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SHELL VARIATION IN THE GENUS *DISCUS* FITZINGER, 1833 (GASTROPODA: PULMONATA: ENDODONTIDAE)

ELŻBIETA KUŹNIK-KOWALSKA

Department of Zoology and Ecology, Wrocław University of Environmental and Life Sciences, Kożuchowska 5b, 51-637 Wrocław, Poland (e-mail: ekow@ozi.ar.wroc.pl)

ABSTRACT: In Europe the genus *Discus* Fitzinger, 1833 is represented by two subgenera: *Gonyodiscus* Fitzinger, with *D. rotundatus* (O. F. Müll.) and *D. perspectivus* (Mühlf.), and *Discus* s. str. with *D. ruderatus* (Fér.). Studies on their shell variation were to ascertain if variation among laboratory-bred individuals differed from such variation in natural populations. The number of whorls, shell height, body whorl height, aperture height, aperture width, shell major and minor diameter, umbilicus major and minor diameter, shell height/major diameter ratio, relative height of body whorl, relative umbilicus diameter and umbilicus major/minor diameter ratio were analysed. Variation ranges of most shell characters in laboratory specimens of *D. rotundatus* and *D. ruderatus* were much wider than those found in natural populations. The natural populations of each species differed statistically significantly among themselves in many characters but the differences were much smaller. Laboratory-bred *D. perspectivus* showed a tendency to produce scalariform shells or descending and partly detached body whorl. Laboratory-bred *D. rotundatus* and *D. ruderatus* tended to form a descending body whorl; in all three species the descending/detached part of the body whorl was formed after sexual maturity had been attained.

KEY WORDS: terrestrial plumonates, *Discus*, shell, variation

INTRODUCTION

In Europe the genus *Discus* Fitzinger, 1833 is represented by two subgenera: *Gonyodiscus* Fitzinger, 1833 with *Discus* (*Gonyodiscus*) *rotundatus* (O. F. Müller, 1774) and *Discus* (*Gonyodiscus*) *perspectivus* (Megerle Von Mühlfeld, 1818), and *Discus* s. str. with *Discus* (*Discus*) *ruderatus* (Férussac, 1821). Other subgenera are known from Madeira (*Atlantica* Ancey), the Canary Islands, Cape Verde Islands (*Keraea* Gude) and North America (*Nematodiscus* Pilsbry) (UMIŃSKI 1962, SOLEM 1976). The subgeneric division of *Discus* is based on shell characters (coloration, number of whorls) and internal structure (genitalia, radula).

D. rotundatus is a West- and Central-European species, in Norway reaching 63° and in Sweden 58°N. In the south its distribution range includes western Mediterranean countries of Europe. The eastern border of its distribution is not exactly known, but it has not been recorded from the Balkans and the southern Carpathian countries. In the Carpathians and Sudetes it reaches up to 1,200 m a.s.l. (in the Alps up to 2,700 m). In Poland it occurs in the whole area except the Bieszczady Mts (UMIŃSKI 1962, RIEDEL & WIKTOR 1974). *D. rotundatus* is primarily a forest-dweller, sometimes penetrating into some anthropogenic habitats (parks, ruins, vegetated and humid rubble dumps, gardens, hothouses). It stays in leaf litter and is strongly associated with rotting timber.

The Carpathian-Dinaric *D. perspectivus* has a disjunct distribution: it inhabits nearly the whole of the Carpathians, in the west reaching the south-western end of Bavaria, vicinity of Munich and Nürnberg, in the north – to the České středohoří, the Sudetes, Lower Silesia, Cracow-Wieluń Jura and the northern foothills of the Carpathians. In Poland it is rather rare, known from the Bieszczady Mts where it reaches up to 1,000 m a.s.l., Pogórze Dynowskie, a part of the Beskidy Mts and the Pieniny (up to 700 m). Outside the Carpathians and their foothills it has scattered localities in the western part of the Sudetes: Złote, Bardzkie and Sowie Mts., and insular ocurrences on

the mountain Biskupia Kopa south of Nysa, nature reserve Muszkowicki Las Bukowy near Ząbkowice Śląskie and in the massif of Ślęża (UMIŃSKI 1962, RIEDEL & WIKTOR 1974). Its northern distribution border crosses Poland. *D. perspectivus* is an inhabitant of montane and submontane forests, usually found at 300–650 m a.s.l. It prefers humid and shaded places where it stays in leaf litter and on rotting timber.

D. ruderatus is widespread in the Palaearctic. In the north in places it reaches to the coast of the Arctic Sea (Arkhangelsk, in Norway to 71°N), in the south to the Crimea, Caucasus and northern part of the Armenian Upland. In Europe the southern border of its range runs along the Southern Carpathians and southern part of the Alps, along the margin of the Pannonian Basin. In Poland it occurs virtually in the whole area, especially in mountainous regions: the Sudetes, Świętokrzyskie Mts, Tatra Mts and other parts of the Carpathians with their foothills; it is absent from the Bieszczady Mts. In the Karkonosze Mts it is found in the zone of 600–1,200 m a.s.l., in the Tatra even up to 1,900 m (UMIŃSKI 1962, RIEDEL & WIKTOR 1974). *D. ruderatus* is a forest-dweller, closely associated with rotting timber. It inhabits deciduous, deciduous-coniferous and also coniferous forests where it stays under bark of tree trunks, in rotting timber and in litter. It is regarded as an indicator species of rather cool and humid forest areas.

This study – another of the series dealing with members of the genus *Discus* (see also KUŹNIK-KOWALSKA 1999, 2005, 2006, KUŹNIK-KOWALSKA & POKRYSZKO 2007) – deals with shell variation in laboratory-bred and wild-living snails of the three species.

MATERIAL AND METHODS

The following material from the collections of the Natural History Museum, Wocław University (MPWr), Museum and Institute of Zoology, Polish Academy of Sciences (MiIZPAN) and the National Museum of Wales, Cardiff (NMW) was used in the study:

D. rotundatus (total 899 shells): laboratory culture (initial material Boboszów, SW. Poland): 60 shells (MPWr); natural populations: SW. Poland: Boboszów, leg. E. KOWALSKA, 6.07. 1997, 31 shells (MPWr); Puszcza Śnieżnej Białki near Bielice, leg. A. WIKTOR, 1.10.1956, 17 shells (MPWr); Mt. Ślęża gabro, leg. A. WIKTOR, 1953/54, 40 shells (MPWr); Mt. Ślęża top, leg. A. WIKTOR, 27.04.1955, 26 shells (MPWr); Mt. Ślęża granite, leg. A. WIKTOR, 1953/54, 18 shells (MPWr); Bardo Śląskie, leg. A. WIKTOR, 22.07.1954, 62 shells (MPWr); Sobótka, leg. A. WIKTOR, 1953, 20 shells (MPWr); Mt. Kościuszko, leg. A. WIKTOR, 24.04.1955, 28 shells (MPWr); Kłodzko, fortress, leg. A. WIKTOR, 22.09.1958, 24 shells (MPWr); Mt. Radosz nr Bardo Śl., leg. A. WIKTOR, 14.08.1956, 21 shells (MPWr); Książ nr Wałbrzych, leg. A. WIKTOR, 23.09.1956, 24 shells (MPWr); Srebrna Mt., no exact data, 21 shells; C. Poland: Wartka, no exact data, 13 shells (MPWr); Austria: Mödling, leg. E. B. KOWALSCY, 9.07. 1998, 66 shells (MPWr); Kärnten, no exact data, 13 shells (MPWr); Karlsbrunn, no exact data, 140 shells (MPWr); Salzburg, no exact data, 32 shells (MPWr); Gastein, no exact data, 10 shells (MPWr); Italy: Nizza, no exact data, 28 shells (MPWr); Piemonte: Netro SW of Biella, leg. A. RIEDEL, 22.10.1996, 24 shells (MiIZPAN); Piemonte: Salussola S of Biella, leg. A. RIEDEL, 24.10.1996, 64 shells (MiIZPAN); Portugal: Madeira, leg. H. WALDÉN, 1984, 31 shells (NMW); Germany: Baberhäuser, no exact data, 35 shells; Switzerland: Basel, no exact data, 20 shells (MPWr); Sion, no exact data, 14 shells (MPWr); Ragatz, no exact data, 17 shells (MPWr).

D. ruderatus (total 149 shells): laboratory culture (initial material Nowa Morawa, SW. Poland): 61 shells (MPWr); natural populations: SW. Poland: Nowa Morawa nr Stronie Śl., leg. A. WIKTOR, 5.09.1957, 19 shells (MPWr); Puszcza Śnieżnej Białki nr Bielice, leg. A. WIKTOR, 1.10.1956, 9 shells (MPWr); Silesia, no exact data, 22 shells (MPWr); Austria: Karlsbrunn, no exact data, 28 shells (MPWr); Germany: Baberhäuser, no exact data, 10 shells (MPWr).

D. perspectivus (total 80 shells): laboratory culture (initial material nature reserve Muszkowicki Las Bukowy), 60 shells; natural population: nature reserve Muszkowicki Las Bukowy nr Ząbkowice Śl. (SW. Poland): 20 shells.

The following shells characters were analysed: number of whorls, shell height, body whorl height, aperture height, aperture width, shell major diameter, shell minor diameter, umbilicus major diameter, umbilicus minor diameter, shell height/shell major diameter ratio, body whorl height/shell height ratio (relative height of body whorl), umbilicus major diameter/shell major diameter ratio (relative diameter of umbilicus), umbilicus minor/major diameter ratio. Whorls were counted with EHRMANN's (1933) method. The shells were measured with calibrated eye-piece, to the nearest 0.025 mm. Besides, such characters as scalariform shells or atypically elevated spires were noted. Statistical analysis was performed with Statistica PL 7. 1 (STANISZ 2006).

RESULTS

Discus perspectivus

The only difference between laboratory-bred specimens and those from the natural population was that some shells of the former group (10 out of 60 cases) showed a tendency to a higher elevation of spire compared to specimens from the wild population, and to formation of scalariform body whorl or its part adjoining the aperture. The number of whorls in scalariform shells ranged from 5.6 to 6.9 (mean = 6.15; SD = 0.47; n = 10). The whorls became scalariform at the level of 5.3–5.75 (mean = 5.55; SD = 0.126; n = 10) (Table 1; Figs 1–3).

Table 1. *Discus perspectivus:* scalariform shells

Specimen	Number of whorls	Point when the shell becomes scalariform
1	6.9	5.75
2	6.0	5.5
3	5.8	5.5
4	5.9	5.5
5	5.9	5.6
6	5.6	5.3
7	5.75	5.6
8	6.9	5.5
9	6.5	5.6
10	6.3	5.7

Discus rotundatus

Ranges of variation of the examined shell parameters among specimens from laboratory culture and selected wild populations are shown in Figs 4–16.

