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SHELL VARIATION IN *HELICODONTA OBVOLUTA* (O. F. MÜLLER, 1774) (GASTROPODA: PULMONATA: HELICIDAE S. LATO)

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ABSTRACT: Biometrical analysis of the material of 668 adult shells of *Helicidonta obvoluta* (Müll.) from Great Britain, Spain, Italy, Switzerland, Germany, Poland, the Czech Republic, Slovakia and Hungary showed a high inter-population variation. Similarity analysis revealed two clusters of populations: one from the centre of the range, another inhabiting its fringes. Snails from the Abruzzi Mts (Central Apennines) had shells similar to those from the central populations, though the area is located on the southern fringe of the distribution range.

KEY WORDS: terrestrial snails, Helicidae, *Helicodonta obvoluta*, shell variation, morphometrics

INTRODUCTION

Helicodonta obvoluta (O. F. Müller, 1774) is among the rare recent snails of Europe. It is a Central European species with the range including the Pyrenees, southern part of the Atlantic coast and the west of France, southern part of Great Britain, Belgium, The Netherlands, Germany, Switzerland, Austria, the Central Sudetes in Poland, southern part of Moravia and Slovakia, as well as northern Hungary, and in the south – a part of Albania and Bosnia, northern Serbia and Calabria in the Apenninic Peninsula (LOŽEK 1955, 1956, KERNEY et al. 1983, RIEDEL 1988, MALTZ 2003b, 2004, WIKTOR 2004). It is a typical forest-dweller, preferring natural, mixed deciduous and deciduous-coniferous forests on calcium-rich substratum in mountainous areas. It lives in humid, shady places, on logs, in litter and under stones, as well as in vegetation-covered ruins and screes (LOŽEK 1955, WIKTOR 1956, 1959, 1972, 2004, KERNEY et al. 1983, RIEDEL 1988, MALTZ 1999, 2003b, 2004), though in the centre of its distribution range it can inhabit also more open and calcium-poorer habitats (CAMERON 1972). The life history of this snail has been thoroughly studied (MALTZ 2003a, 2003c); it is known that *H. obvoluta* lays eggs and hibernates in rotting timber of large logs, only in areas of milder, oceanic climate (Great Britain) can it survive winter in leaf litter (CAMERON 1972). Human interference (clear-felling, removal of dead timber) and climatic changes have a considerable effect on the occurrence of the species. During the climatic optimum (Atlantic Period) its range was probably somewhat wider, extending more to the north and east of the continent, which is indicated e.g. by isolated localities in Schleswig-Holstein or by numerous subfossil sites in the Czech Republic, Slovakia (LOŽEK 1955), Denmark (GIROD 1968), Great Britain (KERNEY 1999), or Spain (ALTONAGA et al. 1994). At present it has small, isolated populations whose survival depends on human activities: on the one hand destruction of natural habitats, on the other – taking proper conservation measures. In Poland it is a species of recognised conservation status (PAWŁOWSKA & POKRYSZKO 1998, WIKTOR & RIEDEL 2002, MALTZ 2004).

Compared with the extensive knowledge of the occurrence, life history and threats, the information on shell variation of *H. obvoluta* is very fragmentary. Identification keys and guides contain various descriptions of its shell (GEYER 1909, EHRMANN 1956, LOŽEK 1956, URBAŃSKI 1957, SHILEYKO 1978, KERNEY et al. 1983, KERNEY 1999, CAMERON 2003, WIKTOR 2004). Adult shells are flattened, with a wide and deep umbilicus, flat spire and tightly coiled whorls, separated by a

Fig. 1. Shells of *Helicodonta obvoluta*: juvenile stages with distinct hairs (A), adult just after lip completion (B), adult with periostracum partly damaged, hairless (C)

deep suture. The surface of the dark brown shell is covered by long, moderately dense hairs, best visible in juvenile or newly mature specimens (Fig. 1). The aperture is surrounded by a lip of pink or pink-brown colour, with two elongate thickenings, one on the basal and one on the palatal part of the lip; sometimes they resemble teeth and their presence makes the aperture three-sinuate. Literature data on the values of basic shell parameters are summarised in Table 1. In most cases they pertain only to the shell diameter, sometimes also shell height and number of whorls are given. There is no published information on the intra- and interpopulation variation of the species, hence the idea of this paper.

Table 1. *Helicodonta obvoluta*. Shell parameters according to various authors

Parameter source	D (mm)	H (mm)	N
GEYER 1909	11	5	6
EHRMANN 1956	11	5	–
LOŽEK 1956	11–13	5–6	6
URBAŃSKI 1957	10–11	5	–
SHILEYKO 1978	10–14	5–6	6
KERNEY et al. 1983	11–15	5–7	5–6
KERNEY 1999	11–14	–	–
WIKTOR 2004	10–11 (15)	5–6	–

MATERIAL AND METHODS

Shell variation in *H. obvoluta* was studied in 2004–2006. The material included 668 adult shells collected in various parts of Europe (Fig. 2), originating from museum and private collections (Table 2). Most of the labels were incomplete. Apart from information on collecting locality (country, town or village and its surroundings, sometimes a brief note on the habitat, e.g. beech forest or slope forest) and date, there were no detailed habitat data.

Biometrical analysis included measurements of the most numerous samples from the following populations: three from Poland (PL-S, PL-M and PL-K), three from Germany (DE-S, DE-B and DE-BW), two from Italy (IT-AB and IT-AL) and one each from Switzerland

Table 2. *Helicodonta obvoluta*. List of material examined

Collection site	Number of specimens Σ = 668	Property of
Poland (PL):	**147**	
Ślęża mountain range (S)	39	Museum of Natural History, Wrocław University, Wrocław
Muszkowicki Las Bukowy reserve (M)	44	
Książ ravine zone (K)	64	
Germany (DE):	**298**	
Saxony (S):	29	Museum für Naturkunde, Berlin
Drezden neighbourhood	29	Zoologische Staatssammlung, München
Bayern (B):	146	Staatliches Museum für Naturkunde, Stuttgart
Günzburg, Banz, Stamberger	107	Staatliches Museum für Naturkunde, Stuttgart
Marktschellenberg	39	
Baden Württemberg (BW):	123	
Kreis Reutlingen – Eningen unter Achalm	57	
Kreis Tübingen – Bad Niedernau	24	
Kreis Heidenheim – Steinheim	42	
Italy (IT):	**38**	
Abruzzi (AB):	8	Zoologische Staatssammlung, München
La Maiella – Fonte Romana	5	Zoologische Staatssammlung, München
Forca d'Acero	3	Zoologisches Museum, Hamburg
Alps (AL):	30	
Provincia Brescia, Covalu (Iseo)	2	
Evemo di San Colombano	12	
Castello di Brendola, Monti Berici	16	
Switzerland (CH):	**34**	
Axenstein ober Brunnen	34	Zoologisches Museum, Hamburg
Great Britain (GB):	**70**	
Buriton	43	Museum of Natural History, Wrocław University, Wrocław
Harting	16	
Rook Clift	11	
Czech Republic (CZ):	**52**	
Moravia:	52	M. HORSÁK & V. LOŽEK collection
Javornik	16	
Suchovske Mlyny	9	
Stary Hrozenkov	9	
Vapenky	11	
Bystrice p. Lopenikem	7	
Slovakia (SK):	**10**	
Stara Lehota	7	M. HORSÁK & V. LOŽEK collection
Biele Karpaty	3	
Spain (ES):	**14**	
Pyrenees, Vulla	14	R. A. D. CAMERON collection
Hungary (HU):	**5**	
Beech Mts.	5	R. A. D. CAMERON collection

(CH), Great Britain (GB), the Czech Republic (CZ), Slovakia (SK), Hungary (HU) and Spain (ES).

Seven metric characters were measured to the nearest 0.01 mm (Fig. 3), whorls were counted to the nearest 0.1 according to EHRMANN's (1956) method; seven coefficients describing shell proportions were calculated (Table 3). The data were subject to basic statistical analysis (mean, median and modal values, variance and standard deviation); the results served as the basis for determining interpopulation variation, correlations among individual parameters of shells from different populations, and betwen latitude and longitude of the sites on the one hand and shell parameters on the other (Pearson correlation (r)).

Similarity among samples and populations was analysed using Nei index (I_N), applied successfully in faunistic and ecological studies to measure similarity

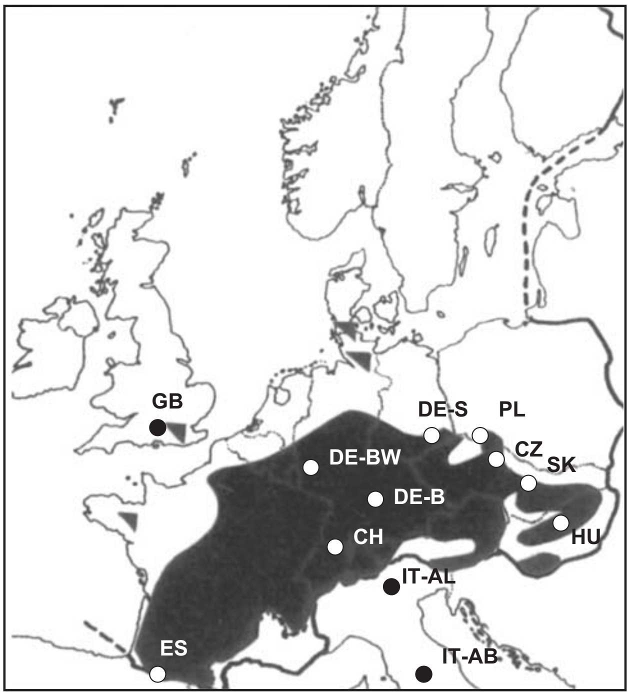

Fig. 2. Sampling sites: IT-AB – Italy-Abruzzi, IT-AL – Italy-Alps, ES – Spain, CH – Switzerland, GB – Great Britain, DE-B – Germany-Bavaria, DE-BW – Germany-Baden Württemberg, DE-S – Germany-Saxony, PL – Poland, CZ – Czech Republic, SK – Slovakia, HU – Hungary

Table 3. *Helicodonta obvoluta*. Abbreviations of shell parameters

Abbreviation	Parameter
D	shell major diameter
d	shell minor diameter
H	shell height
UD	umbilicus major diameter
ud	umbilicus minor diameter
h	mouth height
w	mouth width
N	number of whorls
D/d	shell major diameter/shell minor diameter ratio
D/H	shell major diameter/shell height ratio
UD/D	umbilicus major diameter/shell major diameter ratio
UD/ud	umbilicus major diameter/umbilicus minor diameter ratio
h/w	mouth height/mouth width ratio
hw	mouth height × mouth width index
D/N	shell major diameter/number of whorls ratio

