



SHELL, GENITAL AND COLOUR VARIATION IN *PERFORATELLA INCARNATA* (O. F. MÜLLER, 1774) AND *P. VICINA* (ROSSMÄSSLER, 1842) (GASTROPODA: PULMONATA: HELICIDAE)

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ABSTRACT: *Perforatella incarnata* (O. F. Müll.) and *P. vicina* (Rossm.) are sometimes difficult to distinguish. Variation analysis of the two species, based on over 300 specimens from Poland (the Carpathians, Sudetes, Lower Silesia), was aimed at testing the diagnostic use of shell, genital and body colour characters. Most characters varied within and between populations, and the variation ranges of some characters of the two species overlapped. Syntopic *P. incarnata* and *P. vicina* showed a divergent character displacement. The characters of high diagnostic value are: shell colour and surface sculpture, and mantle colour pattern. The mantle colour pattern can be useful when identifying live specimens, and the surface sculpture can be crucial when examining fossil material.

KEY WORDS: terrestrial snails, Helicidae, variation, identification, *Perforatella incarnata*, *Perforatella vicina*

INTRODUCTION

The genus *Perforatella* Schlüter, 1838 includes nine species, all inhabiting Europe (SHILEYKO 1978); six of them are found in Poland. Two species, classified within the subgenus *Monachoides* Gude et Woodward, 1921: *Perforatella (Monachoides) incarnata* (O. F. Müller, 1774) and *P. (M.) vicina* (RossmäSSLer, 1842), are sometimes difficult to distinguish.

P. incarnata is widespread in central and southeastern Europe, in the west the species reaches central France, in the north – Denmark and southern Sweden, in the east it occurs locally near the Dnieper River. In the south it has been recorded from the Balkan Peninsula (URBAŃSKI 1957, SHILEYKO 1978, RIEDEL 1988, WIKTOR 2004). *P. incarnata* is widely distributed in the whole of Poland, however it becomes less common north- and eastwards. In the Tatra Mts the species has been found only in valleys up to 1,000 m a.s.l. (RIEDEL 1988, WIKTOR 2004).

P. vicina is a rather widely distributed Carpathian species; outside the Carpathians it is found in the uplands of southern Poland and Podole, reaching also

the Sudetes. It has isolated localities in the Franconian Jura (Germany) and Polish lowlands (URBAŃSKI 1957, SHILEYKO 1978, RIEDEL 1988, WIKTOR 2004). In Poland *P. vicina* inhabits all the Carpathians with the Subcarpathian region and the Sudetes; it reaches Roztocze, the Lublin Upland and the Jura, with scattered localities in Białowieża Primeval Forest, the Świętokrzyskie Mts, the region of Trzebnica and Lower Silesia. As subfossil it has been recorded from Małopolska. In the mountains it reaches up to 1,900 m a.s.l. (RIEDEL 1988, WIKTOR 2004).

The two species occupy similar habitats: forest floor in deciduous and mixed forests and scrub, where they are found in litter; the ecological spectrum of *P. incarnata* is somewhat wider than that of *P. vicina* (SHILEYKO 1978).

Because of their overlapping distribution ranges and similar habitats *P. incarnata* and *P. vicina* often co-occur. Usually they are easy to distinguish, based on characters listed in identification keys (e.g.

URBAŃSKI 1957, SHILEYKO 1978, KERNEY et al. 1983, WIKTOR 2004), however in some cases the discrimination can be difficult. The aims of this study were: 1. ascertaining, on the basis of selected populations from Poland, the variation range of the shell, body colour

and genitalia of *P. incarnata* and *P. vicina*, focusing on possibly diagnostic characters, and 2. finding unequivocal characters of the two species which would make identification possible even in doubtful cases.

MATERIAL AND METHODS

The material included samples from the collection of the Natural History Museum in Wrocław (NHMW) and some samples collected in the field especially for the purpose of this study (now also kept at NHMW). Only adult specimens with distinct lip were examined. A total of 165 individuals of *P. incarnata* (59 alcohol-preserved and 106 dry shells) and 135 *P. vicina* (76 alcohol-preserved and 59 dry shells) were analysed. Because of the small number of specimens from several localities in the Carpathians, the material from the Bieszczady Mts., Beskidy Mts., Gorce Mts. and Pieniny Mts. (samples showing no statistically significant differences) was treated as one population. Material from one locality in Germany was also included in the study. In the list of samples below "a" denotes alcohol-preserved material and "d" – dry shells. All scale bars in the figures are 5 mm.

P. incarnata: Oława, nature reserve Zwierzyniec, leg. G. NOTZ, 26.VI, 16. VIII, 28. VIII, 10. IX, 12. IX 1973: 24 a, 23 d; Muszkowice, nature reserve Muszkowicki Las Bukowy, leg. E. PAWŁOWSKA-BANASIAK, 16. IV, 24. X 1998: 20 a, 20 d; Wojcieszów, Mt. Miłek, leg. E. PAWŁOWSKA-BANASIAK, 12. IV 1999: 11 a, 38 d; Wleń, Mt. Zamkowa, leg. E. PAWŁOWSKA-BANASIAK, 12. IV 1999: 4 a, 7 d; Germany: Moosburg on Isar River, leg. M. MAJKOWSKA-PROĆKÓW, 30. VI 1998: 18 d.