Shells of laboratory-bred *D. rotundatus* departed considerably from those of specimens from their original population and from other European populations of the species in nearly all characters. The number of whorls, shell height, body whorl height, aperture height and width, minor and major shell diameter, umbilicus minor diameter, shell height/shell major diameter ratio in laboratory specimens had a much wider range and reached significantly higher mean values than in the original population and other European populations. The examined populations differed also among themselves in many characters in a statistically significant way, but these differences were much smaller (cf. Figs 4–16). The most variable characters in the examined material from various European localities were the number of

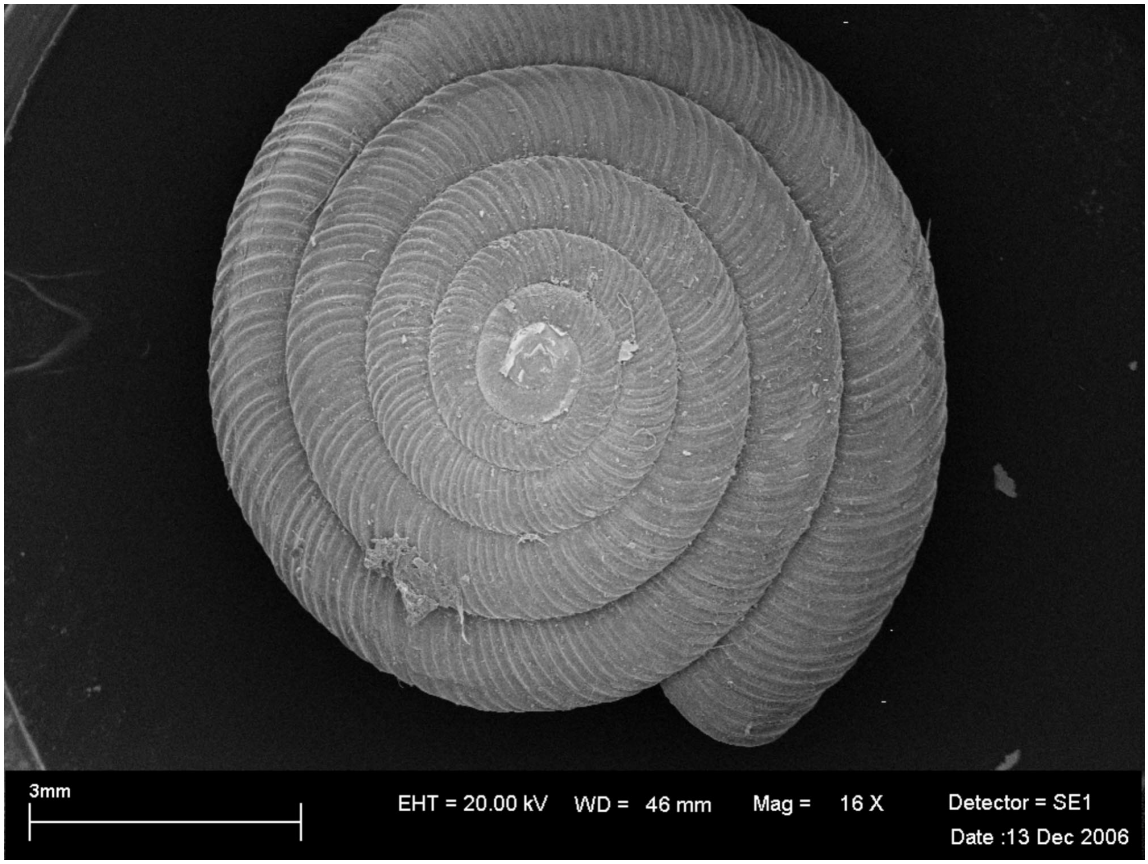

Fig. 1. *Discus perspectivus*: typical shell

Fig. 2. *Discus perspectivus*: scalariform shell

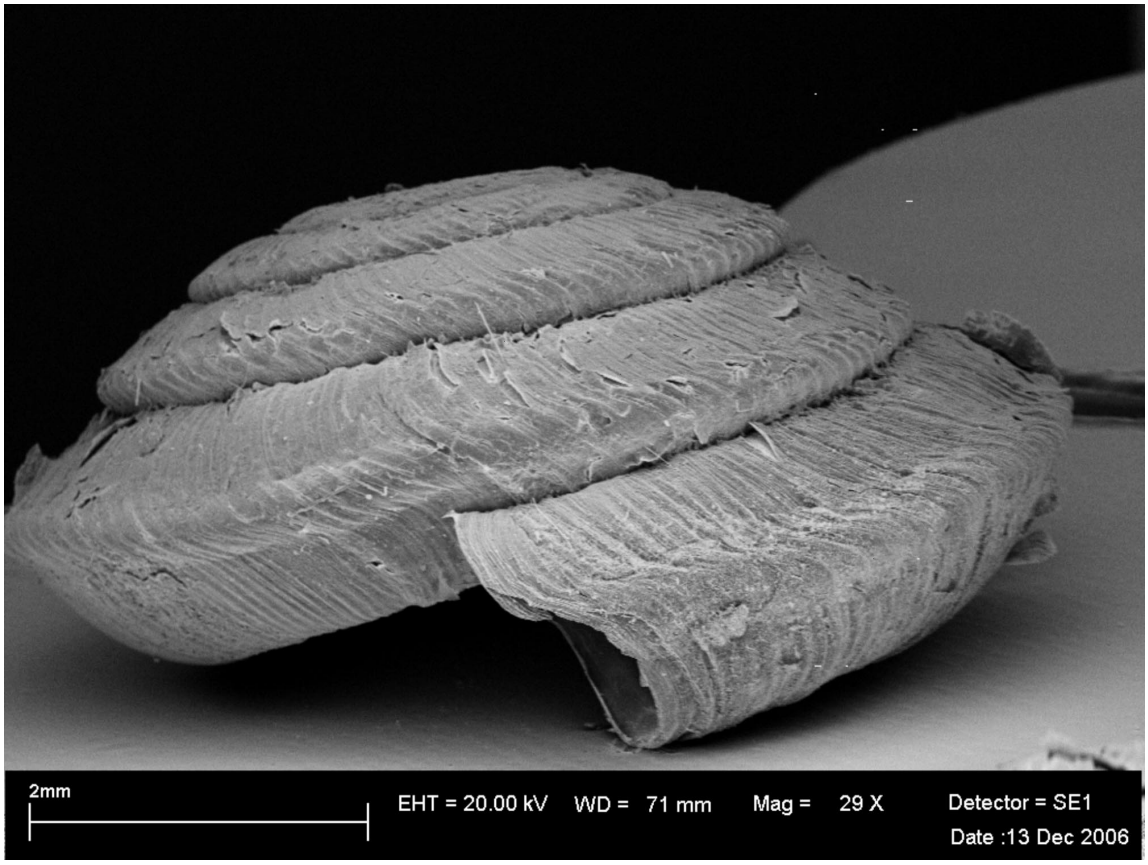

Fig. 3. *Discus perspectivus*: elevated shell

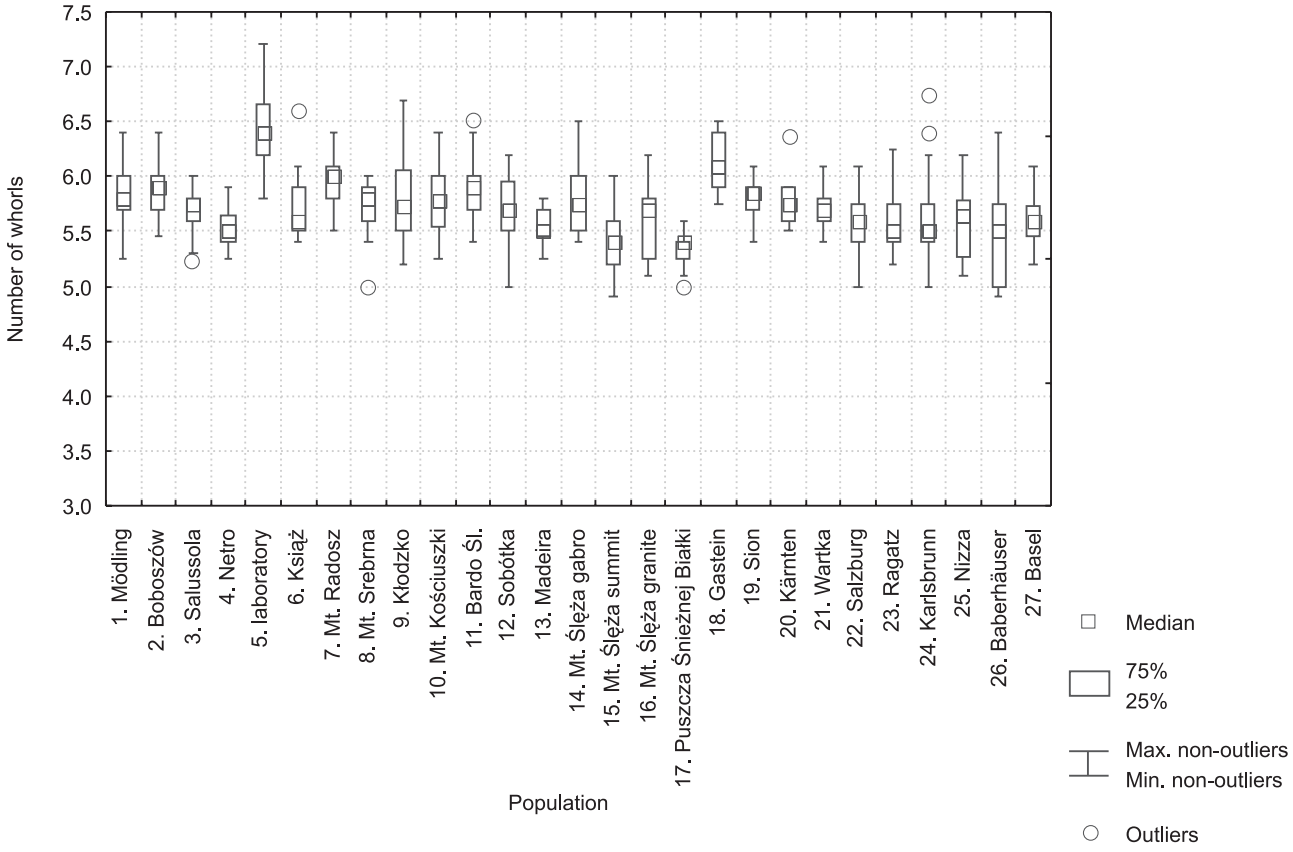

Fig. 4. *Discus rotundatus*: number of whorls, interpopulation variation

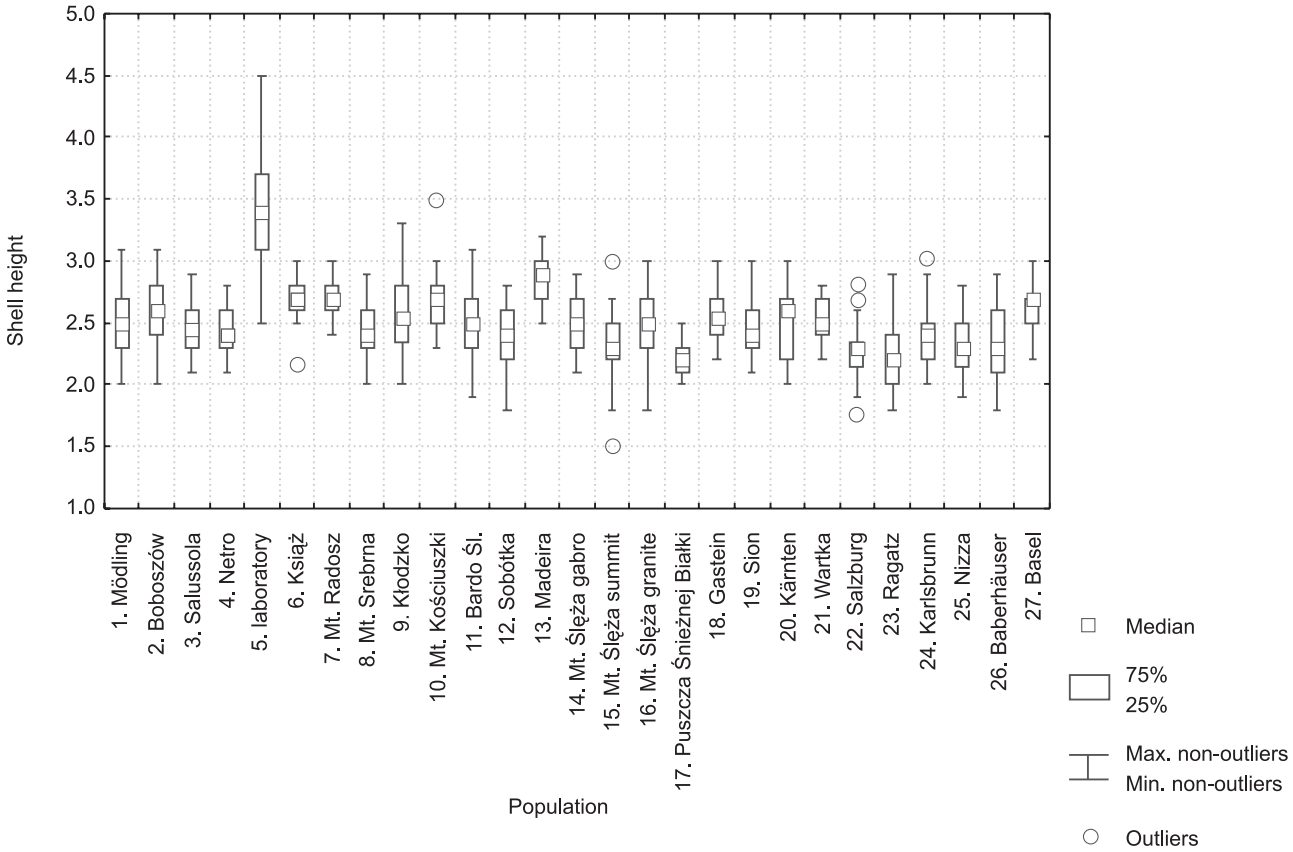

Fig. 5. *Discus rotundatus*: shell height, interpopulation variation

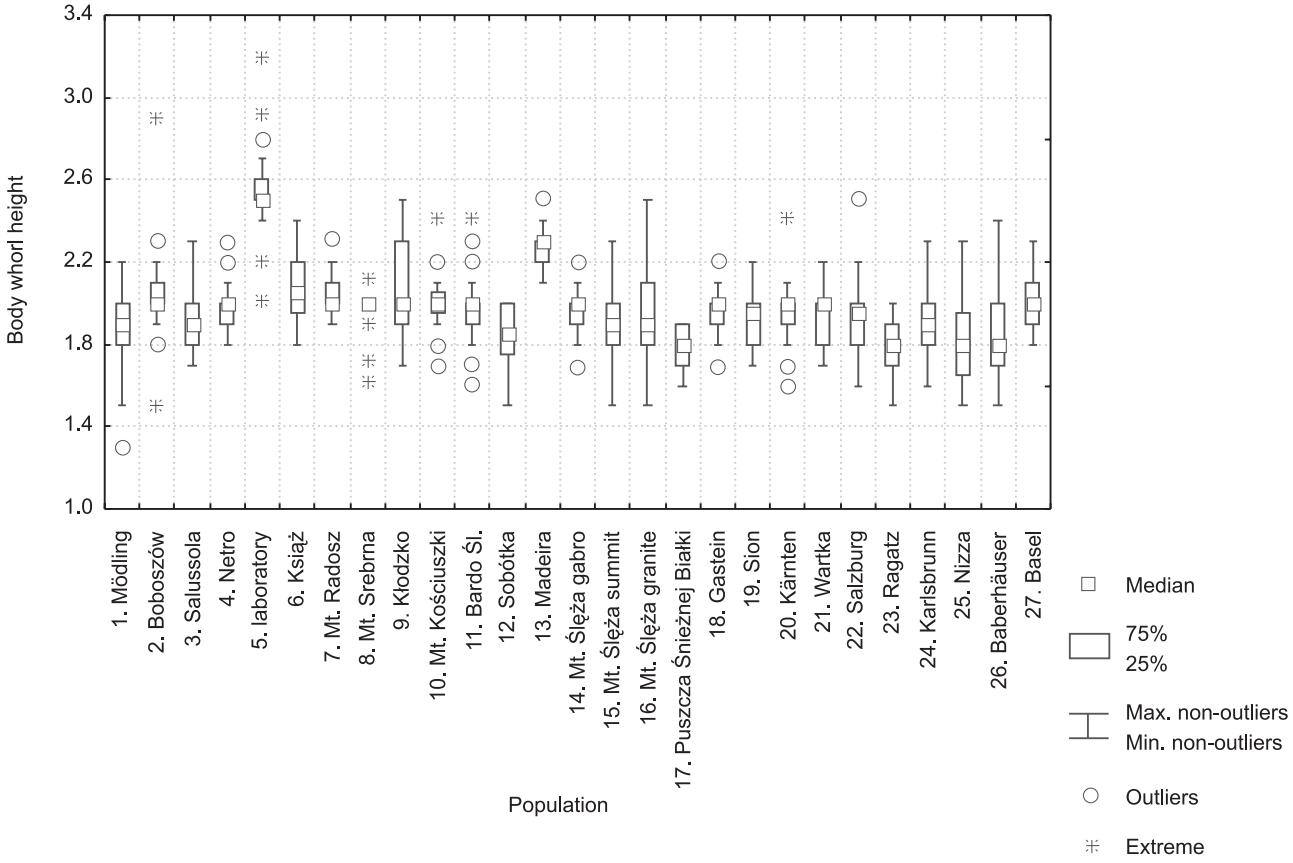