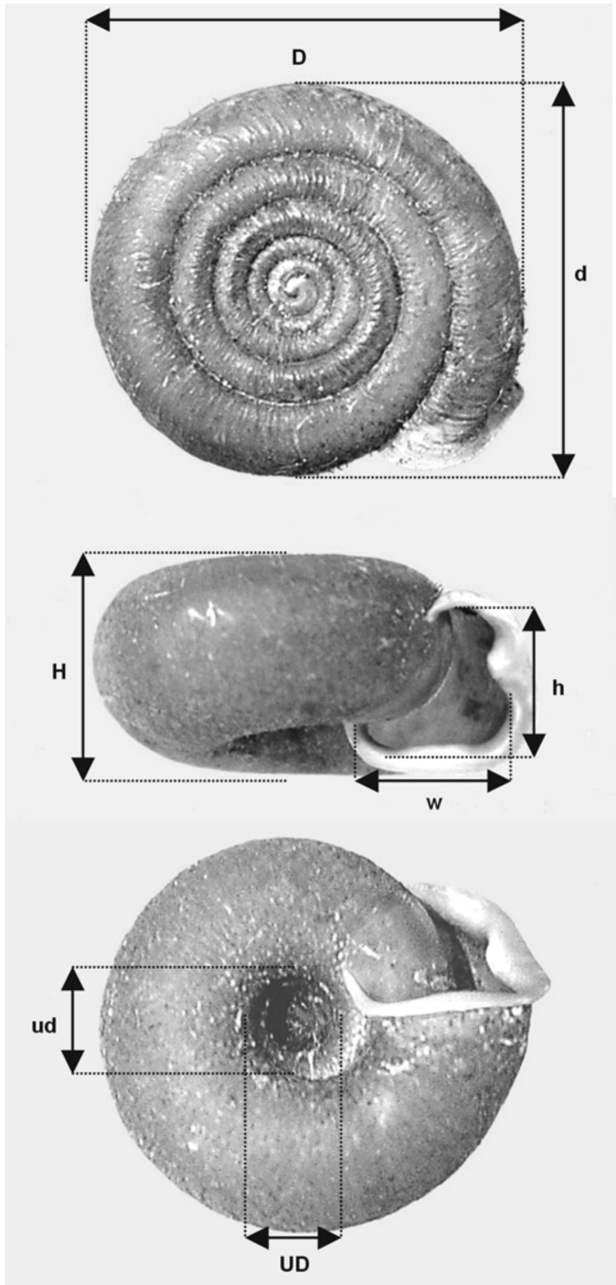

Fig. 3. Shell parameters of *Helicodonta obvoluta* (for designations of variables see Table 3)

between snail communities (e.g. POKRYSZKO & CAMERON 2005). Similarities among the 14 samples were based on mean values of the 15 shell parameters. Intervals grouping similar mean values were determined for each parameter (1. from the highest mean value A to that value decreased by 5%, i.e. A – 5%; 2. from the highest mean value B selected from among the values outside interval 1 to value B – 5%, etc.); symbols were assigned to each interval (interval 1 – a, interval 2 – b, etc.). Then, as a result of pairwise comparison for each parameter (total of 91 pairs) populations were assigned 1 for the same letter symbol and 0 whenever the symbols were different. Sums of these values (range from 0 to 15) were then used to calculate the Nei index (I_N = number of symbols common to each pair of samples divided by the geometric mean of all the symbols for each sample). In order to determine similarity between the populations, Student t-test was used, assuming different variance. The resulting values $t<t_0$ for each pair of populations were assigned 1 while values $t>t_0$ were assigned 0. Sums of values confirming the zero hypothesis (1 values) were used as the basis to calculate the Nei index, in a way analogous to that used for similarity among the samples. Since this was the first attempt at adapting morphometric data to the Nei formula, all intermediate steps are shown below (Tables 4–10). Dendrograms were constructed according to ALEXANDROWICZ (1987).

Statistical analysis was performed with Microsoft Excel, version PL 2003.

RESULTS

Among the 668 examined shells 661 (98.95%) were typical (Fig. 4A). The material included three albino shells (0.45%) (Germany, Bavaria) (Fig. 4E) and shells of atypical shape: two with elevated spire (0.3%) (Germany, Baden Württemberg) (Fig. 4C), one (0.15%) with descending body whorl (Slovakia, Biele Karpaty) (Fig. 4B) and one (0.15%) with a crest on the body whorl (Germany, Bavaria) (Fig. 4E).

Table 4 shows variation ranges of parameters of the examined shells. In the case of shell major diameter (D), shell height (H) and number of whorls (N) most ranges of variation reported by various authors (Fig. 5) are within the ranges determined in this study. Only the ranges for N (5–6) and D (11–15 mm) reported by KERNEY et al. (1983) are outside the determined ranges (N: 5.3–6.3; D: 9.95–14.25). Values of arithmetic means, SD, minima and maxima of the parameters are shown in graphs for the whole of Europe (Fig. 6a–b) and for individual populations (Fig. 7a–h). The widest ranges of variation were displayed by samples from Germany (DE-B for D, d, H, UD, ud, h, w, N and DE-BW for D, d, H, UD, N), the Italian Alps (IT-AL for D, d, w, N), Poland (PL for UD, ud, N), the Czech Republic (CZ for D and H) and Great Britain (GB for H and w), the smallest – by those from Hungary (HU for D, d, H, UD, ud, h, w, N), Spain (ES for D, d, H, UD, ud, w) and the Apennines (IT-AB for UD, ud, w and N).

Table 4. *Helicodonta obvoluta*. Shell variation ranges in the material examined

Parameter	Range (mm)	Parameter	Range
D	9.96–14.25	N	5.30–6.30
d	8.82–12.63	D/d	1.04–1.23
H	4.45–6.93	D/H	1.82–2.52
UD	2.65–5.18	UD/D	0.25–0.42
ud	2.53–4.63	UD/ud	0.99–1.43
h	2.25–6.41	h/w	0.44–1.22
w	4.30–6.30	D/N	1.79–2.36

Assigning mean values of shell parameters of the samples (Table 5) to similarity intervals (within each parameter) expressed as letter symbols is shown in Table 6. Two coefficients, D/d and D/H, showed the greatest scatter of mean values; the smallest scatter was displayed by hw, UD/D and UD. Values of the Nei index (I_N) (Table 8), calculated based on similarities between the means expressed as letter symbols (Table 7), reflect similarities, presented in dendrogram I (Fig. 8). Two main clusters of samples could be distinguished: one (I_N=0.65), including samples from populations from the fringes of the range (PL-M+ES+IT-AL+HU, I_N=0.77; PL-S+PL-K, I_N=0.8; GB+CZ+SK, I_N=0.87), another (I_N=0.6) including samples from the central populations and from Saxony (subcluster from Germany: DE-B+DE-S+DE-BW, I_N=0.74). The two clusters are rather dissimilar (I_N=0.29), the most outlying being the sample from the Apenninic Penisula (I_N=0.17).

Similarities between the populations represented by the samples, based on calculated values of t and t_0 (Student t-test, α=0.05) for individual parameters (Table 9) and sums of values $t<t_0$ (Table 10), are presented in dendrogram II (Fig. 9). There is a high similarity between the populations from the Italian Alps and Hungary as well as the Czech Republic and Slovakia (I_N=0.93). Cluster IT-AL+HU is very similar to the population from Muszkowice (PL-M) (I_N=0.8), while CZ+SK – to that from Spain (ES) (I_N=0.77). The two clusters, together with the English population (GB) (I_N=0.66) and the pair PL-S+PL-K (I_N=0.6), form a group of populations from the fringes of the range (I_N=0.51). The second group includes clusters

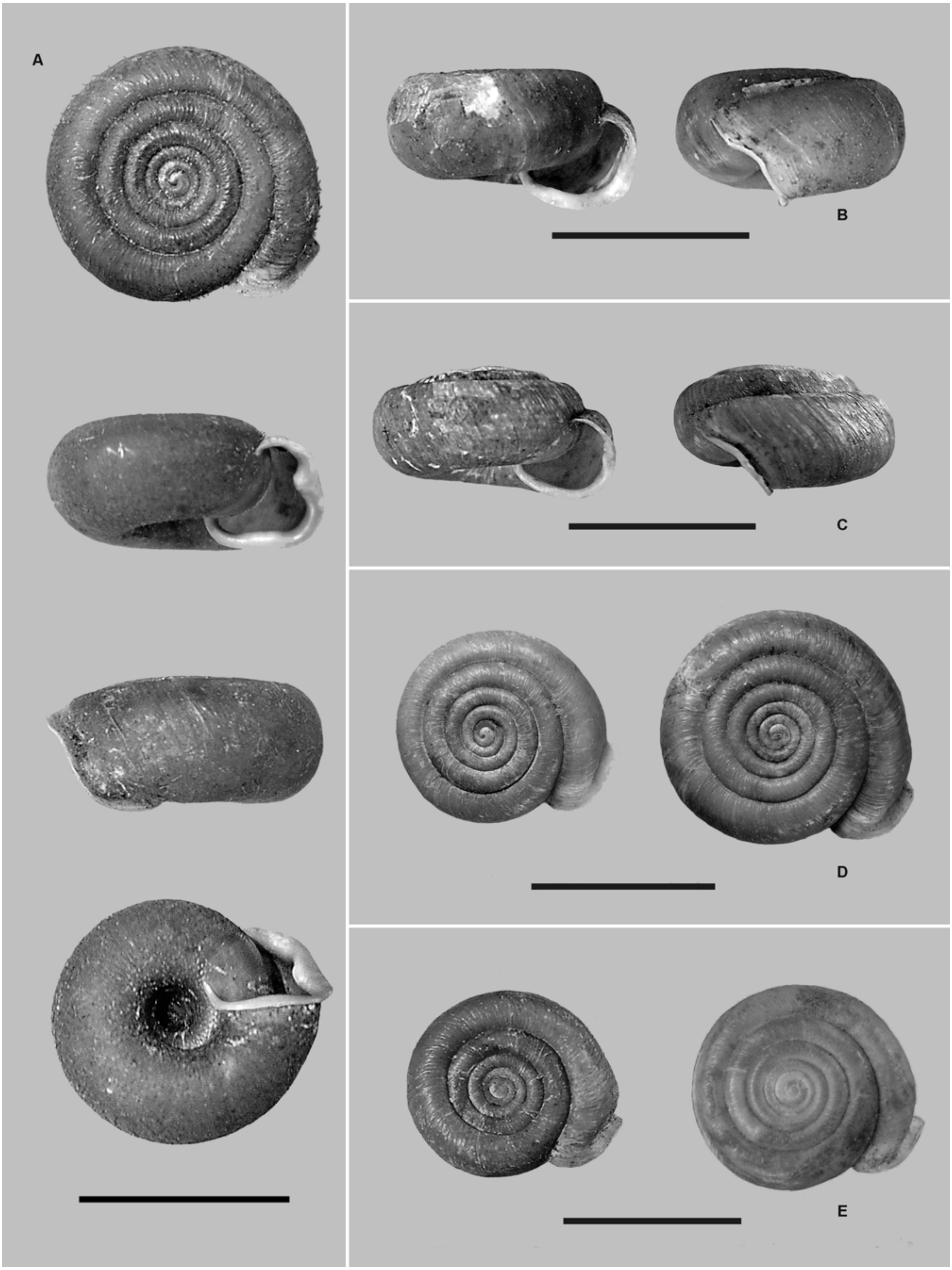

Fig. 4. Shells of *Helicodonta obvoluta*: A – shell shown from four different sides, B – body whorl descending, C – elevated spire, D – extremes of size variation, E – shell with a crest (left) and albino shell (right). Scale bar 10 mm [photo: R. A. D. CAMERON]

Table 5. *Helicodonta obvoluta*. Mean values of shell parameters in the examined populations

	D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
PL-S	12.413	11.013	5.798	4.349	3.739	5.324	5.546	5.835	1.127	2.146	0.350	1.166	0.961	29.580	2.127
PL-K	12.578	11.334	5.800	3.985	3.464	5.347	5.537	5.913	1.110	2.170	0.317	1.153	0.967	29.637	2.127
PL-M	12.720	11.385	5.807	3.806	3.383	5.449	5.574	5.866	1.118	2.192	0.299	1.127	0.978	30.409	2.168
DE-B	11.783	10.349	5.425	3.631	3.225	5.087	5.088	5.714	1.139	2.177	0.308	1.126	1.000	25.951	2.061
DE-BW	11.446	10.085	5.319	3.468	3.109	4.872	4.865	5.657	1.135	2.155	0.303	1.117	1.002	23.767	2.023
DE-S	12.033	10.562	5.675	3.662	3.352	5.030	5.006	5.803	1.139	2.123	0.305	1.093	1.005	25.269	2.073
IT-AB	10.753	9.376	5.214	3.569	3.095	4.664	4.770	5.500	1.148	2.065	0.332	1.156	0.977	22.297	1.955
IT-AL	12.842	11.132	5.946	3.863	3.484	5.715	5.517	5.970	1.154	2.161	0.301	1.111	1.038	31.609	2.151
GB	12.681	11.014	5.931	3.763	3.421	5.420	5.427	5.677	1.152	2.141	0.297	1.101	1.000	29.486	2.233
CZ	12.828	11.238	5.903	3.871	3.511	5.396	5.383	5.800	1.142	2.176	0.302	1.104	1.003	29.086	2.211
SK	12.550	11.107	5.947	3.759	3.423	5.282	5.188	5.820	1.130	2.119	0.299	1.097	1.019	27.458	2.155
CH	11.469	9.974	5.314	3.319	2.955	4.834	4.909	5.741	1.150	2.161	0.289	1.123	0.986	23.764	1.997
ES	12.529	11.006	5.717	3.869	3.479	5.473	5.616	5.886	1.139	2.193	0.309	1.113	0.975	30.768	2.129
HU	12.688	11.188	6.016	3.718	3.416	5.610	5.700	5.860	1.135	2.109	0.293	1.089	0.984	31.983	2.165