P. vicina: Muszkowice, nature reserve Muszkowicki Las Bukowy, leg. E. PAWŁOWSKA-BANASIAK, 16. IV, 24. X 1998: 46 a, 14 d; Wojcieszów, Mt. Miłek, leg. E. PAWŁOWSKA-BANASIAK, 12. IV 1999: 15 a, 27 d; The Carpathians. (total: 22 a and 34 d): Bieszczady Mts.: Wołosate, leg. J. PRASZCZYK, 4. VIII 1972: 1 a; Ustrzyki Górne, leg. J. PRASZCZYK, 5. VIII, 9.VIII 1972: 2 a; Terebowiec Valley near Ustrzyki Górne, leg. J. PRASZCZYK, 6.VIII, 9.VIII 1972: 3 a, 1 d; Zatwarnica, leg. B. MAŁKIN & E. WILCZYŃSKI, 16-19. VIII 1974: 1 a, 1 d; Dukla, Mt. Cergowa, leg. A. WIKTOR, 6. IX 1967, 13.VII 1968: 5 d; Bieszczady Mts., no exact locality, leg. J. PRASZCZYK, 11. VIII 1972: 1 a; Beskid Żywiecki: Ciapków Stream Valley near Rycerka, leg. A. WIKTOR, 26. IX 1976: 1 a; Beskid Sądecki: below Przechybka, leg. A. WIKTOR, 23. VII 1962: 1 d; below Dzwonkówka, leg. A. WIKTOR, 31. VI 1962: 1 d;

Krynica, Czarny Potok Valley, leg. A. WIKTOR, 6. VIII 1973: 1 a; Krynica Zdrój, Krynica Valley, leg. A. WIKTOR, 7. VIII 1973: 1 d; Barnowiec in Jaworzyna range near Krynica, leg. A. WIKTOR, 15. VIII 1973: 1 d; Rytro near Nowy Sącz, leg. A. WIKTOR, 30.VII 1972: 1 d; Mt. Lubomir near Mszana Dolna, leg. A. WIKTOR 11. VIII 1975: 1 d; Gorce: slope of Lubań, leg. A. WIKTOR, 27. VII 1962: 1 d; Valley of Kamienna River near Rzeki, leg. A. WIKTOR, 14. VIII 1975: 1 a; Pieniny Mts: Śrutówka, leg. A. WIKTOR, 6. VIII 1961: 1 a; Kurnikowa Skała, leg. A. WIKTOR, 11. VIII 1961: 1 d; slope of Sokolica, leg. A. WIKTOR, 14. VIII 1961: 1 a; Valley of Pieniński Potok, leg. A. WIKTOR, 26. VIII 1961: 2 a; Rabsztyn, leg. A. WIKTOR, 9. VII 1962: 1 d; Ligarka Glade, leg. A. WIKTOR, 2. VIII 1962: 2 d.

The following shell parameters were measured (stereomicroscope, calibrated eye-piece, to the nearest 0.1 mm): Ws – shell width; Hs – shell height; D – shell diameter; Hbw – body whorl height; Wa – aperture width; Ha – aperture height; Du – umbilicus major diameter; du – umbilicus minor diameter. The following indices of shell shape were calculated: Hs/Ws – shell height/width ratio; Hbw/Hs – relative height of body whorl; Du/D – relative width of umbilicus. Whorls were counted using EHRMANN's (1933) method. Surface sculpture of the shell was examined under stereomicroscope (magnifications 40×, 60×). The data were statistically analysed with Statistica7 for Windows. Statistical significance of the differences between the samples was estimated using Student t-test ($p < 0.05$).

Specimens for anatomical examination were preserved in 70% or 75% ethanol. The following anatomical characters were examined: bend on the penis-epiphallus junction (absent/present); muscle strand fastening the penis-epiphallus bend (absent/present and developed to various extent); length ratio penis : epiphallus : flagellum; number, length and branching of mucus glands; shape of papilla penis lumen in cross-section. Body and mantle colour and pattern were also examined.

RESULTS

SHELL

Perforatella incarnata (O. F. Müller, 1774)

The shell (Figs 1–4) is dextral, most often with 5–6 whorls. Its shape varies from flattened, with only slightly elevated spire, to much elevated, with whorls varying from much flattened to moderately convex, the suture – from shallow to moderately impressed. A small protuberance occurs very seldom on the basal part of the lip. Most specimens have open umbilicus, but sometimes it can be very narrow or even com-

pletely concealed by the lip. Metric characters are shown in Table 1. Surface sculpture consists of elongate, tiny, radial tubercles, very closely spaced, regularly and alternately arranged. The shell colour varies individually and to some extent between populations, from horn- to reddish brown. The body whorl bears a narrow, lighter band of somewhat variable width. Just behind the lip there is a pinkish or pinkish brown radial stripe of variable width. In most specimens it contrasts with the rest of the shell. Only in some shells it is almost the same colour as the rest of the shell or nearly absent. Shells of live individuals appear to be spotted because of the mantle spots shining through. The pink or pinkish-chestnut lip always contrasts with the shell colour.