Fig. 6. *Discus rotundatus*: body whorl height, interpopulation variation

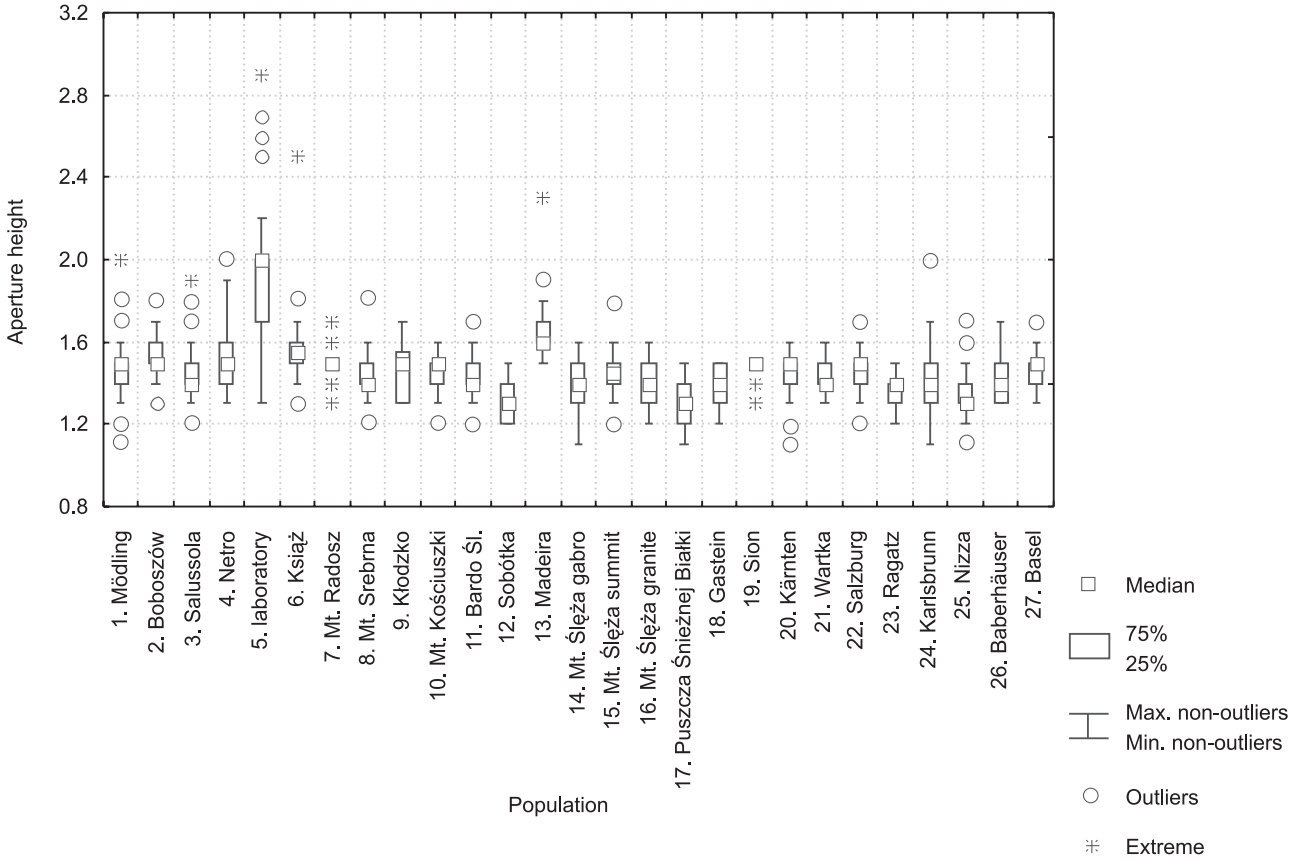

Fig. 7. *Discus rotundatus*: aperture height, interpopulation variation

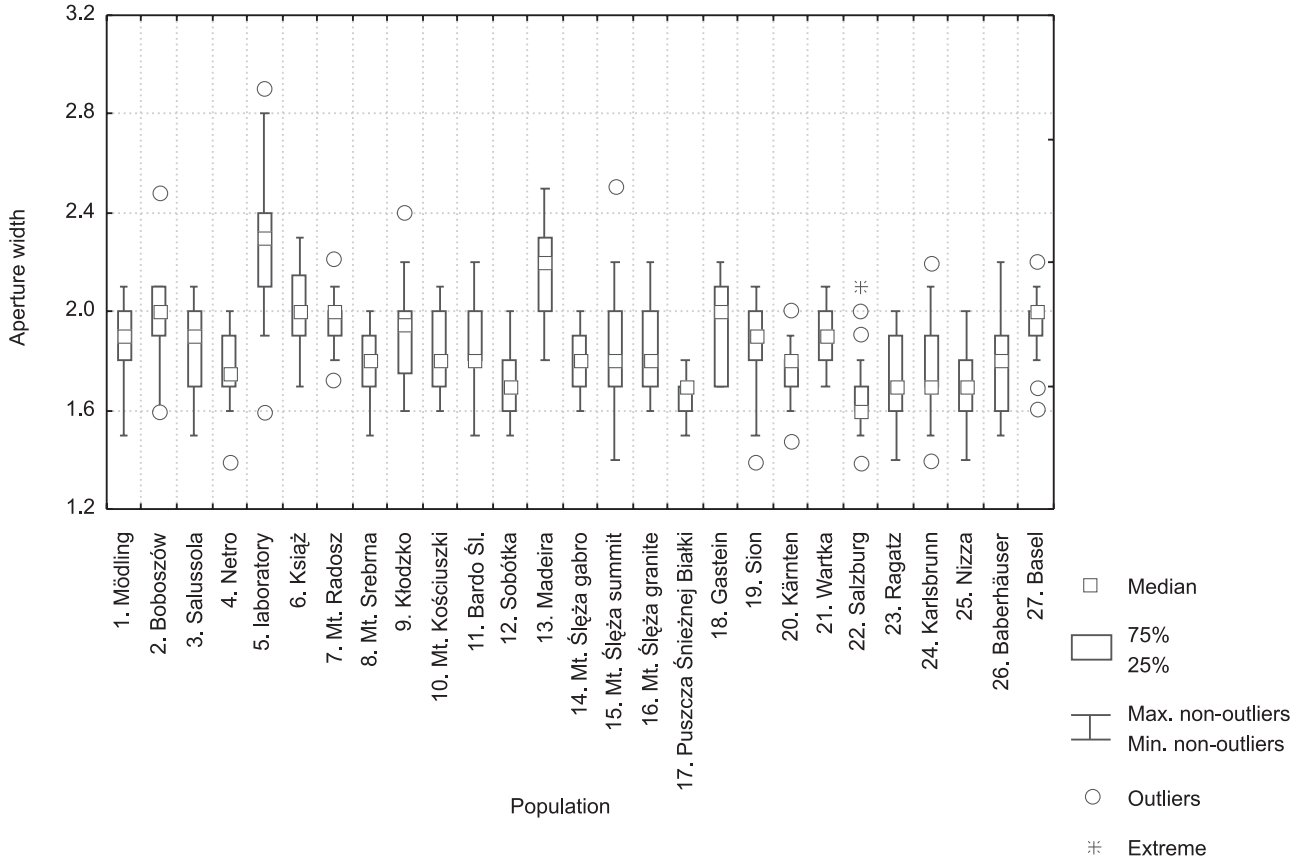

Fig. 8. *Discus rotundatus*: aperture width, interpopulation variation

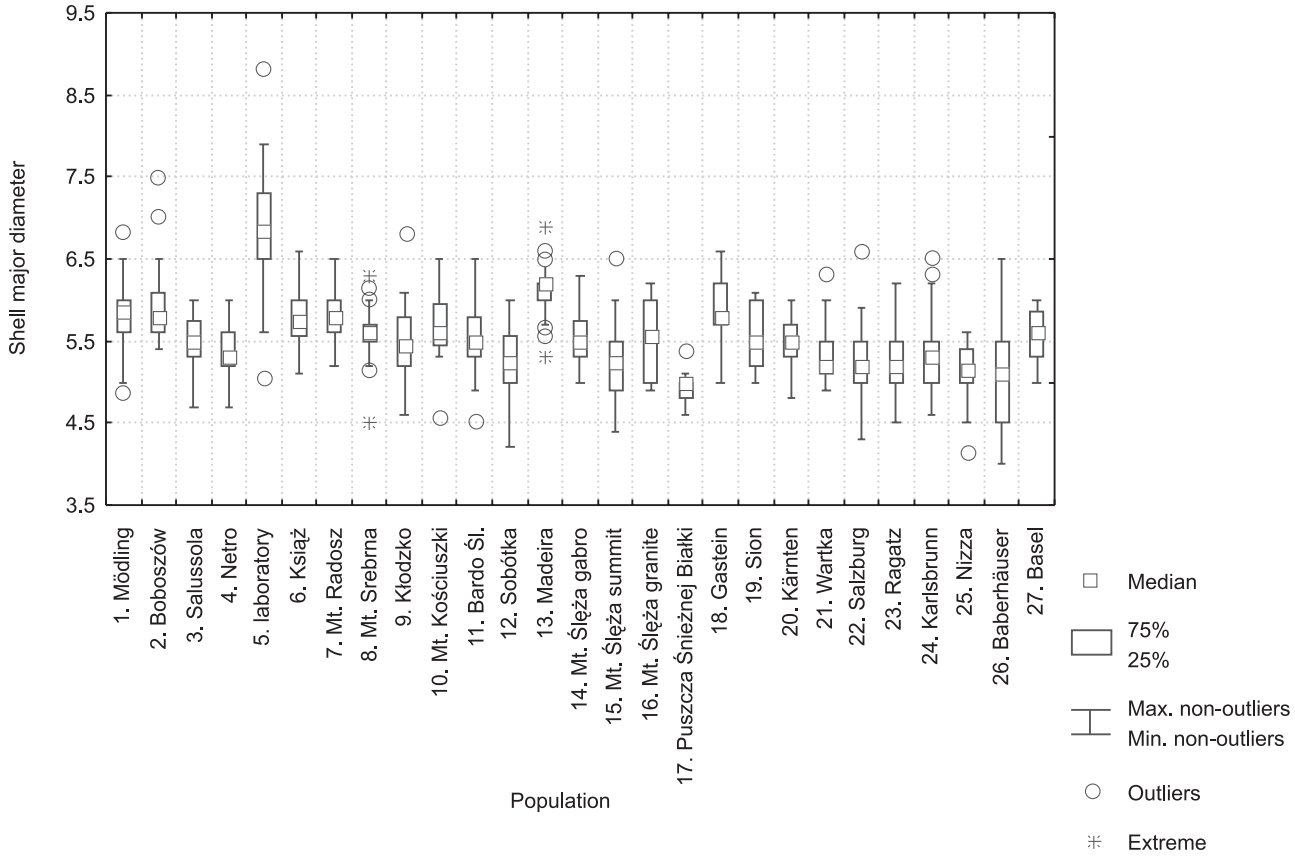

Fig. 9. *Discus rotundatus*: shell major diameter, interpopulation variation

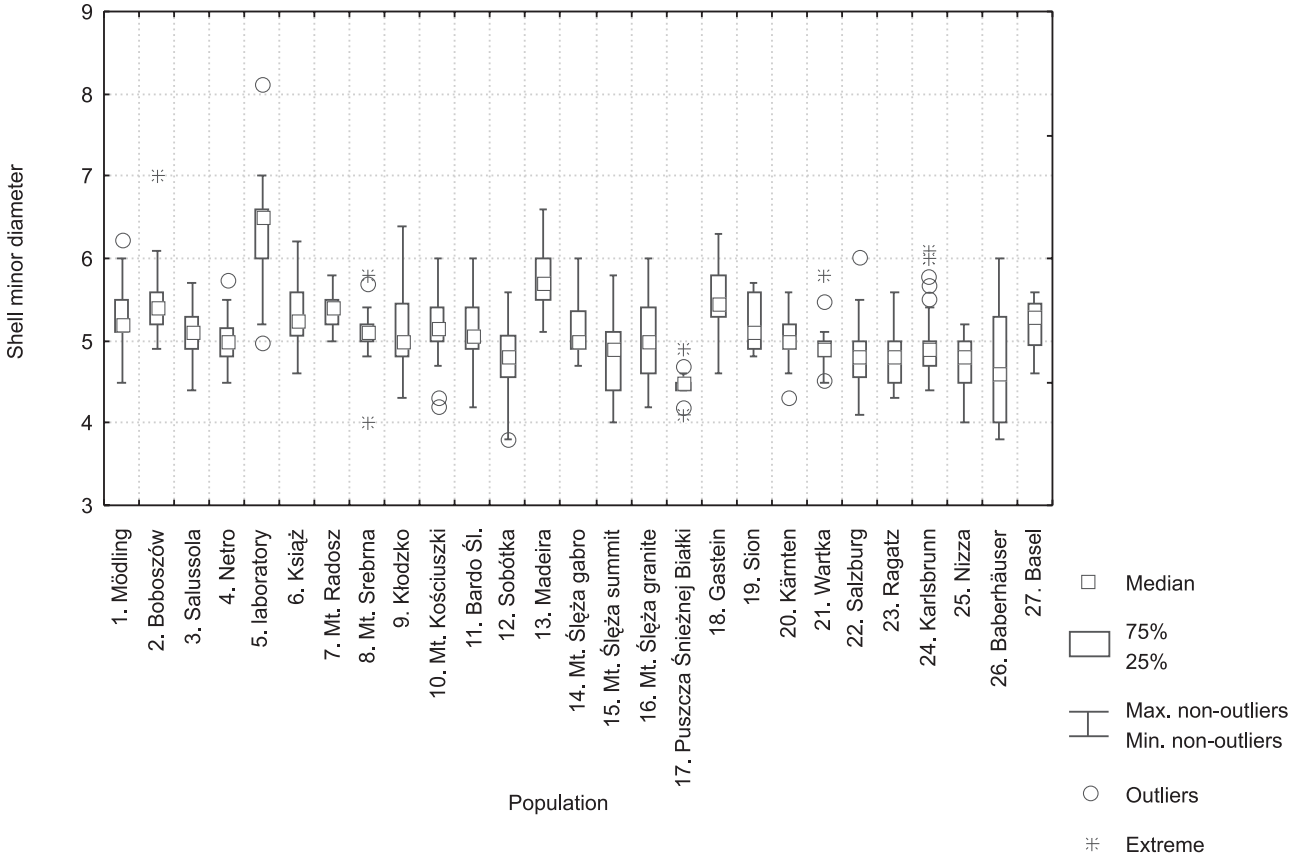

Fig. 10. *Discus rotundatus*: shell minor diameter, interpopulation variation

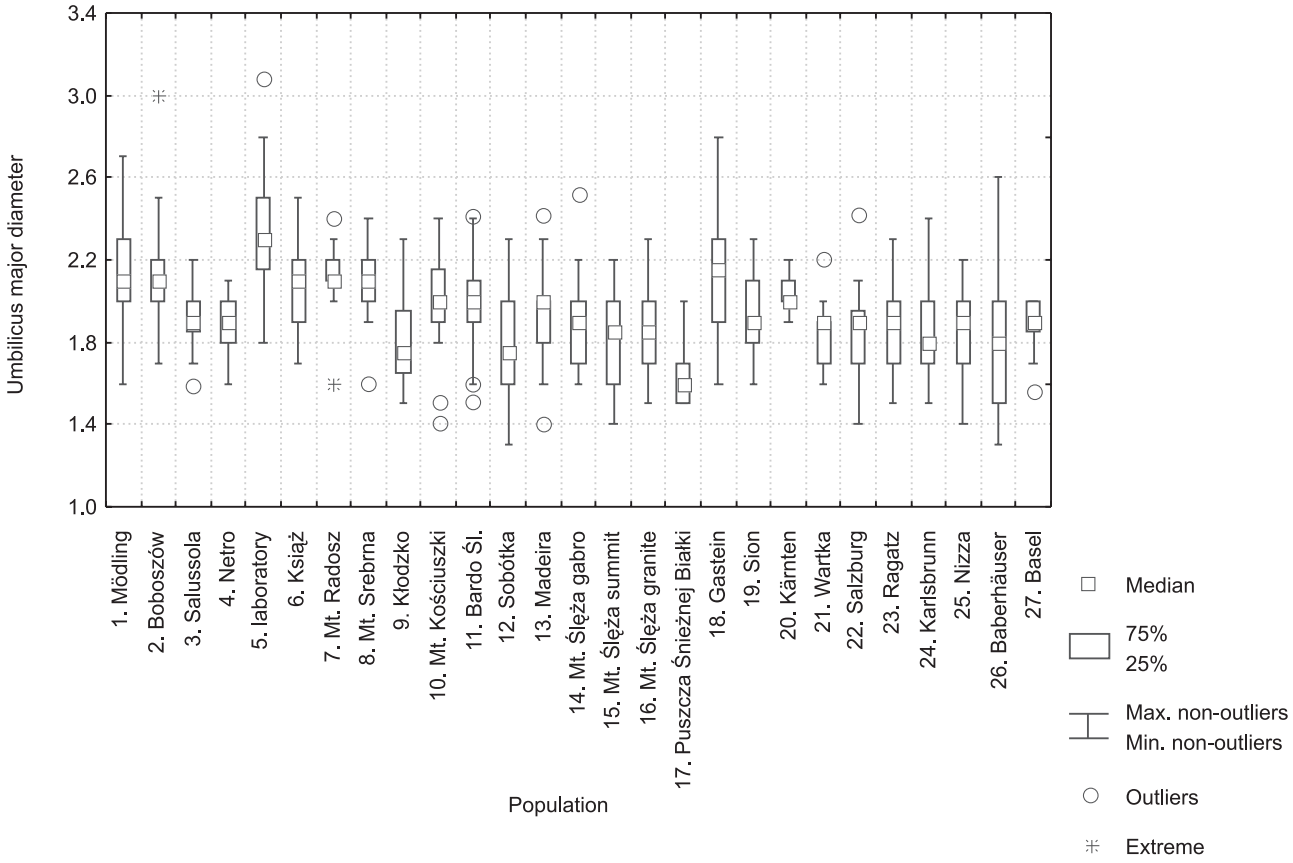

Fig. 11. *Discus rotundatus*: umbilicus major diameter, interpopulation variation