Table 6. *Helicodonta obvoluta*. Intervals of similarity of shell parameters with assignment of symbols a–f (each interval from the highest mean value to that value decreased by 5%)

	D	d	H	UD	ud
a	12.842–12.186	11.385–10.816	6.016–5.715	4.349–4.132	3.739–3.553
b	12.033–11.431	10.562–10.034	5.675–5.391	3.985–3.785	3.511–3.336
c	10.752–	9.973–9.475	5.319–5.053	3.763–3.575	3.225–3.064
d		9.376–		3.569–3.390	2.955–
e					
f					
	h	**w**	**N**	**D/d**	**D/H**
a	5.715–5.429	5.700–5.415	5.970–5.672	1.154–1.097	2.193–2.084
b	5.420–5.149	5.383–5.114	5.657–5.374		2.065–
c	5.087–4.833	5.088–4.834			
d	4.664–	4.770–			
e					
f					
	UD/D	**UD/ud**	**h/w**	**hw**	**D/N**
a	0.350–0.333	1.166–1.107	1.038–0.986	31.983–30.383	2.233–2.122
b	0.332–0.316	1.104–1.049	0.984–0.935	29.637–28.155	2.073–1.969
c	0.309–0.294			27.458–26.086	1.955–
d	0.293–0.278			25.951–24.654	
e				23.767–22.578	
f				22.297–	

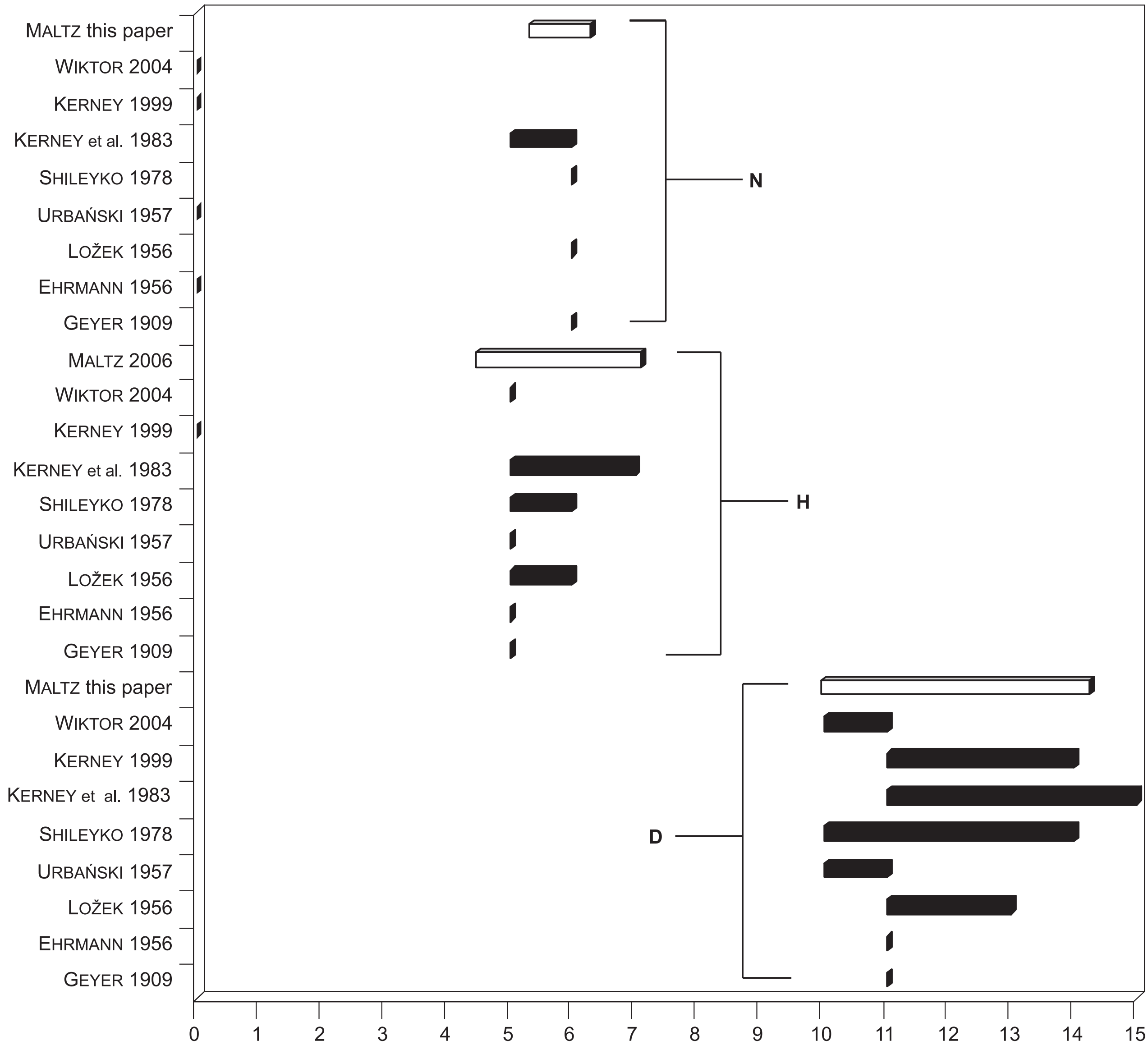

Fig. 5. Variability ranges of three parameters (D, H, N): literature records (black), own measurements (white)

DE-S+DE-B (I_N=0.73) and DE-BW+IT-AB (I_N=0.67), with the Swiss population (CH) (I_N=0.6), for which I_N=0.33. The group represents central populations, as well as those from Saxony and the Abruzzi Mts. The similarity between the two groups is slight (I_N=0.26). The mean values of shell parameters in the first group are higher than European means, in contrast to the mean values of the second group (Fig. 10).

Values of Pearson correlation coefficients among particular parameters of shells from the 14 populations are presented in Table 11. Out of 1,470 correlations, 520 are statistically significant ($|r|$ =0.5). All the populations (100%) show a positive correlation between D and d, D and h, D and hw, D and D/N, d and hw, h and hw, w and hw, as well as hw and D/N, 13 populations (93%) – between D and N, d and h, d and N, d and D/N, Ud and ud, UD and UD/D, 12 (86%) – between D and w, d and H, d and w, h and w, w and D/N, N and hw, 11 (79%) – between H and h, h and D/N, 10 (71%) – between H and hw, ud and UD/D, w and N, nine (64%) – between d and ud, h and h/w, eight (57%) – between D and ud, h and N, and seven (50%) – between H and D/N. The following parameters are negatively correlated: H and D/H (79% populations), ud and UD/ud, w and h/w (14%) as well as D and h/w, h/w and D/N (7%). The greatest number (n_r) of statistically significant correlations among the shell parameters was found for the populations from Hungary (HU) (n_r=67; 72%), Italy (IT-AB) (n_r=47; 51%) and Slovakia (SK) (n_r=43; 46%), the lowest – for those from Poland (PL-S) (n_r=25; 27%) and Spain (ES) (n_r=29; 31%).

Correlations between longitude/latitude and the shell parameters based on Pearson coefficients are shown in Tables 12 and 13. A positive correlation $|r|$ =0.5 was found only between latitude and D, d and D/N, a negative correlation – between longitude and D/d.

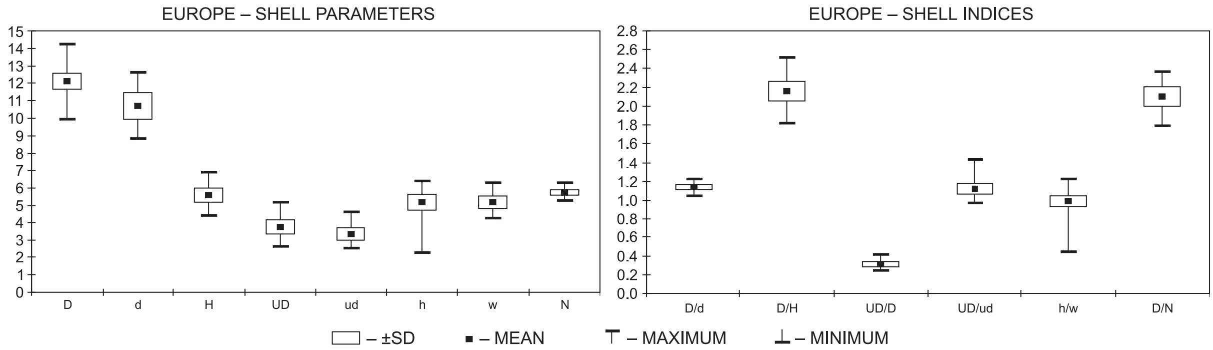

Fig. 6. Parameters of 668 shells of *Helicodonta obvoluta*

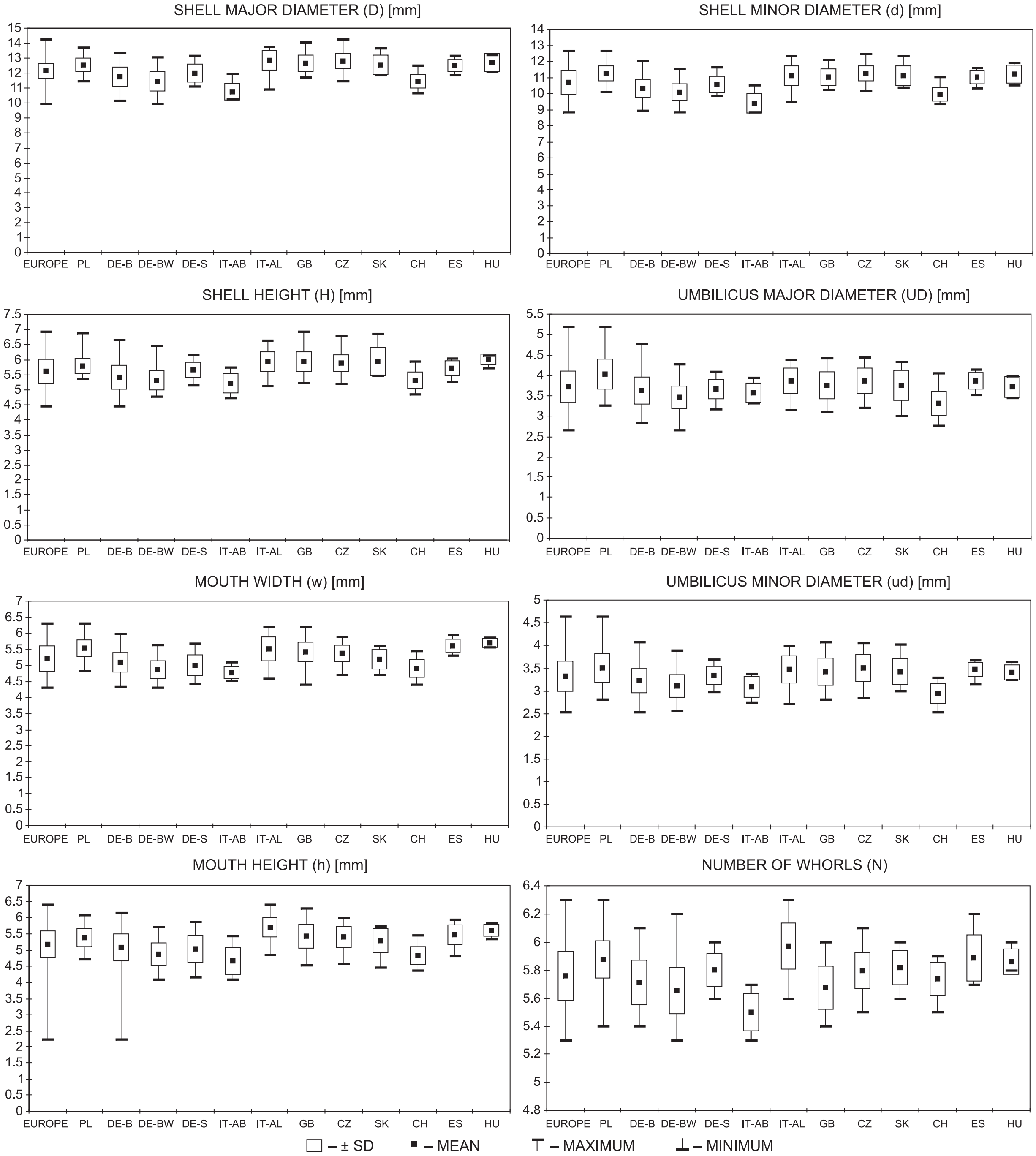

Fig. 7. Variation of eight parameters in populations of *Helicodonta obvoluta*

Table 7. *Helicodonta obvoluta*. Similarities among mean values of shell parameters expressed as letter symbols a–f

