-section of penial papilla, 130 – cross-section of epiphallus. Scale bar 5 mm

Reproductive system (Figs 126–130)

Four pairs of short mucous glands situated around upper vagina, ca. 4 mm upper tips of inner dart sacs, which are slightly longer and narrower than outer ones. Vagina long (6.0–8.7 mm); its expanded dart sac region narrows toward genital atrium. Flagellum considerably longer than epiphallus, which is shorter than fusiform penis. Spermatheca duct straight. Spermatheca elongate, reaching ca. 1/2 spermoviduct length. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 127–130.

Ecology

*T. leucozonus* lives in damp shaded forests, under stones, in leaf litter and in mosses; it is found up to the alpine zone. According to BANK (1995) its various forms reach the following altitudes: *T. leucozonus* s. str. 275–1,900 m a.s.l.; *T. leucozonus ovirensis* 1,700–2,150 m a.s.l. and *T. leucozonus heteromorpha* 220–2,200 m a.s.l.

Distribution (Fig. 131)

A South-East-Alpine species; found in Austria (Carynthia), Slovenia (Pohorje; Kamnik Alps; Carniola; Julian Alps: source of Soča; western Slovenia: the environs of Sava sources and Čaven summit), northern Italy and Croatia (POLIŃSKI 1928, BANK 1995, MANGANELLI et al. 1995).

Remarks

Based on the umbilicus diameter, BANK (1995) distinguished two geographical subspecies: *leucozonus* s. str. (umbilicus open or only partly covered, 1/13–1/7 of shell diameter) and *heteromorpha* (umbilicus covered to a great extent, not more than 1/15 of shell diameter). According to that autor subspecies *ovirensis* represents an Alpine form (living between 1,700 and 2,150 m a.s.l.) derived from *leucozonus* s. str. Besides, he ragards subspecies *erjaveci* as a synonym of *heteromorpha*.

The examined specimens of *ovirensis* had distinctly smaller shells (height 4.1–6.3 mm, width 6.5–9.4 mm) compared to *leucozonus* s. str. (height 4.5–7.6 mm, width 7.7–11.4 mm) and fewer whorls (*ovirensis* 5.1–6.0, mean 5.45; *leucozonus* s. str. 5.25–6.3, mean 5.8).

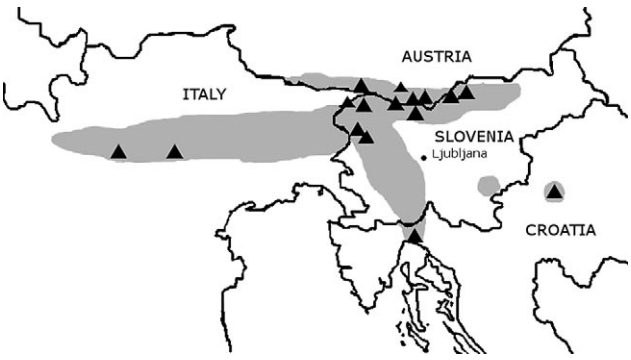



Fig. 131. Distribution of *T. leucozonus*. Black triangles – localities of origin of the examined material

The examined shells of specimens from Mt. Ursula and from "between Rann and Agram", representing *dolopida*, were much larger: height 6.5–8.2 mm, width 9.2–12.2 mm, body whorl height 4.4–6.1 mm, aperture height 4.4–6.1 mm and aperture width 4.8–6.1 mm. On the other hand, their proportions were similar to those of *leucozonus* s. str.: height/width ratio 0.59–0.74, relative height of body whorl 0.68–0.81, umbilicus major diameter/shell diameter ratio 0.04–0.09. The number of whorls (5.8–6.7) and umbilicus diameter (major 0.4–0.9 mm, minor 0.4–0.8 mm) were also very similar. Because of the unavailability of specimens from the locality and alcohol-preserved material, the taxonomic status of this taxon has to remain uncertain. However, BANK (1995) placed *dolopida* among the synonyms of *leucozonus* s. str.

### *Trochulus lubomirskii* (Ślósarski, 1881)

*Helix (Fruticicola) Lubomirski* ŚLÓSARSKI 1881: 319, pl. X, figs A-D. Locus typicus: Poland: Święty Krzyż (Łysa Góra) and Ogrodzieniec.

*Helix Clessini* ULIČNY 1884: 7–8, figs on p. 3. Locus typicus: Czech Republic: Moravia: near Olomouc and Brno.

Material examined

Austria: Wien, MIZW, 1 s.; Korneuburg near Wien, coll. Poliński 228/37, MIZW, 1 s.; Poland: Lower Silesia: Mt. Ślęża, 27.04.1955, leg. A. Wiktor, Nr 98, MPW, 5 s.; Cracow-Wieluń Jura: Mirów castle ruins, leg. E. Polińska 1920, MIZW, 7 s.; Świętokrzyskie Mts: Św. Krzyż [=Łysa Góra], 22.10.1971, leg. A. Piechocki, UŁ, 8 s.; Beskid Wyspowy: Limanowa, 15.08.1999, leg. E. Sułkowski, ZW, 4 alc.; Pogórze Przemyskie: Przemyśl, coll. O. Retowski 41/39, MIZW, 5 s.; Bieszczady Mts: Ustrzyki Górne, 21.08.1996, ZW, 5 alc.; Slovakia: Plaveč castle ruins, reg. Spiš, 540–547 m, 12.08.1922, coll. Poliński 228/37, MIZW, 1 s.; Skalky near Uják [=Údol], reg. Prešov, 12.08.1922, coll. Poliński 228/37, MIZW, 1 s.; Árvaváralja [=Oravský Podzámok], reg. Zilina, coll. Poliński 228/37, MIZW, 1 s.; Ukraine: Złoczów [=Zołocziw], MIZW, 7 s.

Shell (Figs 132–134)

Shell conical, dome-shaped spire with acute apex; 4.7–5 moderately tightly coiled whorls. Dimensions: shell height 5.0–7.0 mm, shell width 7.0–10.0 mm, height/width ratio 0.62–0.77, body whorl height 4.2–5.7 mm, relative height of body whorl 0.82–0.88, aperture height 3.0–3,7 mm, aperture width 4.0–5.3 mm, umbilicus major diameter 0.3–0.9 mm, umbilicus minor diameter 0.3–0.7 mm, umbilicus major diameter/shell diameter ratio 0.06–0.11. Aperture rounded, aperture margin thin with very weakly de-

veloped lip. Umbilicus round and very narrow but always open. Few, very short (0.1 mm) and fine hairs, usually lost in adults. Shell translucent, whitish-yellow to greenish-yellow, weakly shiny.

Reproductive system (Figs 135–139)

Four pairs of short mucous glands situated around upper vagina, ca. 1.5 mm from tips of inner dart sacs which reach beyond outer ones and are much more massive. Vagina rather long and cylindrical. Very short and conical flagellum passes into thick cylindrical epiphallus, which is longer than fusiform penis. Spermoviduct bent just near outlet of free oviduct. Spermatheca duct rather thick, straight and short. Spermatheca big and irregularly club-shaped, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 136–139.

Ecology

*T. lubomirskii* usually lives in dense herbal vegetation (*Petasites* sp.) in relatively damp forests (river plains, mountains up to 1,600 m a.s.l.); it is found under stones, sometimes on limestone rocks and meadows.

Distribution (Fig. 140)

A Carpathian species; known from Austria (only in Lower Austria: Danube valley), the Czech Republic and Slovakia (scattered records in northern Bohemia, northern and eastern Moravia, the Beskidy Mts, the Slovak Carpathians); Poland (Carpathians – localities from the Tatra Mts not confirmed, Carpathian Foothills, to the Eastern Sudetes, single localities in the Świętokrzyskie Mts, Mt. Ślęża – probably absent, Trzebnickie Hills and environs of Krotoszyn) (RIEDEL 1988, WIKTOR 2004), Hungary (Somoskoujfalu, the Zemplén Mts, Bárna) (KERNEY et al. 1983) and western Ukraine (Podolia: Worochta, Transcarpathian region: Jasina [=Yasinya=Yasina=Jasinja=Körösmezö]) (POLIŃSKI 1924).

Remarks

The internal structure of the vagina presented by SHILEYKO (1978a, b) does not correspond with the structure of the examined specimens (fig. 136).

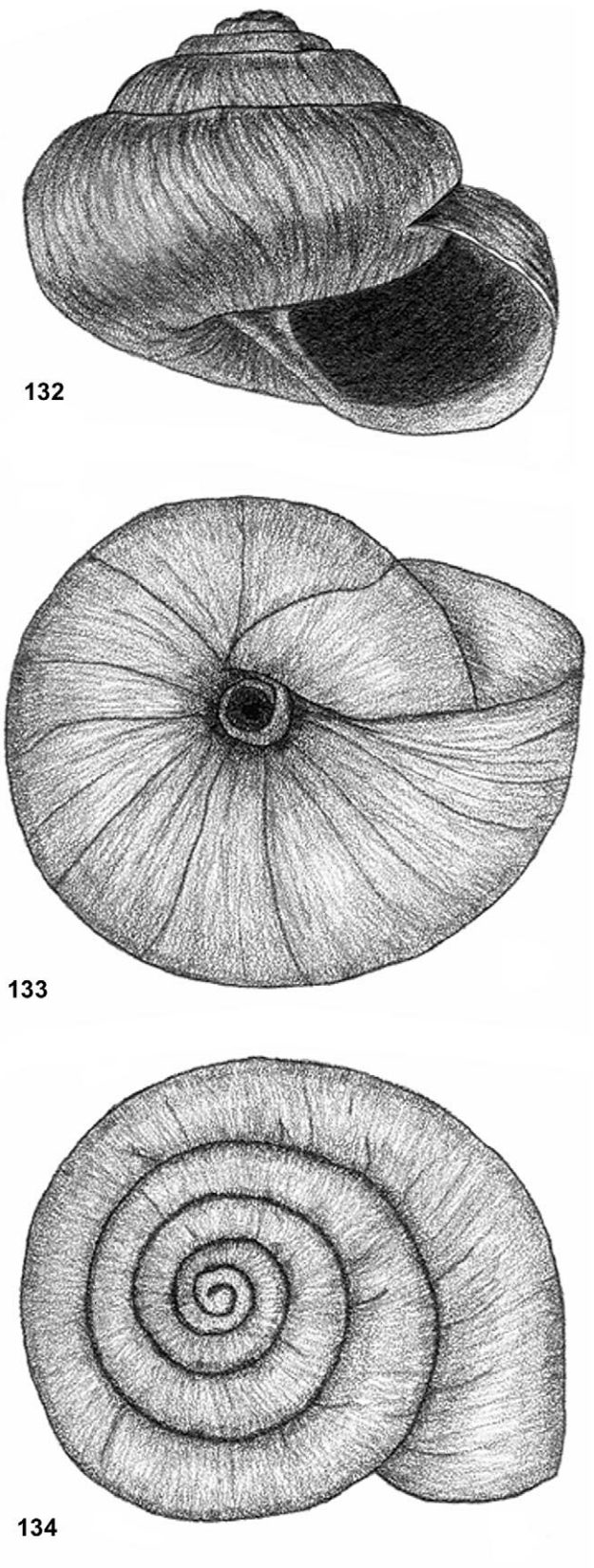
### *Trochulus luridus* (C. Pfeiffer, 1828)

*Helix lurida* C. PFEIFFER 1828: 33, pl. VI, figs 14–15. Terra typica: "Illyrien".

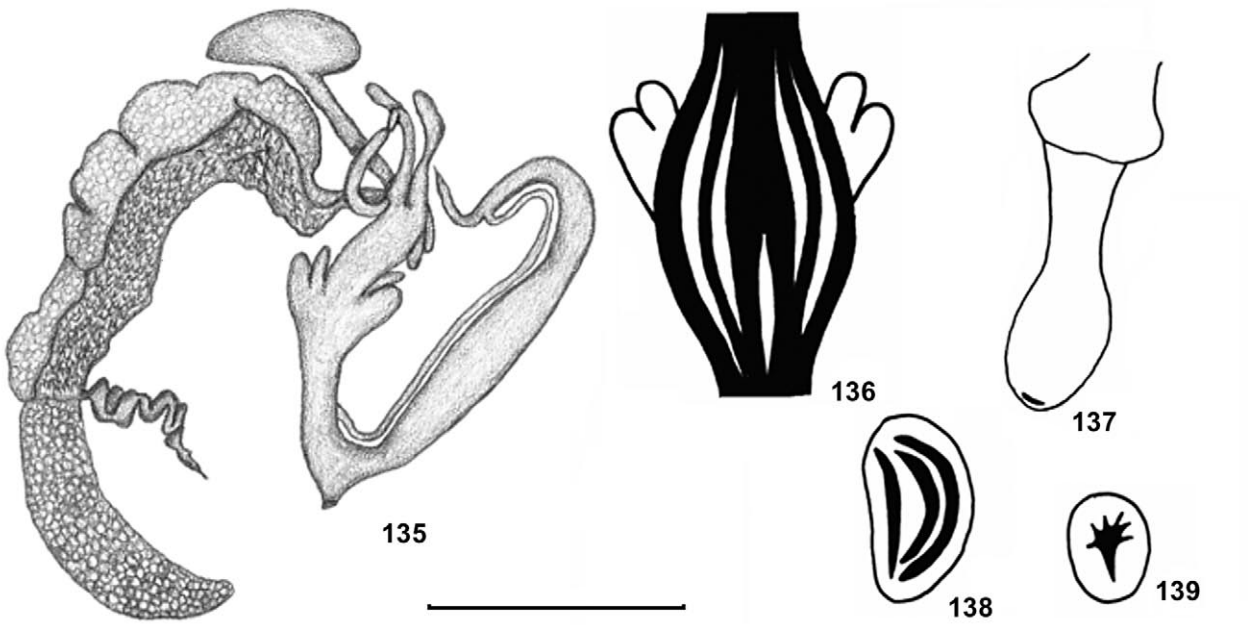
*Helix lurida* var. *separanda* ROSSMÄSSLER 1835: 35, Nr 360. Terra typica: Slovenia: Krain.

Material examined

Austria: Petzen, Karawanken, leg. Gredler, 1927, coll. Poliński, MIZW, 2 s.; Bosnia and Herzegovina: Vlašić mountain range near Travnik, coll. Poliński 228/37, MIZW, 5 s.; Mt. Trebevič near Sarajevo, coll.




Figs 132–134. *T. lubomirskii*. Specimen from Ustrzyki Górne, Bieszczady, Poland, ZW. Shell: 132 – apertural view, 133 – umbilical view, 134 – apical view. Scale bar 5 mm




Figs 135–139. *T. lubomirskii*. Specimen from Ustrzyki Górne, Bieszczady, Poland, ZW. Reproductive system: 135 – general view, 136 – longitudinal section of vagina, 137 – penial papilla, 138 – cross-section of penial papilla, 139 – cross-section of epiphallus. Scale bar 5 mm

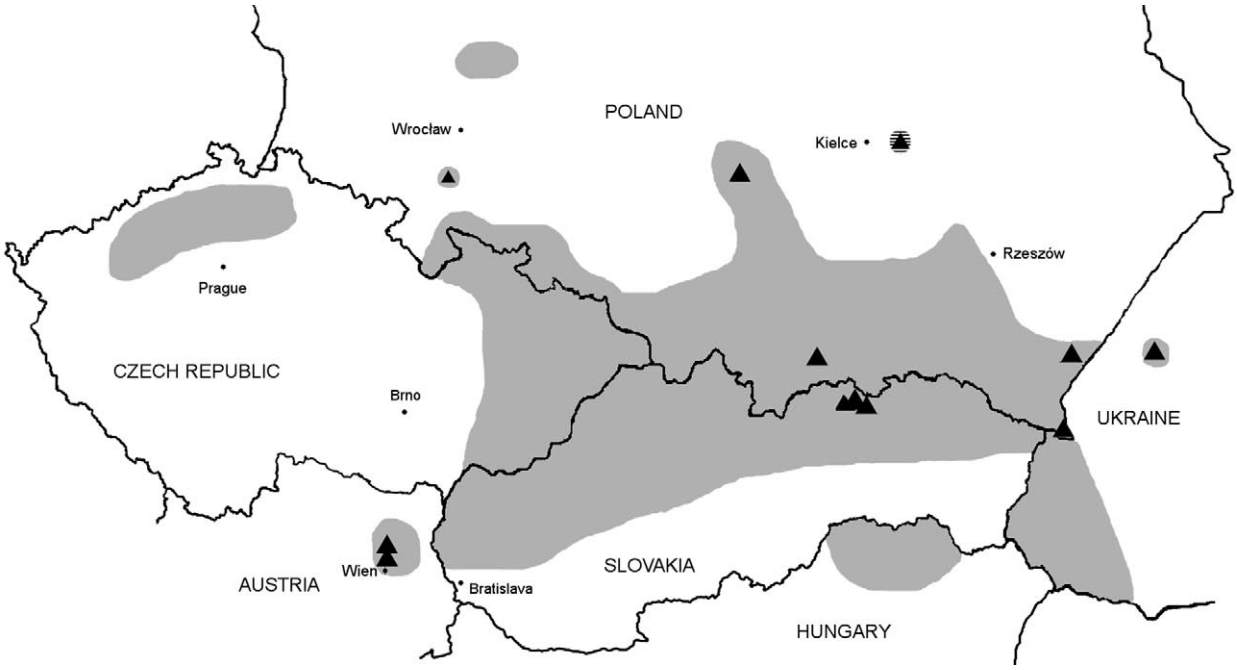



Fig. 140. Distribution of *T. lubomirskii*. Black triangles – localities of origin of the examined material

Poliński 228/37, MIZW, 2 s.; Mt. Dragoljub, N Sarajevo, coll. Poliński 228/37, MIZW, 2 s.; Croatia: Fiume [=Rijeka], MIZW, 1 s.; Šestine near Agram [=Zagreb], coll. Poliński 228/37, MIZW, 7 s.; Agram [=Zagreb], coll. Poliński 228/37, MIZW, 1 s.; Zagreb, 1918, leg. Wagner, MIZW, 2 s.; Lasinjsko, S Zagreb, coll. Poliński 228/37, MIZW, 2 s.; Tuskanec near Zagreb, MIZW, 5 s.; Virovitica, reg. Virovitič-Podravska, MIZW, 2 s.; Jankovac, reg. Brodsko-Posavska, coll. Poliński 228/37, MIZW, 4 s.; Kapela near Jezerane, reg. Ličko-Senjska, coll. Poliński 228/37, MIZW, 5 s.; Ogulin, reg. Karlovačka, coll. Poliński 228/37, MIZW, 3 s.; s. prec. loc., coll. Poliński 228/37, MIZW, 5 s.; Italy: Pazanella, Tyrol, 1,500 m, 1916, coll. Edlauer 6442, NHMW, 3 s.; Cormons, prov. Gorizia, MIZW, 2 s.; Serbia: Mt. Stolac, near Bajina Bašta, coll. Poliński 228/37, MIZW, 1 s.; Slovenia: Kankertal [=Kokra valley], Kamnik Alps, coll. Poliński 228/37, MIZW, 1 s.; environs of Kranj (=Krainburg),03.1928, leg. L. Kuščer, MIZW, 2 alc.; Rothweinklamm [=Radovna valley] near Bled, Julian Alps, 06.1934, leg. Klemm, coll. Klemm 2407, NHMW, 7 s.;

Ulrichsberg [=Šenturška gora], Krain=Carniola, coll. Poliński 228/37, MIZW, 3 s.; s. prec. loc., leg. Kuščer, 03.1928, MIZW, 2 alc.

Shell (Figs 141–143)

Shell roundish with 5.5–6.6 whorls. Shell height 5.0–8.3 mm, shell width 7.8–12.6 mm, height/width ratio 0.51–0.71, body whorl height 3.8–6.0 mm, relative height of body whorl 0.75–0.88, aperture height 2.3–4.0 mm, aperture width 4.0–6.2 mm, umbilicus major diameter 0.2–1.1 mm, umbilicus minor diameter 0.2–1.1 mm, umbilicus major diameter/shell diameter ratio 0.02–0.1. Aperture oblique, aperture margin sharp, slightly reflected with reddish lip inside. Umbilicus very narrow, sometimes partly covered by columellar aperture margin. Short, fine and rather sparse. Shell horny-brown to reddish-brown, slightly shiny, sometimes with light band on body whorl.

Reproductive system (Figs 144–148)

Four pairs of rather long (ca. 4 mm) mucous glands situated around upper vagina, ca. 2 mm from tips of inner dart sacs. Inner and outer dart sacs approximately equal in size. Vagina very long; its very expanded dart sac region narrows toward genital atrium. Flagellum slightly longer the epiphallus which is shorter than fusiform penis, or all three sections of approximately equal length. Spermatheca duct thin and straight. Spermatheca elongate, reaching ca. spermoviduct 2/3 length. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 145–148.

Ecology

*T. luridus* lives in damp, shaded forests, among leaf litter.