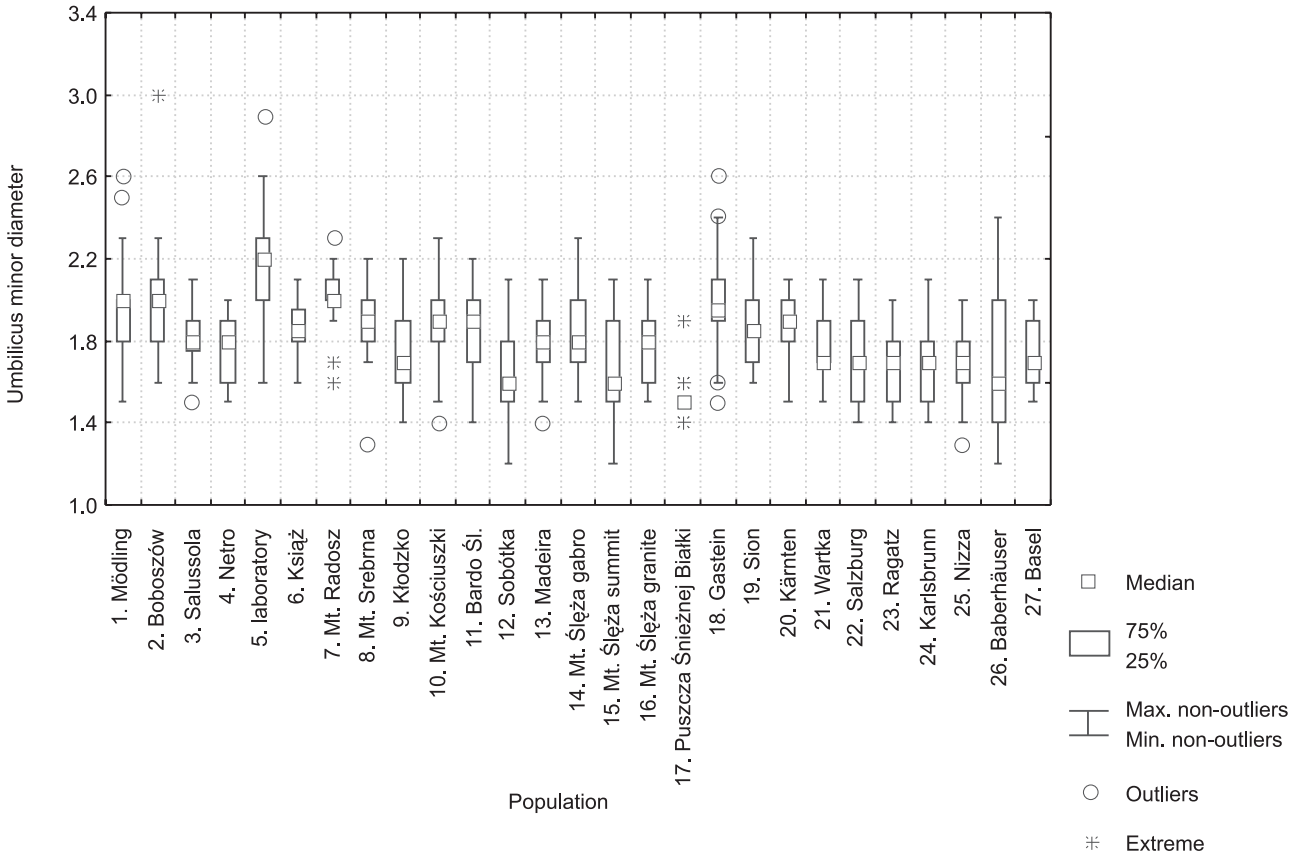

Fig. 12. *Discus rotundatus*: umbilicus minor diameter, interpopulation variation

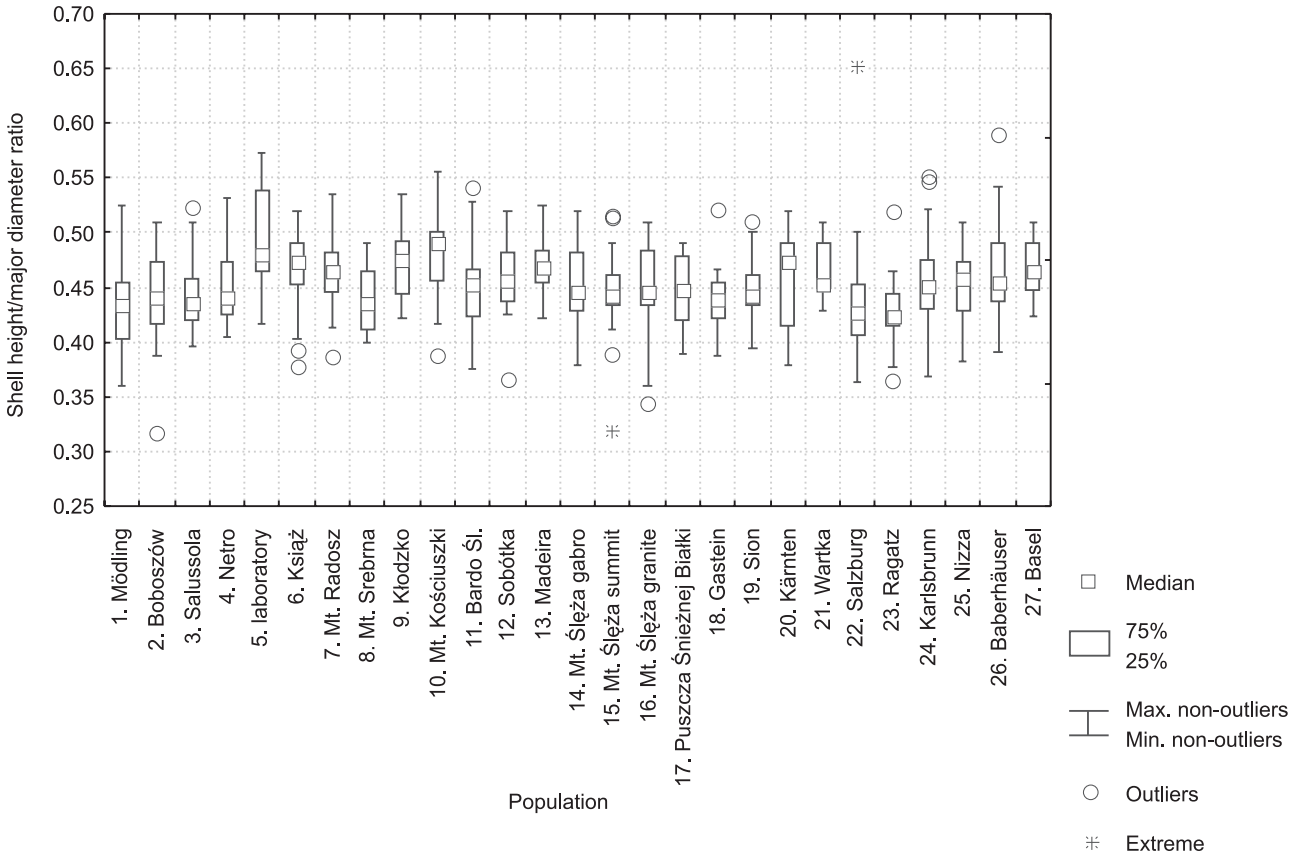

Fig. 13. *Discus rotundatus*: shell height/major diameter ratio, interpopulation variation

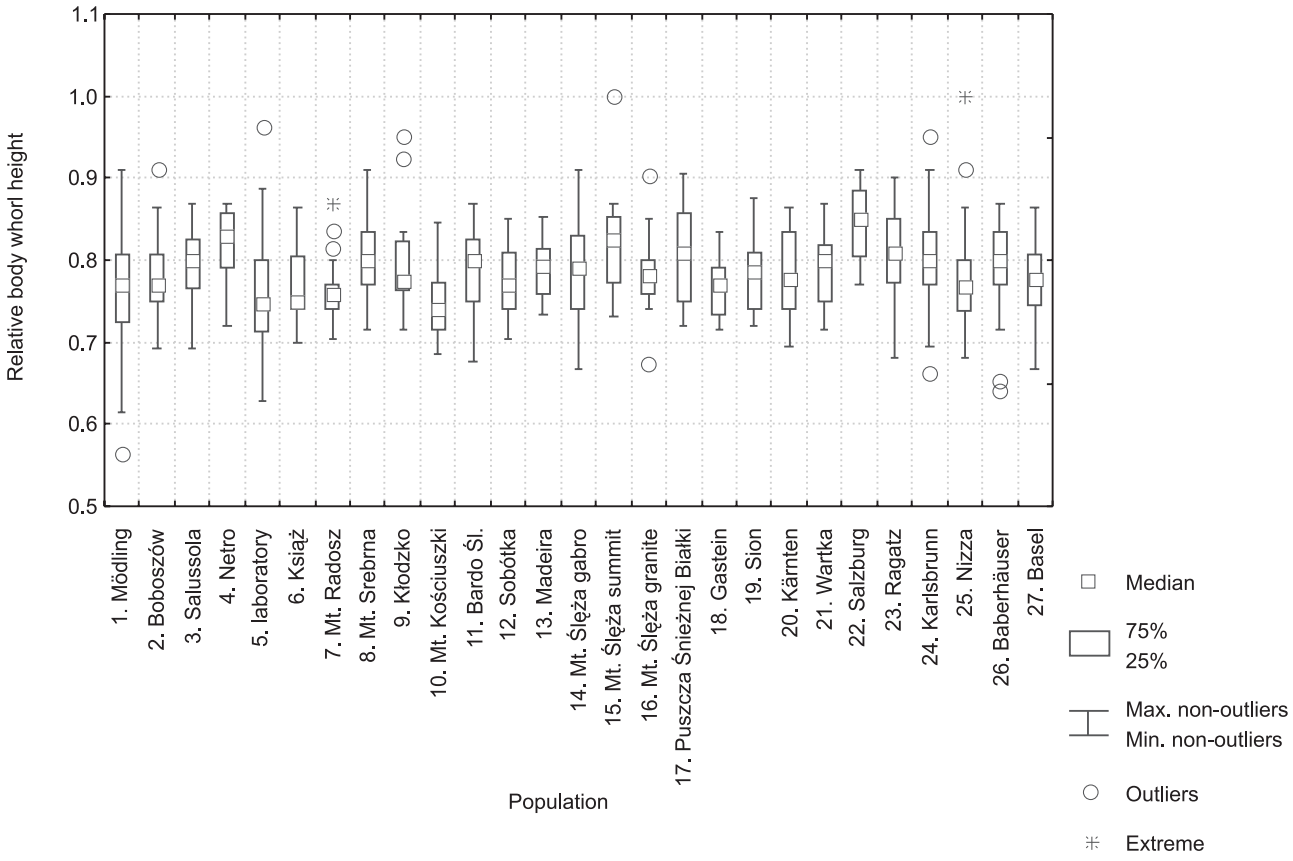

Fig. 14. *Discus rotundatus*: relative body whorl height, interpopulation variation