	D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
PL-S	a	a	a	a	a	b	a	a	a	a	a	a	b	b	a
PL-K	a	a	a	b	b	b	a	a	a	a	b	a	b	b	a
PL-M	a	a	a	b	b	a	a	a	a	a	c	a	b	a	a
DE-B	b	b	b	c	c	c	c	a	a	a	c	a	a	d	b
DE-BW	b	b	c	d	c	c	c	b	a	a	c	a	a	e	b
DE-S	b	b	b	c	b	c	c	a	a	a	c	b	a	d	b
IT-AB	c	d	c	d	c	d	d	b	a	b	b	a	b	f	c
IT-AL.	a	a	a	b	b	a	a	a	a	a	c	a	a	a	a
GB	a	a	a	c	b	b	a	a	a	a	c	b	a	b	a
CZ	a	a	a	b	b	b	b	a	a	a	c	b	a	b	a
SK	a	a	a	c	b	b	b	a	a	a	c	b	a	c	a
CH	b	c	c	e	d	c	c	a	a	a	d	a	a	e	b
ES	a	a	a	b	b	a	a	a	a	a	c	a	b	a	a
HU	a	a	a	c	b	a	a	a	a	a	d	b	b	a	a

Table 8. *Helicodonta obvoluta*. Nei index values for similarities between the samples

	PL-S	PL-K	PL-M	DE-B	DE-BW	DE-S	IT-AB	IT-AL	GB	CZ	SK	CH	ES	HU
PL-S	1	0.8	0.667	0.267	0.2	0.2	0.2	0.6	0.667	0.6	0.533	0.267	0.667	0.6
PL-K	0.8	1	0.8	0.267	0.2	0.267	0.267	0.733	0.733	0.733	0.6	0.267	0.8	0.667
PL-M	0.667	0.8	1	0.333	0.267	0.333	0.2	0.933	0.667	0.667	0.6	0.267	1	0.8
DE-B	0.267	0.267	0.333	1	0.733	0.867	0.2	0.4	0.4	0.333	0.4	0.6	0.333	0.267
DE-BW	0.2	0.2	0.267	0.733	1	0.6	0.4	0.333	0.267	0.267	0.267	0.667	0.267	0.133
DE-S	0.2	0.267	0.333	0.867	0.6	1	0.067	0.4	0.533	0.467	0.467	0.533	0.333	0.4
IT-AB	0.2	0.267	0.2	0.2	0.4	0.067	1	0.133	0.067	0.067	0.067	0.2	0.2	0.133
IT-AL	0.6	0.733	0.933	0.4	0.333	0.4	0.133	1	0.733	0.733	0.667	0.333	0.933	0.733
GB	0.667	0.733	0.667	0.4	0.267	0.533	0.067	0.733	1	0.867	0.867	0.267	0.667	0.733
CZ	0.6	0.733	0.667	0.333	0.267	0.467	0.067	0.733	0.867	1	0.867	0.267	0.667	0.6
SK	0.533	0.6	0.6	0.4	0.267	0.467	0.067	0.667	0.867	0.867	1	0.267	0.6	0.667
CH	0.267	0.267	0.267	0.6	0.667	0.533	0.2	0.333	0.267	0.267	0.267	1	0.267	0.2
ES	0.667	0.8	1	0.333	0.267	0.333	0.2	0.933	0.667	0.667	0.6	0.267	1	0.8
HU	0.6	0.667	0.8	0.267	0.133	0.4	0.133	0.733	0.733	0.6	0.667	0.2	0.8	1

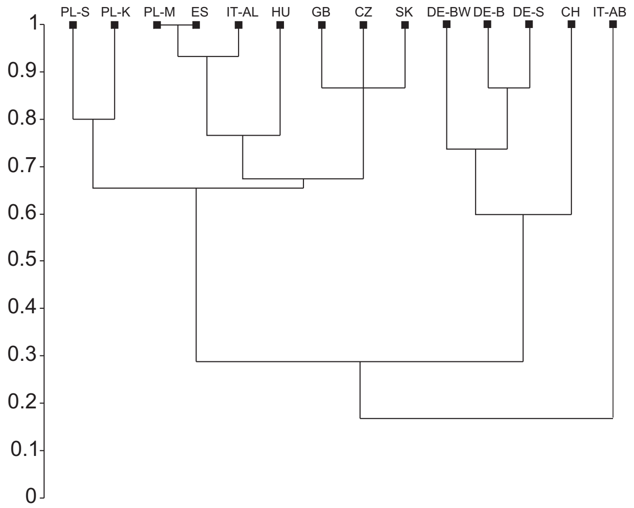

Fig. 8. Dendrogram of Nei similarities among the samples of *Helicodonta obvoluta*

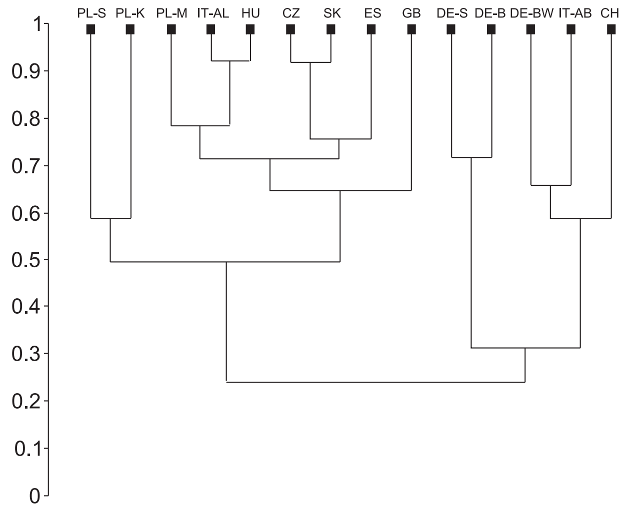

Fig. 9. Dendrogram of Nei similarities among the populations of *Helicodonta obvoluta*

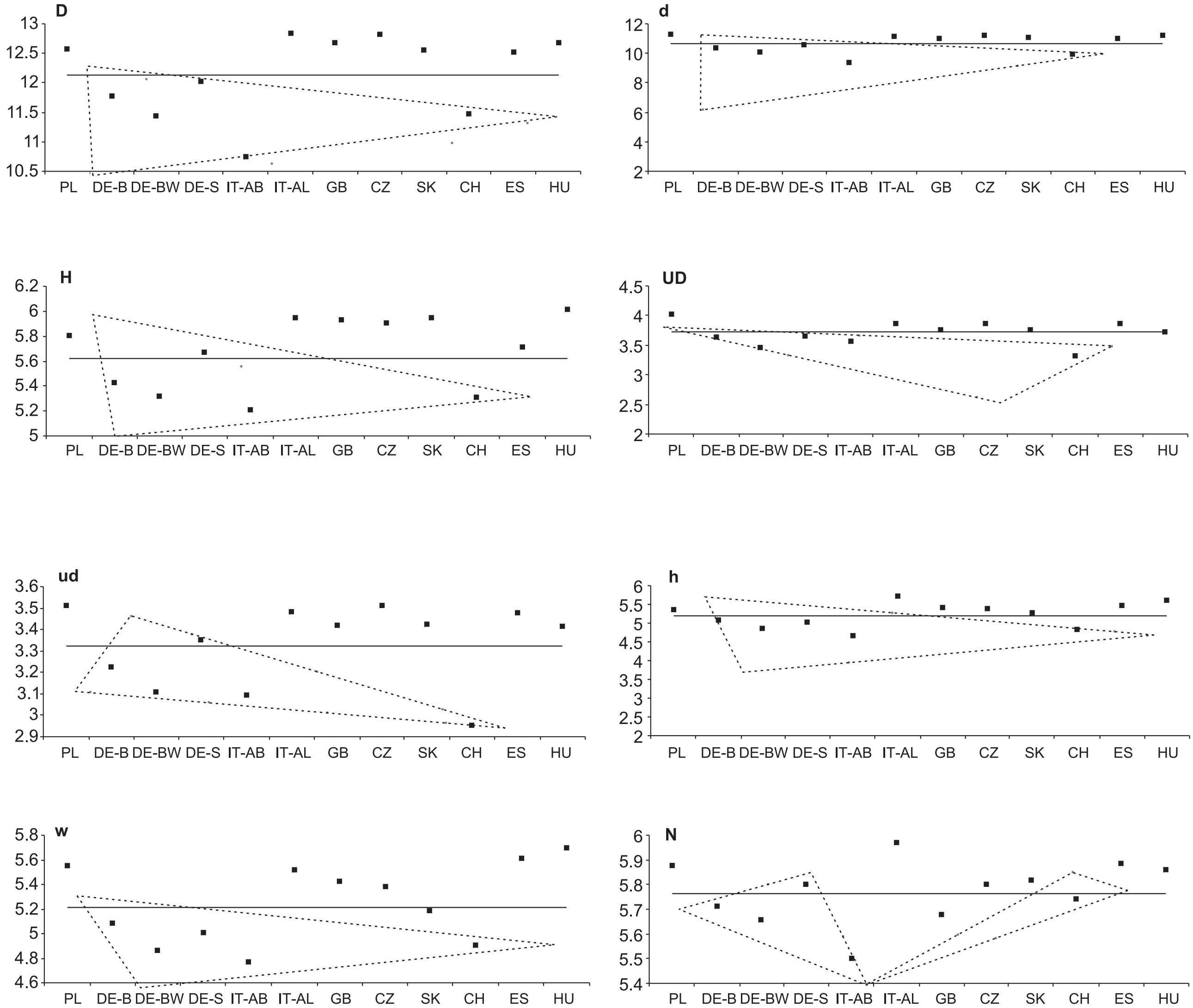

Fig. 10. Mean values of shell parameters: European mean (continuous line), means for populations of group II (triangle)

Table 9. *Helicodonta obvoluta*. Values t i t_0 for shell parameters of each two compared populations (Student t-test, α=0.05)