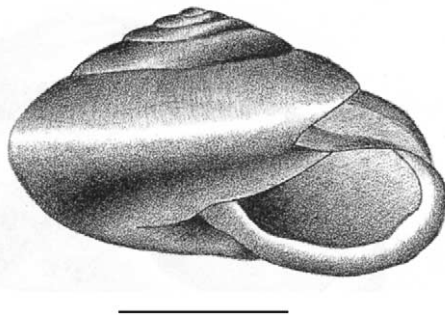


Fig. 1. Shell of *Perforatella incarnata*: a specimen from Muszkowice

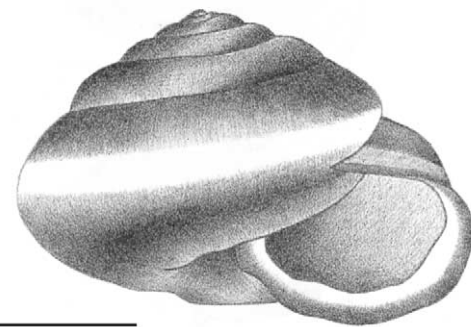


Fig. 2. Shell of *Perforatella incarnata*: a specimen from Muszkowice

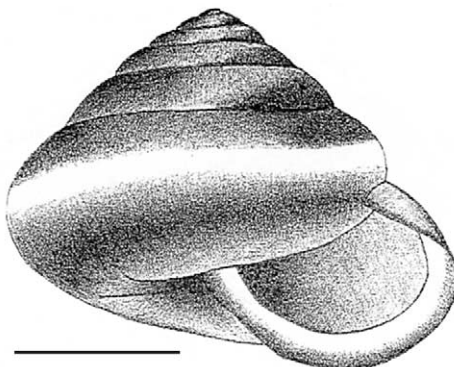


Fig. 3. Shell of *Perforatella incarnata*: a specimen from Oława

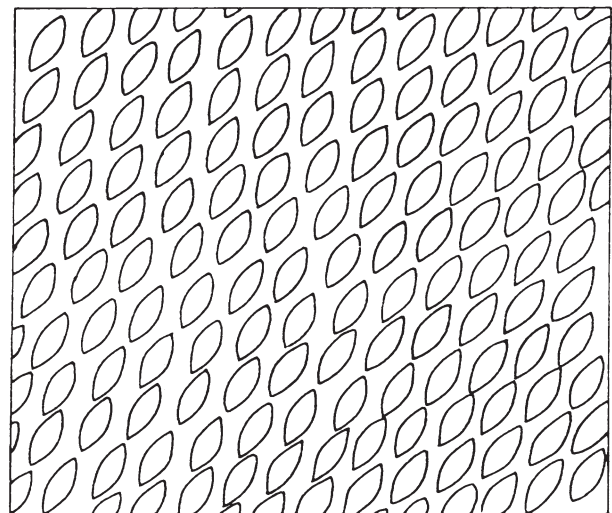


Fig. 4. Shell surface sculpture of *Perforatella incarnata*, diagrammatic

Table 1. Metric shell characters of *Perforatella incarnata*, N=165

Character	Range	Mean	SD
Nw	4.75–7.75	6.03	0.31
Hs	7.00–11.30	8.71	0.70
Ws	10.50–15.60	12.97	0.97
D	10.30–15.00	12.59	0.94
Ha	3.30–6.10	4.53	0.44
Wa	5.90–8.50	7.35	0.57
Hbw	6.00–8.50	7.19	0.48
Du	0.00–1.50	0.67	0.36
du	0.00–1.20	0.59	0.20
Hs/Ws	0.59–1.03	0.67	0.04
Hbw/Hs	0.53–1.00	0.83	0.04
Du/D	0.00–0.11	0.05	0.03

Perforatella vicina (Rossmässler, 1842)

The shell (Figs 5–8) is dextral, most often with 5.5–6.5 whorls. Its shape varies from flattened, but less so than in *P. incarnata*, to much elevated, with whorls varying from much flattened to moderately convex, the suture – from shallow to moderately impressed. A protuberance occurs quite often on the basal part of the lip and it is always situated near its columellar part. Most specimens do not have umbilicus, only some have a very narrow umbilicus almost completely closed by the lip. Metric characters are shown in Table

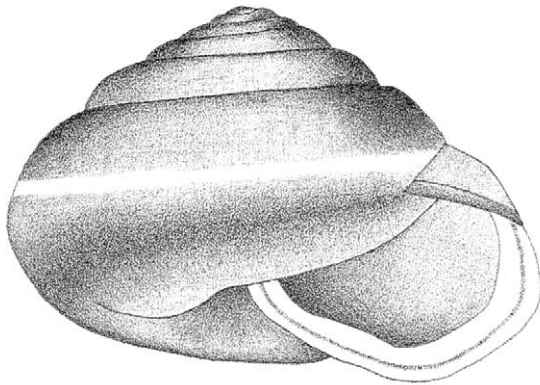


Fig. 5. Shell of *Perforatella vicina*: a specimens from Muszkowice

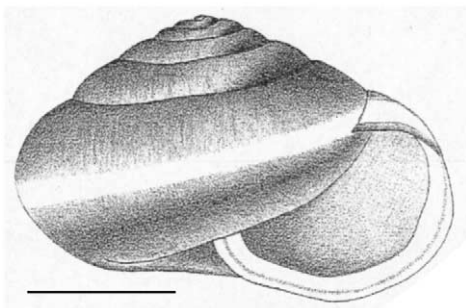


Fig. 6. Shell of *Perforatella vicina*: a specimens from Wojcieszów

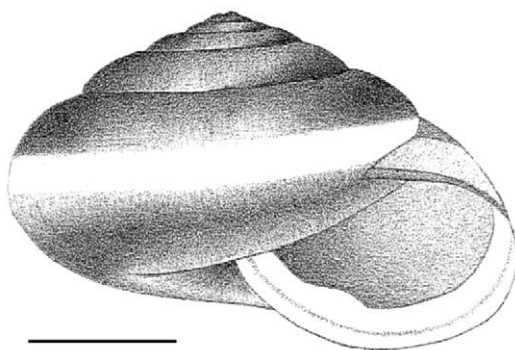


Fig. 7. Shell of *Perforatella vicina*: a specimens from Pieniny Mts., Ligarki Glade

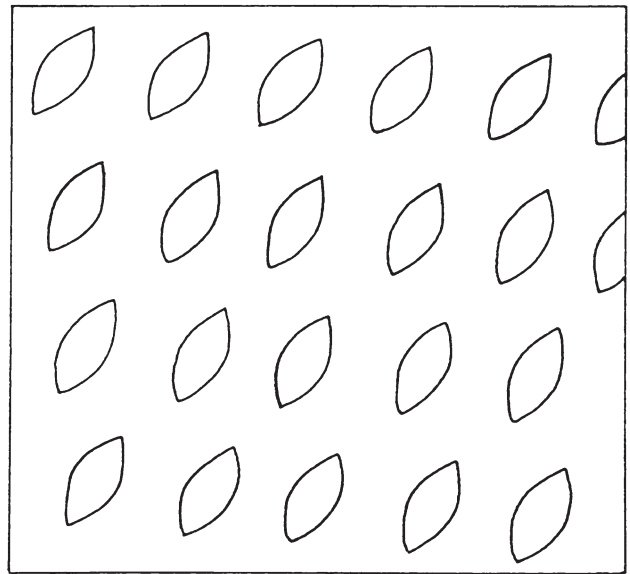


Fig. 8. Shell surface sculpture of *Perforatella vicina*, diagrammatic

Table 2. Metric shell characters of *Perforatella vicina*, N=135

Character	Range	Mean	SD
Nw	5.38–7.00	6.34	0.31
Hs	7.20–10.70	9.31	0.75
Ws	10.90–15.40	13.23	0.90
D	10.50–15.00	12.91	0.93
Ha	3.50–6.00	4.81	0.52
Wa	5.80–8.70	7.36	0.57
Hbw	6.20–8.50	7.37	0.52
Du	0.00–1.00	0.01	0.09
du	0.00–0.50	0.00	0.04
Hs/Ws	0.59–0.81	0.70	0.04
Hbw/Hs	0.73–0.88	0.79	0.03
Du/D	0.00–0.07	0.00	0.01