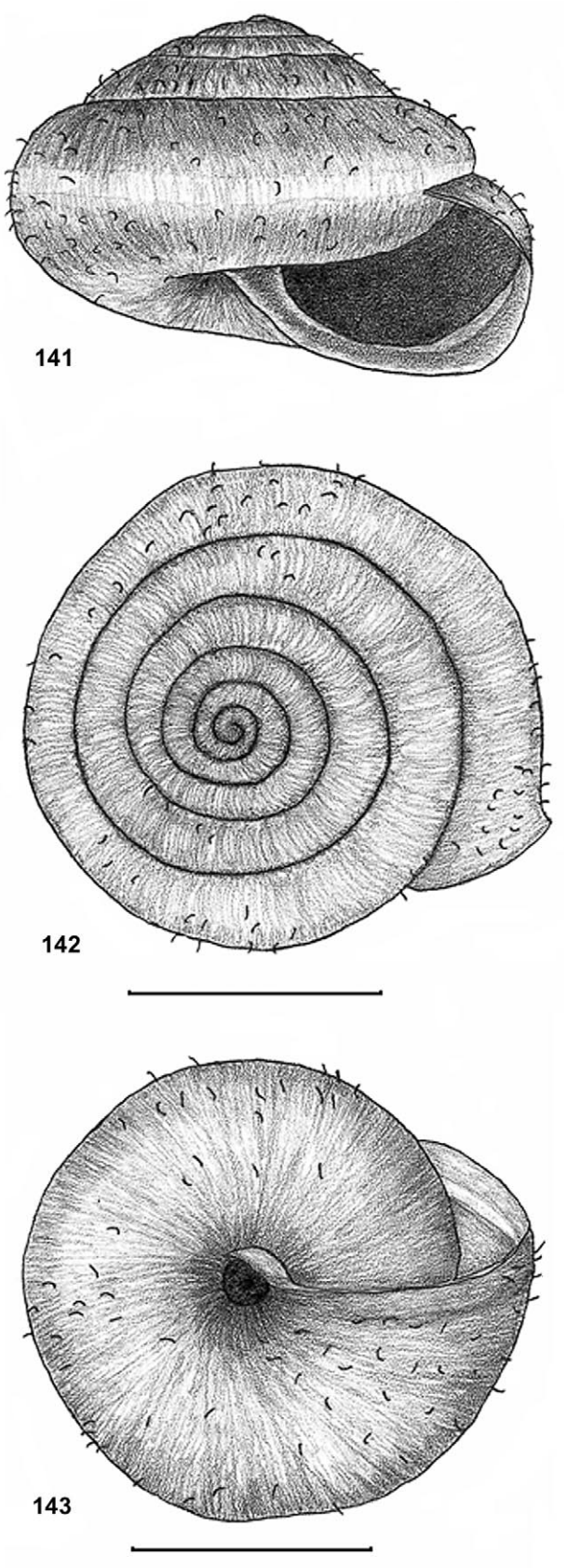
Distribution (Fig. 149)

A South-Alpine species; known from Austria (Carinthia: S slopes of Karawanken), Slovenia (Kamnik Alps, Julian Alps), Croatia (in the east from Zagreb, Korana valley to Velika and Mala Kapela), western Bosnia and Herzegowina, northern Italy (environs of Gorizia, Sette Comuni, S. Tirol) (POLIŃSKI 1928, MANGANELLI et al. 1995).

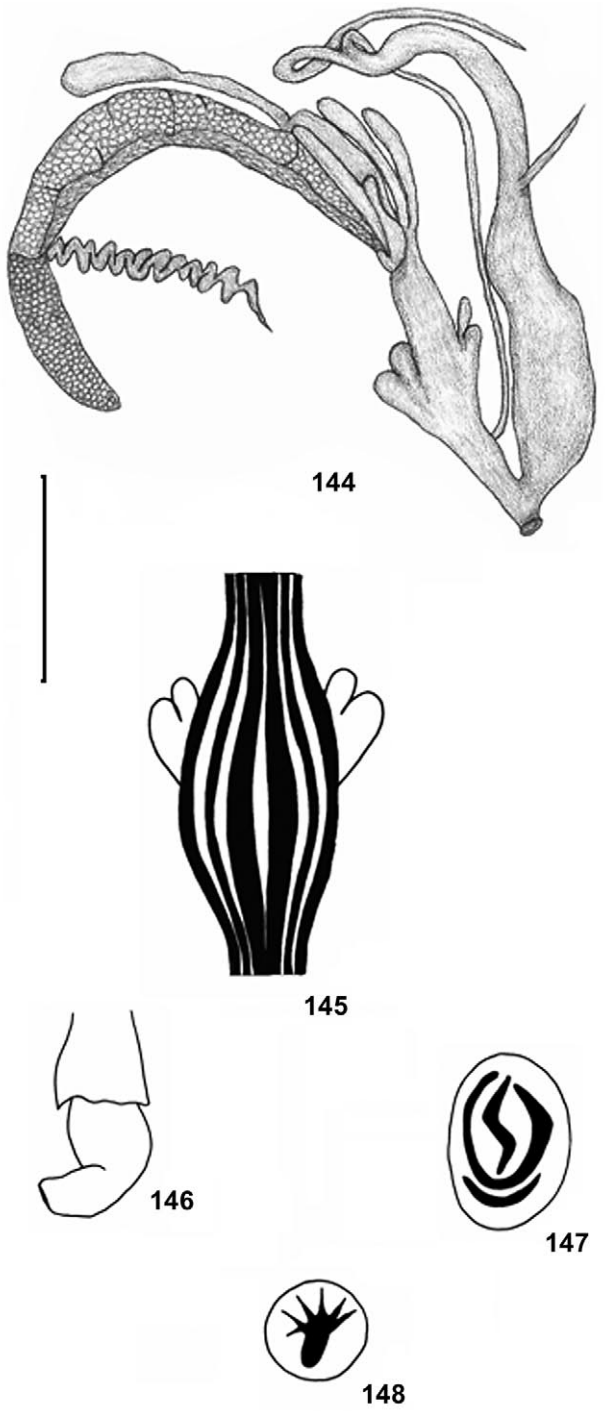
### *Trochulus montanus* (Studer, 1820)

*Glischrus (Helix) montana* STUDER 1820: 86 [12]. Locus typicus: Switzerland: Berner Jura, in forests and on damp rocks. Based on juveniles [see also FORCART 1957: 194]. Lectotype: NHMB.

*Helix submontana* MABILLE 1868: 22. Locus typicus: France: dep. Jura: Saint-Amour; dep. Ain: Bellegarde. = *Helix Pascali* Mabille, 1868: 22. [in synonymy]*




Figs 141–143. *T. luridus*. Specimen from Agram, Croatia, coll. Poliński 228/37, MIZW. Shell: 141 – apertural view, 142 – apical view, 143 – umbilical view. Scale bar 5 mm




Figs 144–148. *T. luridus*. Specimen from Kranj, Slovenia, coll. Poliński 228/37, MIZW. Reproductive system: 144 – general view, 145 – longitudinal section of vagina, 146 – penial papilla, 147 – cross-section of penial papilla, 148 – cross-section of epiphallus. Scale bar 5 mm

*Helix Dubisiana* Coutagne in LOCARD 1882: 77, 318. Locus typicus: France: Haut-Doubs Mountains: Mont Dore; dep. Jura (coll. Coutagne).*

*Helix plebicola* LOCARD 1888: 366. Locus typicus: France: dep. Ain: Tenay and Colombier; N of Lyon: alluvions of Rhône; dep. Haute-Savoie: Évian; dep. Jura: Bief-du-Fourg; dep. Aube (coll. Bourguignat).*


Fig. 149. Distribution of *T. luridus*. Black triangles – localities of origin of the examined material

## Material examined

Switzerland: Taubenlochschlucht near Biel, cant. Berne, 18.07.1935, coll. Edlauer 22122, NHMW, 5 s.; Taubenlochschlucht near Biel, cant. Berne, coll. Klemm 54283, NHMW, 4 s.; Les Roudez near Delémont, cant. Jura, 19.04.1969, leg. Falkner, 85033, NHMW, 5 alc.

## Shell (Figs 150–152)

Shell roundish-conical, 5.25–6.0 convex whorls with moderately deep suture. Shell height 4.5–7.0 mm, shell width 9.3–12.0 mm; height/width ratio 0.47–0.78, body whorl height 4.5–5.3 mm, relative height of body whorl 0.77–0.92, aperture height 3.0–4.1 mm, aperture width 4.5–5.7 mm, umbilicus major diameter 1.7–2.0 mm, umbilicus minor diameter 1.1–1.8 mm, umbilicus major diameter/shell diameter ratio 0.11–0.26. Aperture with white lip. Umbilicus open and moderately wide, earlier whorls visible. Few thin hairs present only in juveniles. Colour variable: from horny-yellow to reddish-brown, shell shiny, finely striated, usually with light band on body whorl.

## Reproductive system (Fig. 153)

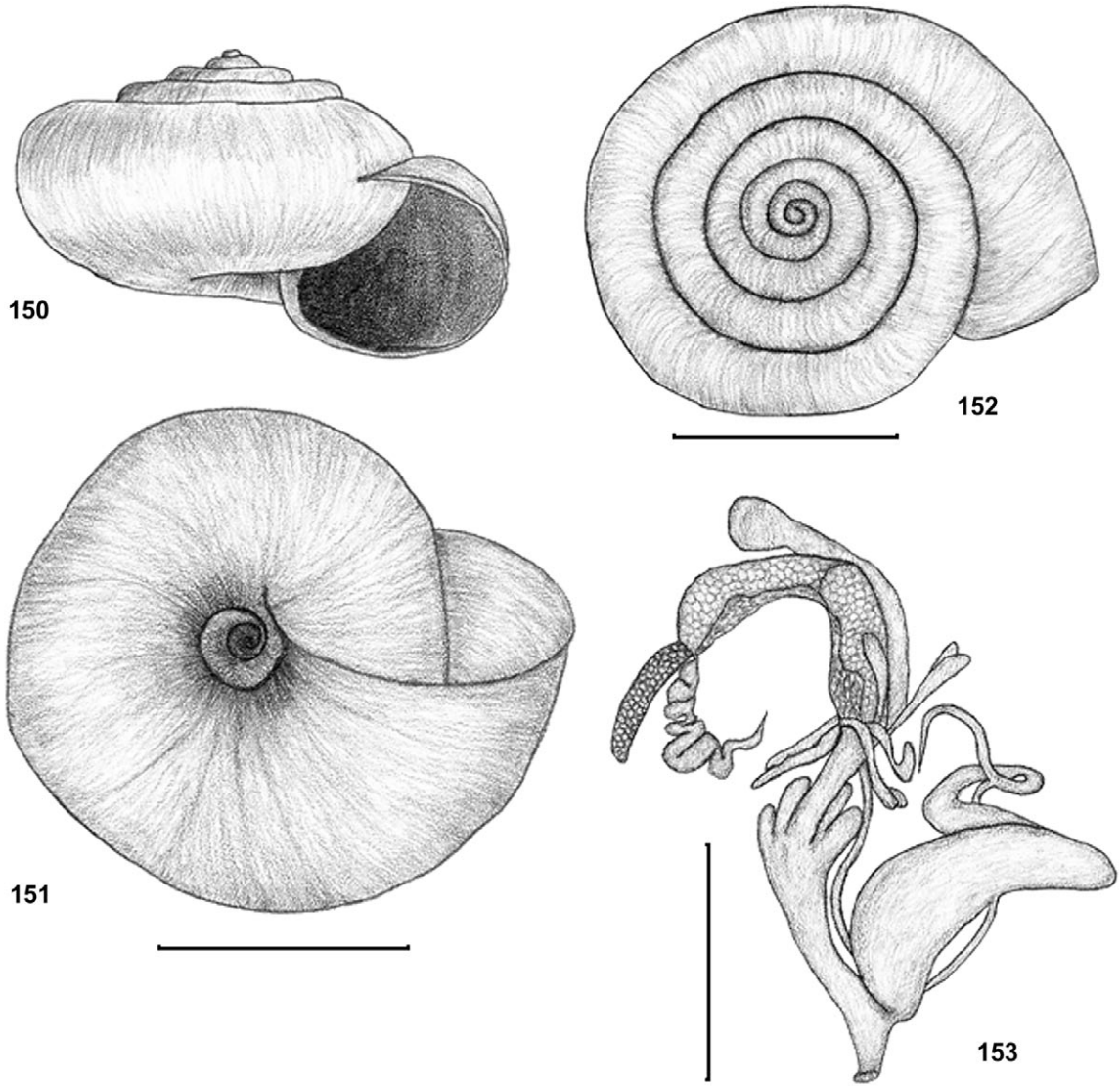
Four pairs of short mucous glands. Inner dart sacs reach beyond outer ones. Vagina long and cylindrical. Flagellum cosiderably longer than epiphallus, which is shorter than massive and fusiform penis. Spermatheca duct long. Spermatheca oval, reaching ca. 2/3 spermoviduct length.

## Ecology

*T. montanus* lives in forests on steep mountain slopes, on shaded rocks; between 400 and 1,600 m a.s.l.

## Distribution (Fig. 154)

A North-Alpine species; known from France (Alps of Savoy: Grand Chartereuse), Switzerland (only in




Figs 150–153. *T. montanus*. Specimen from Les Roudez near Delémont, Switzerland, 85033, NHMW. 150–152 – shell: 150 – apertural view, 151 – umbilical view, 152 – apical view; 153 – reproductive system. Scale bar 5 mm

Jura) and Italy (Western Alps) (FORCART 1965, MANGANELLI et al. 1995, TURNER et al. 1998).

Remarks

It is not always possible to distinguish this species from *T. striolatus* based on conchological characters alone. The two species show only slight differences in the structure of their reproductive system. *T. montanus* has the flagellum considerably longer than the epiphallus, and the inner dart sacs reach far beyond the outer ones. *T. striolatus* has the flagellum as long as the epiphallus or slightly longer, and the inner dart sacs are only slightly longer than the outer ones.

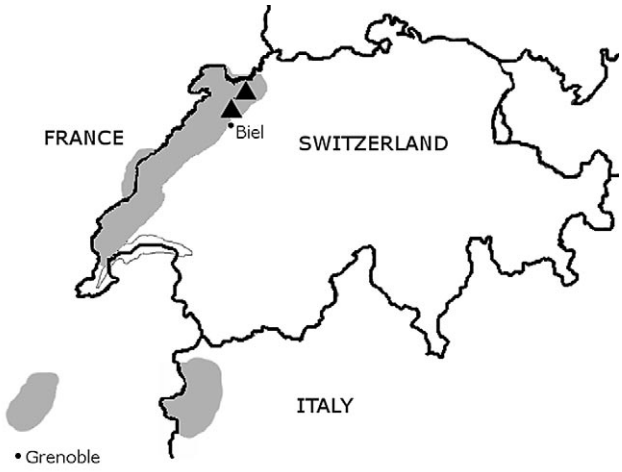



Fig. 154. Distribution of *T. montanus*. Black triangles – localities of origin of the examined material

### *Trochulus piccardi* Pfenninger et Pfenninger, 2005

*Trichia piccardi* HAUSSER 2005: 153. [nomen nudum]

*Trochulus piccardi* PFENNINGER & PFENNINGER 2005: 264, figs 4–5 (shell and genitalia). Locus typicus: Switzerland: canton Vaud: Commune de Chateau d'Oex, meadow at the foot of the church-hill, (46°28'37''N, 07°07'83''E, 970 m a.s.l.). Holotype: Naturmuseum Senckenberg, Frankfurt am Main – SMF 328194; paratypes: Bayerische Staatssammlung, München and Naturhistorische Museum, Bern – SMF 328195/11.

Since the species was described only recently, the original description is detailed and supported with molecular data, and its separate status raises no doubts, the description below is given after PFENNINGER & PFENNINGER (2005).

#### Shell and animal

Shell rather thick-walled, glossy, opaque, light brown, depressed with elevated apex. Mean height 3.9±0.4 (range 3.3–5.0), width 6.4±0.7 (5.6–8.7). Mean number of whorls 4.7±0.3 (4.3–5.3); whorls descending with pronounced suture. Elliptical aperture broader than high, downwards slanted, often with whitish rim inside. Shell increment reflected in slanted striation on upperside. Periphery round and not shouldered. Umbilicus ca. 15% of shell width. Shell hairless; no hair scars visible on first whorls. Body light, with wedge-shaped dark grey pigment spot on head behind ommatophores.

#### Reproductive system

The reproductive system departs in some respects from the typical *Trochulus* structure. Neither male nor female parts are pigmented. The three sections of the male ducts have a length ratio of ca. 1:1.6:1.2 (19.5 mm total length), with a strongly coiled flagellum. The penial retractor muscle attaches to the epiphallus directly behind the penis. No accessory dart sacs are visible in the female tract. However, since the main dart sacs are unusually broad, fusion of the sacs is possible. Eight mucous glands present, inserting directly above dart sacs.

#### Habitat

The snail lives on extensively used pastures on south-facing slopes; it is found on the ground, among the vegetation composed of typical alpine herbs and grasses.

#### Distribution (Fig. 155)

Plain d'Afflon, near Enney. Fresh shells were found in various, ecologically similar places in the lower Saanen-valley.

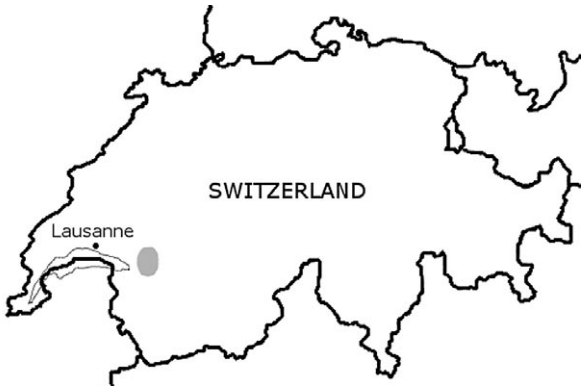



Fig. 155. Distribution of *T. piccardi*

### *Trochulus striolatus* (C. Pfeiffer, 1828)

*Cochlea rufescens* DA COSTA 1778: 80, pl. IV, fig. 6. Locus typicus: England: Cornwall and Hampshire; Wales: Flintshire: Leeswood and others. [see also FALKNER 1995: 99]

*Helix striolata* C. PFEIFFER 1828: 28, pl. VI, fig. 8. Locus typicus: Germany: near Heidelberg, in gardens.

*Helix montana* C. PFEIFFER, 1828: 33, pl. VI, fig. 9. Locus typicus: Germany: near Heidelberg, the castle hill; Austria: forests near Vienna.

*Helix danubialis* CLESSIN 1874: 184, pl. VIII, fig. 4. Locus typicus: Germany: Bavaria: near Dillingen, woods on the border of the Bavarian Danube.

*Helix altenana* Klees in LOCARD 1882: 79. Locus typicus: France: dep. Nord: vicinity of Lille; dep. Pas-de-Calais: Boulogne-sur-Mer; dep. Aube: Bar-sur-Seine (coll. Bourguignat) and Courtenot.*

*Helix abludens* LOCARD 1888: 334. Locus typicus: Jersey; Ireland: environs of Dublin; France: dep. Pas-de-Calais: Boulogne-sur-Mer. [see Falkner et al. 2001: 57 – *Trochulus striolatus abludens* (Locard, 1888)]

*Helix rufescentella* LOCARD 1894: 128–129. Locus typicus: France: dep. Nord: Valenciennes and Lille.*

*Helix (Trichia) britannica* WESTERLUND 1894: 164. Locus typicus: England: London.*

*Helix (Hygromia, Fruticicola) montana* var. *juvavensis* GEYER 1914: 276. Locus typicus: Austria: north slopes of Schafberg. Paratypes: NHMW.

#### Material examined

Austria: Hollerberg, north of See am Mondsee, Upper Austria, 1945, coll. Klemm 56657, NHMW, 19 s.; Scharflingerpass, Salzkammergut, 600 m, 8.09.1997, leg. A. Riedel & F. Seidl, MIZW, 19 s.; Schafberg, Salzkammergut, ± 1,700 m, 8.09.1997, leg. A. Riedel & F. Seidl, MIZW, 7 alc. [*juvavensis*]; Schafberg, Salzkammergut, coll. Rusnov R/105/5, NHMW, 5 s. [paratypes *T. striolatus juvavensis*]; Höllengebirge, Upper Austria, 21.09.1968, coll. Klemm 86624, NHMW, 4 alc. [*juvavensis*]; Höllengebirge, cable car station, Upper Austria, NHMW, 10 s. [*juvavensis*];

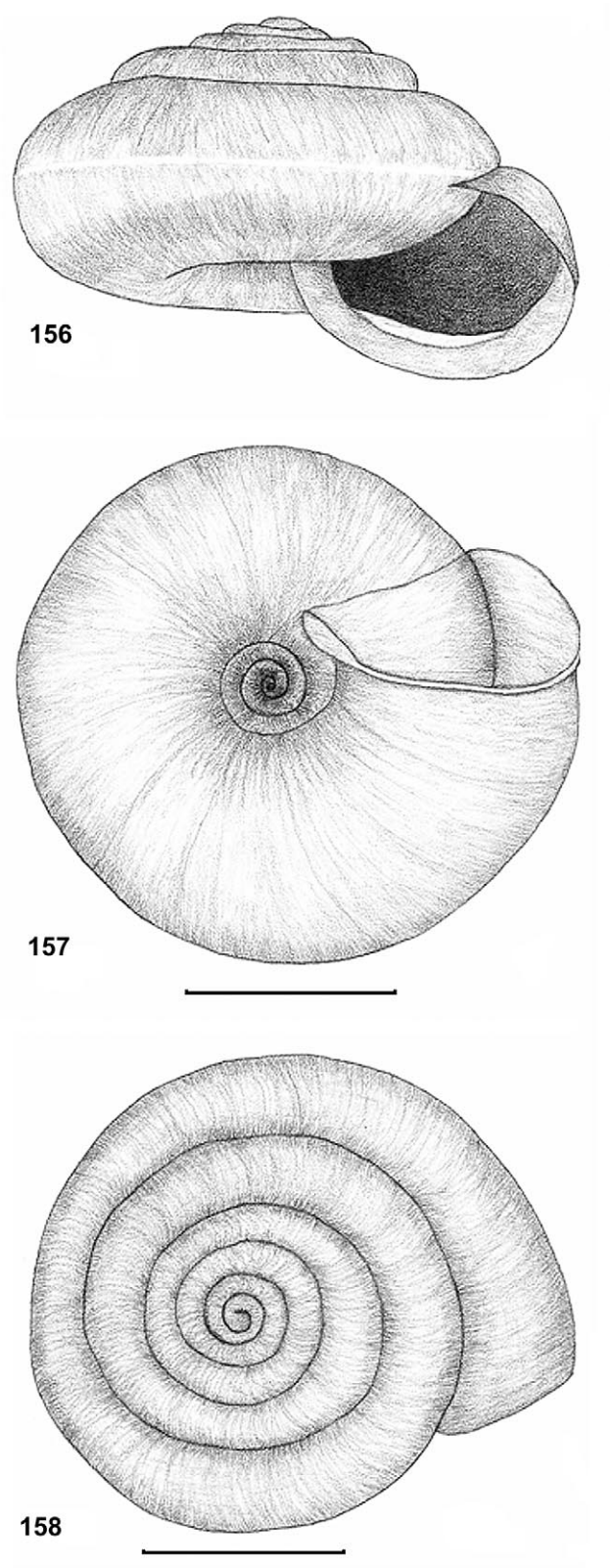
Höllengebirge, cable car station, Upper Austria, coll. Klemm 80844: NHMW, 19 s.; Mt. Hochlecken, Höllengebirge plateau, 1,600 m, Upper Austria, NHMW, 30 s.; Mt. Feuerkogel, Höllengebirge near Ebensee, Upper Austria, 1927, coll. Edlauer 6873, 11 s.; Fischamend, Lower Austria, coll. Rusnov, NHMW, 22 s. [*danubialis*]; Grimsing, Wachau valley, Lower Austria, coll. Klemm 63024, NHMW, 12 s. [*danubialis*]; Britain: Box Hill near Dorking, county Surrey, 18–25.09.1963, leg. J. F. Peake & A. J. Knight, BMNH, 18 alc.; Epsom, county Surrey, V 1939, leg. A. E. Ellis, Nr 2136, BMNH, 16 s.; Durrington near Salisbury, county Wiltshire, leg. A. E. Ellis, Nr 2136, BMNH, 9 s.; Porton near Salisbury, county Wiltshire, 08.1917, leg. Boycott, Nr 1218, BMNH, 32 s.; Cheltenham, county Gloucestershire, 2.06.1954, leg. I. S. Hawkins, Nr 1392–1396, BMNH, 29 s.; Germany: Ulm, Württemberg, leg. Prinzing, MIZW, 19 s.; Geislingen an der Steige, Württemberg, coll. Edlauer 9103, NHMW, 16 s.; Mt. Hohenstausen near Göppingen, Schwäbische Alb, leg. Regius, coll. Geyer 47033, NHMW, 13 s.; Nürburg castle ruins near Adenau, Rhineland-Palatinate, coll. O. Retowski 41/39, MIZW, 8 s.; Günzburg, Bavaria, coll. Edlauer 36332, NHMW, 26 s.; Sonthofen, Bavarian Alps, leg. Gutten, MIZW, 10 s.

