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Shell-morphometrical characterization of populations of *Arianta arbustorum* (L.) (Gastropoda, Helicidae) in the Ennstaler Alpen (Styria, Austria)

H. Baminger*

Abstract

Because of the highly variable shell shape, numerous subspecies of *Arianta arbustorum* (LINNAEUS, 1758) have been described. These descriptions are frequently based on few specimens. However, determinations based on a typological species concept, i.e. typological thinking, are always problematic. An alternative approach is the investigation of populations, i.e. population thinking.

The following shell characters were measured or estimated in 28 populations of *A. arbustorum* (N = 1331) from the Ennstaler Alpen (Styria, Austria): shell height (sh), shell breadth (sb), height-breadth-ratio (hb) = shell shape, degree of umbilication (du), umbilical width (uw), number of whorls (nw) and intensity of the brown band (bb).

The results of the shell-morphometrical characterizations are:

1) Similarity analyses (UPGMA and minimum spanning tree) reveal four clusters (= groups): high altitude group, valley group, alpine pasture group and *Arianta arbustorum* "*styriaca*" group. Three populations cannot unambiguously be attributed to any of the groups.

2) The character analysis (PCA) reveals that shell shape, degree of umbilication, shell height and umbilical width represent a major part of the total variance.

3) Pairwise comparisons of the characters by their confidence intervals frequently show significant differences between the populations for the characters of shell height, shell breadth, shell shape and degree of umbilication. In particular, shell shape is a most suitable tool for a rough distinction of *Arianta* populations.

4) The different groups seem to be characteristic for certain ranges in altitude and certain habitats. As a consequence, the populations of the high altitude group, the valley group and the alpine pasture group are considered as eco-morphological units or eco-phenotypes. The populations of the *Arianta arbustorum* "*styriaca*" group are assumed to be members of a geographical subspecies, descending from a globular ancestor.

5) The results show that populations of *A. arbustorum* can be discriminated and a grouping (= classification) is possible, though with restrictions.

Key words: *Arianta arbustorum*, classification, grouping, Pulmonata, shell shape, morphometrical characterization, similarity analyses, PCA, eco-phenotypes, geographical subspecies

Zusammenfassung

Aufgrund der äußerst variablen Schalenform wurden innerhalb von *Arianta arbustorum* (LINNAEUS, 1758) bislang verschiedenste Unterarten beschrieben, wobei diese Beschreibungen oft anhand weniger Individuen erfolgten. Individuelle Zuordnungen, welchen ein typologischer Artbegriff zugrunde liegt, stellen sich meist als problematisch heraus. Als Alternative bietet sich hier die Bearbeitung von Populationen an.

* Helmut Baminger, Institute of Zoology, University of Vienna, Althanstr. 14, A - 1090 Vienna, Austria. Present address: Conservation Biology Research Group (NLU), University of Basel, St. Johanns-Vorstadt 10, CH - 4056 Basel, Switzerland.

Insgesamt wurden 1331 Individuen der Art *A. arbustorum* aus 28 Populationen aus den Ennstaler Alpen (Steiermark, Österreich) einer schalenmorphometrischen Untersuchung unterzogen, wobei folgende Schalenmerkmale gemessen bzw. geschätzt wurden: Schalenhöhe (sh), Schalenbreite (sb), Höhen-Breiten-Verhältnis (hb) = Schalenform, Nabelung (du), Nabelweite (uw), Anzahl der Umgänge (nw) und Bänderung (bb).

Die schalenmorphometrische Charakterisierung der verschiedenen Populationen von *A. arbustorum* brachte folgende Ergebnisse:

1) Die Ähnlichkeitsanalysen (UPGMA und minimum spanning tree) führen zur Bildung von vier Clustern (= Gruppen): Höhengruppe, Talgruppe, Almgruppe und *Arianta arbustorum "styriaca"* - Gruppe. Für 3 Populationen ergibt sich keine eindeutige Zuordnung.

2) Bei der Merkmalsanalyse (PCA) zeigt sich, daß die Merkmale Schalenform, Schalenhöhe, Nabelung und Nabelweite einen wesentlichen Anteil an der Gesamtvarianz haben.

3) Beim paarweisen Vergleich der verschiedenen Merkmale anhand der Konfidenzintervalle zeigen sich bei den Merkmalen Schalenhöhe, Schalenbreite, Schalenform und Nabelung häufig signifikante Unterschiede zwischen den Populationen. Vor allem das Höhen-Breiten-Verhältnis stellt sich dabei als ein besonders geeignetes Merkmal zur groben Unterscheidung von *Arianta* - Populationen heraus.

4) Die verschiedenen Gruppen scheinen für bestimmte Höhenbereiche bzw. bestimmte Habitate charakteristisch zu sein. Die Populationen der Höhengruppe, der Talgruppe und der Almgruppe werden deshalb in diesem Zusammenhang als ökomorphologische Einheiten oder Ökophänotypen bezeichnet. Die Populationen der *Arianta arbustorum "styriaca"* - Gruppe werden als einer geographischen Rasse zugehörig betrachtet, die aus einer globulären Stammform hervorgegangen ist.

5) Die Ergebnisse zeigen, daß die verschiedenen Populationen voneinander unterschieden werden können und daß, mit Einschränkungen, eine Gruppierung (= Klassifikation) möglich ist.

Introduction

Arianta arbustorum (LINNAEUS, 1758) is a highly variable helicid land snail occurring in central, northern (including Iceland) and western Europe up to 2700 m above sea level (FECHTNER & FALKNER 1990, SCHLESCH 1921).