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
PL-S	PL-K	**1.67**	3.362	**0.029**	4.939	4.277	**0.415**	**0.154**	2.742	4.087	**1.251**	6.223	**0.796**	**0.614**	**0.102**	**0.004**
		1.992	1.993	2.002	1.999	1.994	1.995	1.994	1.997	1.991	1.999	2.001	1.998	1.992	1.995	1.989
PL-S	PL-M	3.036	3.731	**0.133**	7.715	5.789	2.164	**0.450**	**1.033**	2.005	2.194	9.727	2.539	**1.883**	**1.404**	3.351
		1.993	1.992	1.998	2.007	2.000	1.994	1.994	1.993	1.989	1.993	2.006	2.004	1.997	1.993	1.993
PL-S	DE-B	6.525	7.209	5.702	10.246	8.827	4.012	8.242	4.373	2.956	**1.618**	8.215	2.700	4.109	6.717	5.682
		1.992	1.993	1.998	2.007	2.007	1.989	2.002	1.999	1.998	1.998	2.009	2.012	1.988	1.988	1.993
PL-S	DE-BW	9.845	10.222	7.493	12.652	10.842	7.988	12.134	6.256	**1.809**	**0.843**	9.335	3.338	4.584	10.884	8.335
		1.990	1.995	2.001	2.008	2.008	1.993	2.001	1.995	1.989	1.997	2.011	2.009	1.996	1.999	1.986
PL-S	DE-S	2.751	3.674	**1.681**	8.911	5.826	3.265	6.998	**0.952**	2.608	**0.845**	7.565	4.449	3.380	5.425	3.235
		2.005	2.001	1.997	1.999	1.998	2.011	2.000	1.997	1.997	2.001	1.997	1.999	2.005	2.004	2.006
PL-S	IT-AB	8.054	7.656	4.641	7.565	6.684	4.328	9.201	6.399	**2.153**	2.600	**2.099**	**0.361**	**0.685**	6.799	5.409
		2.228	2.262	2.201	2.101	2.145	2.262	2.119	2.201	2.262	2.145	2.145	2.179	2.262	2.201	2.262
PL-S	IT-AL	3.125	**0.876**	**1.814**	5.640	3.225	5.373	**0.346**	3.506	5.069	**0.734**	7.874	3.454	6.569	2.570	**1.410**
		2.003	2.004	1.997	1.996	1.997	1.999	2.002	2.000	1.999	1.997	1.996	2.001	1.999	2.002	2.003
PL-S	GB	2.573	**0.009**	**1.953**	7.713	4.932	**1.520**	**1.918**	5.138	5.769	**0.199**	10.032	4.324	3.891	**0.153**	8.552
		1.988	1.990	1.995	1.996	1.994	1.986	1.991	1.989	1.992	1.992	2.002	2.007	1.988	1.988	1.989
PL-S	CZ	3.898	2.251	**1.518**	6.176	3.369	**1.134**	2.683	**1.154**	3.320	**1.392**	8.700	3.883	4.059	**0.831**	6.541
		1.989	1.990	1.994	1.995	1.991	1.989	1.994	1.993	1.992	1.991	1.998	1.999	1.989	1.991	1.989
PL-S	SK	**0.627**	**0.448**	**0.915**	4.441	3.036	**0.332**	3.453	**0.319**	**0.317**	**0.519**	5.918	3.384	2.793	**1.979**	**1.089**
		2.179	2.179	2.179	2.131	2.119	2.179	2.131	2.109	2.179	2.201	2.101	2.052	2.179	2.145	2.179
PL-S	CH	8.280	9.524	6.591	12.476	11.998	7.212	9.273	2.977	4.059	**0.674**	10.073	2.432	**1.976**	9.405	9.658
		1.994	1.994	1.994	1.995	1.997	1.994	1.994	1.994	1.998	1.994	1.995	1.995	1.998	1.994	1.994
PL-S	ES	**0.812**	**0.057**	**0.955**	5.644	3.869	**1.579**	**0.897**	**1.034**	**1.792**	**1.770**	5.829	2.505	**0.940**	**1.429**	**0.084**
		2.056	2.048	2.030	2.015	2.011	2.074	2.035	2.074	2.059	2.037	2.030	2.032	2.069	2.056	2.074
PL-S	HU	**1.178**	**0.699**	**0.025**	4.941	3.468	3.045	**2.005**	**0.542**	**0.547**	**1.115**	8.964	2.737	**1.397**	3.044	**1.342**
		2.571	2.571	2.262	2.365	2.262	2.365	2.179	2.365	2.571	2.306	2.109	2.365	2.447	2.262	2.571
PL-K	PL-M	**1.688**	**0.614**	**0.157**	3.944	**1.752**	2.286	**0.749**	1.999	**1.756**	**1.421**	5.269	2.506	**1.520**	**1.651**	3.830
		1.984	1.985	1.986	1.983	1.983	1.985	1.984	1.986	1.988	1.988	1.983	1.983	1.983	1.986	1.983
PL-K	DE-B	10.118	13.303	8.690	7.898	5.714	5.657	10.871	10.076	9.048	**0.547**	2.750	2.865	4.177	9.166	6.592
		1.974	1.975	1.973	1.977	1.981	1.972	1.979	1.975	1.978	1.973	1.978	1.983	1.973	1.975	1.976
PL-K	DE-BW	14.045	17.257	11.812	11.726	8.501	11.091	15.982	12.299	6.939	**1.095**	4.548	3.816	4.854	14.903	9.449
		1.975	1.976	1.974	1.979	1.981	1.974	1.978	1.974	1.974	1.974	1.979	1.981	1.977	1.976	1.974

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
PL-K	DE-S	4.319	7.026	2.299	5.852	2.112	3.864	7.848	4.135	7.420	2.073	2.707	5.064	3.203	6.169	3.449
		2.017	2.011	2.009	1.996	1.993	2.026	2.012	2.005	1.995	2.021	2.004	1.993	2.015	2.019	2.013
PL-K	IT-AB	9.203	9.472	5.059	4.728	4.217	4.618	10.130	8.494	4.135	3.826	**2.003**	**0.103**	**0.445**	7.278	5.503
		2.306	2.306	2.306	2.228	2.228	2.306	2.201	2.306	2.306	2.262	2.262	2.262	2.306	2.306	2.306
PL-K	IT-AL	2.106	**1.637**	2.249	**1.805**	**0.302**	5.863	**0.263**	**1.721**	9.219	**0.551**	3.309	3.732	6.787	**0.037**	**1.515**
		2.014	2.015	2.015	2.007	2.007	2.011	2.015	2.017	2.006	2.000	2.007	1.990	2.006	2.017	2.009
PL-K	GB	**1.173**	3.964	2.807	4.139	**0.849**	**1.418**	2.212	9.908	11.719	**1.859**	5.791	5.220	3.890	**0.304**	9.734
		1.978	1.978	1.989	1.978	1.978	1.979	1.978	1.979	1.978	1.979	1.978	1.980	1.978	1.979	1.978
PL-K	CZ	2.763	**1.143**	2.126	2.041	**0.874**	**0.943**	3.195	4.910	8.632	**0.356**	3.925	4.371	4.051	**1.166**	7.371
		1.983	1.982	1.984	1.983	1.982	1.985	1.981	1.983	1.981	1.985	1.982	1.981	1.983	1.983	1.982
PL-K	SK	**0.135**	**1.124**	**0.949**	**1.857**	**0.425**	**0.542**	3.604	2.226	2.239	**1.042**	2.295	3.312	2.596	**2.158**	**1.121**
		2.228	2.228	2.228	2.201	2.179	2.228	2.179	2.179	2.201	2.228	2.201	2.131	2.201	2.201	2.201
PL-K	CH	11.176	14.143	8.916	10.645	9.932	9.006	10.867	6.937	7.764	**0.488**	6.118	2.222	**1.667**	11.692	10.739
		1.997	1.996	2.001	1.997	1.989	2.001	1.997	1.995	2.004	2.002	1.998	1.994	2.006	1.995	1.992
PL-K	ES	**0.383**	2.716	**1.199**	**1.755**	**0.290**	**1.448**	**1.158**	**0.589**	4.919	**1.018**	**1.319**	2.246	**0.582**	**1.509**	**0.091**
		2.086	2.086	2.093	2.059	2.028	2.109	2.074	2.119	2.086	2.093	2.093	2.086	2.093	2.101	2.093
PL-K	HU	**0.484**	**0.598**	2.613	**2.302**	**0.569**	3.041	2.432	**1.232**	**1.890**	**2.082**	4.827	**2.490**	**1.105**	3.341	**1.376**
		2.571	2.776	2.571	2.571	2.447	2.571	2.365	2.571	2.776	2.571	2.365	2.571	2.571	2.447	2.571
PL-M	DE-B	11.504	13.043	8.179	4.519	4.222	7.521	11.126	6.803	5.344	**0.953**	3.072	**0.049**	2.915	10.017	10.959
		1.981	1.983	1.979	1.979	1.985	1.977	1.989	1.986	1.996	1.985	1.981	1.987	1.975	1.985	1.982
PL-M	DE-BW	15.275	16.693	10.972	8.902	7.345	12.771	15.792	8.968	4.035	2.320	**1.331**	**1.229**	3.507	15.176	13.438
		1.980	1.985	1.982	1.980	1.986	1.980	1.988	1.983	1.986	1.984	1.984	1.985	1.980	1.987	1.978
PL-M	DE-S	5.367	7.246	2.306	2.865	**0.619**	5.031	8.217	2.199	4.691	2.860	**1.258**	3.088	2.303	7.009	6.098
		2.014	2.008	2.003	2.008	2.002	2.023	2.009	1.999	1.994	2.011	2.012	2.002	2.019	2.014	2.015
PL-M	IT-AB	9.861	9.626	5.059	2.792	3.367	5.284	10.438	7.363	3.187	4.431	4.336	**1.141**	**0.059**	7.903	6.831
		2.262	2.306	2.306	2.262	2.262	2.306	2.201	2.262	2.262	2.201	2.306	2.306	2.306	2.262	2.306
lPL-M	IT-AL	**0.956**	**1.997**	2.066	**0.898**	**1.575**	4.128	**0.741**	2.971	6.833	**1.727**	**0.359**	**1.565**	5.879	**1.649**	**1.176**
		2.012	2.012	2.011	2.017	2.014	2.009	2.013	2.009	1.998	1.995	2.014	1.998	2.012	2.012	2.012
PL-M	GB	**0.432**	4.330	2.479	**0.895**	**0.831**	**0.536**	2.847	7.262	7.945	2.896	**0.872**	2.938	2.664	**1.739**	6.085
		1.982	1.983	1.982	1.982	1.981	1.981	1.983	1.982	1.989	1.983	1.982	1.984	1.981	1.982	1.982
PL-M	CZ	**1.162**	**1.659**	**1.861**	**1.278**	2.529	**0.984**	3.804	2.613	5.496	**0.903**	**0.667**	2.217	2.903	2.597	3.840
		1.986	1.986	1.986	1.988	1.987	1.986	1.986	1.986	1.989	1.986	1.987	1.986	1.987	1.986	1.986
PL-M	SK	**0.805**	**1.363**	**0.898**	**0.396**	**0.430**	**1.386**	3.945	**1.071**	**1.355**	**1.477**	**0.003**	**1.821**	**2.046**	2.872	**0.519**
		2.201	2.201	2.228	2.228	2.201	2.201	2.179	2.160	2.179	2.228	2.201	2.160	2.228	2.179	2.201