### Shell (Figs 156–158)

Shell roundish-conical with 5.3–6.5 moderately convex whorls, body whorl slightly expanded and often angled. Shell height 5.2–8.8 mm, shell width 8.5–14.0 mm; height/width ratio 0.51–0.7, body whorl height 4.3–7.1 mm, relative height of body whorl 0.75–0.94, aperture height 3.0–5.5 mm, aperture width 3.9–7.2 mm, umbilicus major diameter 1.5–2.7 mm, umbilicus minor diameter 0.9–2.4 mm, umbilicus major diameter/shell diameter ratio 0.1–0.24. Aperture with white lip, aperture margin very slightly reflected. Umbilicus open, earlier whorls visible. Adults usually hairless. Shell dark reddish-brown to creamy-yellow, usually with light band on body whorl.

### Shell variation

Almost every studied population differs statistically significantly from the remaining ones in at least one character (Figs 159–171). Some pairs of populations differ in all or nearly all the parameters examined, e.g. those from Höllengebirge, Schafberg and Scharflingerpass. Some characters, such as shell height and width (Figs 159, 160), aperture height and width (Figs 161, 162), body whorl height (Fig. 163), and umbilicus major and minor diameter (Figs 165, 166) are very much variable. The least variable characters are those describing the shell proportions i.e. height/width ratio (Fig. 168), relative height of body whorl (Fig. 171) and umbilicus relative diameter (Fig. 169). The shell diameter (Fig. 164) and umbilicus minor/major diameter ratio (Fig. 170) show no statistically significant differences between the examined populations.




Figs 156–158. *T. striolatus*. Specimen from Ulm, Württemberg, Germany, MIZW. Shell: 156 – apertural view, 157 – umbilical view, 158 – apical view. Scale bar 5 mm

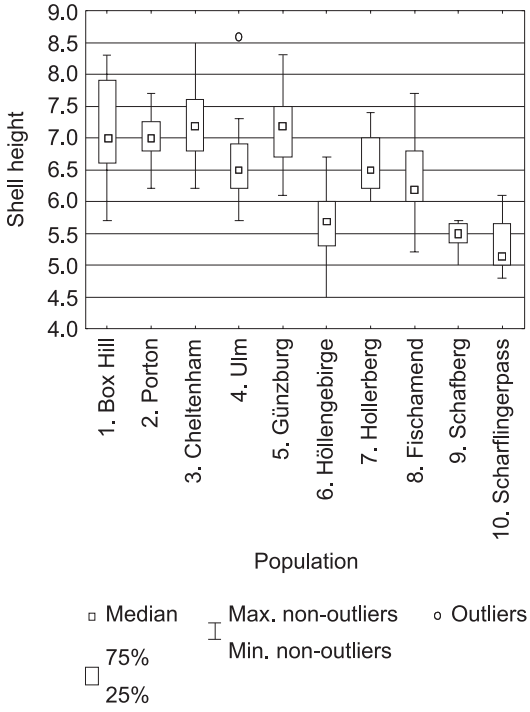



Fig. 159. Interpopulation variation of *T. striolatus*: shell height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–6, 1–8, 1–9, 1–10, 2–6, 2–8, 2–9, 3–4, 3–6, 3–7, 3–8, 3–9, 3–10, 4–6, 4–9, 4–10, 5–6, 5–8, 5–9, 5–10, 6–7, 6–8, 6–10, 7–8, 7–9, 7–10, 8–9, 8–10

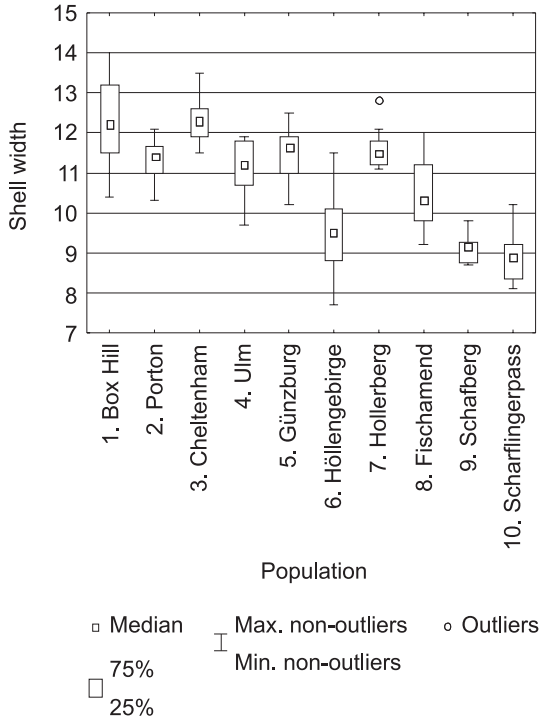



Fig. 160. Interpopulation variation of *T. striolatus*: shell width. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–4, 1–5, 1–6, 1–7, 1–8, 1–9, 1–10, 2–3, 2–6, 2–8, 2–9, 2–10, 3–4, 3–6, 3–7, 3–8, 3–9, 3–10, 4–6, 4–8, 4–9, 4–10, 5–6, 5–8, 5–9, 5–10, 6–7, 6–8, 6–9, 6–10, 7–8, 7–9, 7–10, 8–9, 8–10

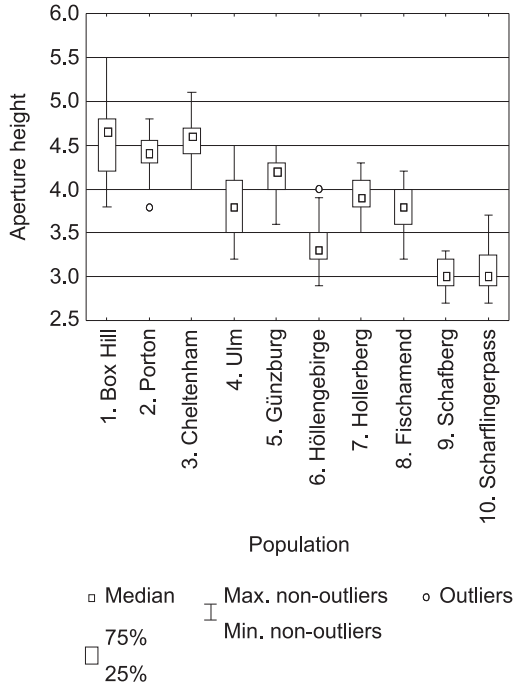



Fig. 161. Interpopulation variation of *T. striolatus*: aperture height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–4, 1–5, 1–6, 1–7, 1–8, 1–9, 1–10, 2–4, 2–5, 2–6, 2–7, 2–8, 2–9, 2–10, 3–4, 3–5, 3–6, 3–7, 3–8, 3–9, 3–10, 4–5, 4–6, 4–9, 4–10, 5–6, 5–8, 5–9, 5–10, 6–7, 6–8, 6–9, 6–10, 7–9, 7–10, 8–9, 8–10

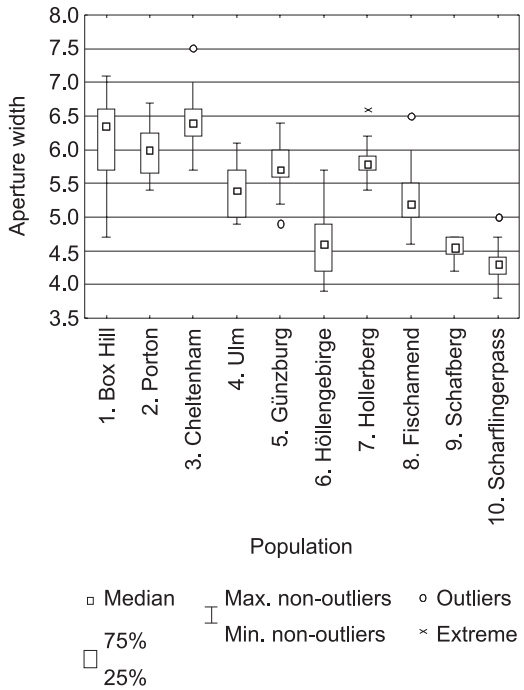



Fig. 162. Interpopulation variation of *T. striolatus*: aperture width. Statistical significance of differences (Duncan test, $p < 0.05$) are between the following populations: 1–3, 1–4, 1–5, 1–6, 1–8, 1–9, 1–10, 2–3, 2–4, 2–5, 2–6, 2–8, 2–9, 2–10, 3–4, 3–5, 3–6, 3–7, 3–8, 3–9, 3–10, 4–5, 4–6, 4–7, 4–9, 4–10, 5–6, 5–8, 5–9, 5–10, 6–7, 6–8, 6–10, 7–8, 7–9, 7–10, 8–9, 8–10

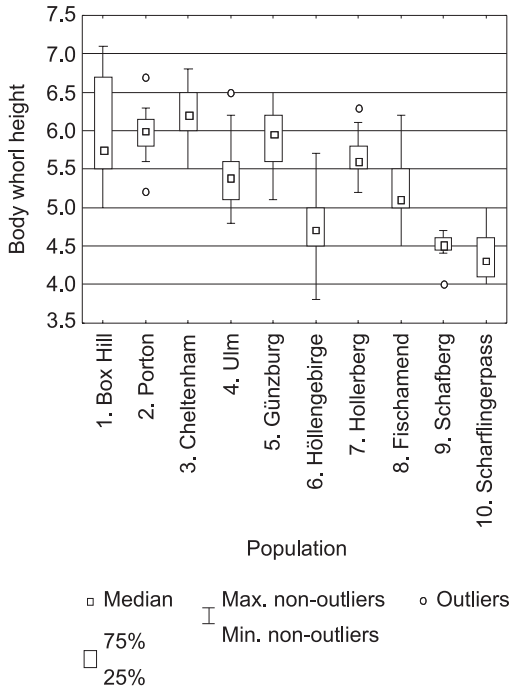



Fig. 163. Interpopulation variation of *T. striolatus*: body whorl height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–4, 1–6, 1–8, 1–9, 1–10, 2–3, 2–4, 2–6, 2–8, 2–9, 2–10, 3–4, 3–6, 3–7, 3–8, 3–9, 3–10, 4–5, 4–6, 4–9, 4–10, 5–6, 5–8, 5–9, 5–10, 6–7, 6–8, 6–9, 6–10, 7–8, 7–9, 7–10, 8–9, 8–10

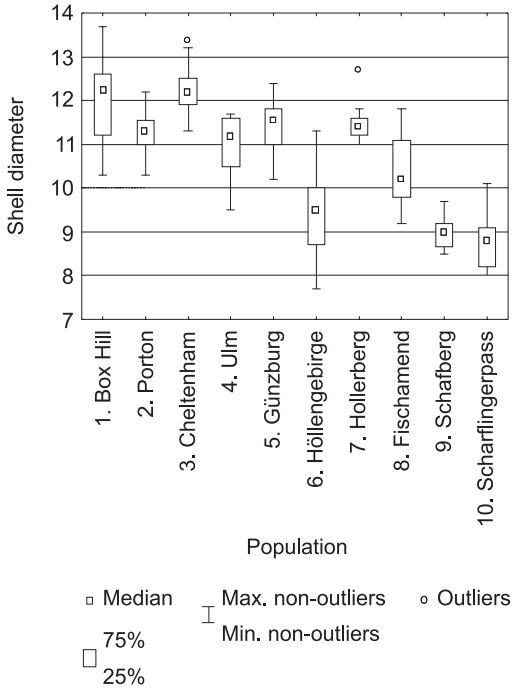



Fig. 164. Interpopulation variation of *T. striolatus*: shell diameter. No statistically significant differences between the studied populations

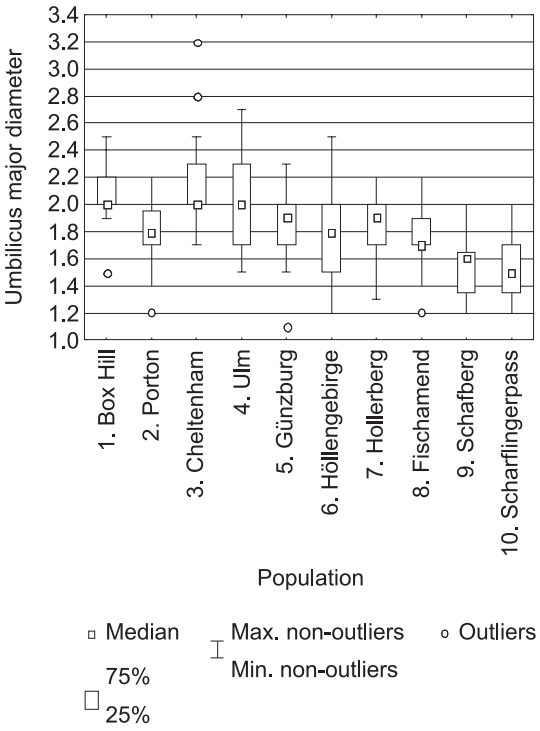



Fig. 165. Interpopulation variation of *T. striolatus*: umbilicus major diameter. Statistically significant differences (Duncan test, $p < 0{,}05$) between the following populations: 1–2, 1–5, 1–6, 1–8, 1–9, 1–10, 2–3, 2–4, 2–9, 2–10, 3–5, 3–6, 3–7, 3–8, 3–9, 3–10, 4–5, 4–6, 4–8, 4–9, 4–10, 5–9, 5–10, 6–9, 6–10, 7–10, 8–9, 8–10

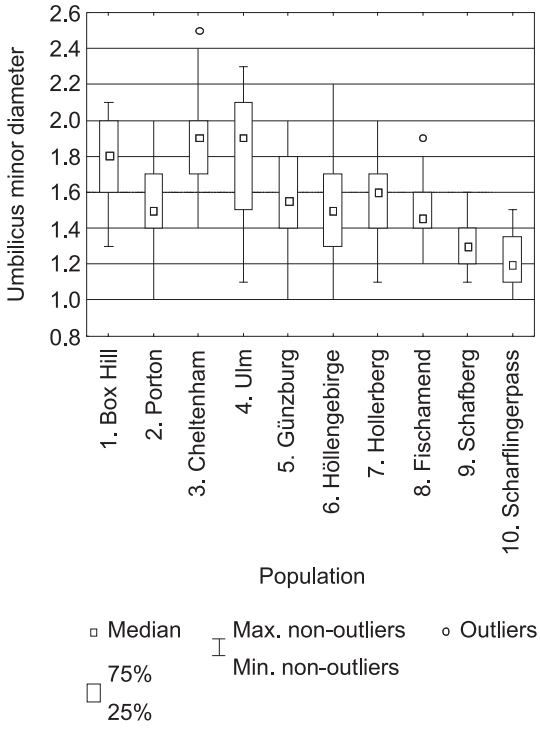



Fig. 166. Interpopulation variation of *T. striolatus*: umbilicus minor diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–5, 1–6, 1–7, 1–8, 1–9, 1–10, 2–3, 2–5, 2–6, 2–9, 2–10, 3–5, 3–6, 3–7, 3–8, 3–9, 3–10, 4–5, 4–6, 4–7, 4–8, 4–9, 4–10, 5–9, 5–10, 6–9, 6–10, 7–10, 8–9, 8–10

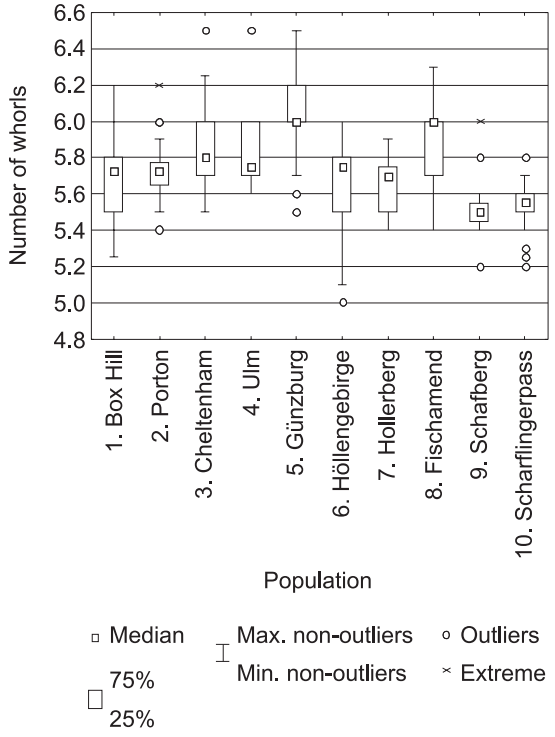



Fig. 167. Interpopulation variation of *T. striolatus*: number of whorls. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–5, 2–5, 3–9, 3–10, 4–9, 4–10, 5–6, 5–7, 5–9, 5–10, 6–10, 7–8, 8–9, 8–10

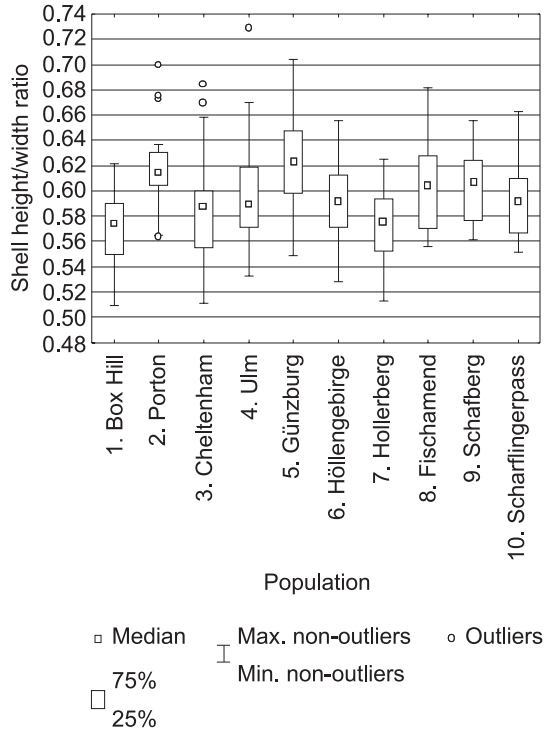



Fig. 168. Interpopulation variation of *T. striolatus*: shell height/width ratio. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–5, 2–3, 2–6, 2–7, 3–5, 5–6, 5–7

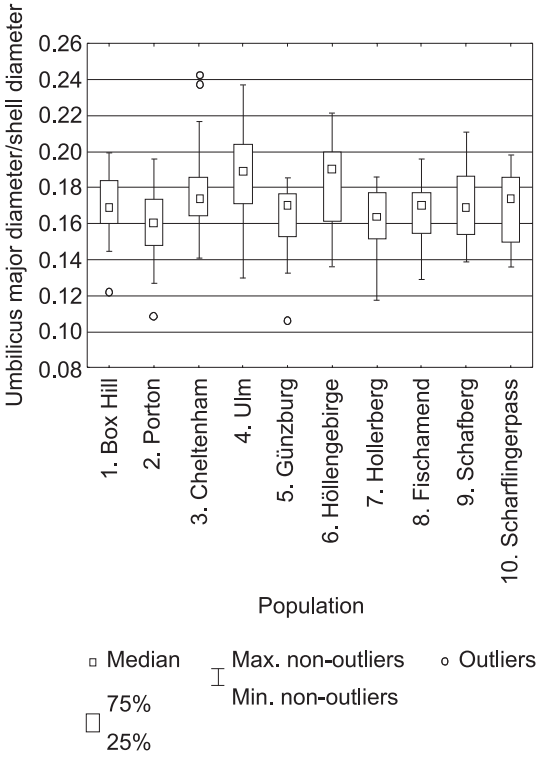



Fig. 169. Interpopulation variation of *T. striolatus*: umbilicus major diameter/shell diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 2–4, 2–6, 4–5, 4–7, 5–6, 6–7, 6–8, 6–10