2. Surface sculpture consists of elongate radial tubercles, larger than in *P. incarnata*, spaced so widely that the distances between them are almost as large as the tubercles themselves, and arranged regularly and alternately. The shell colour shows little variation: from almost white, light yellowish, to very light horn brown. The body whorls bears a narrow, white band of somewhat variable width. There is a white, radial stripe of variable width immediately behind the lip. In most specimens the stripe contrasts with the rest of the shell, but in some it is almost the same colour as the rest of the shell or nearly absent. Shells of live individuals appear to be spotted because of the mantle spots shining through. The white lip is always clearly distinct from the shell colour.

INTERPOPULATION VARIATION OF THE SHELL

The inter-specific differences in metric characters of the shell and the ratios describing its proportions, except for aperture width, are statistically significant ($p < 0.05$), though their variation ranges overlap to a great extent.

There are considerable differences between individual populations within each species. The studied populations of *P. incarnata* differ statistically significantly ($p < 0.05$) in the following characters: Moosburg/Muszkowice: Ws, D, Hbw/Hs; Moosburg/Oława: Hs, Du, Du/D, Hs/Ws; Wojcieszów/Muszkowice: Hs, D, Nw, Du, Du/D; Wojcieszów/Oława: Ws, Wa, D, Hbw, Du, du, Du/D; Wleń/Muszkowice: D; Wleń/Oława: Hs, Ws, Du, Du/D; Muszkowice/Oława: Hs, Ws, Wa, D, Ha, Hbw, Nw, Du, Du/D, Hbw/Hs. Three populations: from Moosburg in Germany, Wojcieszów and Wleń did not show statistically significant differences. The examined populations of *P. vicina* differed statistically significantly ($p < 0.05$) in the following characters: Wojcieszów/Muszkowice: Hs, Ha, Nw, Hs/Ws, Hbw/Hs; Wojcieszów/Carpathians: Ws, Wa, D, Ha, Hbw, Hbw/Hs; Muszkowice/Carpathians: Hs, Ws, Wa, D, Ha, Hbw, Nw.

Sympatric populations of *P. vicina* and *P. incarnata* from Wojcieszów and Muszkowice differed statistically significantly in several characters. The populations of the two species from Wojcieszów differed in their Ha, Nw, Du, du, Du/D, from Muszkowice – in Hs, Nw, Du, du, Du/D, Hs/Ws, Hbw/Hs. The population of *P. vicina* from the Carpathians, from the localities with no *P. incarnata*, differs from *P. vicina* from Oława (where *P. vicina* does not occur) only in Hbw/Hs, Du/D, Du and du, and the variation ranges overlap to a great extent.

BODY COLOUR AND MANTLE PATTERN

Perforatella incarnata

The coloration of the body, including head is dark graphite or slightly lighter, some specimens are grey; the sole is slightly lighter than the rest of the body. The mantle ground colour is yellowish-beige, with graphite, brown-black, brown, or – very rarely – black spots. The size, density and shape of these spots vary: they can be fine, very dark (24% specimens), brown with blurred margins, or large, merging to completely merged (15%), so that the light mantle background forms a reticulate pattern (Figs 9, 10). The variation is individual; specimens with very different colour pattern can be found in the same population. The large, merging spots with irregular shapes are most frequent (61%). The mantle spots always have a very high ratio of perimeter to surface.

Perforatella vicina

The body is light, flesh-coloured or cream-yellow, with darker, brown or rusty stripe on the head and neck between the ommatophores. The whitish mantle bears inky black spots; only very rarely the spots are missing (some specimens from the Carpathians). The size, density and shape of the spots vary from very small and sparse (20% specimens), through medium-sized to very large, round or oval, sometimes merging (8%) (Fig. 11). The variation is individual; specimens with different mantle patterns occurring in the same population. Medium-sized, oval or round spots, sometimes partly merging, are recorded most frequently (72%). The spots always have a very low ratio of perimeter to surface.

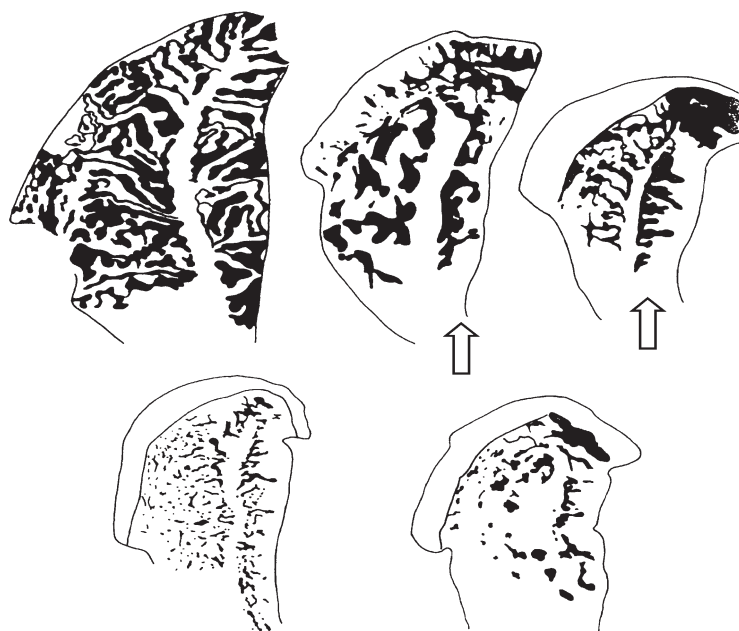


Fig. 9. Mantle pattern of *Perforatella incarnata*, specimens from Muszkowice; the most frequent pattern indicated with arrow