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
PL-M	CH	12.322	14.304	8.594	8.342	8.974	10.470	11.175	4.644	5.725	**1.557**	2.338	**0.278**	**0.716**	12.368	14.364
		1.977	1.995	1.998	2.007	1.995	1.999	1.997	1.993	1.997	1.995	2.005	2.002	2.011	1.993	1.996
PL-M	ES	**1.454**	3.053	**1.258**	**1.017**	**1.929**	**0.269**	**0.598**	**0.424**	3.335	**0.029**	**1.738**	**0.799**	**0.249**	**0.461**	2.135
		2.079	2.074	2.079	2.086	2.045	2.101	2.063	2.101	2.056	2.064	2.101	2.101	2.109	2.079	2.101
PL-M	HU	**0.143**	**0.801**	2.471	**0.777**	**0.409**	**1.834**	**1.836**	**0.135**	**1.284**	2.734	**1.363**	**1.501**	**0.396**	**2.163**	**0.137**
		2.571	2.571	2.447	2.571	2.571	2.571	2.306	2.447	2.571	2.447	2.447	2.571	2.571	2.365	2.571
DE-B	DE-BW	4.325	3.874	2.435	4.324	3.703	4.648	6.417	2.877	**1.207**	**1.619**	2.027	**1.444**	**0.193**	5.956	3.785
		1.969	1.969	1.969	1.969	1.969	1.969	1.969	1.969	1.970	1.969	1.969	1.969	1.969	1.969	1.969
DE-B	DE-S	**2.010**	**1.995**	4.430	**0.622**	2.833	**0.686**	**1.302**	3.511	**0.079**	2.387	**0.829**	3.405	**0.378**	**0.984**	**0.743**
		2.018	2.014	2.001	2.005	2.011	2.021	2.021	2.008	2.005	2.019	2.015	2.014	2.012	2.024	2.019
DE-B	IT-AB	5.222	4.739	**1.804**	**0.728**	**1.568**	2.842	4.423	4.440	**0.966**	4.084	3.203	**1.178**	**1.045**	3.661	3.428
		2.306	2.306	2.306	2.262	2.306	2.306	2.262	2.306	2.306	2.262	2.306	2.365	2.306	2.306	2.306
DE-B	IT-AL	8.590	6.469	7.845	3.687	4.229	9.621	5.966	7.823	3.418	**1.006**	**1.599**	**1.722**	3.539	8.228	6.077
		2.015	2.019	2.009	2.017	2.024	2.004	2.026	2.019	2.017	1.997	2.018	2.009	2.002	2.021	2.017
DE-B	GB	10.539	8.659	10.388	2.729	4.681	6.084	7.785	**1.599**	4.084	2.319	3.773	3.439	**0.107**	7.463	**1.654**
		1.975	1.975	1.974	1.978	1.979	1.975	1.978	1.997	1.976	1.976	1.976	1.976	1.974	1.978	1.975
DE-B	CZ	11.877	11.129	9.456	4.768	6.126	5.614	7.000	3.928	**0.844**	**0.092**	**1.852**	2.475	**0.297**	6.964	14.275
		1.981	1.980	1.979	1.985	1.989	1.979	1.983	1.981	1.982	1.983	1.985	1.987	1.979	1.982	1.981
DE-B	SK	3.659	3.784	3.365	**1.076**	**2.153**	**1.609**	**1.064**	2.589	**0.956**	**1.190**	**1.189**	**1.883**	**0.917**	**1.508**	3.810
		2.228	2.228	2.228	2.228	2.228	2.201	2.228	2.201	2.228	2.228	2.228	2.201	2.201	2.228	2.228
DE-B	CH	3.235	4.115	**1.964**	5.360	6.257	4.245	3.403	**1.153**	2.334	**0.886**	4.515	**0.267**	**1.187**	4.545	5.686
		1.997	1.997	1.995	2.006	2.001	1.993	2.007	1.997	2.014	2.000	2.008	2.013	2.003	1.997	1.996
DE-B	ES	5.800	5.552	4.127	3.875	5.535	4.342	8.263	3.822	**0.067**	**0.695**	**0.180**	**0.809**	**1.853**	6.549	3.751
		2.093	2.093	2.079	2.086	2.074	2.101	2.101	2.119	2.109	2.093	2.109	2.131	2.093	2.109	2.109
DE-B	HU	4.019	3.459	7.056	**0.770**	**2.408**	5.919	9.744	3.474	**0.331**	**2.329**	3.276	**1.513**	**1.003**	8.776	3.857
		2.776	2.776	2.447	2.571	2.571	2.447	2.571	2.571	2.776	2.571	2.447	2.777	2.571	2.447	2.776
DE-BW	DE-S	4.668	4.510	6.513	3.914	5.424	**1.917**	2.198	5.555	**1.049**	**1.407**	**0.423**	2.325	**0.271**	2.182	3.115
		2.017	2.017	2.007	2.008	2.011	2.024	2.023	2.003	1.992	2.018	2.019	2.009	2.023	2.026	2.011
DE-BW	IT-AB	3.500	3.452	**0.909**	**1.189**	**0.172**	**1.404**	**1.312**	3.231	**1.372**	3.263	3.914	**1.570**	**1.122**	**1.477**	**2.169**
		2.306	2.306	2.306	2.262	2.306	2.306	2.262	2.306	2.306	2.262	2.306	2.306	2.306	2.306	2.306
DE-BW	IT-AL	11.206	8.725	9.662	6.314	6.126	13.356	9.016	9.372	3.998	**0.379**	**0.456**	**0.631**	3.615	11.485	8.279
		2.014	2.021	2.015	2.018	2.024	2.009	2.026	2.015	2.005	1.995	2.021	2.004	2.013	2.023	2.007
DE-BW	GB	14.182	12.354	13.145	6.175	7.459	10.507	12.698	**0.852**	4.671	**0.875**	2.183	2.027	**0.301**	12.255	19.149
		1.975	1.976	1.976	1.979	1.979	1.977	1.978	1.976	1.973	1.976	1.978	1.975	1.977	1.979	1.973

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
DE-BW	CZ	15.389	14.717	12.041	8.096	8.618	9.992	12.089	6.244	**1.798**	**1.247**	**0.372**	**1.322**	**0.152**	12.012	16.391
		1.980	1.982	1.982	1.986	1.989	1.983	1.982	1.979	1.977	1.982	1.987	1.984	1.985	1.983	1.978
DE-BW	SK	5.246	5.119	4.061	2.443	3.413	3.422	3.428	3.924	**0.518**	**0.736**	**0.499**	**1.227**	**0.859**	3.706	5.267
		2.228	2.228	2.228	2.228	2.228	2.228	2.228	2.179	2.201	2.228	2.228	2.201	2.228	2.228	2.201
DE-BW	CH	**0.232**	**1.236**	**0.104**	2.596	3.580	**0.656**	**0.816**	3.411	2.945	**0.327**	3.349	**0.577**	**1.371**	**0.007**	2.123
		1.995	2.000	1.999	2.008	2.001	1.999	2.005	1.993	2.003	1.999	2.011	2.009	2.011	1.999	1.988
DE-BW	ES	8.340	7.854	5.734	6.572	8.069	6.889	11.669	5.031	**0.597**	**1.659**	**1.121**	**0.206**	**2.025**	9.577	5.687
		2.086	2.101	2.093	2.093	2.074	2.109	2.101	2.119	2.086	2.086	2.119	2.119	2.109	2.109	2.093
DE-BW	HU	5.497	4.557	8.439	**2.206**	3.870	8.508	13.192	4.766	**0.034**	**1.563**	**2.211**	**1.112**	**1.120**	12.038	5.207
		2.571	2.776	2.571	2.776	2.571	2.571	2.447	2.571	2.776	2.571	2.571	2.776	2.571	2.571	2.571
DE-S	IT-AB	5.804	5.375	3.795	**1.024**	2.890	2.234	2.624	5.925	**0.905**	**1.746**	3.373	2.411	**1.161**	2.572	3.526
		2.179	2.228	2.228	2.201	2.201	2.201	2.093	2.228	2.262	2.109	2.201	2.262	2.228	2.145	2.228
DE-S	IT-AL	5.119	3.908	3.649	2.845	**1.909**	7.268	5.702	4.484	2.984	**1.577**	**0.679**	**1.467**	2.394	7.034	4.068
		2.002	2.003	2.004	2.006	2.008	2.008	2.003	2.006	2.006	2.012	2.002	2.002	2.004	2.002	2.002
DE-S	GB	4.968	4.045	4.337	**1.737**	**1.310**	4.472	6.102	4.388	3.207	**0.771**	**1.858**	**0.704**	**0.445**	5.616	10.159
		2.011	2.008	1.998	1.992	1.993	2.013	2.008	1.995	1.997	2.011	2.004	2.003	2.009	2.009	2.013
DE-S	CZ	6.011	5.937	3.771	3.501	2.809	4.186	5.531	**0.123**	**0.617**	2.148	**0.633**	**0.962**	**0.146**	5.183	8.577
		2.009	2.007	1.998	1.993	1.993	2.013	2.011	1.999	1.997	2.008	1.999	1.996	2.006	2.013	2.009
DE-S	SK	2.229	2.519	**1.714**	**0.787**	**0.729**	**1.817**	**1.687**	**0.371**	**0.956**	**0.071**	**0.669**	**0.241**	**0.634**	**1.892**	3.001
		2.131	2.145	2.201	2.201	2.160	2.109	2.109	2.131	2.201	2.160	2.145	2.119	2.131	2.101	2.119
DE-S	CH	4.074	4.826	5.508	5.159	7.388	2.160	**1.288**	2.106	2.061	**1.479**	2.946	2.197	**1.261**	**1.992**	4.523
		2.006	2.003	1.999	2.000	2.000	2.011	2.003	2.001	2.003	2.005	1.999	2.000	2.000	2.011	2.009
DE-S	ES	3.056	3.091	**0.540**	2.986	2.272	3.961	7.316	**1.703**	**0.109**	2.401	**0.695**	**1.099**	**1.841**	5.859	2.582
		2.032	2.037	2.052	2.048	2.030	2.032	2.030	2.086	2.074	2.028	2.056	2.079	2.039	2.032	2.042
DE-S	HU	2.663	**2.445**	3.782	**0.477**	**0.748**	5.204	8.407	**1.240**	**0.347**	**0.389**	**2.108**	**0.179**	**1.128**	7.450	3.122
		2.447	2.571	2.365	2.571	2.447	2.160	2.145	2.365	2.776	2.262	2.201	2.571	2.262	2.145	2.365
IT-AB	IT-AL	9.499	7.707	5.793	2.988	3.960	6.781	7.791	8.520	**0.695**	3.342	3.749	**1.757**	2.592	8.080	5.907
		2.179	2.179	2.201	2.131	2.131	2.262	2.069	2.145	2.228	2.201	2.179	2.262	2.262	2.145	2.228
IT-AB	GB	9.590	7.887	6.073	**2.159**	3.728	5.013	8.539	3.549	**0.445**	2.675	4.659	**2.191**	**0.998**	6.919	8.895
		2.262	2.306	2.262	2.201	2.228	2.306	2.179	2.262	2.306	2.228	2.262	2.306	2.306	2.262	2.306
IT-AB	CZ	10.261	8.916	5.801	3.325	4.629	4.849	8.047	6.058	**0.647**	3.816	3.893	**2.006**	**1.147**	6.600	8.146
		2.262	2.306	2.262	2.201	2.201	2.306	2.201	2.262	2.306	2.201	2.262	2.306	2.262	2.262	2.306
IT-AB	SK	6.471	6.223	3.882	**1.346**	2.738	3.332	3.689	5.294	**1.391**	**0.994**	3.217	**2.045**	**1.444**	3.790	5.191
		2.119	2.119	2.119	2.131	2.119	2.145	2.119	2.131	2.119	2.145	2.119	2.179	2.131	2.119	2.145