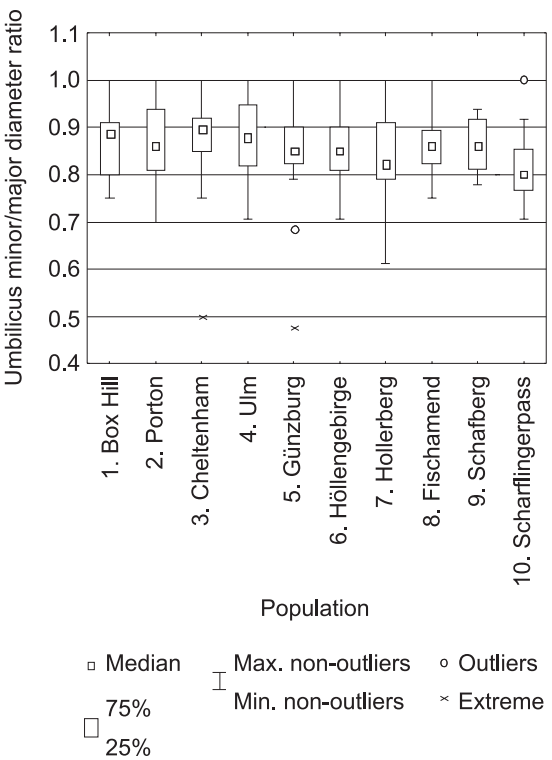



Fig. 170. Interpopulation variation of *T. striolatus*: umbilicus minor/major diameter ratio. No statistically significant differences between the studied populations

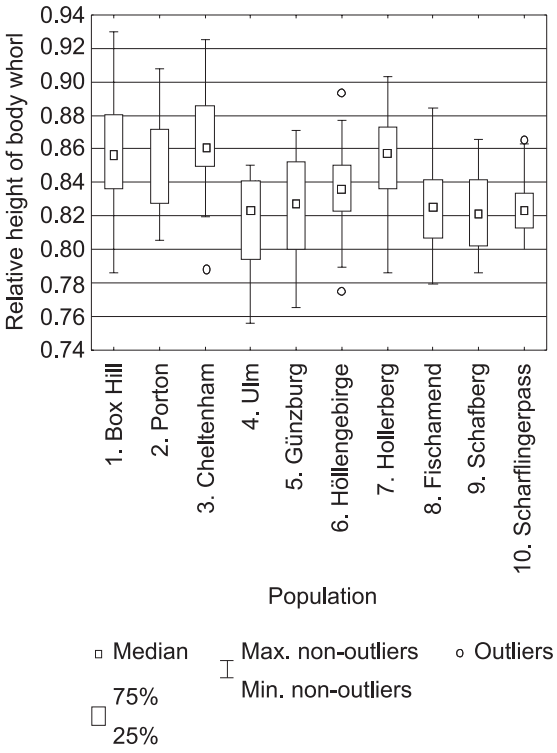



Fig. 171. Interpopulation variation of *T. striolatus*: relative height of body whorl. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–4, 2–4, 2–5, 2–8, 2–9, 2–10, 3–4, 3–5, 3–6, 3–8, 3–9, 3–10, 4–7, 5–7, 7–8, 7–10

## Reproductive system (Figs 172–176)

Four pairs of short mucous glands. Inner dart sacs reach only slightly beyond outer ones, which are considerably more massive. Vagina long, its dart sac region narrows toward genital atrium. Flagellum longer than epiphallus. Epiphallus as long as massive and fusiform penis, or longer. Spermatheca duct thick. Spermatheca roundish, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 172–176.

## Ecology

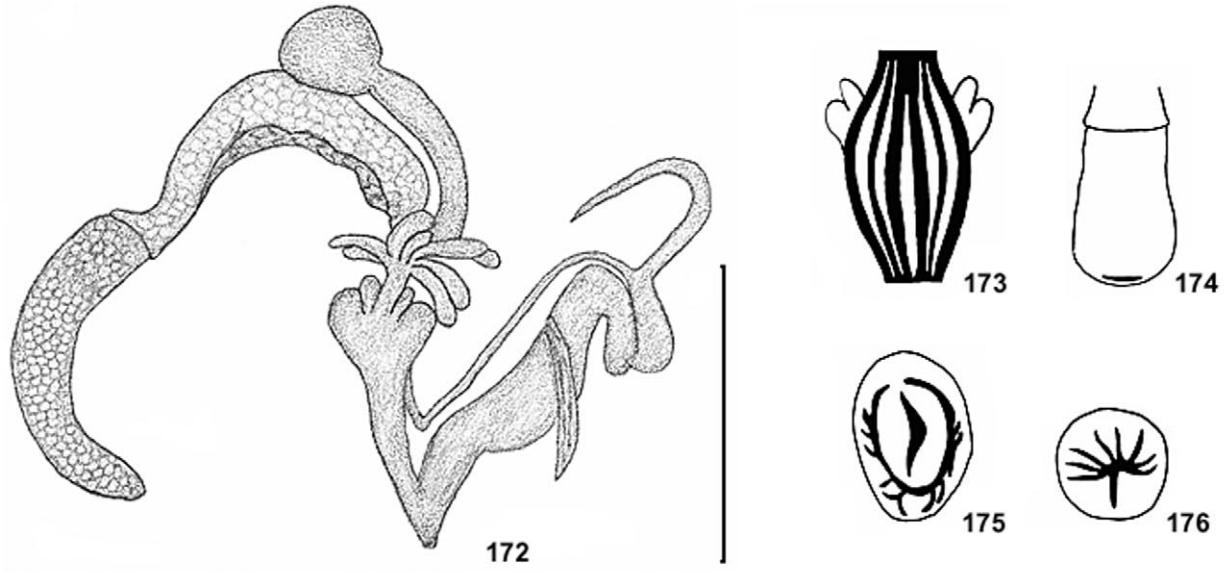
*T. striolatus* lives in humid and shaded habitats in forests, scrub and roadsides; also in gardens (especially in northern France and the British Isles where it is an introduced synanthrope); in Austria found between 150 and 2,000 m a.l.s. (KLEMM 1974), in northern Switzerland at 400–800 m a.s.l.

## Distribution (Fig. 177)

A North-West-European species; known from the British Isles, northern France (to the Seine River), southern part of the Netherlands, southern Germany (to the middle Rhine River; mainly in river valleys and on lowlands), northern Switzerland (canton Schaffhausen), Austria (except the southern part) and Slovakia (Danube floodplain, southern part of Little Carpathians and Žilinská Basin) and Hungary (FORCART 1965, KERNEY et al. 1983, ČEJKA 2000).

## Remarks

The specimens from Fischamend were determined as *Trochulus striolatus danubialis* (Clessin, 1874). However, the shell variation ranges of this population and those of *T. striolatus* from the remainig localities overlap (Figs 159–171). Besides, the differences between this population and the remaining ones are as statistically significant as those among the populations of *T. striolatus* s. str. Moreover, the reproductive



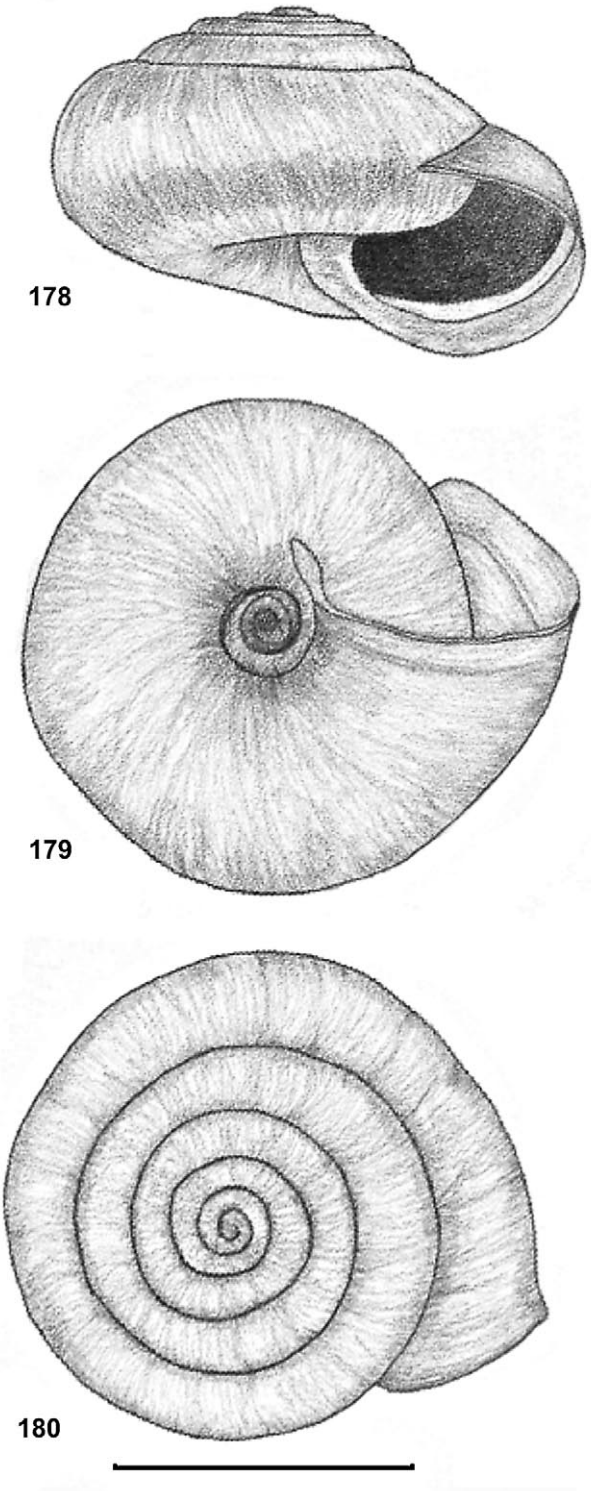

Figs 172–176. *T. striolatus*. Specimen from Box Hill near Dorking, Great Britain, BMNH. Reproductive system: 172 – general view, 173 – longitudinal section of vagina, 174 – penial papilla, 175 – cross-section of penial papilla, 176 – cross-section of epiphallus. Scale bar 5 mm


Fig. 177. Distribution of *T. striolatus*. Black triangles – localities of origin of the examined material

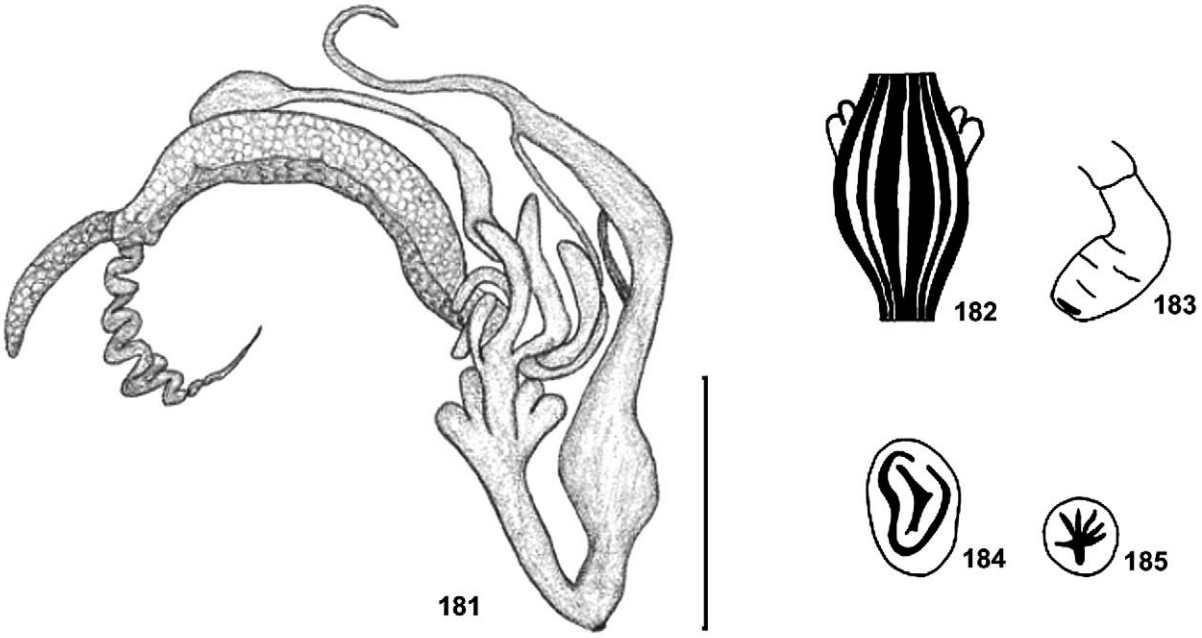
system of the examined specimens from Great Britain displays characters which are present in both *striolatus* and *danubialis* described in SHILEYKO (1978b), i.e. the expanded dart sac region narrows toward the genital atrium and the flagellum is longer than the epiphallus (like in *striolatus*; SHILEYKO 1978b). However, the spermatheca duct is short and thick, and the spermatheca does not reach the albumen gland (like in *danubialis*; SHILEYKO 1978b). Thus, the above data support FORCART's (1965) statement that "we cannot recognize geographical subspecies, but that the area of distribution of *T. striolata* is split up into colonies with local variations". In this context, it is likely that the subspecies *danubialis* is conspecific with *Trochulus striolatus* (C. Pfeiffer, 1828), despite the fact that SHILEYKO (1978b) regards it as a distinct species.

The pecularities of the external morphology of the reproductive system of *T. striolatus danubialis* were previously noted by HUDEC (1964). He did not compare its structure to *T. striolatus* s. str., but to other members of *Trochulus* (*T. hispidus, T. villosulus, T. sericeus* and *T. lubomirskii*) inhabiting the Czech Republic. Two charactes were recognized as subspecific i.e. the inner dart sacs considerably thinner than the outer ones and the relatively thick spermathecal duct, compared to free oviduct. The features given by HUDEC (1964) are, in fact, identical with those of *T. striolatus* s. str. from Great Britain (specimens examined cf. Figs 172–176).

Specimens from Schafberg and Höllengebirge represent subspecies *T. striolatus juvavensis* (Geyer, 1914) (Figs 178–180). They differ most of all in smaller shell height and width (mean values 5.61 mm and 9.23 mm, respectively). The mean aperture height and width are also small (3.22 mm and 4.61 mm, respectively). In *T. striolatus* s. str. the values are in the following ranges: shell height 5.7–7.2 mm (mean 6.82 mm) (Fig. 159), shell width 9.8–12.4 mm (mean 11.59 mm) (Fig. 160), aperture height 3.3–4.6 mm (mean 4.27 mm) (Fig. 161) and aperture width 4.7–6.4 mm (mean 5.91 mm) (Fig. 162). The coefficients describing the shell proportions are similar in all the studied populations, and their variation ranges overlap (Figs 168–171). The




Figs 178–180. *T striolatus juvavensis*. Paratype. Specimen from Schafberg, Salzkammergut, Austria, coll. Rusnov R/105/5, NHMW. Shell: 178 – apertural view, 179 – umbilical view, 180 – apical view. Scale bar 5 mm




Figs 181–185. *T. striolatus juvavensis*. Specimen from Schafberg – Salzkammergut, Austria, MIZW. Reproductive system: 181 – general view, 182 – longitudinal section of vagina, 183 – penial papilla, 184 – cross-section of penial papilla, 185 – cross-section of epiphallus. Scale bar 5 mm

mean number of whorls is 5.53 in *T. striolatus juvavensis* and a slightly higher in *T. striolatus* s. str. (5.65–5.89, mean of all populations 5.76); but also their variation ranges overlap (Fig. 167).

The reproductive systems in *T. striolatus* s. str. (Figs 172–185) and *T. striolatus juvavensis* (Figs 181–185) display considerable similarities both in shape and proportions of their component parts. Thus, FORCART's (1965) suggestion that *juvavensis* Geyer, 1914 from Schafberg is probably conspecific with *T. suberecta* seems ungrounded.

### *Trochulus suberectus* (Clessin, 1878)

*Helix suberecta* CLESSIN 1878b: 46. Locus typicus: Germany: Bavaria: Dreifaltigkeitsberg above Kleinprüfening near Regensburg (higher fossil loess layers), near Passau; Austria: Linz; Elbe and Rhine valleys.

#### Material examined

Austria: Mühl near St. Jodok, Tyrol, 2.07.1998, ZW, 4 alc.

#### Shell (Figs 186–188)

Shell roundish-conical with 5–5.2 convex whorls. Shell height 4.0–5.6 mm, shell width 5.0–7.5 mm, height/width ratio 0,63–0,71, body whorl height 3.5–3.9 mm, relative height of body whorl 0.79–0.83, aperture height 2.7–3.0 mm, aperture width 3.7–3.9 mm, umbilicus major diameter 0.7–1.1 mm, umbilicus minor diameter 0.6–1.0 mm, umbilicus major diameter/shell diameter ratio 0.14–0.15. Aperture with thin white lip. Umbilicus entirely open and wide, earlier whorls visible. Hairs thin, short and slightly curved, often lost in adults, leaving pronounced scars. Shell light to dark brown, some specimens with light band on body whorl.

#### Reproductive system (Figs 189–193)

Six short mucous glands. Inner and outer dart sacs approximately equal in size. Vagina long and cylindrical. Flagellum longer than epiphallus, which is shorter than conical penis. Spermatheca duct rather thick. Spermatheca oval, reaching ca. 1/2 spermoviduct length. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 190–193.

#### Ecology

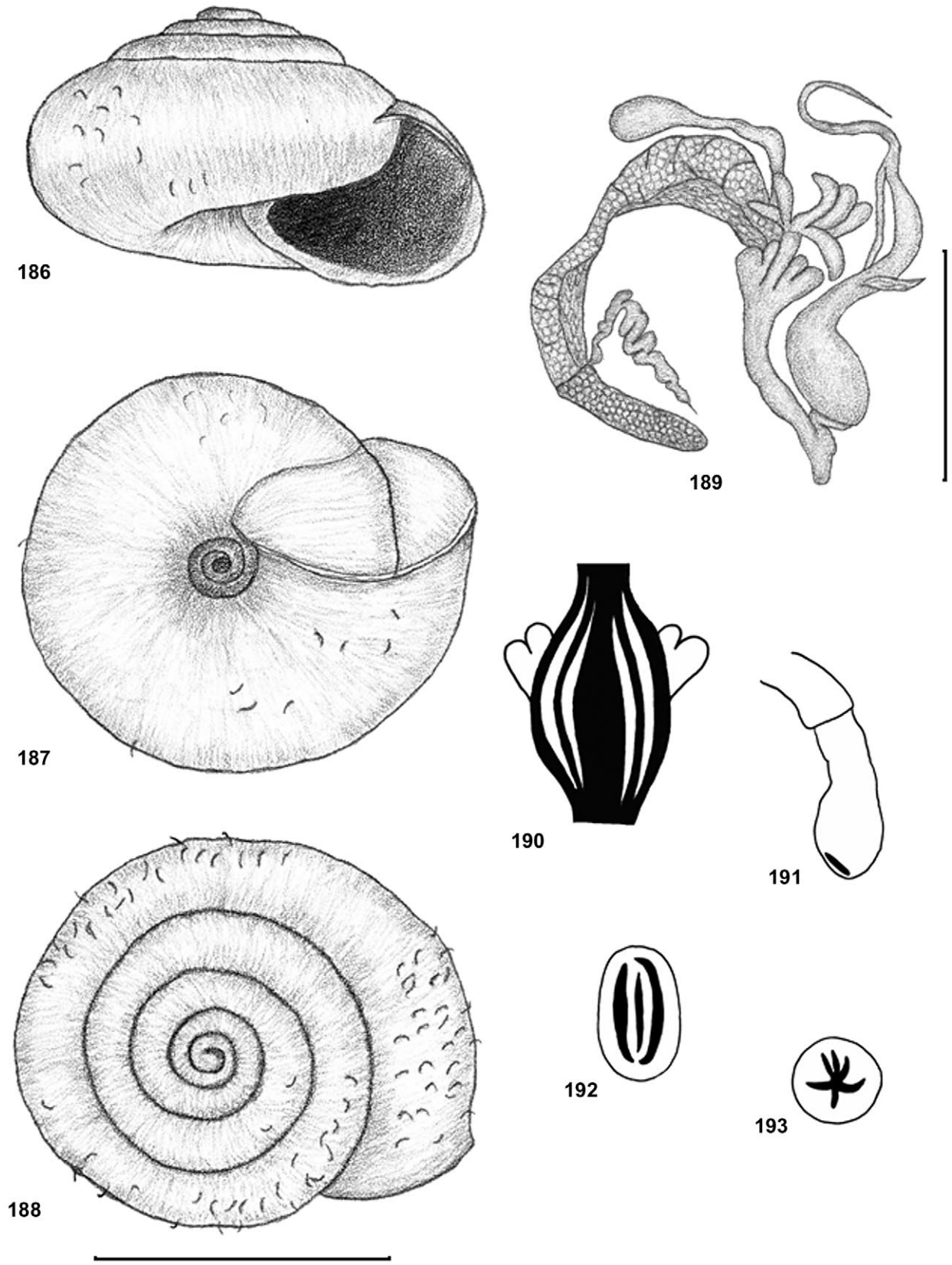
*T. suberectus* lives in montane habitats between 1,000 and 2,000 m a.s.l., in shaded scrub along streams; it shelters in tussocks of vegetation or under fallen leaves.