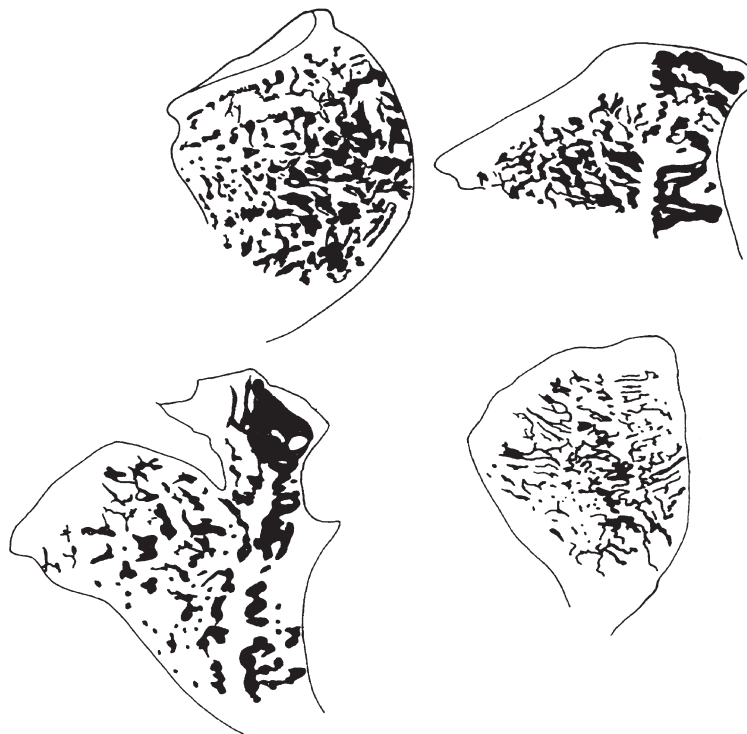


Fig. 10. Mantle pattern of *Perforatella incarnata*, specimens from Olawa



Fig. 11. Mantle pattern of *Perforatella vicina*, specimens from Muszkowice; the most frequent pattern indicated with arrow

GENITALIA

Perforatella incarnata

The gonad is not divided into distinct lobes. The first, short section of hermaphroditic duct is thin and straight, the next one four times longer, thick walled and coiled. The albumen gland, elongated, tongue shaped, consists of very fine lobules. The spermoviduct is roughly as long as the free oviduct and vagina combined. The spermatheca duct is long, the spermatheca large and globular, not reaching the albumen gland. The club-shaped stylophore is approximately as long as the atrium and vagina combined. The vagina is thick walled, the atrium very short. There are two clusters of mucus glands. Their total number is ranges from 4 to 7 (mostly 4, 5 or 6) arranged in pairs (2+2; 44% specimens), 2+3 (27%), 3+3 (17%) or 3+4 (12%). In most specimens (90%) at least one of the glands is branched. The number and arrangement of the glands vary within the popula-

tions. The penis (Figs 12, 13) is a muscular tube of approximately the same length as epiphallus. There is a single or double bend on the penis-epiphallus junction; very rarely the bend is absent. More than half of the examined individuals have a muscle strand fastening the bend; the muscle is developed to various extent: it can be strong and thick (42% specimens) or flat, membraneous, or else reduced to single fibres (11%). The bend and the muscle strand vary within the populations. The shape of the penial papilla lumen varies widely (Fig. 14). The flagellum is slightly shorter than the epiphallus in most cases (67%) or longer (30%), only exceptionally of the same length (3%). None of the parts of the genital system is pigmented.

Perforatella vicina

The gonad, hermaphroditic duct, albumen gland, spermoviduct, spermatheca with its duct, stylophore, vagina and atrium are identical with those of the