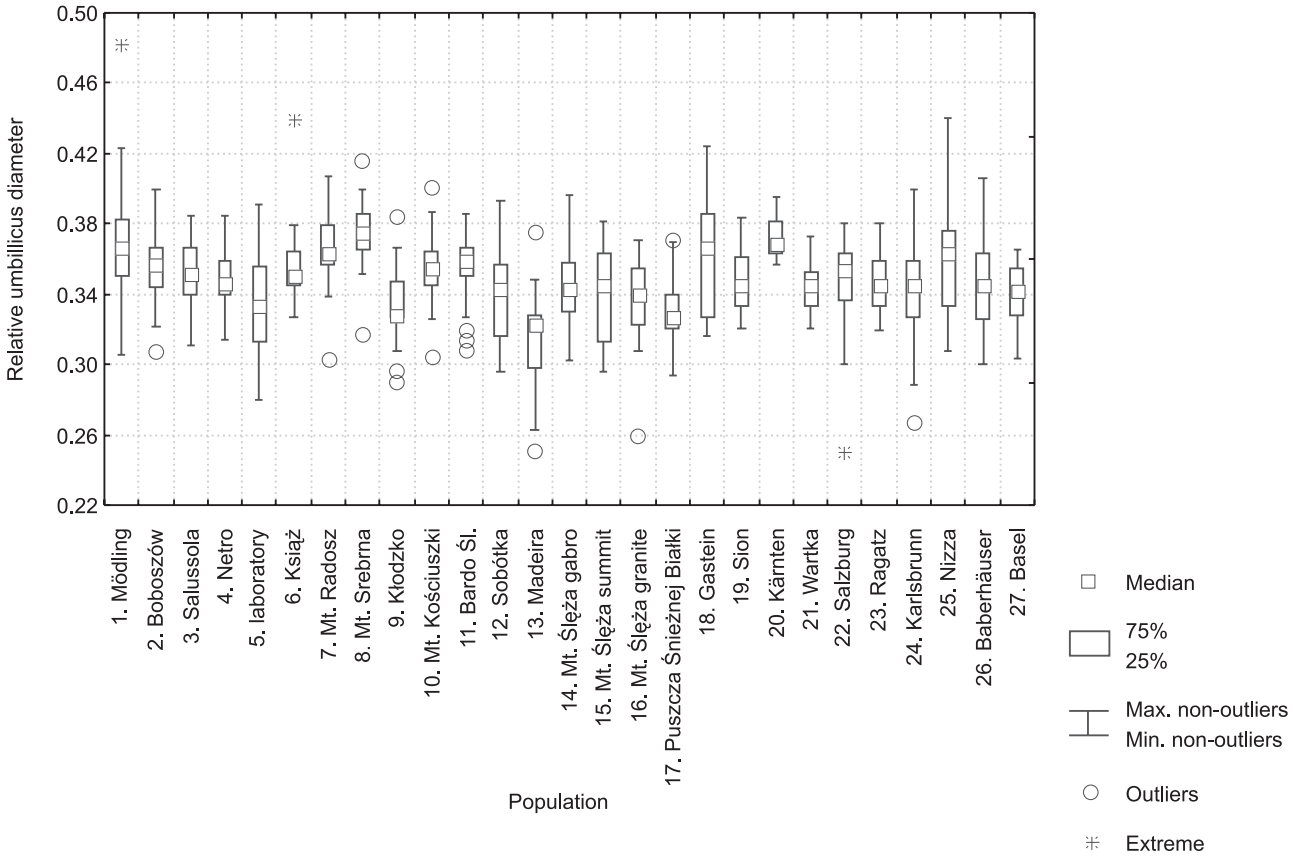

Fig. 15. *Discus rotundatus*: relative umbilicus diameter, interpopulation variation

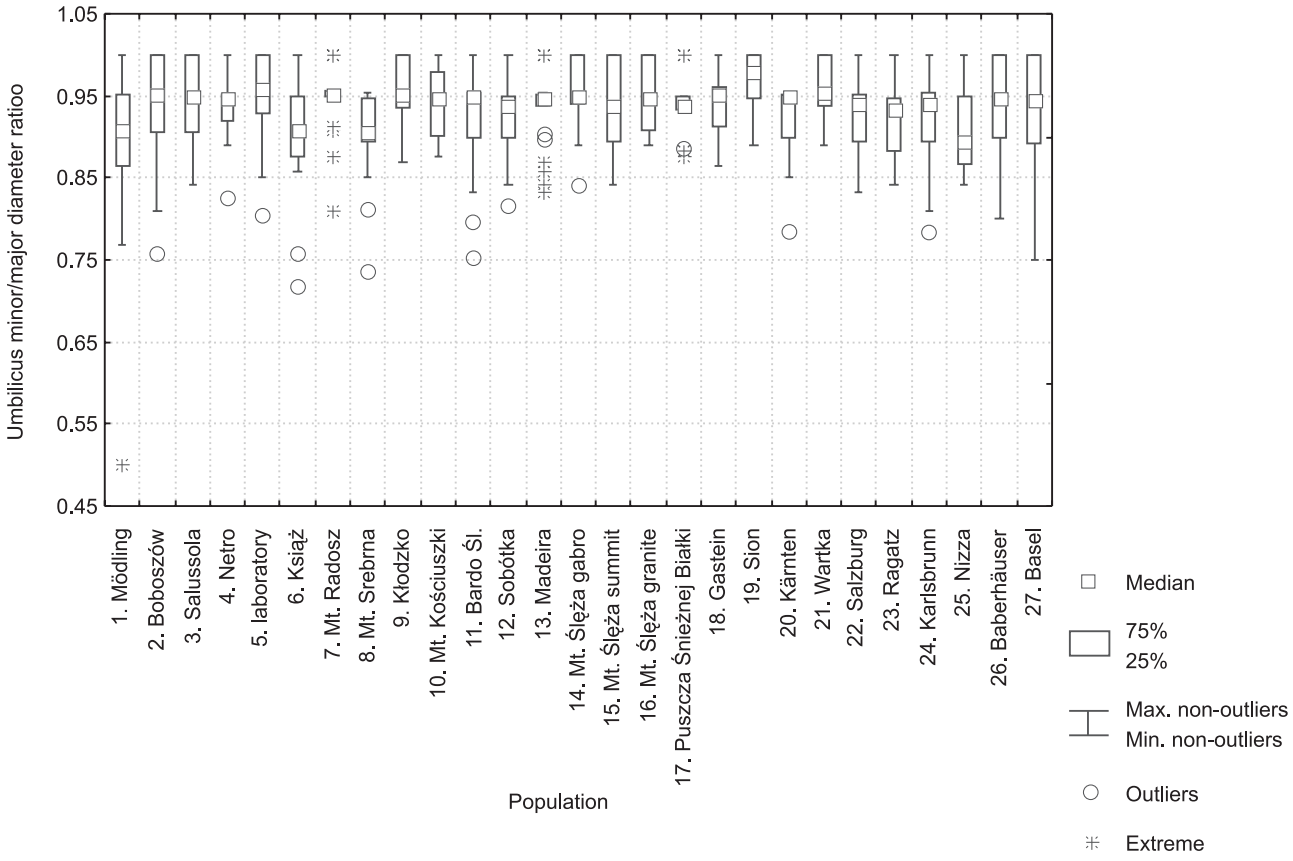

Fig. 16. *Discus rotundatus*: umbilicus minor/major diameter ratio, interpopulation variation

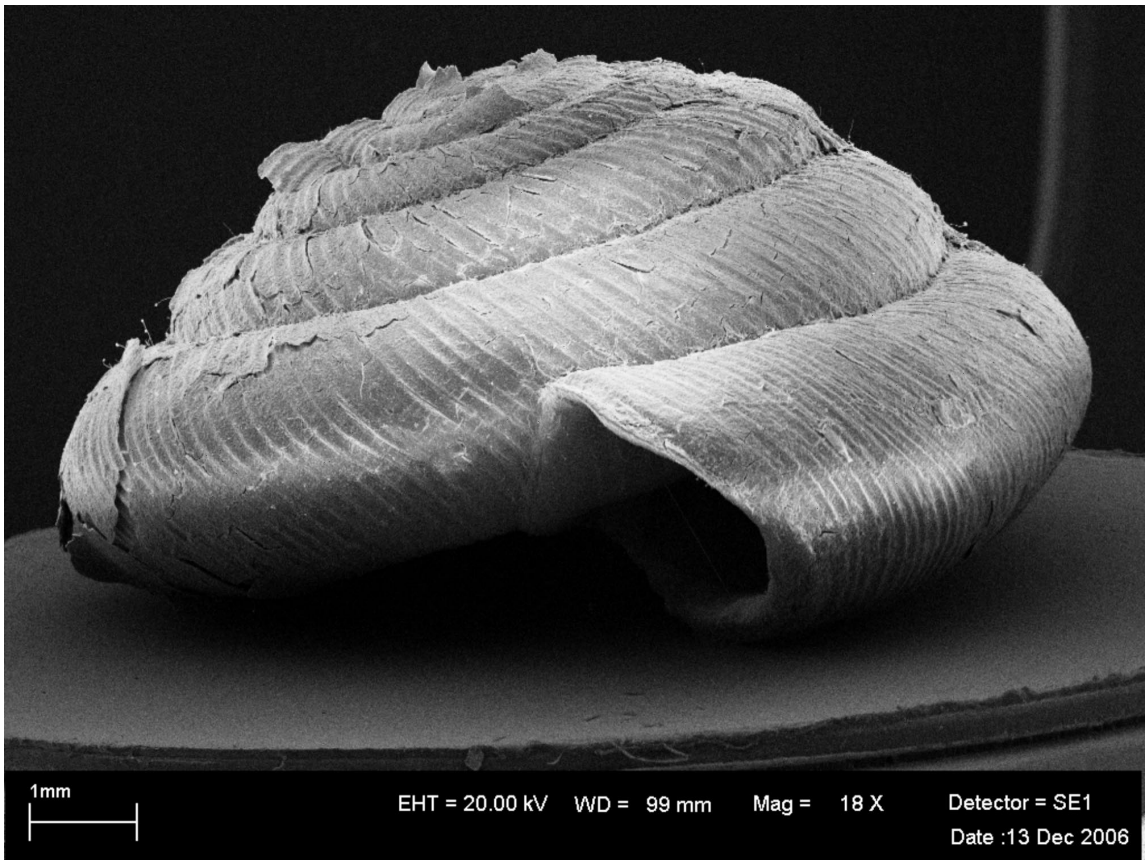

Fig. 17. *Discus rotundatus*: elevated shell

whorls, body whorl height, aperture width, minor and major shell diameter, minor and major umbilicus diameter and relative umbilicus diameter. The characters in most cases varied both between and within populations.

Some shells of laboratory-bred specimens (27 out of 66 cases) were more elevated i.e. had a higher spire compared to wild populations (Fig. 17), and the number of whorls ranged from 6.25 to 7.2 (mean = 6.58; SD = 0.26).

Discus ruderatus

Ranges of variation of the examined characters among laboratory-bred individuals and from selected European populations are shown in Figs 18–30.

The examined populations of *D. ruderatus* were few. Laboratory specimens departed very much from the wild populations in their ranges of variation and mean values of the following characters: number of whorls, shell height, body whorl height, aperture height and width, shell height/shell major diameter ratio, umbilicus minor and major diameter, shell minor and major diameter. Mean values of all these characters in these shells were higher than in the wild populations, while the relative height of body whorl was on average smaller. The examined natural populations did not differ among themselves in a very significant way and it was difficult to point to the most variable characters.

Shells of laboratory-bred specimens (second generation) often had a much more elevated spire (36 out of 61 cases; Fig. 31). The number of whorls in such specimens was 4.75–5.6 (mean = 5.12; SD = 0.29; n = 36).