#### Distribution (Fig. 194)

A species known from some localities in southern Germany (Schwäbische Alb), western Austria (Tirol: Trins, Mühl near St. Jodok, Lech valley), north-western Italy and eastern Switzerland (Unter Engadin: Swiss National Park, Münster valley) (FORCART 1965, KERNEY et al. 1983).

#### Remarks

Conchologically *T. suberectus* is very similar to *T. hispidus*. It differs from other members of *Trochulus* in




Figs 186–193. *T. suberectus*. Specimen from Mühl near St. Jodok, Tirol, Austria, ZW. 186–188 – shell: 186 – apertural view, 187 – umbilical view, 188 – apical view; 189–193 – reproductive system: 189 – general view, 190 – longitudinal section of vagina, 191 – penial papilla, 192 – cross-section of penial papilla, 193 – cross-section of epiphallus. Scale bar 5 mm

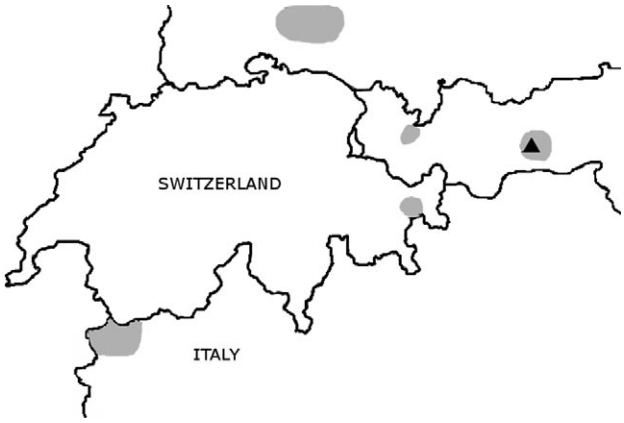



Fig. 194. Distribution of *T. suberectus*. Black triangle – locality of origin of the examined material

having 6 branches of the mucous glands. However, dissection of eastern Swiss specimens showed that the form was conspecific with *Trochulus sericeus* sensu Draparnaud, 1801, where occasionally some of the eight mucous glands can be missing (TURNER et al. 1998).

### *Trochulus unidentatus* (Draparnaud, 1805)

*Helix unidentata* DRAPARNAUD 1805: 81, pl. VII, fig. 15. Terra typica: France: Bresse. Type specimen: NHMW.

*Helix Cobresiana* ALTEN 1812: 79, pl. IX, fig. 18. Locus typicus: Germany: vicinity of Lechhausen [now a part of Augsburg] and outside Ublaß.

*Helix monodon* FÉRUSSAC 1821–1822: 35 [quarto edition], no 122. Locus typicus: France: La Franche-Comté; Germany: Augsburg; E Switzerland.

*Helix ventricosa* CRISTOFORI & JAN 1832: 1, no 6–54. Terra typica: Amer. Jamaica (labels probably mislead) [non *Helix ventricosa* Müller].*

*Helix unidens* Ziegler in L. PFEIFFER 1848: 151. [in synonymy] Terra typica: Germany, France, Italy: Alpine summits".*

*Helix (Fruticicola) unidentata* var. *alpestris* CLESSIN 1878a: 84, pl. III, fig. 12. Locus typicus: Austria: Tyrol: Lafatsch and Styria [not Kärnten]: Schneealpe (notified by Tschapeck).

*Helix unidentata* var. *anodonta* TSCHAPECK 1880: 190, pl. VI, fig. 4. Locus typicus: Austria: Styria: Prebichel-Passe.

*Fruticicola unidentata* var. (natio) *norica* POLIŃSKI 1928: 161–163, pl. XXVII, fig. 20. Locus typicus: Austria: Styria: Präbühel-Pass [=Prebichl]; Lower Austria: Schönbühel near Melk; Kuchl near Salzburg; Salzburg Alterbachgenist; Ach near Burghausen [near Salzburg].

*Fruticicola unidentata* var. *subalpestris* POLIŃSKI 1928: 163–165, tab, XXVII, figs 22–23. Locus typicus: Switzerland: "Basler Jura" and Valzeina (canton Graubünden); Italy: Tyrol: Glisenklamm near Sterzing [= Vipiteno]; Germany: Bavaria: Burgkirchen an der Alz; Austria: Styria: Seegraben near Aflenz.

*Fruticicola unidentata* var. (natio) *subtecta* POLIŃSKI 1928: 167, pl. XXVII, figs 24–26. Locus typicus: Austria: various localities near Vienna: Markenstein ruins near Vöslau; Gutenstein in Piestingtal; gorges near Fischau; Hoche Wand – Dürnbachklamm; Hoche Wand near Stollhof; Hoche Wand above Leitergrabens; Sirningtal (between Puchberg and Stixenstein); vicinity of Payerbach; Klause near Mariensee in Wechselgebiet; Pittental valley (Scheiblingkirchen). [see FALKNER 1990: 206, FALKNER et al. 2001: 58 – *Petasina subtecta*]

*Fruticicola unidentata* var. *carpatica* POLIŃSKI 1928: 170–172, pl. XXVII, figs 27–28. Locus typicus: Poland: Carpathians: Zamki Orawskie (S slopes of Carpathians between Babia Góra and Tatra Mts); Zaryte (gm. Limanowa), Mszana Dolna; Homole gorge near Jaworki; Łomnica (commune Nowy Sącz); Mt. Cisownice; Trzy Korony; Tatra Mts (N slopes); Kopa Magóry (Tatra Mts); "Jatki Bialskie" (Tatry Bialskie).

Material examined

Austria: Tirol: Trins, 1.07.1998, ZW, 5 s.; St. Jodok, 2.07.1998, ZW, 5 alc.; Vals, 2.07.1998, ZW, 5 alc.; Mühl near St. Jodok, 2.07.1998, ZW, 5 alc.; Putzalpe near Reutte, coll. O. Retowski 41/39, MIZW, 5 s. [*alpestris*]; Austria: Rottenbach near Haag am Hausruck, 9.09.1997, leg. A. Riedel et F. Seidl, MIZW, 3 s.; Pupping near Eferding, 9.09.1997, leg. A. Riedel et F. Seidl, MIZW, 1 s.; Überackern, Braunau am Inn, 7.09.1997, leg. A. Riedel et F. Seidl, MIZW, 1 s.; Wildshut, on Salzbach River near St. Pantaleon, 7.09.1997, leg. A. Riedel et F. Seidl, MIZW, 7 s.+7 alc.; Sengsengebirg Wald, 1380 m, 08.1958, NHMW, 28 s.; Ramsau, Salzkammergut, 4.07.1998, ZW, 5 alc.; Salzburg: Salzach-Klamm Gorge near Pass Lueg, 6.09.1997, leg. A. Riedel et F. Seidl, MIZW, 5 s.+3 alc.; Golling near Salzburg, 6.09.1997, leg. A. Riedel et F. Seidl, MIZW, 23 s.; Scharflingerpass, Salzkammergut, 8.09.1997, leg. A. Riedel et F. Seidl, MIZW, 1 s.; Mt. Schafberg, Salzkammergut, 8.09.1997, leg. A. Riedel et F. Seidl, MIZW, 4 s.+6 alc.; Kuchl, Salzburg, leg. A. Wagner 12, MIZW, 10 s.; Alterbachgeniste, Salzburg, coll. Rusnov, NHMW, 68 s.; Hinterseegenist near Faistenau, Salzburg, coll. Klemm 64768, NHMW, 25 s. [*norica*]; Tiefbrunnau, Salzkammergut, 4.07.1998, ZW, 10 alc.; Ebenau, Salzkammergut, 4.07.1998, ZW, 7 alc.; between Fuschl and St. Gilgen, Salzkammergut, 5.07.1998, ZW, 5 alc.; environs of Vienna and Lower Austria: Dornbacher Park near Wien, coll. Poliński 228/37, MIZW, 6 s.; Augarten Wien, coll. Poliński 228/37, MIZW, 3 s.; Schneeberg near Wien, 1,900 m, 1918, coll. Poliński 228/37, MIZW, 3 s. [*alpestris*]; Hinterbrühl near Mödling, coll. Poliński 228/37, MIZW, 1 s.; Maleiten near Fischau, coll. Poliński 228/37, MIZW, 10 s.; Gutenstein in Piestingtal, coll. Poliński 228/37, MIZW, 1 s.; Dürnbachklamm, coll. Poliński 228/37,

MIZW, 6 s.; Styria: Mt. Leobner Mauer, Eisenerzer Alpen, 1,800–2,000 m, coll. Edlauer 43925, NHMW, 30 s. [*subalpestris*]; Prebichl, ex coll. A. J. Wagner, coll. Poliński 228/37, MIZW, 4 s.; Präbuhel, cotypes, ex coll. Tschapeck, coll. Poliński 228/37, MIZW, 2 s. [*anodonta*]; Gleisdorf, on Raba River, coll. Poliński 228/37, MIZW, 4 s.; Mürzenist near Kapfenberg, coll. Poliński 228/37, MIZW, 3 s.; between Aussee and Grundlsee, 15.08.1912, leg. A. J. Wagner, coll. Poliński 228/37, MIZW, 3 s.; Klachau near Mitterndorf [=Bad Mitterndorf], coll. Rusnov, NHMW, 13 s. [*anodonta*]; Carynthia: Villach, coll. Poliński 228/37, MIZW, 3 s.; Magdalensberg, coll. Edlauer 50642, NHMW, 31 s.; *s. prec. loc.*, Catynthia, coll. Poliński 228/37, MIZW, 2 s.; Croatia: s. prec. loc., ex coll. Jickeli, coll. Poliński 228/37, MIZW, 2 s.; Czech Republic: Srbsko near Karlštejn, Březnice, 25.09.1960, leg. A. Riedel, 66/60, MIZW, 3 alc.; Ruine Landsberg b. Geiersberg [=Lanšperk castle ruins near Letohrad, reg. Pardubice], coll. O. Retowski 41/39, MIZW, 6 s.; Landsberg [=Lanšperk], Böhmen, coll. Poliński 228/37, MIZW, 5 s.; Germany: Bavaria: Ulm, leg. Prinzing, coll. Poliński 228/37, MIZW, 1 s.; München, on Isar River, coll. Poliński 228/37, MIZW, 1 s.; Moosburg, 30.06.1998, ZW, 39 alc.; Raitenhaslach near Burghausen, 7.09.1997, leg. A. Riedel et F. Seidl, MIZW, 1 s.; Grafussing near Simbach, 10.09.1997, leg. A. Riedel et F. Seidl, MIZW, 9 s.; Gemeinde Ering, 5.09.1997, MIZW, 11 alc.; Italy: Ugovizza, Friuli Val Canale valley (between Drava and Tagliamento Rivers), leg. Alzona, 09.1925, MIZW, 5 s.; Poland: Sudetes: Kletno, Kleśnica stream valley, 17.08.1996, ZW, 35 s.+12 alc.; Beskid Śląski: Cisownica near Ustroń, 1918, leg. Wagner, MIZW, 4 s. [*carpatica*]; Beskid Żywiecki: Ciapków Stream Valley near Rycerka, 24.09.1976, leg. A. Wiktor, Nr 1920, MPW, 3 alc.; Abrahamów Stream Valley near Rycerka, 26.09.1976, leg. A. Wiktor, Nr 1921, MPW, 2 alc.; stream valley on Przegibek, 24.09.1976, leg. A. Wiktor, Nr 1917, MPW, 2 alc.; nature reserve Śrubita, 13.08.1970, leg. A. Wiktor, Nr 1759, MPW, 2 alc.; Mt. Babia Góra, 4.08.1970, leg. A. Wiktor, Nr 1705, MPW, 5 alc.; below Palice, Mt. Babia Góra, 25.05.1964, leg. A. Wiktor, Nr 1172, MPW, 2 alc.; above Widły, Mt. Babia Góra, 23.08.1964, leg. A. Wiktor, Nr 1164, MPW, 2 alc.; Gorce: Rzeki, 16.08.1975, leg. A. Wiktor, Nr 1897, MPW, 6 alc.; Mt. Marszałek, 7.07.1962, leg. A. Wiktor, Nr 846, MPW, 5 alc.; Mt. Luboń, 27.08.1962, leg. A. Wiktor, Nr 874, MPW, 1 alc.; Beskid Sądecki: Valley of Szczawny Potok, 19.08.1961, leg. A. Wiktor, Nr 822a, MPW, 1 alc.; Sopotnicki Stream Valley, 4.07.1962, leg. A. Wiktor, Nr 843, MPW, 2 alc.; Pieniny Mts: Czorsztyn, 28.08.1963, leg. A. Wiktor, Nr 1063, MPW, 4 alc.; Valley of Pieniński Potok, 8.08.1972, leg. A. Riedel, 10/72, MIZW, 9 s.; Mt. Sokolica, 14.08.1961, leg. A. Wiktor, Nr 821, MPW, 2 alc.; Trzy Skałki near Jarmuta massif, 9.07.1962, leg. A. Wiktor, Nr 850, MPW, 1 alc.; Mt. Góra Zamkowa, 22.08.1961, leg. A. Wiktor, Nr 827, MPW, 1 alc.; Valley of Ociemny Potok, 19.08.1961, leg. A. Wiktor, Nr 822b, MPW, 3 alc.; Ligarka Glade, 8.08.1962, leg. A. Wiktor, Nr 881, MPW, 4 alc.; Tatra Mts: Zakopane, Pod Capkami quarry, 1914, leg. W. Poliński, coll. Poliński 228/37, MIZW, 8 s.; Mała Łąka Valley, 7.07.1997, ZW, 11 s.+15 alc.

### Shell (Figs 195–200)

Shell dome-shaped with 5–7 tightly coiled convex whorls, rounded at periphery. Shell height 3.4–6.6 mm, shell width 5.1–9.5 mm, height/width ratio 0.54–0.82, body whorl height 2.9–4.9 mm, relative height of body whorl 0.62–0.89, aperture height 1.7–3.2 mm, aperture width 3.0–5.2 mm, umbilicus diameter 0.2–0.8 mm, umbilicus major diameter/shell diameter ratio 0.03–0.11. Aperture with whitish or pinkish lip inside and prominent white tooth on basal margin. Umbilicus very narrow, punctured, sometimes partly or entirely covered by columellar aperture margin. Juveniles with dense and fine hairs, in adults hairs easily lost. Shell horny to reddish-brown, finely striated, sometimes with light band on body whorl.

### Shell variation

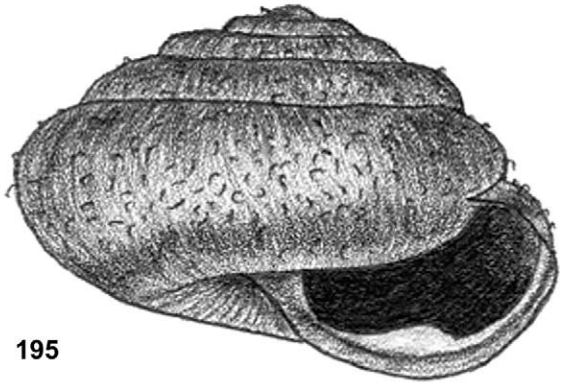
Almost every examined population differs statistically significantly from the remaining ones in at least one character (Figs 201–211). Some pairs of populations differ in all or nearly all the parameters examined, e.g. those from Kletno in the Sudetes, Dolina Małej Łąki in the Tatra Mts., Alterbachgeniste in Austria. The shell height (Fig. 201), aperture width (Fig. 202) and body whorl height (Fig. 205) vary very widely. The least variable characters are those describing the shell proportions i.e. height/width ratio (Fig. 210), relative height of body whorl (Fig. 211).

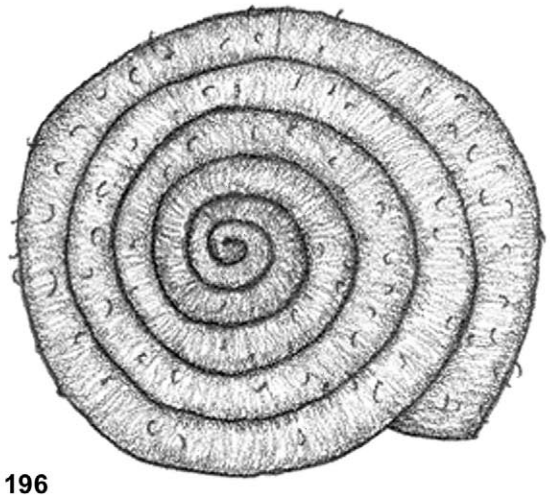
### Reproductive system (Figs 212–216)

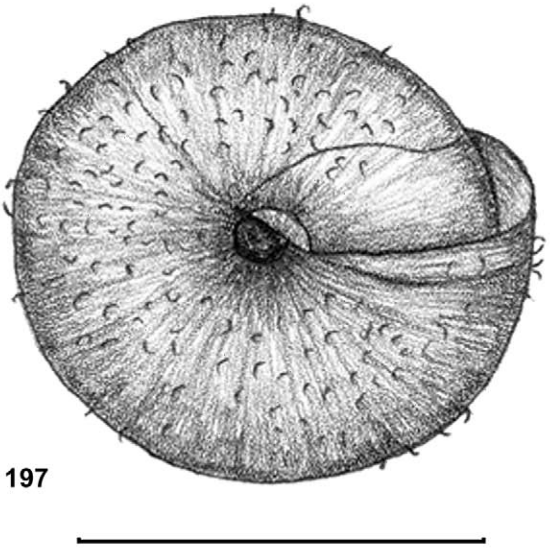
Four pairs of long (ca. 2 mm) mucous glands. Inner pair of long, well-separated dart sacs reaches outlet of mucous glands, outer pair considerably shorter. Vagina long and cylindrical. Flagellum reaches ca. 2/3 length of straight, cylindrical epiphallus, which is longer than straight or bent cylindrical penis. Spermatheca duct slightly coiled. Spermatheca massive, hammer-shaped, not reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 213–216.

### Ecology

*T. unidentatus* lives in damp montane forest habitats between 500 and 1,500 m a.s.l.; it is also quite frequent above the timberline in various habitats, up to 2,000 m a.s.l.; it is found along streams in leaf-litter, rotting wood and, rarely, on vegetation.




Figs 195–197. *T. unidentatus*. Specimen from Kletno, Sudetes, Poland, ZW. Shell: 195 – apertural view, 196 – apical view, 197 – umbilical view. Scale bar 5 mm


Figs 198–200. *T. unidentatus*. Specimen from Draparnaud's collection, NHMW. Shell: 198 – apertural view, 199 – apical view, 200 – umbilical view. Scale bar 5 mm

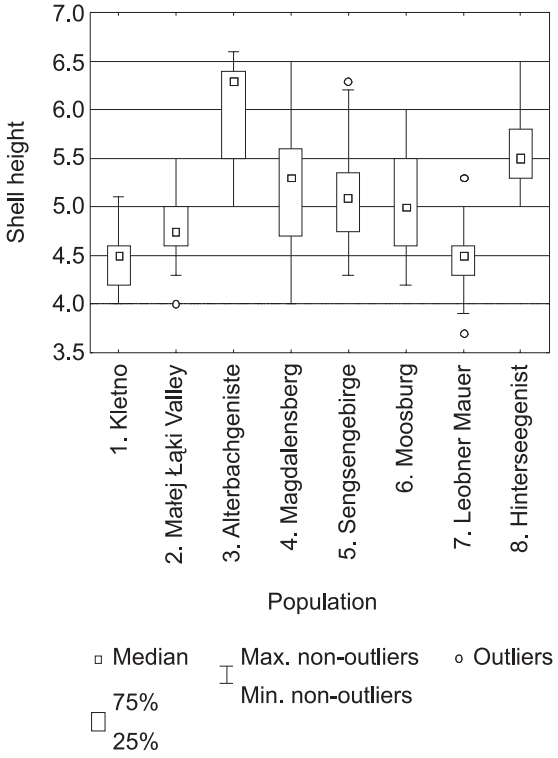



Fig. 201. Interpopulation variation of *T. unidentaus*: shell height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 4–7, 4–8, 5–7, 5–8, 6–7, 6–8, 7–8

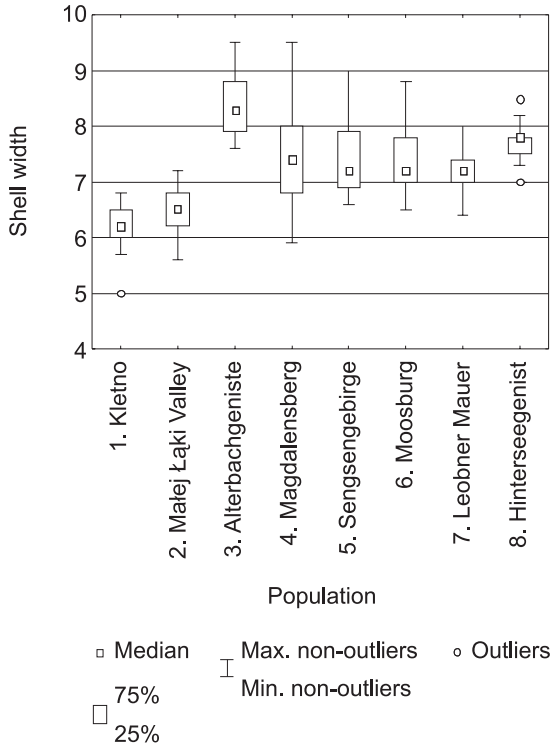



Fig. 202. Interpopulation variation of *T. unidentaus*: shell width. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 3–8, 6–8, 7–8