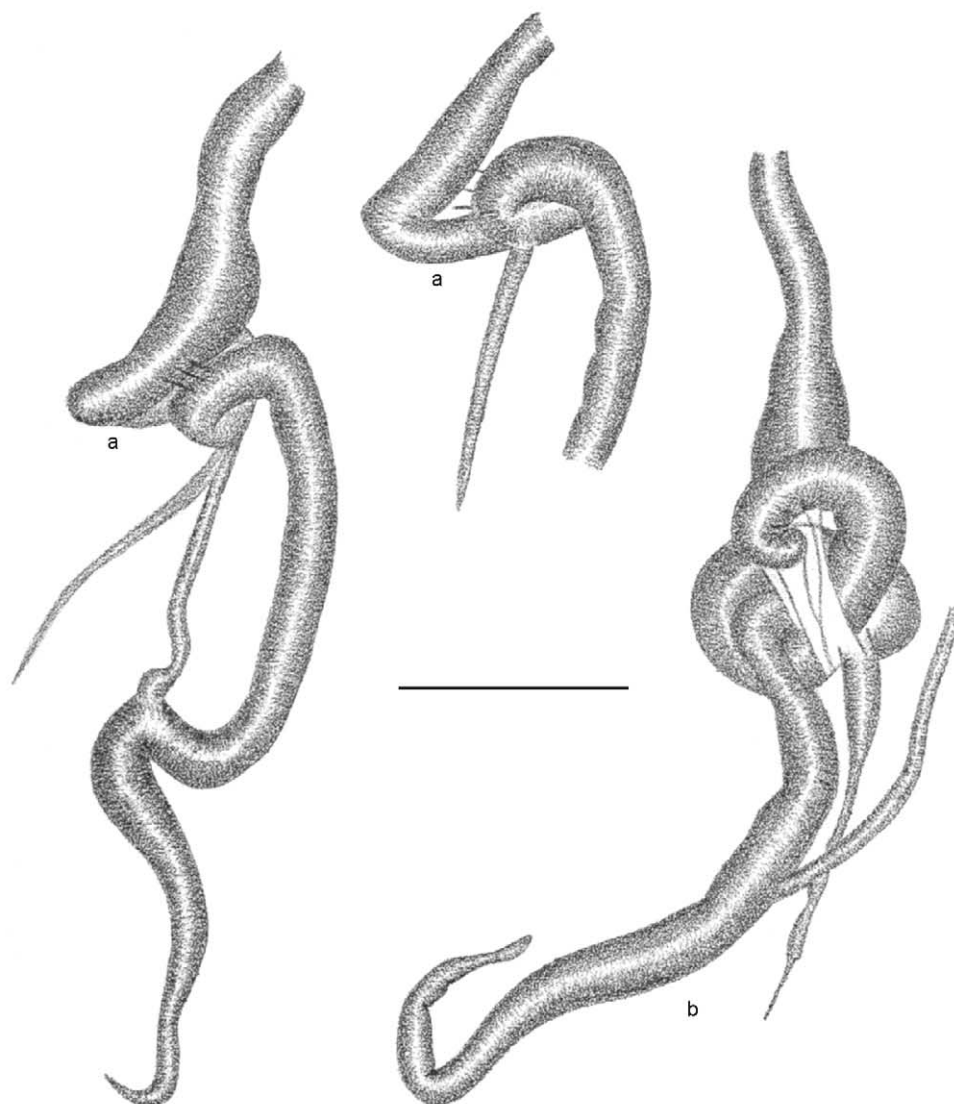


Fig. 12. Male genitalia of *Perforatella incarnata*, specimens from: a – Muszkowice, b – Wleń

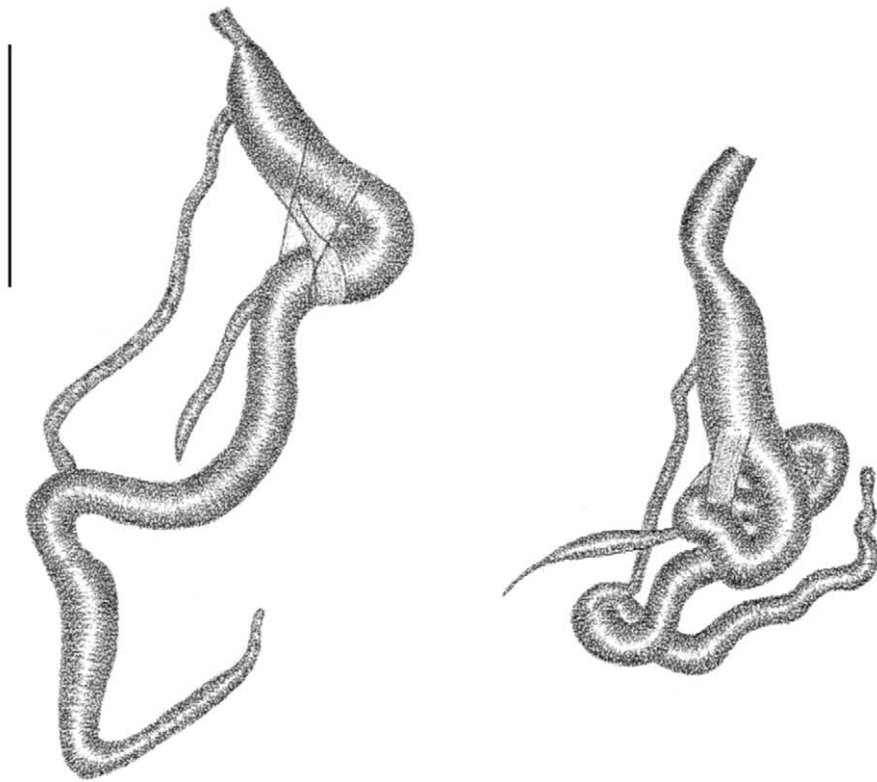


Fig. 13. Male genitalia of *Perforatella incarnata*: a specimen from Oława

preceding species. The mucus glands (3 to 6; usually 4 or 5) are arranged as 2+1 (9% specimens), 2+2 (42%), 2+3 (41%), 3+3 (8%). In most specimens (88%) at least one of the glands is branched. The variation has an intra-population character. The penis (Figs 15, 16) is a muscular tube, roughly as long as epiphallus, in most cases with a single or double bend on the penis-epiphallus junction; very rarely the bend is absent. In ca. 40% specimens the muscle fastening

the bend is present in the form of a strong, thick strand (16%), in others it is a flat membrane, or is reduced to single fibres (24%). The characters of the bend and muscle vary within populations. The penial papilla lumen varies in shape (Fig. 17). The flagellum is almost always longer than the epiphallus (93%), very rarely shorter (4%) or of the same length (3%). None of the parts of the genital system is pigmented.