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
IT-AB	CH	3.470	2.799	**0.821**	2.618	**1.589**	**1.115**	**1.678**	4.788	**0.288**	3.193	5.259	**1.215**	**0.395**	**1.407**	**1.326**
		2.228	2.262	2.228	2.160	2.228	2.262	2.131	2.228	2.201	2.160	2.201	2.228	2.228	2.228	2.306
IT-AB	ES	7.966	7.199	3.907	3.079	4.294	4.865	9.395	6.102	0.886	3.877	2.575	**1.464**	**0.080**	7.169	5.010
		2.179	2.201	2.179	2.145	2.201	2.179	2.109	2.109	2.179	2.131	2.145	2.160	2.179	2.145	2.201
IT-AB	HU	6.681	5.844	5.883	**1.094**	2.906	5.698	10.417	5.884	**0.833**	**1.175**	4.671	**1.936**	**0.286**	8.405	5.244
		2.262	2.262	2.201	2.306	2.228	2.228	2.201	2.201	2.306	2.228	2.201	2.228	2.201	2.201	2.201
IT-AL	GB	**1.239**	**0.938**	**0.225**	**1.444**	**0.935**	4.239	**1.166**	8.288	**0.559**	**1.123**	**0.949**	**0.991**	3.534	2.847	5.412
		2.008	2.013	2.006	2.001	2.006	1.998	2.012	2.006	2.008	1.990	2.008	1.999	2.001	2.007	2.009
IT-AL	CZ	**0.101**	**0.839**	**0.612**	**0.113**	**0.386**	4.577	**1.765**	4.889	2.605	**0.786**	**0.152**	**0.557**	3.077	3.452	3.883
		2.007	2.011	2.004	2.000	2.002	1.999	2.015	2.009	2.006	1.992	2.002	1.993	1.998	2.011	2.007
IT-AL	SK	**1.262**	**0.110**	**0.004**	**0.806**	**0.576**	3.373	2.904	3.055	2.475	**0.849**	**0.203**	**0.783**	**0.897**	3.599	**0.179**
		2.131	2.131	2.179	2.145	2.109	2.160	2.086	2.079	2.160	2.228	2.131	2.131	2.160	2.109	2.131
IT-AL	CH	9.995	8.616	8.505	7.095	7.777	11.995	7.375	6.360	**0.633**	**0.005**	2.128	**0.961**	3.788	10.452	9.472
		2.005	2.006	2.002	2.000	2.008	2.000	2.006	2.008	1.999	1.999	1.999	2.001	1.999	2.009	2.006
IT-AL	ES	**1.943**	**0.817**	2.669	**0.075**	**0.068**	2.456	**1.097**	**1.607**	2.374	**1.309**	**1.234**	**0.145**	4.107	**0.901**	**1.004**
		2.032	2.026	2.032	2.026	2.018	2.059	2.023	2.056	2.045	2.069	2.045	2.086	2.056	2.032	2.045
IT-AL	HU	**0.626**	**0.215**	**0.719**	**1.171**	**0.715**	**1.069**	**2.051**	**0.028**	**1.458**	**1.707**	**1.388**	**0.848**	3.086	**0.416**	**0.323**
		2.447	2.447	2.262	2.447	2.262	2.306	2.101	2.262	2.571	2.447	2.160	2.571	2.365	2.145	2.447
GB	CZ	**1.527**	2.604	**0.512**	**1.859**	**1.657**	**0.406**	**0.888**	4.790	2.769	**1.903**	**1.386**	**0.384**	**0.384**	**0.749**	**1.933**
		1.981	1.981	1.981	1.981	1.982	1.980	1.980	1.980	1.981	1.981	1.982	1.983	1.981	1.980	1.981
GB	SK	**0.616**	**0.457**	**0.103**	**0.030**	**0.019**	**1.121**	2.446	3.313	2.336	**0.450**	**0.372**	**0.204**	**0.956**	**1.949**	3.107
		2.201	2.201	2.228	2.201	2.179	2.179	2.179	2.145	2.228	2.228	2.201	2.179	2.201	2.179	2.201
GB	CH	11.591	10.775	10.454	6.811	9.084	9.119	8.722	2.349	**0.233**	**1.000**	**1.622**	**1.862**	**1.087**	10.197	19.565
		1.992	1.994	1.993	1.993	1.988	1.990	1.993	1.988	2.006	1.993	1.999	2.005	2.002	1.987	1.992
GB	ES	**1.138**	**0.069**	2.929	**1.561**	**1.084**	**0.572**	2.712	4.446	2.263	2.155	2.197	**0.737**	**1.760**	**1.622**	5.626
		2.074	2.074	2.069	2.045	2.026	2.079	2.064	2.101	2.093	2.069	2.093	2.109	2.086	2.074	2.093
GB	HU	**0.029**	**0.709**	**0.995**	**0.381**	**0.061**	**2.073**	3.980	4.142	**1.299**	**1.061**	**0.749**	**0.476**	**0.935**	3.349	**2.529**
		2.571	2.571	2.447	2.571	2.447	2.447	2.306	2.447	2.776	2.447	2.365	2.776	2.447	2.306	2.571
CZ	SK	**1.299**	**0.643**	**0.278**	**0.908**	**0.897**	**0.923**	**2.004**	**0.469**	**1.236**	**1.139**	**0.314**	**0.419**	**0.768**	**1.581**	2.212
		2.201	2.201	2.228	2.179	2.160	2.179	2.179	2.160	2.201	2.228	2.179	2.145	2.179	2.179	2.201
CZ	CH	12.719	12.768	9.729	8.280	10.054	8.713	8.119	2.218	**1.669**	**0.715**	2.644	**1.448**	**1.343**	9.828	17.089
		1.993	1.994	1.993	1.993	1.989	1.992	1.997	1.992	2.004	1.993	1.995	1.997	1.999	1.992	1.992
CZ	ES	2.203	**1.869**	2.509	**0.029**	**0.554**	**0.835**	3.399	**1.844**	**0.532**	**0.704**	**1.241**	**0.497**	**1.969**	2.167	4.369
		2.069	2.069	2.064	2.042	2.017	2.079	2.069	2.101	2.086	2.059	2.074	2.086	2.074	2.079	2.086

		D	d	H	UD	ud	h	w	N	D/d	D/H	UD/D	UD/ud	h/w	h x w	D/N
CZ	HU	**0.612**	**0.205**	**1.299**	**1.298**	**1.099**	**2.335**	4.695	**1.373**	**0.537**	**2.169**	**1.731**	**0.612**	**1.137**	3.964	**1.707**
		2.571	2.571	2.447	2.571	2.365	2.447	2.365	2.447	2.774	2.447	2.306	2.571	2.447	2.365	2.571
SK	CH	4.953	5.431	3.989	3.465	4.844	3.566	2.733	**1.806**	**2.032**	**0.834**	**1.243**	**1.428**	**1.482**	3.539	6.176
		2.179	2.179	2.201	2.160	2.179	2.179	2.145	2.145	2.145	2.201	2.145	2.093	2.131	2.179	2.179
SK	ES	**0.092**	**0.456**	**1.397**	**0.857**	**0.575**	**1.346**	3.947	**1.133**	**0.804**	**1.416**	**1.108**	**0.726**	**1.917**	2.798	**0.904**
		2.131	2.145	2.179	2.160	2.160	2.109	2.119	2.074	2.131	2.179	2.101	2.074	2.119	2.109	2.109
SK	HU	**0.463**	**0.264**	**0.405**	**0.256**	**0.059**	2.318	4.751	**0.717**	**0.276**	**0.176**	**0.779**	**0.307**	**1.416**	3.923	**0.262**
		2.228	2.262	2.179	2.179	2.179	2.160	2.160	2.201	2.306	2.160	2.160	2.365	2.160	2.160	2.228
CH	ES	7.455	7.820	5.151	7.293	9.591	6.725	9.354	3.049	**1.714**	**1.235**	3.102	**0.537**	**0.712**	8.813	6.834
		2.056	2.052	2.048	2.030	2.030	2.069	2.042	2.093	2.035	2.048	2.052	2.059	2.039	2.074	2.079
CH	HU	5.227	4.866	7.787	3.282	5.445	8.208	10.593	2.661	**1.159**	**1.636**	**0.622**	**1.297**	**0.109**	10.954	6.057
		2.571	2.571	2.365	2.447	2.447	2.365	2.228	2.447	2.571	2.365	2.178	2.447	2.262	2.306	2.571
ES	HU	**0.643**	**0.699**	2.993	**1.227**	**0.735**	**1.191**	**1.017**	**0.438**	**0.283**	2.430	2.422	**0.837**	**0.492**	**1.300**	**1.149**
		2.447	2.477	2.228	2.447	2.447	2.179	2.179	2.160	2.571	2.262	2.131	2.306	2.228	2.160	2.306

Table 10. *Helicodonta obvoluta*. Nei index values for similarities between the populations

	PL-S	PL-K	PL-M	DE-B	DE-BW	DE-S	IT-AB	IT-AL	GB	CZ	SK	CH	ES	HU
PL-S	1	0.6	0.33	0.07	0.13	0.2	0.27	0.33	0.4	0.33	0.6	0.13	0.73	0.6
PL-K	0.6	1	0.6	0.07	0.07	0	0.2	0.53	0.33	0.33	0.6	0.13	0.8	0.67
PL-M	0.33	0.6	1	0.13	0.13	0.13	0.13	0.73	0.4	0.47	0.87	0.2	0.8	0.87
DE-B	0.07	0.07	0.13	1	0.27	0.73	0.4	0.2	0.2	0.27	0.67	0.33	0.33	0.4
DE-BW	0.13	0.07	0.13	0.27	1	0.4	0.67	0.2	0.2	0.33	0.33	0.6	0.33	0.4
DE-S	0.2	0	0.13	0.73	0.4	1	0.27	0.27	0.4	0.33	0.8	0.33	0.4	0.6
IT-AB	0.27	0.2	0.13	0.4	0.67	0.27	1	0.13	0.27	0.2	0.33	0.6	0.2	0.33
IT-AL	0.33	0.53	0.73	0.2	0.2	0.27	0.13	1	0.67	0.6	0.67	0.2	0.73	0.93
GB	0.4	0.33	0.4	0.2	0.2	0.4	0.27	0.67	1	0.8	0.73	0.33	0.53	0.8
CZ	0.33	0.33	0.47	0.27	0.33	0.33	0.2	0.6	0.8	1	0.93	0.27	0.67	0.83
SK	0.6	0.6	0.87	0.67	0.33	0.8	0.33	0.67	0.73	0.93	1	0.4	0.87	0.8
CH	0.13	0.13	0.2	0.33	0.6	0.33	0.6	0.2	0.33	0.27	0.4	1	0.27	0.33
ES	0.73	0.8	0.8	0.33	0.33	0.4	0.2	0.73	0.53	0.67	0.87	0.27	1	0.8
HU	0.6	0.67	0.87	0.4	0.4	0.6	0.33	0.93	0.8	0.83	0.8	0.33	0.8	1

Table 11. *Helicodonta obvoluta*. Values of significant Pearson coefficients of correlation among shell parameters

	PL-S	PL-K	PL-M	DE-B	DE-BW	DE-S	IT-AB	IT-AL	GB	CZ	SK	CH	ES	HU
D : d	0.911	0.882	0.821	0.937	0.895	0.961	0.944	0.937	0.919	0.913	0.895	0.864	0.884	0.857
D : H	0.572	0.592		0.676	0.602		0.832	0.783	0.522			0.588	0.566	0.646
D : UD				0.570	0.648				0.659		0.655	0.553		0.942
D : ud	0.502			0.516	0.649				0.708	0.565	0.638	0.624		0.567
D : h	0.528	0.784	0.755	0.616	0.714	0.853	0.725	0.640	0.759	0.688	0.710	0.682	0.767	0.583
D : w		0.624	0.698	0.804	0.787	0.824	0.898	0.891	0.655	0.702		0.790	0.826	0.929
D : N	0.708	0.608	0.710	0.790	0.624	0.800		0.734	0.766	0.746	0.836	0.811	0.579	0.849
D : D/H						0.643								0.674
D : UD/D													–0.540	0.730
D : UD/ud							0.656							0.684
D : h/w								–0.580						
D : hw	0.525	0.808	0.789	0.780	0.807	0.903	0.837	0.826	0.786	0.785	0.680	0.860	0.898	0.898
D : D/N	0.765	0.836	0.770	0.887	0.854	0.941	0.883	0.831	0.785	0.843	0.947	0.905	0.649	0.952
d : H	0.599	0.658	0.567	0.732	0.674		0.698	0.789	0.649	0.510	0.713	0.674	0.676	
d : UD				0.583	0.535				0.721		0.503	0.500		0.899
d : ud	0.526	0.518		0.543	0.596				0.731	0.532	0.633	0.557		0.634
d : h	0.516	0.782	0.796	0.603	0.671	0.819	0.655	0.684	0.742	0.644	0.750	0.553	0.740	
d : w		0.513	0.636	0.819	0.689	0.755	0.848	0.877	0.657	0.667		0.684	0.820	0.964
d : N	0.630	0.628	0.716	0.797	0.721	0.791		0.729	0.808	0.704	0.883	0.743	0.611	0.898
d : D/d							–0.605	–0.517						–0.579
d : D/H						0.535								0.876
d : UD/D							–0.526							0.815
d : UD/ud							0.683							0.558
d : h/w								–0.510			0.510			
d : hw	0.510	0.743	0.775	0.779	0.735	0.852	0.768	0.845	0.778	0.742	0.664	0.726	0.876	0.707
d : D/N	0.711	0.673	0.514	0.789	0.656	0.892	0.795	0.743	0.620	0.751	0.766	0.747		0.716
H : UD							0.624		0.525					
H : ud	0.502								0.561					0.512
H : h	0.627	0.647	0.764	0.526	0.528		0.659	0.768		0.514	0.518		0.696	0.911
H : w				0.686	0.514		0.694	0.840				0.553		
H : N			0.522	0.584	0.531			0.618	0.612					