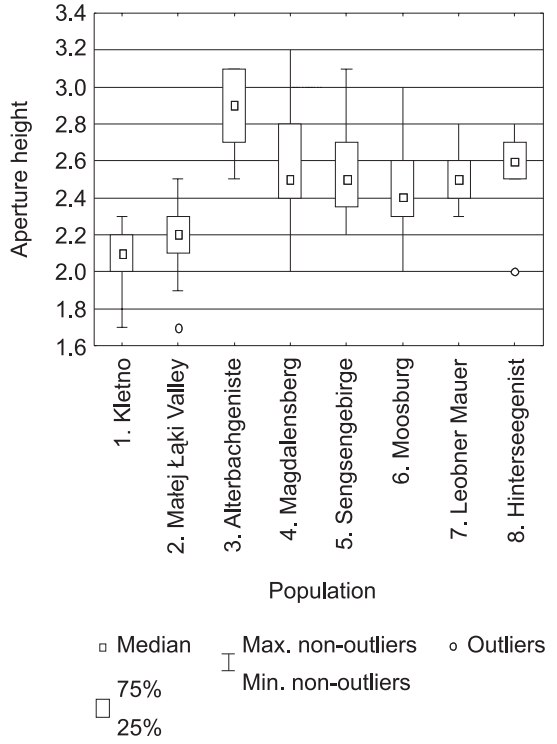



Fig. 203. Interpopulation variation of *T. unidentatus*: aperture height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 3–8

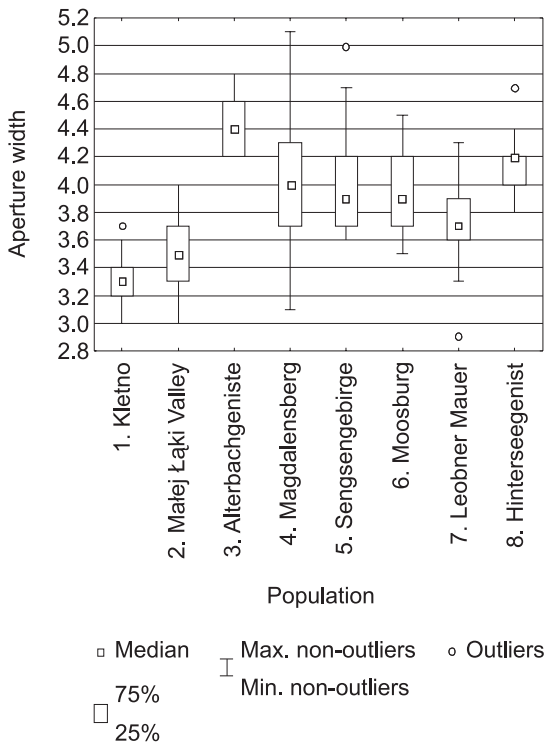



Fig. 204. Interpopulation variation of *T. unidentatus*: aperture width. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 3–7, 3–8, 4–7, 4–8, 5–7, 6–7, 6–8, 7–8

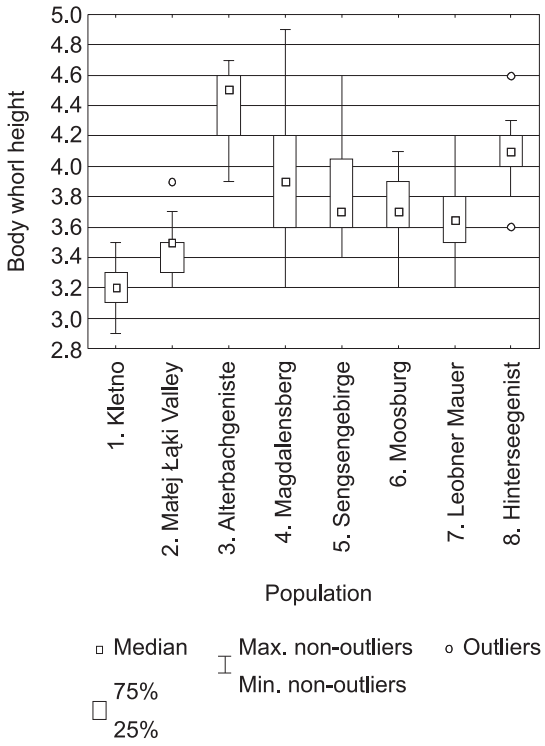



Fig. 205. Interpopulation variation of *T. unidentatus*: body whorl height. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 4–7, 4–8, 5–8, 6–8, 7–8

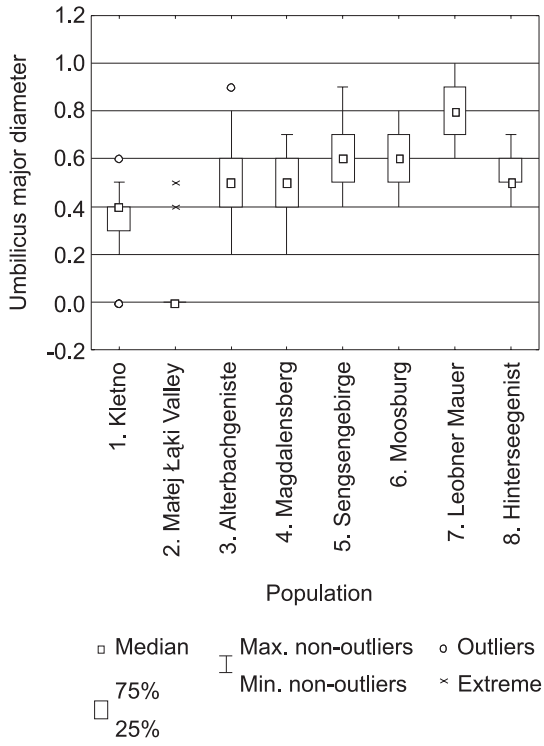



Fig. 207. Interpopulation variation of *T. unidentatus*: umbilicus major diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–3, 1–4, 1–5, 1–6, 1–7, 3–7

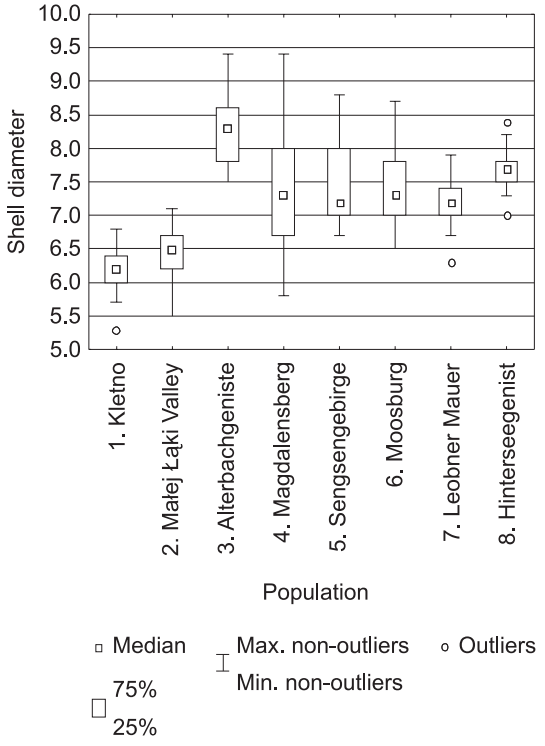



Fig. 206. Interpopulation variation of *T. unidentatus*: shell diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–2, 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–4, 3–5, 3–6, 3–7, 2–8, 7–8

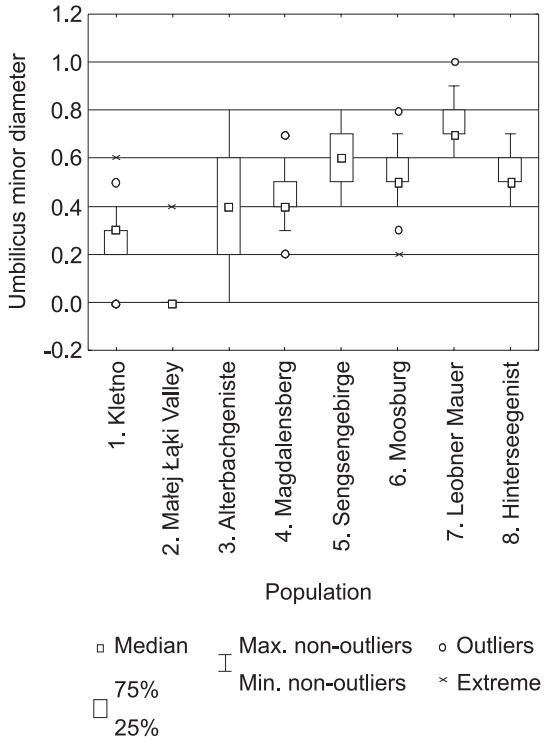



Fig. 208. Interpopulation variation of *T. unidentatus*: umbilicus minor diameter. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–7, 3–4, 3–5, 3–7, 4–5, 4–6, 4–7, 4–8, 5–7, 6–7, 7–8

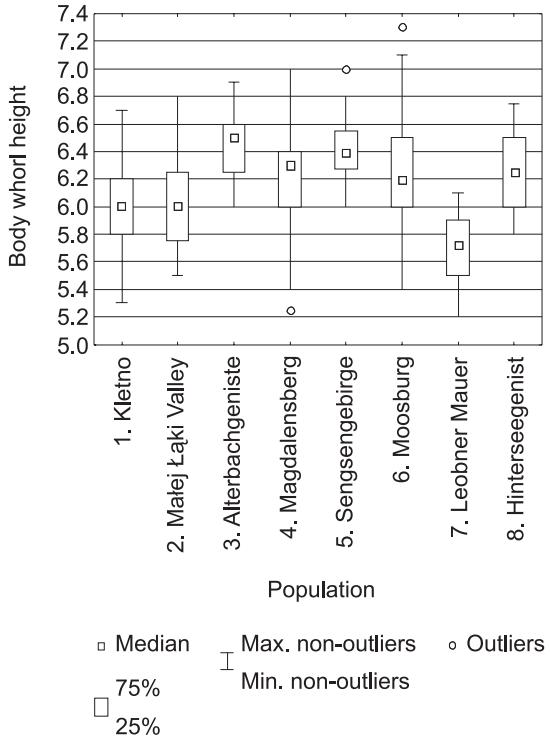



Fig. 209. Interpopulation variation of *T. unidentatus*: number of whorls. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–3, 1–4, 1–5, 1–6, 1–7, 1–8, 2–3, 2–4, 2–5, 2–6, 2–7, 2–8, 3–6, 3–7, 4–7, 5–7, 6–7, 7–8

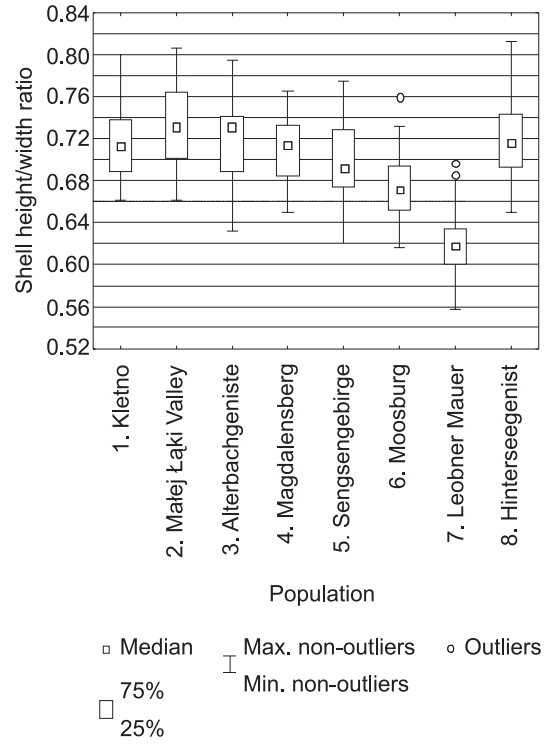



Fig. 210. Interpopulation variation of *T. unidentatus*: shell height/width ratio. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 1–6, 1–7, 2–5, 2–6, 2–7, 3–6, 3–7, 4–6, 4–7, 5–6, 5–7, 6–7, 6–8, 7–8

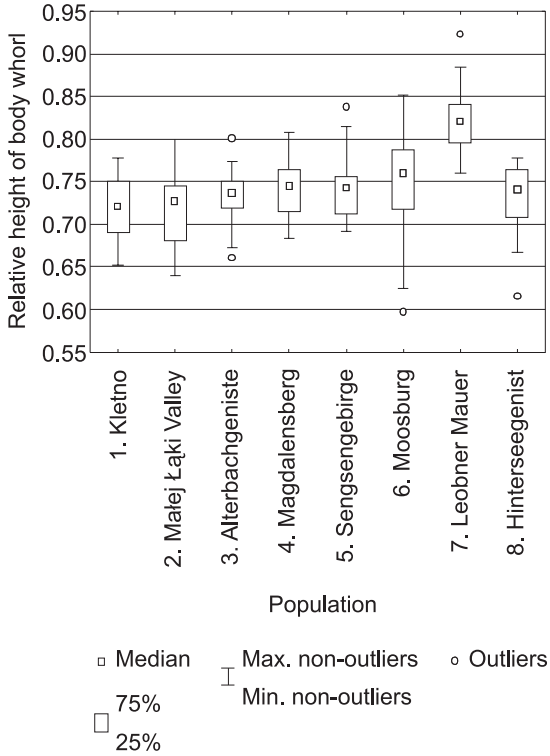


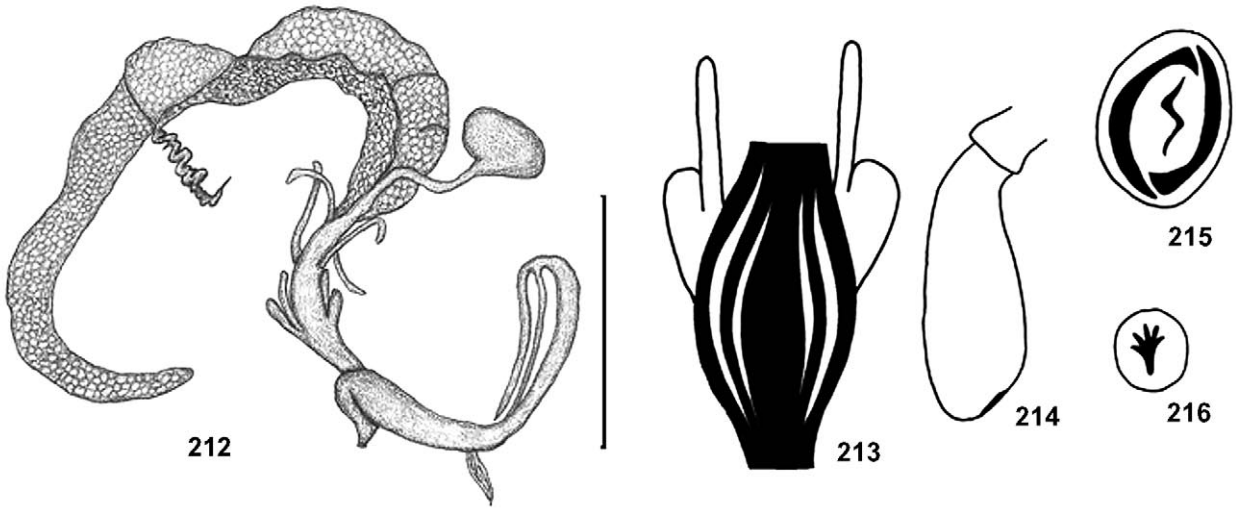

Fig. 211. Interpopulation variation of *T. unidentatus*: relative height of body whorl. Statistically significant differences (Duncan test, $p < 0.05$) between the following populations: 7–1, 7–2, 7–3, 7–4, 7–5, 7–6, 8–7

## Distribution (Fig. 217)

An East-Alpine and Carpathian species; known from eastern and north-eastern Switzerland (two distribution centres: 1. Samnaun, Engadin and Val Müstair; 2. Alpenrheintal and Nordbünden; to Walensee, near Zürich, Thurtal, near Bodensee, the High Rhine), Germany (Alpine regions, single localities in the north to the Main River, Erzgebirge), Austria (widespread), the Czech Republic and Slovakia (Danube valley, Carpathians, "Böhmische Masse") (POLIŃSKI 1928, KERNEY et al. 1983, TURNER et al. 1998), also from Poland (Carpathians except Bieszczady Mts, Cracow-Wieluń Jura, Sudetes: in the north to Srebrna Góra) (RIEDEL 1988) and from northern Hungary. It is also found in northern Italy (MANGANELLI et al. 1995). Although, the species was described from France its distribution there is doubtful (FALKNER 1990).

## Remarks

Six local forms, varieties, races or subspecies were described within *unidentatus*. Their identification is sometimes very difficult. Five of the six were described from Austria but only two of them occupy separate range fragments and their populations are fairly easily distinguished. The populations of the remaining three forms are heterogeneous, which means that the race-specific specimens are found among "typical" shells.




Figs 212–216. *T. unidentatus*. Specimen from Kletno – Sudetes, Poland, ZW. Reproductive system: 212 – general view, 213 – longitudinal section of vagina, 214 – penial papilla, 215 – cross-section of penial papilla, 216 – cross-section of epiphallus. Scale bar 5 mm

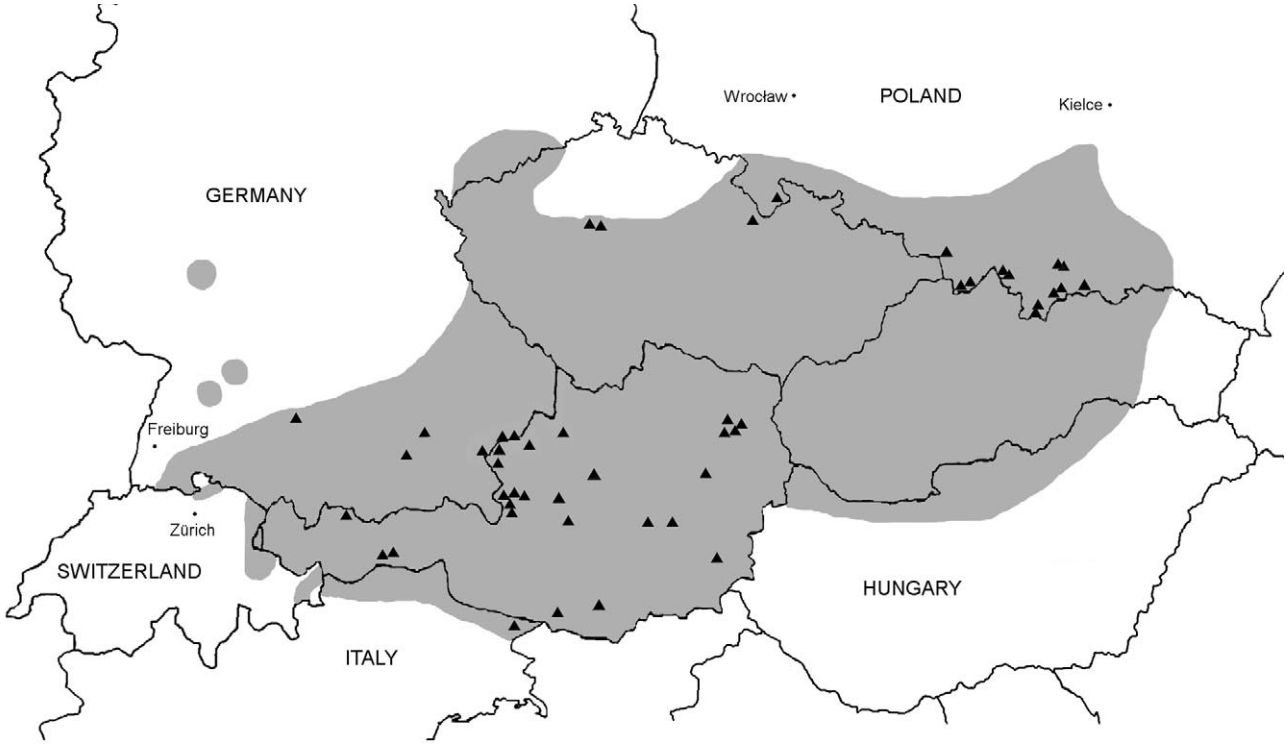



Fig. 217. Distribution of *T. unidentatus*. Black triangles – localities of origin of the examined material

The first group includes *alpestris* – a very small roundish form (shell height 3–4.5 mm, shell width 5–7 mm) from the high Alps (800–2,300 m a.s.l.), with open umbilicus and the tooth more or less reduced, and *subtecta* [2] – also small (shell width 5–6 mm) but with punctured or covered umbilicus, lower spire and convex underside; with fine, very short and regular hairs (POLIŃSKI 1928, KLEMM 1974).

The second group comprises *subalpestris*, described from various localities in the Alps as characterised by a lower spire, narrower, partly covered umbilicus, often less distinct tooth, and dense but easily lost hairs (POLIŃSKI 1928), and *norica* – generally distinguished by its larger size (shell diameter 8–10.2 mm) and the tooth developed to various extent (POLIŃSKI 1928). Shells, of approximately the same

[2] KLEMM (1954) adopted *Trichia* (*Petasina*) *unidentata subtecta* (Poliński) as the valid name of a subspecies (Art. 45.6.4.1 ICZN). FALKNER (1990: 106, 1991) regarded it as a separate species "Rasse des Ostalpenrandes" (from "südlicher Wienerwald bis ins Grazer Bergland"). It prefers drier and warmer places than *unidentata* s. str.

size as *norica* but with no tooth were named *Fruticicola unidentata* f. *anodonta*, and often misidentified with *edentulus* or *leucozonus* (KLEMM 1974).

Finally, the shells of "natio" *carpatica* are more conical, spire dome-shaped, with the umbilicus almost covered, the tooth variously developed, and hairs more durable, very dense and short. The form is not easily distinguishable from *unidentatus* s. str. (POLIŃSKI 1928).