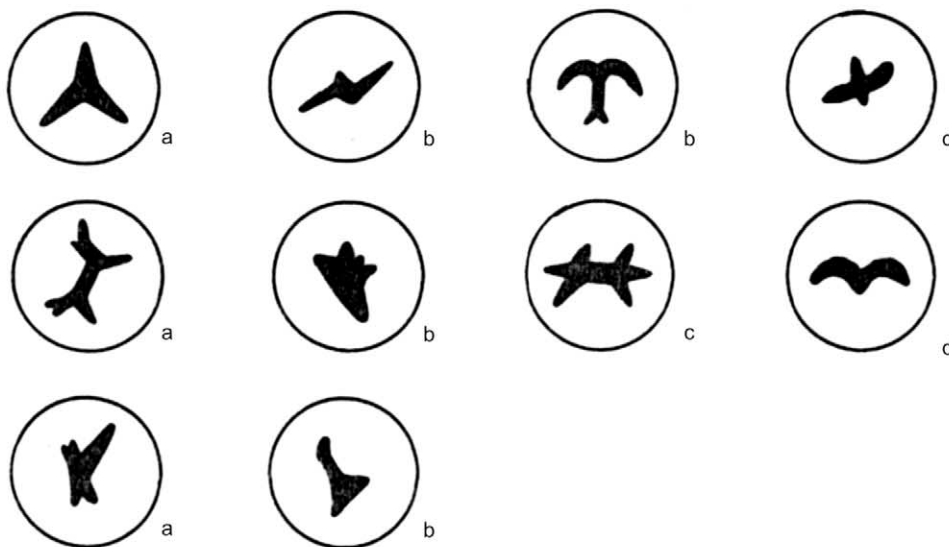


Fig. 14. *Perforatella incarnata*, cross-section of penial papilla, diagrammatic. Papilla lumen marked with black. Specimens from: a – Oława, b – Muszkowice, c – Wleń and d – Wojcieszów

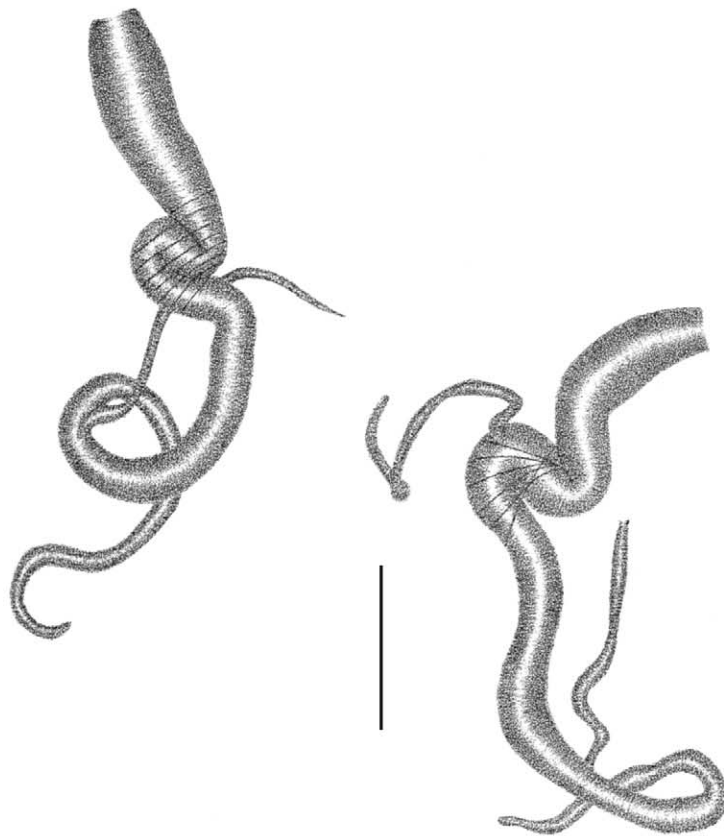


Fig. 15. Male genitalia of *Perforatella vicina*: specimens from Muszkowice

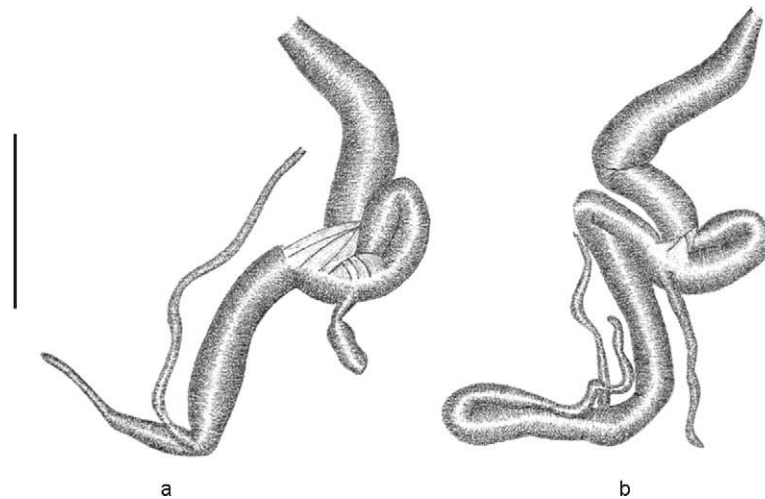


Fig. 16. Male genitalia of *Perforatella vicina*, specimens from the Pieniny Mts.: a – Valley of Pieniński Potok (Dolina Pienińskiego Potoku), b – Sokolica

DISCUSSION

DIAGNOSTIC VALUE OF CHARACTERS

The following distinctive conchological characters of *P. incarnata* are specified in the identification keys (URBAŃSKI 1957, SHILEYKO 1978, KERNEY et al. 1983, WIKTOR 2004): shell with umbilicus; horn- or reddish

brown, with pink lip; no protuberance on the lip; surface sculpture of radial, elongate and closely set tubercles. The keys specify for *P. vicina*: umbilicus absent, shell yellowish or light horn brown, with white lip (less often lip pink); often small protuberance on basal part of the lip; surface sculpture of radial tuber-