	PL-S	PL-K	PL-M	DE-B	DE-BW	DE-S	IT-AB	IT-AL	GB	CZ	SK	CH	ES	HU
H : D/d											–0.720			0.552
H : D/H	–0.740	–0.510	–0.650	–0.640	–0.510		–0.590		–0.600	–0.630	–0.790	–0.620	–0.610	
H : UD/ud							0.546				–0.580			
H : h/w														0.666
H : hw		0.624	0.600	0.671	0.567		0.714	0.866		0.542		0.557	0.653	0.822
H : D/N	0.579			0.560			0.744	0.616		0.358		0.519		0.791
UD : ud	0.691	0.744	0.754	0.847	0.807	0.771	0.614	0.896	0.873	0.819	0.914	0.801		0.642
UD : h									0.515		0.371			0.529
UD : w					0.558									0.934
UD : N									0.581		0.569			0.778
UD : D/H					0.508									0.769
UD : UD/D	0.893	0.858		0.794	0.749	0.698	0.699	0.818	0.876	0.867	0.856	0.892	0.829	0.917
UD : UD/ud											0.591	0.559	0.676	0.691
UD : hw					0.563				0.547					0.862
UD : D/N					0.516		0.583				0.608	0.596		0.909
ud : h									0.508	0.572				0.758
ud : w					0.529								0.539	
ud : N					0.500		–0.720		0.693		0.671		0.517	
ud : D/d							0.724							
ud : D/H			0.535											
ud : UD/D	0.510	0.551		0.653			0.769	0.714	0.680	0.623	0.741	0.621		0.644
ud : UD/ud			–0.590				–0.580							
ud : hw					0,531				0.521					0.800
ud : D/N						0.519					0.521	0.629		0.647
h : w	0.602	0.506	0.679	0.552	0.700	0.742	0.734	0.736	0.508	0.548	0.585		0.542	
h : N			0.688	0.524	0.557	0.793	0.708	0.538		0.594	0.813			
h : UD/ud							0.863							
h : h/w				0.732	0.579	0.629	0.907		0.537		0.631	0.544	0.729	0.769
h : hw	0.893	0.857	0.909	0.923	0.937	0.947	0.975	0.914	0.923	0.904	0.912	0.858	0.917	0.871
h : D/N	0.627	0.660		0.517	0.532	0.742			0.538	0.517	0.541	0.663	0.633	0.781
w : N			0.510	0.672		0.753	0.580	0.636	0.508	0.530		0.679	0.639	0.947
w : D/H						0.586								0.894

	PL-S	PL-K	PL-M	DE-B	DE-BW	DE-S	IT-AB	IT-AL	GB	CZ	SK	CH	ES	HU
w : UD/D														0.798
w : UD/ud							0.810							0.741
w : h/w		–0.558						–0.637						
w : hw	0.896	0.877	0.922	0.829	0.904	0.918	0.866	0.946	0.891	0.852	0.867	0.853	0.832	0.724
w : D/N		0.572	0.523	0.685	0.681	0.721	0.699	0.756	0.507	0.588	0.511	0.685		0.791
N : D/N														0.865
N : UD/D							–0.530							0.573
N : UD/ud							0.720							0.716
N : h/w							0.621				0.707			–0.530
N : hw			0.652	0.661	0.560	0.831	0.696	0.627	0.642	0.641	0.643	0.684	0.510	0.564
N : D/N						0.550					0.615	0.485		0.645
D/d : D/H									0.523		0.826			–0.630
D/d : UD/D							0.744							
D/d : UD/ud											0.738			
D/d : h/w														0.604
D/d : D/N					0.515									
D/H : UD/D						–0.510								0.763
D/H : UD/ud											0.831			0.763
D/H : h/w														–0.720
D/H : hw						0.519								
D/H : D/N			0.517			0.624			0.519					
UD/D : UD/ud											0.584	0.624	0.724	0.584
UD/D : hw														0.693
UD/D : D/N														0.721
UD/ud : h/w							0.684							–0.518
UD/ud : hw							0.891							
UD/ud : D/N														0.571
h/w : hw							0.790							
autoh/w : D/N								–0.560						
hw : D/N	0.558	0.706	0.524	0.656	0.649	0.789	0.568	0.671	0.578	0.620	0.600	0.786	0.594	0.970

Table 12. *Helicodonta obvoluta*. Values of Pearson coefficients of correlation between latitude and shell parameters

Parameter	Pearson coefficient value
D	0.508
d	0.567
H	0.463
UD	0.368
ud	0.422
h	0.283
w	0.302
N	0.323
D/d	–0.491
D/H	0.322
UD/D	–0.085
UD/ud	–0.109
h/w	–0.026
h x w	0.283
D/N	0.538

Table 13. *Helicodonta obvoluta*. Values of Pearson coefficients of correlation between longitude and shell parameters

Parameter	Pearson coefficient value
D	0.138
d	0.234
H	0.243
UD	0.245
ud	0.223
h	0.093
w	0.115
N	0.245
D/d	–0.514
D/H	–0.254
UD/D	0.169
UD/ud	0.111
h/w	–0.057
h x w	0.104
D/N	0.047

DISCUSSION

The shell of *H. obvoluta* is regarded as much variable (KERNEY et al. 1983) (Table 1, Fig. 5), which is confirmed in this study. Based on similarities among the shell parameters, two groups of populations can be distinguished: one from the fringes of the distribution range, with much more varied and relatively larger shells, another, including populations mainly from the centre of the range, with less varied and smaller shells. Many factors which may affect ultimate size of snail shell and/or contribute to inter- and intrapopulation variation have been mentioned in the literature. They fall in two major groups: external (among others, effect of habitat conditions, interactions among individuals of the same/different species) and internal (genetic factors, metabolic processes, etc.) (GROMADSKA & PRZYBYLSKA 1960, WOLDA 1972, CAMERON & CARTER 1979, BAUR 1984, GOODFRIEND 1986, BAUR & RABOUD 1988, SULIKOWSKA-DROZD 2001).

Altitude can have an effect on the shell size. In *Arianta arbustorum* from the Swiss Alps the shell size (volume) has been found to decrease with increasing altitude (BAUR & RABAUD 1988). Individuals from montane populations have considerably smaller shell diameter compared to those from valleys (BAUR 1984). Likewise, shells of *Vestia turgida*, collected in lower-situated sites, are higher than those from sites located at greater altitudes (SULIKOWSKA-DROZD 2001). According to SULIKOWSKA-DROZD (2001) the kind of habitat rather than the altitude per se is the significant factor influencing the shell size. Snails collected above the timberline were significantly smaller than those living in a forest at the same altitude. Shells of *H. obvoluta* from populations representing the first group (GB, PL, CZ, SK, HU, ES?) were collected in areas not exceeding 600 m a.s.l. (CAMERON, HORSÁK, POKRYSZKO, WIKTOR personal communication). There were no altitudinal data for the central populations (DE, CH). It is only known that in Germany the snail reaches up to 1,300 m a.s.l., in the Swabian Jura – 1,600–1,699 m a.s.l., and in the German part of the Alps – 1,700–1,800 m a.s.l. (EHRMANN 1956, GODAN 1979). In the Austrian and Swiss Alps it has been recorded even at 2,260 m a.s.l. (KLEMM 1973). Probably shells from the populations included in the second group were collected in montane areas. However, a latitudinal effect compared to the altitudinal one could be expected as well. Actually, most shell parameters show no clear geographical trend. Three of them (D, d and D/N) tend to increase – and not decrease – northwards. Besides, one (D/d) decreases eastwards, with increasing continentalisation of the climate.

Shell size may also depend on the temperature and humidity. It has been found that smaller individuals of *Cepaea nemoralis* prefer less shaded habitats since they absorb less heat and lose it faster. Larger snails absorb heat to a greater extent, lose it more slowly and in consequence are limited to more shaded places (HEATH 1975, KNIGHTS 1979). *C. nemoralis* is a polymorphic species, which also has a significant effect on preferred microhabitats, activity and –

possibly – shell size. *H. obvoluta* is monomorphic with respect to shell colour and is fairly stenoecious, preferring humid and shaded places in deciduous or deciduous-coniferous forests. However, in the central part of its range it is more catholic and found also in more open and calcium-poorer habitats (CAMERON 1972), which may explain the relatively smaller shell size and the presence of albino snails in such populations.

Population density can also have an effect on the growth rate and attainment of ultimate size. Individuals of *C. nemoralis* and *C. hortensis* kept singly grew faster and had larger shells compared to those kept in groups (CAMERON & CARTER 1979). The effect was probably a result of the excess of mucus containing pheromones which affect growth (GOODFRIEND 1986). In the wild *H. obvoluta* has been observed to form very dense populations (some sites in England and Poland) (CAMERON 1972, MALTZ 2003c), where large individuals constitute a majority. Laboratory observations indicate that in this species there is no correlation between the growth rate and the ultimate shell size (fast-growing snails may have either small or big shells; the same is true of slow-growing individuals) (MALTZ 2002). Similar results have been obtained for *C. nemoralis* (WOLDA 1972). Thus, the density is not the main decisive factor for the adult shell size; reasons for the differences should be sought in genetic factors (WOLDA 1972). Studies on *A. arbustorum* show that individuals collected at high altitudes produce relatively larger offspring in laboratory conditions, but the size of parents and progeny from low-altitude lineages is similar (BAUR 1984).

The shell variation may also depend on the structure of the distribution range: whether it is continuous or consists of isolated localities. Shells of *Vestia elata* from the isolated population in the Świętokrzyskie Mts are smaller and less varied in their size than those from the Bieszczady Mts or S. Carpathians (ABRASZEWSKA-KOWALCZYK & SULIKOWSKA 1998), which is probably a result of a limited gene pool of small, isolated populations. POKRYSZKO (1990) has shown that shell variation (mainly apertural barriers) in numerous species of *Vertigo* does not depend on habitat conditions. Many members of the genus are stenoecious species of very fragmented ranges, composed of isolated populations, while the snails are only capable of passive dispersal. Few dispersing individuals get into favourable habitats, while the ability to self-fertilise makes it possible for a single or a few colonisers to establish a new population. The shell variation depends thus mainly on the genetic material brought by the coloniser(s) that gave rise to the local population. The present range of *H. obvoluta* is also much fragmented, composed of insular populations among which gene flow is rendered difficult. The reason is no doubt human impact (clearfelling for agricultural or timber industry purposes) which, especially in the 19th c., confined natural habitats of the species to small submontane areas (nature reserves or places of difficult access), and higher parts of the lower forest zone in the mountains, often replaced with planted forests. In many cases the population abundance was considerably decreased and its recovery, if any (establishing nature reserves, restitution), was based on gene pool of a small number of individuals. Hence the large variation of shell characters among the populations could be expected – a situation similar to that observed for the phylogenetically remote genus *Vertigo*.

Mutual correlations among the various shell parameters were found to differ among the populations (cf. Table 11). Such differences indicate different growth patterns. In a few instances the correlations differ between the two groups of populations, and some appear to be characteristic of group II (mainly central) in which they occur much more frequently. These are: D:UD, d:UD, h:h/w, H:w, UD:D/N and h:N. The populations of group I (fringes of the range) seem to show no characteristic growth patterns. Inter-population differences in the mode of shell growth, expressed as correlation among different shell parameters, have never been studied and require a wider approach based on a more extensive material of more than one species.

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