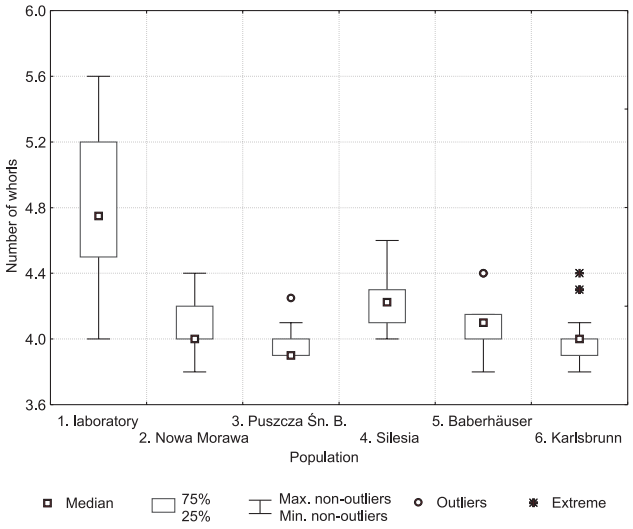

Fig. 18. *Discus ruderatus*: number of whorls, interpopulation variation

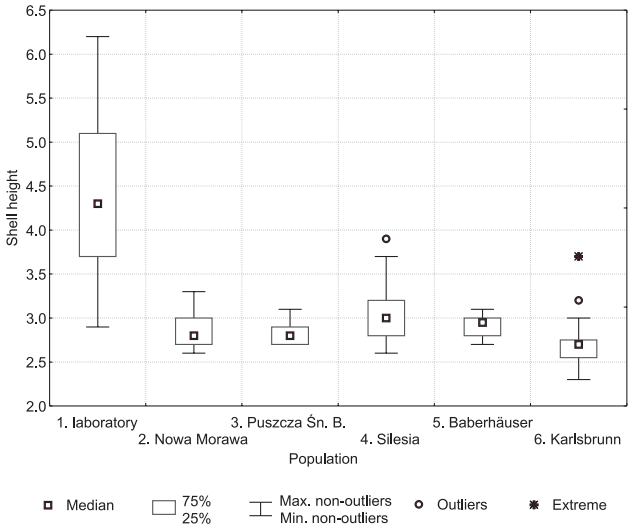

Fig. 19. *Discus ruderatus*: shell height, interpopulation variation

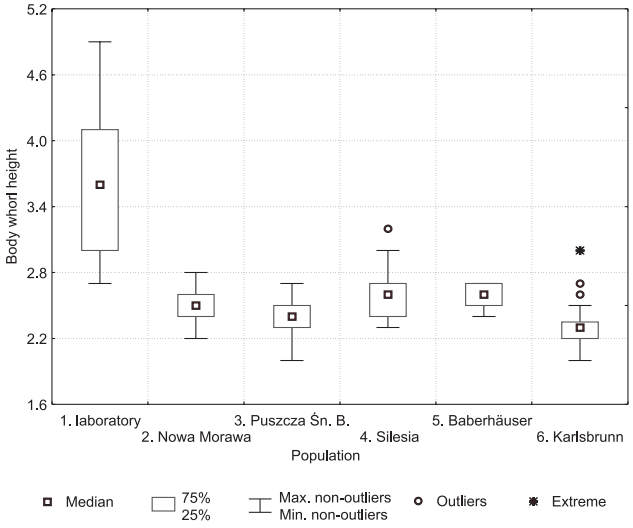

Fig. 20. *Discus ruderatus*: body whorl height, interpopulation variation

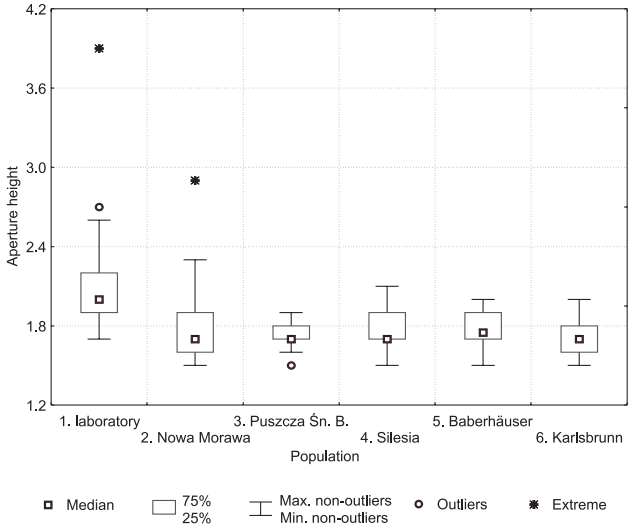

Fig. 21. *Discus ruderatus*: aperture height, interpopulation variation

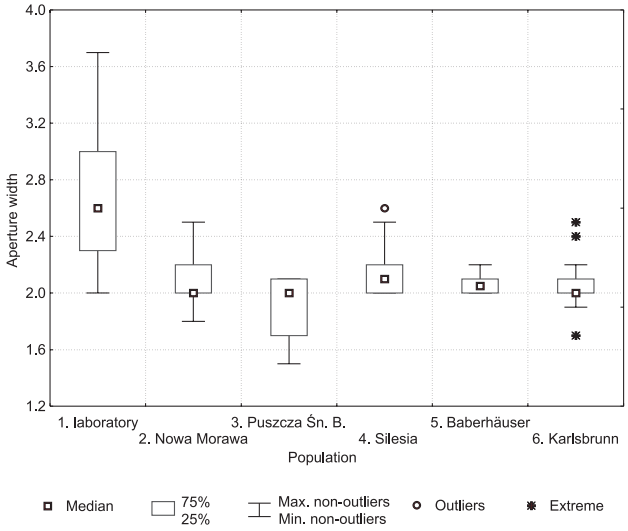

Fig. 22. *Discus ruderatus*: aperture width, interpopulation variation

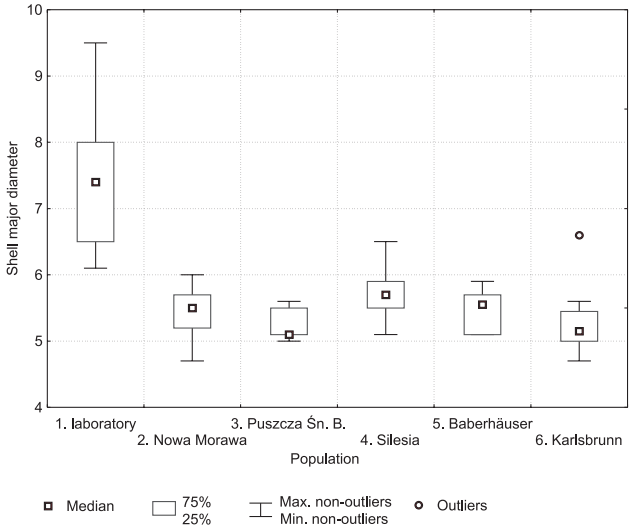

Fig. 23. *Discus ruderatus*: shell major diameter, interpopulation variation

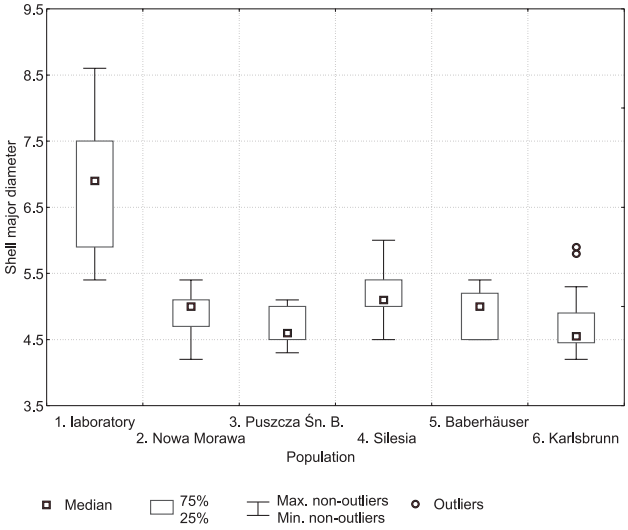

Fig. 24. *Discus ruderatus*: shell minor diameter, interpopulation variation

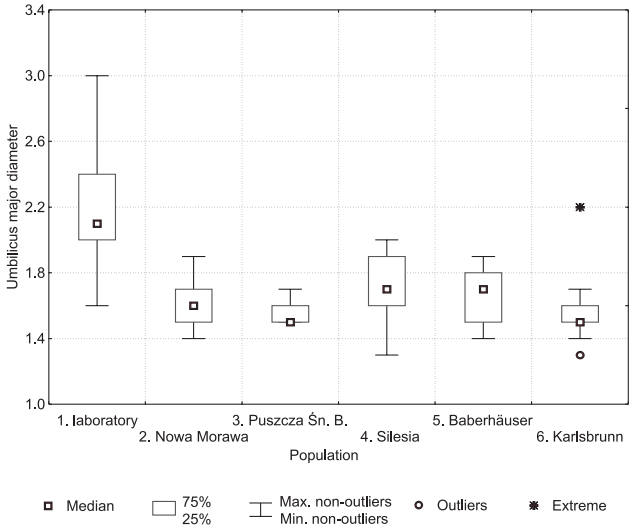

Fig. 25. *Discus ruderatus*: umbilicus major diameter, interpopulation variation

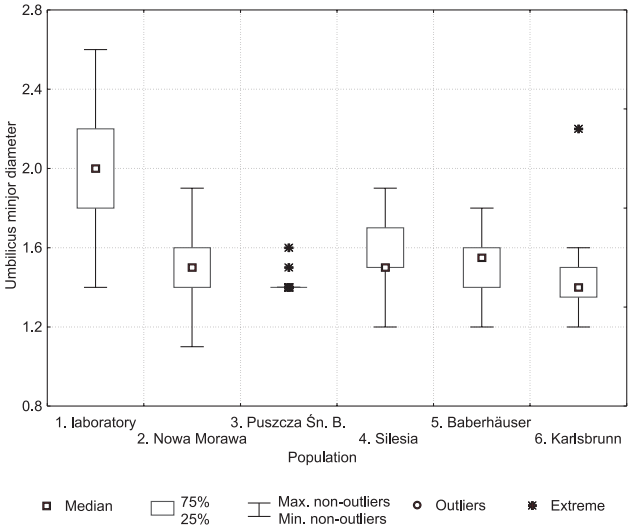

Fig. 26. *Discus ruderatus*: umbilicus minor diameter, interpopulation variation

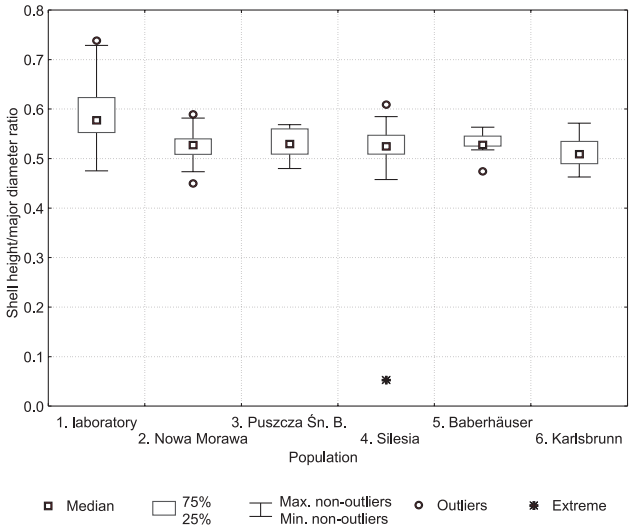

Fig. 27. *Discus ruderatus*: shell height/major diameter ratio, interpopulation variation

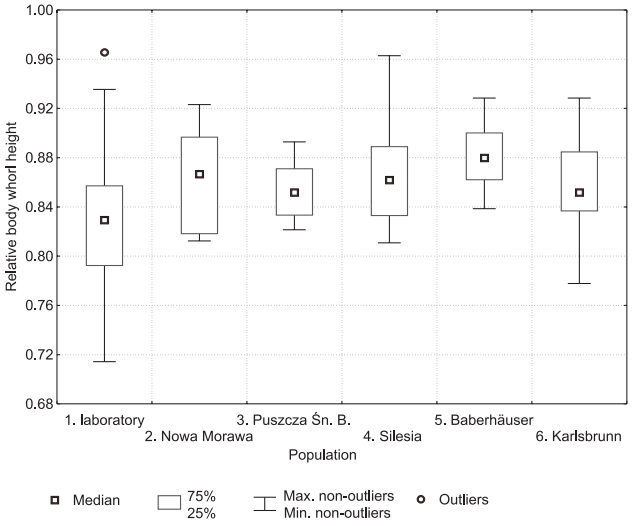

Fig. 28. *Discus ruderatus*: relative body whorl height, interpopulation variation