In order to solve the taxonomic status of these taxa further investigations are required, including detailed conchological and anatomical analyses, and their distribution ranges.

In this study the specimens from Leobner Mauer were determined as *Trochulus unidentatus subalpestris* (Poliński, 1928), and from Hinterseegenist as *Trochulus unidentatus norica* (Poliński, 1928). However, the shell variation ranges of these populations overlap with that of *T. unidentatus* s. str. from the remainig localities (figs 201–211). Besides, the differences between those populations and the remaining ones, and among the populations of *T. unidentatus* s. str. are equally statistically significant. Likewise, it was impossible to indicate any characters which would allow to distinguish the subspecies unequivocally. Consequently, it is assumed here that both names are synonyms of *Trochulus unidentatus* (Draparnaud, 1805).

### *Trochulus villosulus* (Rossmässler, 1838)

*Helix villosula* ROSSMÄSSLER 1838: 1. Terra typica: Hungary.

*Helix Pietruskyana* L. PFEIFFER, 1853: 124, no 615. Terra typica: Ukraine: Podolia. [In Schnirkelschnecken, Dritter Theil: 418, pl. 148, figs 11, 12. Terra typica: Ukraine: Podolia. No title page with reference on publication year, but according to WELTER-SCHULTES (1999) it is 1854.]

*Fruticicola (Trichia) pietruskiana* f. *elatior* POLIŃSKI 1914: 28. Locus typicus: Poland: vicinity of Ojców.

#### Material examined

Poland: Cracow-Wieluń Jura: Ojców National Park, near church, 16.08.1970, leg. A. Wiktor, Nr 1722, MPW, 5 alc.; Ojców National Park, Prądnik Valley, 23.08.1973, leg. A. Wiktor, Nr 1846, MPW, 19 alc.; Pieniny Mts.: Mt. Sokolica, 14.08.1961, leg. A. Wiktor, Nr 821, MPW, 4 alc.; Czorsztyn, 31.08.1963, leg. A. Wiktor, Nr 1069, MPW, 1 alc.; Śrutówka, 6.08.1961, leg. A. Wiktor, Nr 809, MPW, 1 alc.; Valley of Pieniński Potok, 26.08.1961, leg. A. Wiktor, Nr 829, MPW, 12 alc.; between Rabsztyn and Homole Gorge, 9.07.1962, leg. A. Wiktor, Nr 854, MPW, 4 alc.; Krościenko on Dunajec, 11.08.1961, leg. A. Wiktor, Nr 808, MPW, 5 alc.; Bieszczady Mts: Ustrzyki Górne, 21.08.1996, ZW, 10 s.+25 alc.; Slovakia: Rosenberg [=Ružomberok], Čebra a/d Waag, [=Mt. Čebra on Váh River], coll. O. Retowski, 41/39, MIZW, 11 s.; Vratnathal [=Vratna valley], Comitatus Trencsin [presently in W. Slovakia], dr C. Brancsik, coll. O. Retowski, 41/39, MIZW, 5 s.

#### Shell (Figs 218–220)

Shell roundish-conical, sometimes nearly flattened, with 5–5.75 moderately tightly coiled whorls. Shell height 4.5–6.0 mm, width 7.0–9.0 (10) mm; height/width ratio 0.52–0.68, body whorl height 3.3–4.8 mm, relative height of body whorl 0.73–0.96, aperture height 2.6–3.6 mm, aperture width 3.2–4.7 mm, umbilicus major diameter 0.9–2.0 mm, umbilicus minor diameter 0.9–1.8 mm, umbilicus major diameter/shell diameter ratio 0.13–0.22. Aperture with weakly developed, white lip. Umbilicus entirely open. Hairs long, curved and rather durable. Shell dark brown, with no band on body whorl.

#### Reproductive system (Figs 221–225)

Four pairs of short mucous glands. Dart sacs long and massive. Inner dart sacs always reach beyond outer ones. Vagina long, its dart sac region narrows toward cylindrical lower vagina. Flagellum shorter than epiphallus, which is longer than fusiform penis. Spermatheca duct long and thin. Spermatheca oval, almost reaching albumen gland. Longitudinal section of vagina, penial papilla, cross-section of penial papilla and epiphallus shown in Figs 222–225.

#### Ecology

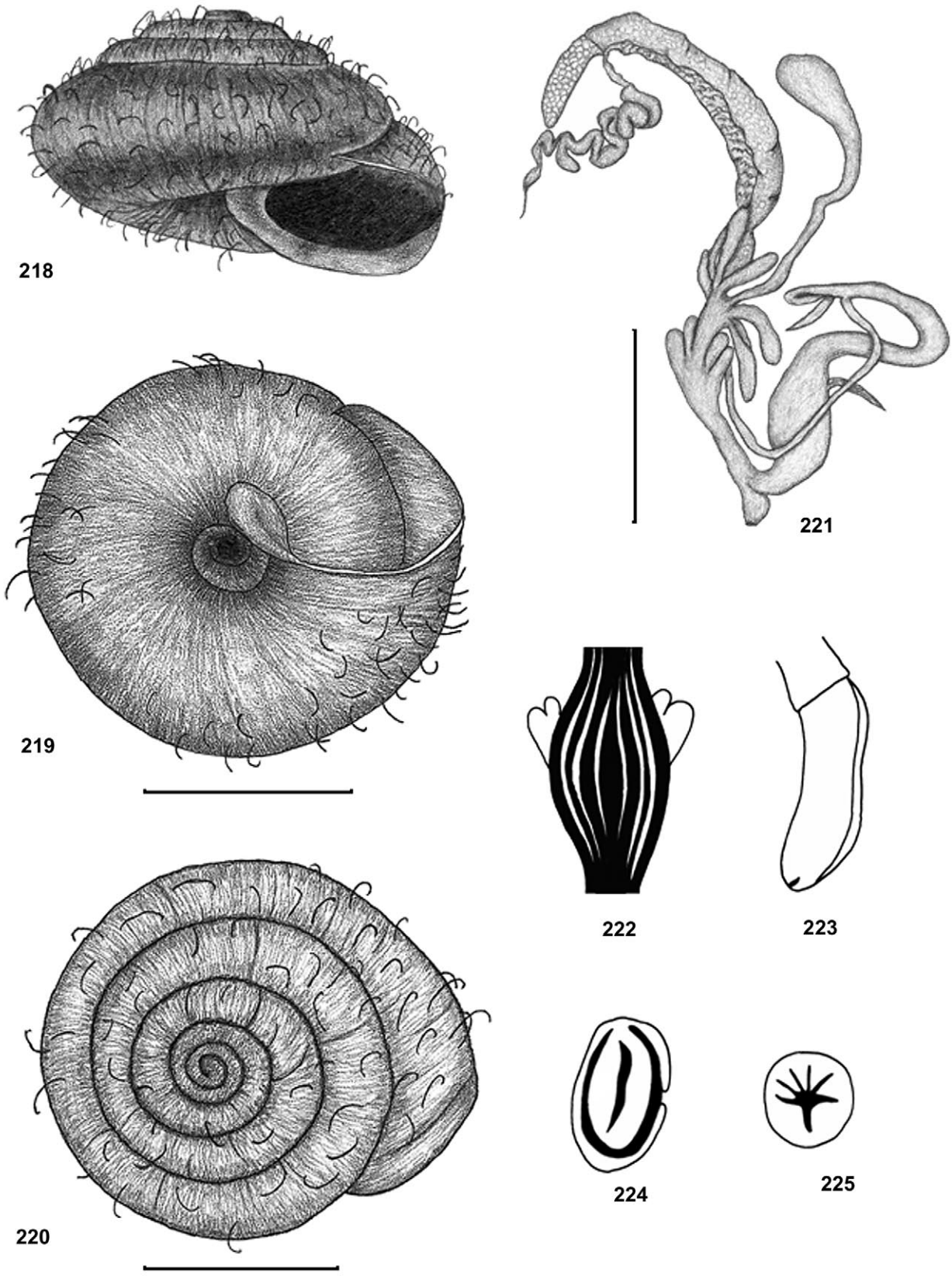
*T. villosulus* lives in mountains up to 1,600 m a.s.l., also in foothills in humid habitats: scrub along streams, wet alder forests, preferably in tussocks of vegetation (*Petasites* sp.) or rarely on the ground, among the vegetation and rotting leaves (RIEDEL 1988).

#### Distribution (Fig. 226)

A West-Carpathian species; found in the Czech Repulic and Slovakia (in the Carpathians to the Moravian Gate) (KERNEY et al. 1983, JUŘIČKOVÁ et al. 2001) and Poland (Carpathians with their foothills: in the north to the Cracow-Wieluń Jura and the Sandomierska Lowland; in the west probaly to Upper Silesia and along the Skawa River) (RIEDEL 1988). Isolated localities in the Polish Eastern Sudetes have not been confirmed (RIEDEL 1988).

#### Remarks

According to POLIŃSKI (1924) the flagellum is as long as the epiphallus or slightly longer, and shorter than the penis. In all the adult specimens anatomically examined, both the flagellum and the penis were shorter than the epiphallus.




Figs 218–225. *T. villosulus*. Specimen from Ustrzyki Górne, Bieszczady, Poland, ZW. 218–220 – shell: 218 – apertural view, 219 – umbilical view, 220 – apical view; 221–225 – reproductive system: 221 – general wiev, 222 – longitudinal section of vagina, 223 – penial papilla, 224 – cross-section of penial papilla, 225 – cross-section of epiphallus. Scale bar 5 mm

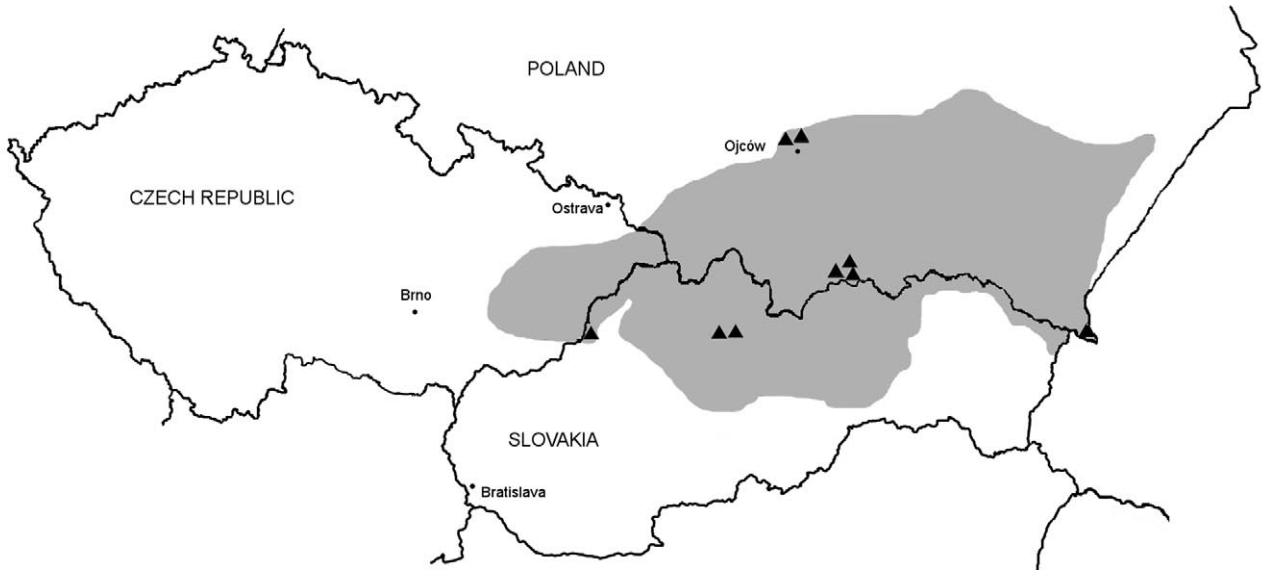



Fig. 226. Distribution of *T. villosulus*. Black triangles – localities of origin of the examined material

### *Trochulus villosus* (Draparnaud, 1805)

*Helix Villosa* Studer in COXE 1789: 385. [nomen nudum]

*Helix villosa* DRAPARNAUD 1805: 104, pl. VII, fig. 18. Locus typicus: France: montagnes de Savoie.

*Helix pilosa* ALTEN 1812: 46, pl. IV: fig. 7. Locus typicus: Germany: Siebenbrunnenfeld [near Augsburg], "an den Lechkanalen" and environs of Stätzling.*

*Helix phorochaetia* BOURGUIGNAT 1864: 52, pl. VI: figs 9–14. Locus typicus: France: dep. Isère: Grande-Chartreuse 3 km NW Saint-Pierre-de-Chartreuse, between Saint-Bruno and Chartreusette. [see WINTER 1990 and FALKNER et al. 2001 – *Trochulus phorochaetius* (Bourguignat, 1864)]

*Fruticicola villosa* var. *alpicola* EDER 1921: 228. Locus typicus: Switzerland: canton Nidwalden: Bannalppass. [see GITTENBERGER & NEUTEBOOM 1991, FALKNER et al. 2001 – *Trochulus alpicola* (Eder, 1921)]

#### Material examined

Austria: Vorarlberg: Bregenz, MIZW; 7 s.; Bregenz, coll. Klemm 69410, NHMW, 6 s.+1 alc.; Bregenzer Wald, 74368, NHMW, 5 alc.; France: Besançon, 07.1924, leg. M. Dyrdowska, coll. Poliński 228/37, MIZW, 3 s.; Germany: Donaugehölze near Ulm, Württemberg, leg. Prinzing, MIZW, 20 s.; Ulm, Württemberg, MIZW, 6 s.; Sigmaringen a/Donau, Württemberg, coll. Geyer 47014, NHMW, 8 s.; Güzburg, Bavaria, coll. O. Retowski 41/39, MIZW, 3 s.; Switzerland: Schindellegi, cant. Schwyz, coll. Edlauer 15611, NHMW, 8 s.; Ragatz [=Bad Ragaz], cant. St. Gallen, MPW, 23 s.

#### Shell (Figs 227–229)

Shell flattened, with low spire and blunt apex, 5.5–6.0 convex whorls with deep suture. Shell height 6.0–8.0 mm (most often 7.0–7.5 mm), shell width 11.0–14.0 mm, height/width ratio 0.5–0.65, body whorl height 5.6–6.8 mm, relative height of body whorl 0.83–0.94, aperture height 3.6–4.8 mm, aperture width 5.0–7.0 mm, umbilicus major diameter 2.1–3.2 mm, umbilicus minor diameter 1.9–2.7 mm, umbilicus major diameter/shell diameter ratio 0.16–0.23. Aperture rounded with weakly developed lip. Umbilicus wide and deep. Hairs long, up to 1.5 mm, and rather sparce. Shell pale yellowish to reddish-brown, body whorl slightly descending, without band.

#### Reproductive system (Fig. 230)

Four pairs of short mucous glands. Tips of inner dart sacs reach beyond outer ones. Lower vagina expanded in dart sac region and narrowing toward long genital atrium. Flagellum slightly shorter than epiphallus, which is shorter than cylindical penis. Spermatheca duct straight. Spermatheca small, oval, reaching ca. 1/2 spermoviduct length.

#### Ecology

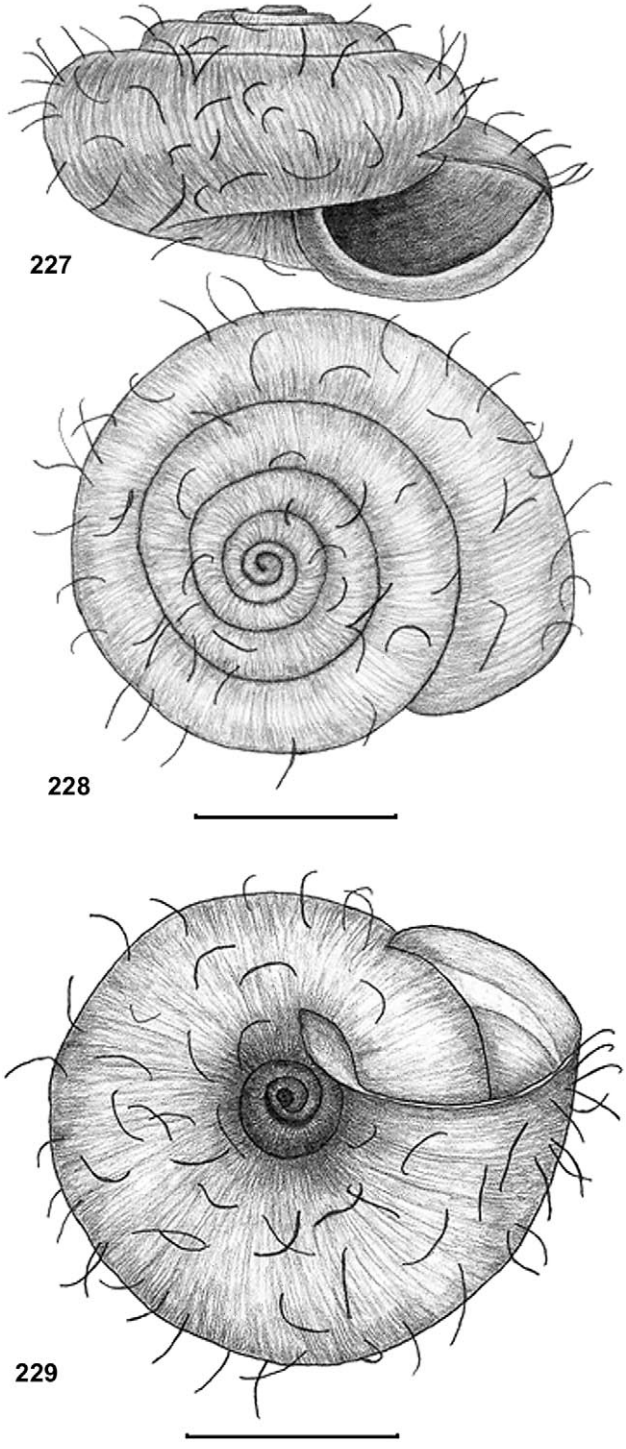
*T. villosus* lives in shaded and humid montane habitats, usually in forests, also alpine pastures; its occurrence depends on high air humidity (in the Alps usually found between 500 and 2,000 m a.s.l.).

#### Distribution (Fig. 231)

A North-West-Alpine species; known from eastern France (Vosges Mts, Jura, Alps), Switzerland (Jura, northern Alps, Mittelland) and southern Germany (from the upper Rhine River valley to south-eastern Bavaria; an isolated locality in Zippendorf near Schwerin (Mecklenburg)) (KERNEY et al. 1983, KRAUSP 1952); found also in western Austria (Vorarlberg and northern Tirol) (KERNEY et al. 1983).

Remarks

The taxonomic status of *alpicola* Eder, 1921 has remained controversial. Some authors (GITTENBERGER & NEUTEBOOM 1991, FALKNER et al. 2001) regard it as a distinct species, whereas others (TURNER et al. 1998) consider it to be a small alpine form of *T. villosus*. Its reproductive system does not differ from that of typical *T. villosus*, which was already shown by EDER (1921) in his original work. Moreover, PFENNINGER et al. (2005) found a comparatively small genetic distance between




Figs 227–229. *T. villosus*. Specimen from Ragatz, Switzerland, MPW. Shell: 227 – apertural view, 228 – apical view, 229 – umbilical view. Scale bar 5 mm

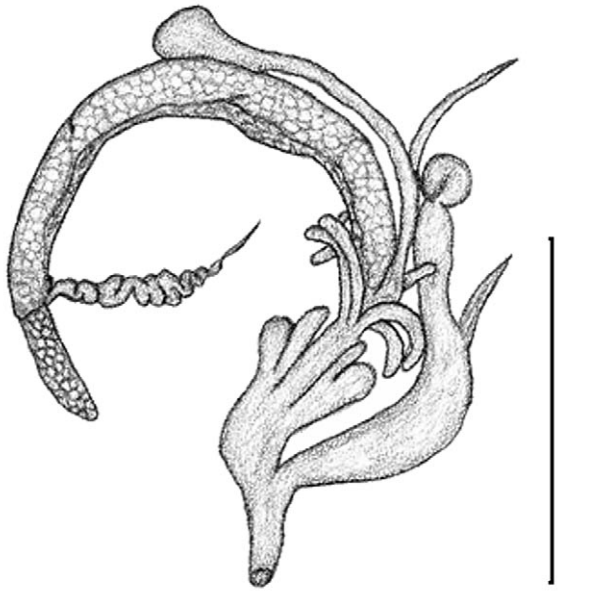


Fig. 230. *T. villosus*. Specimen from Bregenz, Vorarlberg, Austria, coll. Klemm 69410, NHMW. Reproductive system. Scale bar 5 mm

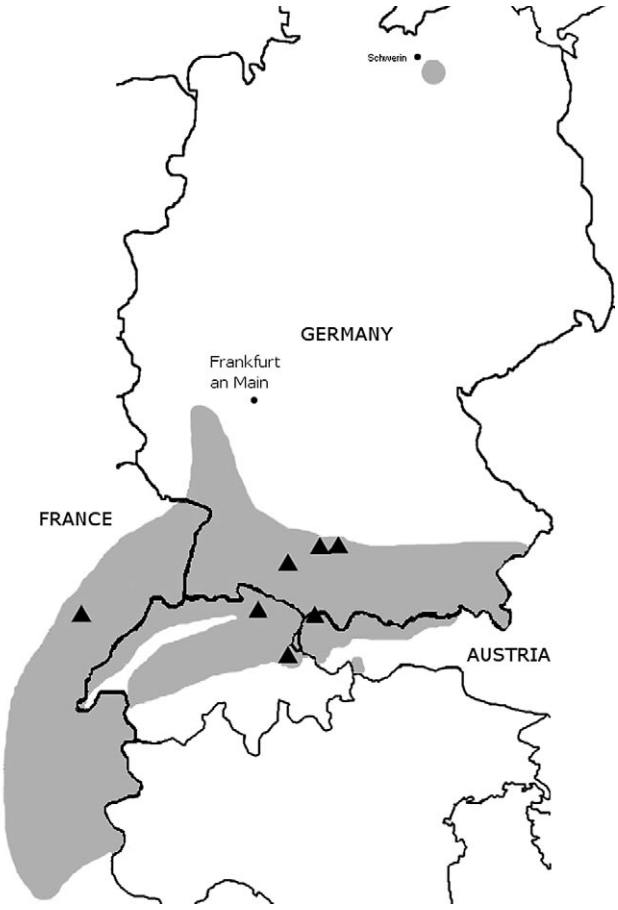



Fig. 231. Distribution of *T. villosus*. Black triangles – localities of origin of the examined material

*T. villosus* and *T. alpicolus*, indicating a questionable specific distinction between these two taxa.