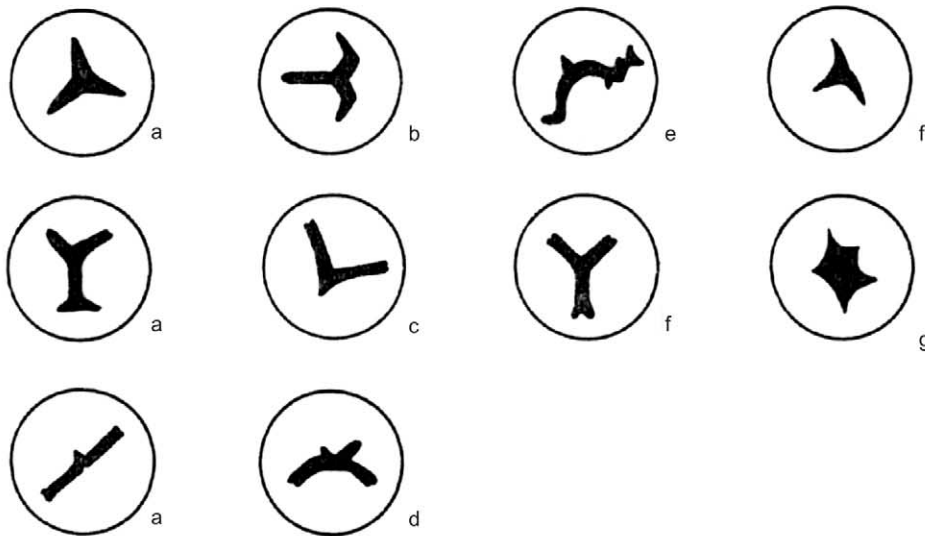


Fig. 17. *Perforatella vicina*, cross-section of penial papilla, diagrammatic. Papilla lumen marked with black. Specimens from: a – Bieszczady Mts., Terebowiec valley, b – Beskid Żywiecki, Ciapków stream valley near Rycerka, c – Bieszczady Mts, Ustrzyki Górne, d, e: Pieniny Mts: Śrutówka (d) and Valley of Pieniński Potok (e), f – Muszkowice, g – Wojcieszów

cles looking like tiny ribs, alternately arranged. SHILEYKO (1978) is the only author to list the characters of genitalia. *P. incarnata*: no bends on penis and epiphallus; lumen of papilla penis cross-shaped with thick beams; number of mucus glands $2 \times 3-5$, glands branched; flagellum and epiphallus are more or less the same length. *P. vicina*: one or two distinct bends on penis-epiphallus junction; lumen of papilla penis irregularly comb-shaped; number of mucus glands 2×3 , glands unbranched; thin flagellum slightly shorter than epiphallus. Distinctive characters found in this study are listed in Table 3.

The variation ranges of most of the characters specified in Table 3 overlap (number of whorls, umbilicus, lip protuberance, number of mucus glands, muscle fastening the penial bend, length ratio flagellum : epiphallus). *P. incarnata* and *P. vicina* can be effectively and univocally separated by four of the analysed characters: shell surface sculpture, shell colour, body colour and mantle pattern. The coloration can be useful when identifying live specimens in the field, and the surface sculpture can be crucial in examination of fossil material, when only shell fragments are available. The anatomical characters indicated by SHILEYKO (1978) as diagnostic, after examination of a more extensive material, appear to be of no value. This is one of the very few cases among helicids when features of the genital system are of less diagnostic value than shell and coloration characters.

INTERPOPULATION VARIATION

No data on shell and genitalia variation in the two species exist in the literature. In spite of statistically significant differences in metric shell characters and the indices of shell shape, the two species are con-

chologically very similar, and their variation ranges overlap. In most cases conspecific populations display differences greater than those between the species. The differences between syntopic *P. incarnata* and *P. vicina* from Muszkowice and Wojcieszów on the one hand, and the absence of differences between the populations of *P. incarnata* from Germany, Wleń and Wojcieszów, as well as considerable differences between the three examined populations of *P. vicina* are noteworthy. The syntopic populations of *P. incarnata* and *P. vicina* from Muszkowice and Wojcieszów differ more than the populations of the species from Oława (*P. incarnata*) and the Carpathians (*P. vicina*), suggesting a divergent character displacement (RIDLEY 1993). Because it is not known which of the Carpathian samples of *P. vicina* actually come from localities with no *P. incarnata*, testing the hypothesis requires biometrical examination of material collected especially for the purpose.

The populations of *P. incarnata* from Moosburg in Germany, Wojcieszów and Wleń do not differ from each other statistically significantly, whereas each of them shows some differences in relation to the populations from Muszkowice and Oława, though all four investigated Polish localities are geographically very close. It is not known if the variation is geographical or purely ecological, or maybe a result of some past colonisation and extinction events.

The differences between the populations of *P. vicina* from Wojcieszów and Muszkowice (both in the Sudetes) on the one hand and the Carpathians on the other are statistically significant. *P. vicina* is a Carpathian species, its outlying localities in the western Sudetes and Lower Silesia are remote from the main distribution range. Similar differences between populations from outlying localities and those from the

Table 3. Shell, genital and body colour characters of *Perforatella incarnata* and *Perforatella vicina*

No.	Character	<i>P. incarnata</i>	<i>P. vicina</i>
Shell			
1	number of whorls	4.75–6.75 (most often 5–6)	5.37–7.00 (most often 5.5–6.5)
2	lip protuberance	occurs very rarely	occurs quite often
3	umbilicus	most often present but sometimes very narrow or even completely closed	most often absent, very rarely narrow and almost completely closed
4	surface sculpture	fine, closely spaced tubercles	large, widely spaced tubercles
5	shell colour	always brown though of varied hue	yellowish
6	lip and stripe behind it	pink or reddish	white
Body colour and mantle pattern			
7	body colour	dark graphite or grey	yellowish or flesh-coloured
8	colour of mantle spots	graphite, brown, very rarely black	always black
9	shape of mantle spots	irregular, very high perimeter:surface ratio	more regular, very low perimeter:surface ratio
Genitalia			
10	number of mucus glands	4–7	3–6
11	muscle fastening penis bend	present in over 60% specimens	present in ca. 40% specimens
12	degree of development of muscle fastening penis bend	usually well developed	vestigial in ca. 50% specimens with muscle
13	length ratio flagellum:epiphallus	flagellum mostly slightly shorter than epiphallus	flagellum almost always longer than epiphallus

Carpathians have been observed for some Carpathian clausiliids (ABRASZEWSKA-KOWALCZYK & SULIKOWSKA 1998).

The observed variation pattern is complicated; its character may suggest a rather recent speciation, a

possible role played by past colonisation and extinction events, and indicates a necessity of studies on a more extensive material, possibly including molecular characters as well as details of ecology and life histories.

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