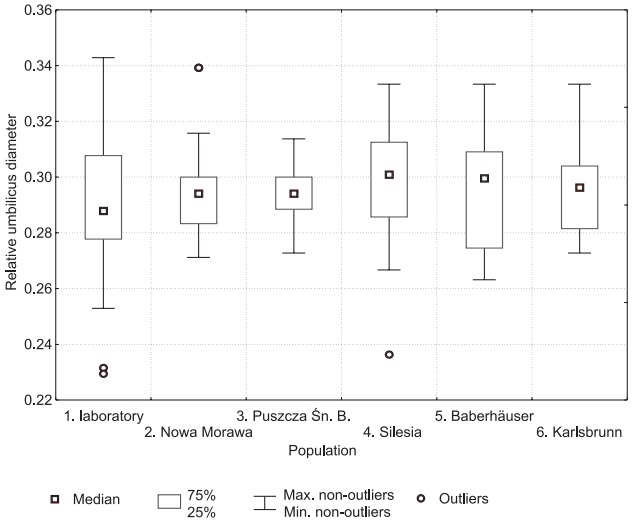

Fig. 29. *Discus ruderatus*: relative umbilicus diameter, interpopulation variation

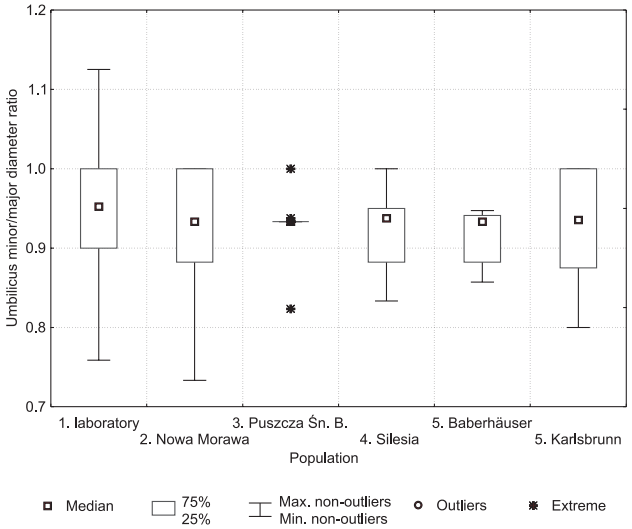

Fig. 30. *Discus ruderatus*: umbilicus minor/major diameter ratio, interpopulation variation

DISCUSSION

Studies on shell variation in the three species of *Discus* had two aims: 1. to ascertain if variation among laboratory-bred individuals departed from such varation in wild populations; 2. to solve the problem of variation and subspecies/varieties within *D. ruderatus* and *D. rotundatus*.

The ranges of variation of the number of whorls and shell measurements are wide in all members of *Discus* (UMIŃSKI 1962), like in all snails which continue growing when sexually mature (POKRYSZKO 1990a). The variation ranges of most parameters of shell size and proportions in laboratory-bred individuals of *D. rotundatus* and *D. ruderatus* are much wider than those of wild populations (cf. Figs 4–16 and 18–30).

Shells of laboratory-bred *D. rotundatus* depart considerably from those of snails from the original population and other European populations in nearly all characters. The examined wild populations also differ among themselves statistically significantly in many characters, but the differences are much smaller. The examined populations of *D. ruderatus* were much fewer than those of *D. rotundatus*, but their characters indicate that the species displays the same shell variation tendency as *D. rotundatus* (cf. Figs 4–16 and 18–30).

Morphometric differences between the laboratory culture material and the original population(s) have been studied only in few snails. Many shell characters in laboratory-bred *Vertigo pusilla* O. F. Müller show a wider range of variation, compared to the original population, but do not assume higher values (POKRYSZKO 1990b). The wider range of variation can be at least partly explained by constant, comfortable conditions of the laboratory culture, which no doubt causes a slackened selection pressure and thus a lower mortality. The higher values of measurements in the laboratory may be explained in a similar way, especially that the growth of both species of *Discus* in the laboratory was faster as a result of the whole-year activity, and the life span was probably longer than in the wild which allowed some individuals to reach a larger size.

However, one of the parameters describing shell proportions – relative height of body whorl – in laboratory-bred *D. rotundatus* was not higher than in the wild populations, in spite of the much higher absolute body whorl height, and in *D. ruderatus* it was even lower, though also in this species the absolute body whorl height was higher than in the wild populations (cf. Figs 6, 14, 22, 28). Such differences in proportions result probably from the tendency to form a descending body whorl and more pronounced spire elevation observed in the laboratory culture.

Laboratory-bred *D. perspectivus* shows a tendency to produce partly scalariform shells, with the body whorl or its part adjacent to the aperture descending, and

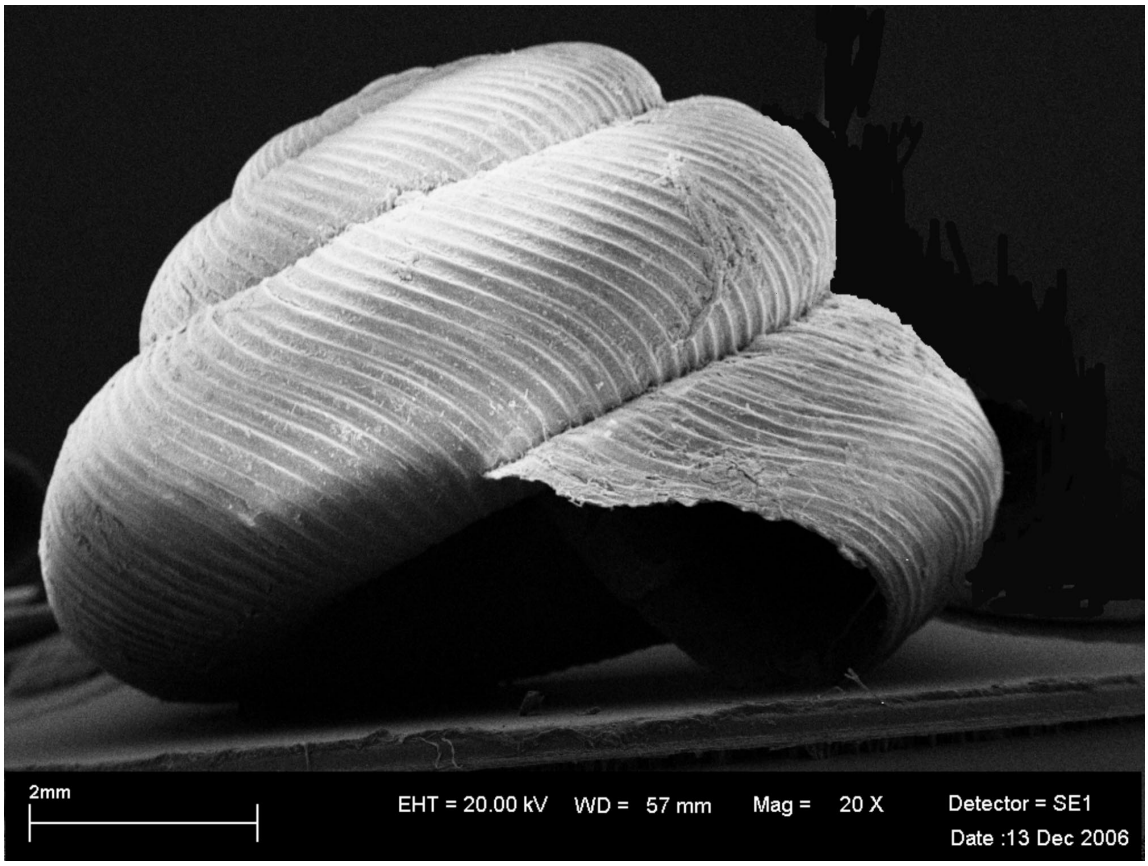

Fig. 31. *Discus ruderatus*: elevated shell

nearly completely separated from the preceding whorl, so that the suture between these two whorls becomes very deep. In this species the last half or, less often, the whole body whorl is scalariform, the phenomenon beginning at 5.3–5.7 whorls (cf. Table 1, Figs 1–3). *D. rotundatus* and *D. ruderatus* in the laboratory culture show only a tendency to form a descending body whorl, sometime erroneusly termed scalariform (UMIŃSKI 1962). In all three species separation and/or descending of the body whorl begins during or just after sexual maturation, and the phenomenon is difficult to explain.

In wild populations specimens showing the above-described shell characters are very rare. BOETTGER (1929), who kept *D. rotundatus* in high-humidity conditions, obtained specimens with very much elevated spire and often with a descending body whorl, already in the first generation hatched from eggs laid in the laboratory; such characters were also observed in individuals collected in caves (BOETTGER 1931). Individuals of *D. ruderatus*, kept by this author for comparison, also in the first generation obtained in the laboratory, showed a tendency to form an elevated spire and descending body whorl. Similar forms of *D. rotundatus* have been described from greenhouses in Berlin (BOETTGER 1930), caves in Belgium (BOETTGER 1939), and of *D. ruderatus* – from the Karkonosze Mts (UMIŃSKI 1962). BOETTGER (1929, 1930) explains this change of shape by humidity and temperature conditions (no sub-zero temperatures). However, since similar forms of *D. rotundatus* are also found in Algeria (see below), where it is difficult to expect favourable humidity conditions, UMIŃSKI (1962) explains such shell modifications by the hibernation period: hibernating snails build flattened shells, and those not forced to hibernate – elevated shells with descending body whorl. According to that author this is a better explanation of the distribution of populations in which the described forms are found (UMIŃSKI 1962: map 3).

Earlier data on the variation of *D. rotundatus, D. ruderatus* and *D. perspectivus* in the taxonomic context have been summarised by UMIŃSKI (1962), who has shown that distinguishing many of the varieties described in literature is unjustified. He accepted the existence of only two subspecies within *D. ruderatus: D. ruderatus ruderatus* and *D. ruderatus pauper,* and the existence, apart from the typical one, of another form within *D. rotundatus: D. rotundatus* f. *abietina*. Based on materials from various parts of the distribution range UMIŃSKI (1962) pointed to the wide range of individual shell variation in *Discus*.

D. ruderatus pauper was described by GOULD (1858) from Petropavlovsk in Kamchatka and from Hakodate on the island of Yeso in Japan, based on considerably flattened shells with a keel on the body whorl. Later,

the subspecies was recorded under different names from Japan (ADAMS 1868, EHRMANN 1933, EHRMANN & BÜTTNER 1927), Tibet (DESHAYES 1870), North Korea (MÖLLENDORFF 1887), Siberia (MOUSSON 1887), Behring Strait islands (WESTERLUND 1889), Amur River shores, northern China (MÖLLENDORFF 1885, 1899) and the vicinity of Lake Baikal (DYBOWSKI 1903) (for synonymy see UMIŃSKI 1962). In populations from localities listed by these authors a varied proportion of specimens have a tendency to form the keel on the body whorl, pronounced to a varied degree, and the tendency is the strongest in populations from the Amur River basin (UMIŃSKI 1962). Since the range of *D. ruderatus pauper* is limited to the eastern part of the range of *D. ruderatus* and the two ranges do not overlap (cf. UMIŃSKI 1962: map 1), and in the examined populations from the remaining part of the range I found no specimens with a keel, regarding *D. ruderatus pauper* as a subspecies seems justified.

D. rotundatus f. *abietina* was described by BOURGUIGNAT (1864) as *Helix abietina* from Algeria; it differs from the typical form in a more elevated spire and deeper suture. In the context of the above data on the variation of all three species, it can be supposed that the form is only an expression of the effect of climatic factors on some populations of *D. rotundatus* and as such is of no taxonomic significance.

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