Another taxon requiring taxonomic clarification is *phorochaetia* Bourguignat, 1864, which was regarded as a distinct species by WINTER (1990) and FALKNER et al. (2001). According to WINTER (1990) its shell closely resembles either *T. sericeus* (Draparnaud, 1801) or *T. plebeius* (Draparnaud, 1805), whereas its genitalia are similar to the figure and measurements of *T. 'sericea'* given by KLOETI-HAUSER (1920).

Nomen dubium

***Trochulus waldemari*** (Wagner, 1912)

*Fruticicola waldemari* WAGNER 1912: 250. Locus typcus: Bosnia and Herzegovina: near Sarajevo, Jajce and Bočac near Banja Luka.

No specimens were available; no original material was found in the collections of the two institutions that keep Wagner's material: Naturhistorisches Museum Wien or Museum and Institute of Zoology, Polish Academy of Science in Warsaw. According to WAGNER's (1912) description and later paper of MAASSEN (1985), it is impossible to establish which species they are related to. The taxonomic status of *T. waldemari* requires further studies.

## PHYLOGENETIC ANALYSIS

### CHARACTER ANALYSIS

Since it is difficult to specify the sister group of *Trochulus*, the following genera of the Trichiinae sensu Shileyko 1978b, were adopted as out-groups: *Nanaja* Shileyko, 1978, *Odontotrema* Lindholm, 1927, *Leucozonella* Lindholm, 1927, *Hygrohelicopsis* Shileyko, 1977, *Teberdinia* Shileyko, 1977, *Kokotschashvilia* Hudec et Lezhava, 1969, *Caucasigena* Lindholm, 1927 and *Anoplitella* Lindholm, 1929. The Helicoidea seem to have undergone much parallel evolution, both in their shell characters and anatomy. Within numerous genera, otherwise well-defined by their synapomorphies, the same or similar structures have been acquired or reduced, so that intermediate stages of the evolution are similar as well (for references and character review see: SHILEYKO 1978a, b). Consequently, only some of the analysed characters could be polarised unequivocally.

The following shell and reproductive system characters were used in the phylogenetic analysis (numbers correspond with the numbers in the character matrix – Table 1).

1. Shell colour: body whorl banded (0) or monochrome (1). In the outgroups and other members of the Hygromiidae banded shells are common. Thus, this state, even when expressed only in some individuals of the species, was regarded as plesiomorphic.
2. Lip: distinct, well developed (0) or weakly developed (1). In the outgroups the lip is mostly well developed, often stronger on the basal aperture margin, and sometimes provided with callus.
3. Hairs: absent in adults (0) or present in adults (1). In outgroups short hairs, easily lost in adults are common. Only exceptionally, in phylogenetically remote genera, such as *Helicodonta* Férussac, 1821, *Causa* Shileyko, 1971 and *Isognomostoma* Fitzinger, 1833, hairs are preserved in adults.
4. Length of hairs: short or absent (0); long (1) or very long (up to 1.5 mm) (2). Hairs in the outgroups are short. The character was treated as ordered and additively coded.
5. Umbilicus: wide open (0); or partly or entirely covered, punctured (1). In the outgroups the umbilicus is wide or narrow, but at least a part of the previous whorl is always visible; the umbilicus is never punctured.
6. Penis shape: fusiform (00); cylindrical (10) or conical (01). The penis in the outgroups is fusiform.
7. Penis/epiphallus length ratio: penis as long as or slightly shorter than epiphallus (0) or penis longer than epiphallus (1). In the outgroups the penis is as long as epiphallus or slightly shorter.
8. Flagellum/epiphallus length ratio: flagellum shorter than epiphallus (00); flagellum slightly longer than or as long as epiphallus (10) or flagellum 1.5–2× longer than epihallus (01). In the outgroups the flagellum is shorter than epiphallus.
9. Penial papilla lumen (cross-section): simple (0); complicated as a result of division in 2–3 parts (1) or very complicated, divided in more than 3 parts (2). All three character states are present in the outgroups. Initially two alternative polarizations were applied, one of which was chosen because it yielded a more parsimonious cladogram. The character was regarded as ordered character and coded additively.
10. Epiphallus lumen: low folds (00); few folds of medium height + two high folds (10) or high folds (01). In the outgroups the situation with some low and two higer folds is common.

11. Number and position of mucous glands: eight glands grouped in pairs (1); four glands not grouped in pairs (0) or six glands not grouped in pairs (0). In the outgroups the mucous glands are clearly grouped (two groups of 2–3) and tend to branch secondarily to various extent. This state may have given origin to the other two states through division or reduction of some components; 4 or 6 mucous glands are autapomorphies in *biconicus* and *suberectus*, respectively, and they were excluded from the phylogenetic analysis.
12. Length of mucous glands: short (0) or long (1). The mucous glands in the outgroups are long.
13. Dart sacs: inner and outer dart sacs of approximately equal length (00); inner dart sacs slightly longer than outer ones (10); inner dart sacs much longer than outer ones (01); dart sacs fused (02). In the outgroups the inner dart sacs are longer than the outer ones. The character was treated as partly ordered.
14. Section from outlet of mucous glands to tips of inner dart sacs: short or absent (0) or long (1). In the outgroups this section is short or absent.
15. Shape of vagina: cylindrical (0) or narrowing toward genital atrium (1). In the outgroups the vagina is cylindrical or slightly narrowing towards the genital atrium.
16. Internal structure of vagina: two plicae inside (01); three plicae inside (10) or four plicae inside, arranged in pairs (00). In the outgroups in which plicae are present, they are arranged in pairs i.e. the outlet of the dart sacs, on both sides, is flanked by plicae.
17. Shape of spermatheca: oval (0); roundish (10) or different shape (01). In the outgroups the spermatheca is oval.
18. Length of spermatheca duct: short (0) or long (1). In the outgroups the spermatheca duct is short.

## RELATIONSHIPS AND CLASSIFICATION

PAUP programme (version 4.0b10 for Windows) yielded 96 equally parsimonious trees; the strict consensus procedure resulted in the cladogram (Fig. 232) 81 steps long, CI = 0.33, RI = 0.49, RC = 0.16. The cladogram shows numerous polytomies. Both this and the relatively low values of the CI, RI and RC indices result from the characters being distributed in such a way that only few of them characterise consistent species groups, and from many instances when character states for the species were unknown (cf. Table 1). Confirming or rejecting the phylogeny tentatively proposed here would require complete knowledge of character states for all taxa and support from molecular studies. Nevertheless the cladogram makes it possible to question some classifications proposed in the past.

None of the previous authors included in their classifications all or even most of the species then known. The subgenera in which WAGNER (1915) placed members of *Trochulus* in its present sense were: *Fruticicola* s. str. and *Perforatella* Schlüter, 1838, including *erjaveci*, *villosa*, *villosula*, *hispida*, *caelata*, *lubomirskii*, and *unidentata*, *edentula*, *leucozona*, *lurida* and *bielzi*, respectively. In the cladogram species of none of these groups form monophyletic units; they do not seem to be closer related within the group than with the species from outside the group. Some members of WAGNER's *Fruticicola* s. str. are close to the common ancestor, some are interspersed with species included in his *Perforatella*. POLIŃSKI's (1928) sections, corresponding to subgenera, comprised the following species: *Petasina* Beck, 1847: *unidentata*, *Filicinella* Poliński, 1928: *filicina*, *leucozona* and *bielzi*, *Edentiella* Poliński, 1928: *edentula* and *bakowskii*. In the cladogram in Fig. 232 *unidentata*, representing the monotypic *Petasina*, is the sister group to *bielzi* which was included in *Filicinella*, the other two members of which form the sister group to *lurida* (not considered by POLIŃSKI 1928) and then to *edentula* and *bakowskii*. Only the last two species, which POLIŃSKI classified within *Edentiella*, are closely related in the cladogram (sister species). From phylogenetic point of view the section *Filicinella* would not be monophyletic. According to SHILEYKO (1978a, b) members of *Trochulus* and *Petasina* should be placed in the following genera: *Plicuteria* Shileyko, 1978 (*lubomirskii*), *Trichia* Hartmann, 1840, with subgenera *Petasina* Beck, 1847 (*unidentata*) and *Trichia* s. str. (*hispida*, *villosula*, *striolata*), and *Edentiella* Poliński, 1924 (*bakowskii*). These genera and subgenera were defined on the basis of certain conchological and genital characters, but their significance was not specified. The species of the only non-monotypic taxon given by the author do not form a monophyletic group in the cladogram. Special attention should be paid to the monotypic genus *Plicuteria*. In the original version of his classification (SHILEYKO 1978a) the author defined it as having "vaginal plicae divided into rows of folds, flagellum considerably shorter than epiphallus, spermatheca duct very short and spermatheca very massive". In the English edition of the treatise (SHILEYKO 1978b) he pointed out that "regular transverse prismatic folds that form a dense pattern on the internal wall of the vagina" were unique to the genus *Plicuteria*, and not found in any other species (cf. SHILEYKO 1978a: 204, fig. 215, 1978b: 31, fig. 107). Examining nine specimens of *T. lubomirskii,* in none of them did I find such a pattern of folds on the vaginal walls; their structure did not differ from the corresponding structures in other members of *Trochulus* (cf. Fig. 136). Reasons for describing a non-existent character by SHILEYKO (1978b) are uknown; perhaps it was a mistake (misplaced labels, figures, etc.). *T. lubomirskii*, like *T. unidentatus* and *bakowskii*, included by SHILEYKO (1978a, b) in other, monotypic, genera and subgenera do not depart from the remaining members of *Trochulus*.

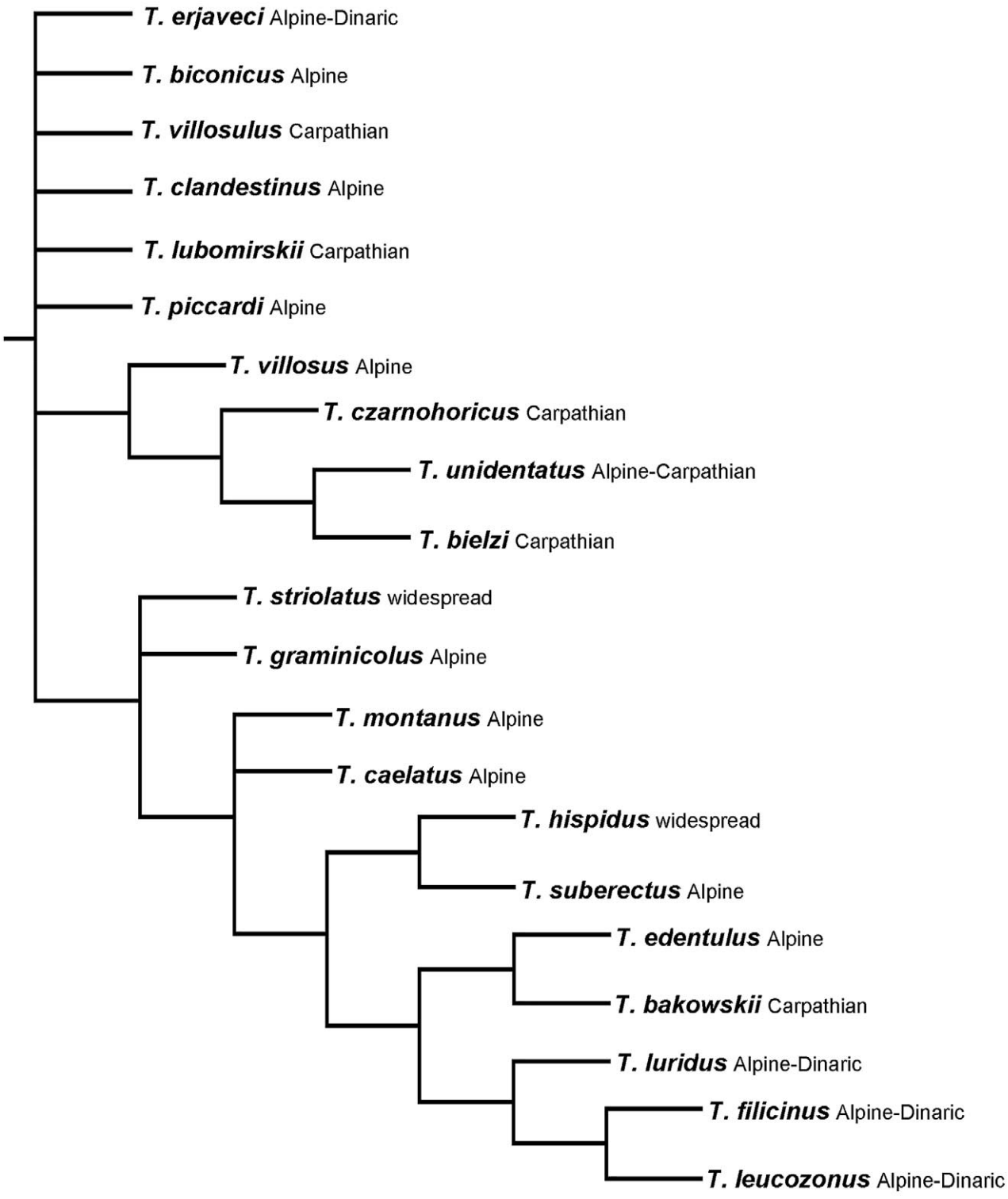



Fig. 232. Cladogram of *Trochulus*

In the cladogram (Fig. 232), despite it being not completely resolved, two distinct monophyletic groups of species can be distinguished, the *villosus* group including *villosus*, *czarnohoricus*, *unidentatus* and *bielzi*, and the *striolatus* group, with *striolatus*, *graminicolus*, *montanus*, *caelatus*, *hispidus*, *suberectus*, *edentulus*, *bakowskii*, *luridus*, *filicinus* and *leucozonus*. These two groups and *erjaveci*, *biconicus*, *villosulus*, *clandestinus*,

Table 1. Genus *Trochulus* – character matrix. Hyphens represent missing data

| Taxon/character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *erjaveci* | 0 | 0 | 0 | 0 | 0 | 00 | 0 | 00 | – | – | – | 0 | 00 | 0 | 0 | – | 00 | 0 |
| *biconicus* | 1 | 0 | 0 | 0 | 0 | 00 | 0 | 10 | 0 | 00 | 0 | 1 | 00 | 0 | 0 | 01 | 00 | 0 |
| *czarnohoricus* | 1 | 1 | 1 | 0 | 1 | – | – | – | – | – | – | – | – | – | – | – | – | – |
| *hispidus* | 0 | 0 | 1 | 0 | 0 | 00 | 0 | 10 | 0 | 01 | 1 | 0 | 10 | 0 | 0 | 01 | 00 | 0 |
| *suberectus* | 0 | 0 | 1 | 0 | 0 | 01 | 1 | 10 | 0 | 01 | 0 | 0 | 10 | 0 | 0 | 01 | 00 | 0 |
| *villosulus* | 1 | 1 | 1 | 1 | 0 | 00 | 0 | 00 | 0 | 01 | 1 | 0 | 00 | 0 | 0 | 00 | 00 | 1 |
| *villosus* | 1 | 1 | 1 | 2 | 0 | 10 | 1 | 00 | – | – | 1 | 0 | 00 | 0 | 1 | – | 00 | 0 |
| *striolatus* | 0 | 0 | 0 | 0 | 0 | 00 | 0 | 10 | 0 | 01 | 1 | 0 | 00 | 0 | 1 | 10 | 10 | 0 |
| *montanus* | 0 | 0 | 0 | 0 | 0 | 00 | 1 | 10 | – | – | 1 | 0 | 00 | 0 | 0 | – | 00 | 0 |
| *caelatus* | 0 | 0 | 0 | 0 | 0 | 00 | 1 | 10 | 0 | 00 | 1 | 0 | 00 | 0 | 0 | 10 | 00 | 0 |
| *clandestinus* | 0 | 1 | 0 | 0 | 0 | 01 | 0 | 00 | 2 | 01 | 1 | 0 | 00 | 0 | 0 | 10 | 00 | 0 |
| *graminicolus* | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 10 | – | – | 1 | 0 | 00 | 1 | 0 | – | 00 | 0 |
| *lubomirskii* | 1 | 1 | 0 | 0 | 0 | 00 | 0 | 00 | 0 | 10 | 1 | 0 | 00 | 0 | 0 | 10 | 01 | 0 |
| *unidentatus* | 0 | 0 | 1 | 0 | 1 | 10 | 0 | 00 | 0 | 10 | 1 | 0 | 01 | 0 | 0 | 01 | 01 | 0 |
| *edentulus* | 0 | 0 | 1 | 0 | 1 | 00 | 0 | 00 | 2 | 10 | 1 | 1 | 10 | 0 | 0 | 10 | 00 | 1 |
| *filicinus* | 0 | 0 | 1 | 0 | 1 | 10 | 1 | 01 | 1 | 01 | 1 | 1 | 00 | 1 | 1 | 10 | 00 | 0 |
| *leucozonus* | 0 | 0 | 0 | 0 | 1 | 10 | 1 | 01 | 1 | 01 | 1 | 1 | 00 | 1 | 1 | 01 | 00 | 0 |
| *luridus* | 0 | 0 | 1 | 0 | 1 | 00 | 1 | 10 | 1 | 01 | 1 | 1 | 10 | 1 | 1 | 10 | 00 | 0 |
| *bakowskii* | 0 | 0 | 1 | 0 | 1 | 01 | 1 | 01 | 1 | 10 | 1 | 1 | 10 | 0 | 0 | 10 | 00 | 1 |
| *bielzi* | 0 | 0 | 1 | 0 | 1 | 10 | 0 | 01 | 2 | 10 | 1 | 0 | 00 | 0 | 1 | 01 | 00 | 0 |
| *piccardi* | 1 | 0 | 0 | 0 | 0 | 00 | 0 | 00 | – | – | 0 | 0 | 02 | 0 | 0 | – | 00 | 0 |

*lubomirskii* and *piccardi*, form a phylogenetic bush. The monophyletic groups appearing in the cladogram (Fig. 232) are not compatible with any of the proposed divisions. At present it is impossible to attempt any subgeneric classification; any such attempt would result in two (supposedly) monophyletic groups, viz. *villosus* group and *striolatus* group being distinguished as subgenera, plus either a paraphyletic subgenus including all the remaining species, or six monotypic subgenera. Since anyway the genus includes only about 20 species of rather small diversity of characters, distinguishing any subgenera does not seem justified.

## DISTRIBUTION AND EVOLUTION

Discounting the North African species of very doubtful relationship with the genus (see Introduction), most members of *Trochulus* inhabit the Alps and the Carpathians (Fig. 12). The only widely distributed species is *T. hispidus*, widespread in Western, Central and Eastern Europe, and partly Northern Europe. *T. striolatus* is the second most widespread species. It inhabits the British Isles, northern France, Switzerland and Austria, the Netherlands, southern Germany and south-western Slovakia. The remaining species are endemics with limited ranges and can be divided into four grous: 1. Alpine group, with distribution restricted to the Alps or their parts – 9 species (*T. suberecus, T. villosus, T. biconicus, T. caelatus, T. edentulus, T. clandestinus, T. graminicolus, T. montanus, T. piccardi*), 2. Carpathian group, distributed in the Carpathians or their parts – 5 species *(T. villosulus, T. bakowskii, T. bielzi, T. lubomirskii, T. czarnohoricus*), 3. Alpine-Carpathian group – 1 species (*T. unidentatus*) and 4. East-Alpine-Dinaric group, comprising species widespread in the Eastern Alps and/or in the Dinaric Alps – 4 species *(T. erjaveci, T. filicinus, T. leucozonus, T. luridus*). Like the previously proposed classifications within the genus, the distributional groups do not match the phylogenetic lineages in the cladogram (cf. Fig. 232).

The number of species within particular parts of the range points to the Alpine-Carpathian area as the diversity centre of the genus. Superimposing the distribution ranges on the cladogram (Fig. 232) reveals that often distribution changes must have been accompanied by speciation events, since the members of the two main monophyletic groups are encountered in a few (2–3) distribution areas. In this context the position of sister-species pairs is noteworthy. In the cladogram (Fig. 232) there are four such pairs: *unidentatus/bielzi*, *hispidus/suberectus*, *edentulus/bakowskii*, and *filicinus/leucozonus*. Only one of such pairs (*edentulus/bakowskii*) is vicariating.

From the point of view evolution and distributional changes, phylogenetic position of the two most widespread species *hispidus* and *striolatus* is relevant. The plesiomorphic nature of their characters could point to their previously wider distribution, with later reduction of the distribution ranges and the origin of endemic species, whereas their position in the terminal parts of the cladogram could suggest the evolution within a limited area, with later spreading of few species. Meanwhile in the cladogram (Fig. 232) the two species belong to the *striolatus* group, of which *striolatus* (with *graminicolus*) is the most plesiomorphic member, whereas *hispidus* is a member of a more derived cluster in the same group. Their position and the fact that the evolution of the genus most likely started in the Alpine area, suggests an independent expansion of their ranges.

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