The shell characters of *A. arbustorum* according to KERNEY & CAMERON (1979) are a globular shell with a convex or conical spire of 5 - 6 whorls with rather shallow sutures; an umbilicus with a tiny crescent-shaped slit almost closed by the reflected columellar lip; a nearly round aperture with a white, everted lip and an opaque, brown or yellow shell usually with a dark brown spiral band at the periphery and nearly always with extensive paler fleckings distributed over the shell. Because of the high variability within the species *A. arbustorum*, mainly with regard to shell shape, shell colour and shell size, numerous varieties have been mentioned, e.g. by PFEIFFER (1848; 10 var.), MOQUIN-TANDON (1855; 12 var.), KOBELT (1881, 8 var.), CLESSIN (1882; 20 var.) or TAYLOR (1882; 23 var.). KLEMM (1974, pp. 432 - 445) recognized five subspecies of *A. arbustorum* for Austria. Two out of these five subspecies are recorded for the present study area: *Arianta a. arbustorum* (LINNAEUS, 1758) and *Arianta a. styriaca* (KOBELT, 1876). The shell of the nominotypical *Arianta a. arbustorum* is globular with 5 - 6 whorls, banded and not umbilicated. *Arianta a. styriaca* was originally described as a separate species, *Campylaea styriaca* n. sp., by FRAUENFELD (1868). He describes the shell as being very flat vaulted on the upper side with about 5.5 whorls. The umbilicus has mediocre dimensions, the mouth is big with a white lip and the spiral band is visible up to the fourth whorl and then covered by the suture. Concerning the shell shape, *Campylaea styriaca* is seen to be similar to *Helix phalerata* (= *Arianta chamaeleon* L. PFEIFFER, 1842) by

Frauenfeld. KOBELT (1876) mentions *Campylaea styriaca* FRAUENFELD as *Helix arbustorum var. styriaca* and he describes it as a flat umbilicated form with a great resemblance to *Helix schmidtii* (= *Arianta schmidti* ROSSMÄSSLER, 1836). KLEMM (1974) terms *Helix arbustorum var. styriaca* as *Arianta a. styriaca* (KOBELT, 1876). In his opinion, *Arianta a. styriaca* is a race of higher altitudes and he summarized in this subspecies all those forms which have flatter and more or less umbilicated shells and therefore are different from the nominotypical *Arianta a. arbustorum*. Klemm also stated that *Arianta a. styriaca* is, because of the shell colour, more similar to *Arianta chamaeleon* than to *Arianta a. arbustorum*.

Most recently, the subspecies *Arianta a. arbustorum* and *Arianta a. styriaca* are recorded by GITTENBERGER (1991) for the Ennstaler Alpen. He discriminates *Arianta a. arbustorum* from *Arianta a. styriaca* by the shape index (= shell height/shell breadth x 100) (*Arianta a. arbustorum*: 71.9 - 89.3; *Arianta a. styriaca*: 58.8 - 69.2) and the umbilication. The umbilicus of *Arianta a. styriaca* is more or less opened, whereas that of *Arianta a. arbustorum* is closed by a reflected columellar lip.

Quite frequently, descriptions of subspecies were based on few specimens, e.g., the description of *Arianta a. styriaca* made by Frauenfeld is based on four specimens. But the variation in shell shape can be large even within populations (as shown in *Polygyra septemvolva* by EMBERTON 1988) and is hardly reflected by only few specimens. Consequently, shell variation cannot be based on only a few specimens for description. Since the shell characters of *A. arbustorum* are very variable, the individual assignment of specimens (= shells) to certain subspecies can be quite ambiguous (BISENBERGER 1993, KOTHBAUER & al. 1991). Individual determination based on a typological concept is highly problematic (KOTHBAUER & al. 1991, MAYR 1963). Not only in *A. arbustorum* have individual typological assignments led to problems in classification. GIUSTI & al. (1986) had similar difficulties with the classification of *Medora* (Clausiliidae), as had GOODIN & JOHNSON (1992) with *Partula* (Partulidae). As an alternative to the typological concept, i.e. typological thinking, the investigation of populations, i.e. population thinking, is suggested (MAYR 1963). "... All organisms and organic phenomena are composed of unique features and can be described collectively only in statistic terms. Individuals, or any kind of organic entities, form populations of which we can determine the arithmetic mean and the statistics of variation. ..." (MAYR 1959c). In the case of *A. arbustorum*, this approach was pioneered by BISENBERGER (1993).

The character states of the shell assumed to be typical for *Arianta a. styriaca* - comparatively flat and umbilicated - show transitions to among others the nominotypical *Arianta a. arbustorum*. They therefore prove to be unsuitable for determination of individuals. Consequently, the taxon *Arianta a. styriaca* based only on shell characters has to be rejected (KOTHBAUER & al. 1991). In the same way, *Arianta a. alpicola* is not separable within the species *A. arbustorum* by shell shape. Although *Arianta a. alpicola* is characterized by specimens with predominantly small shells in absolute scale, there are, like in *Arianta a. styriaca*, gradients to - among others - *Arianta a. arbustorum* (NEMESCHKAL & KOTHBAUER 1988). Both results were achieved by means of biometrical methods. EHRMANN (1910) sees a so-called 'Formenkette' (a gradual change in size and shape) for *Campylea phalerata* (= *Arianta chamaeleon*) for certain areas in the Southern Alps of Austria. Diminution of shell size in *A. arbustorum* with increasing altitude has been demonstrated by BURLA & STARHEL (1983) and BAUR & RABOUD (1988). Also, in determination literature, the occurrence of individuals with smaller shells (KERNEY & CAMERON 1979) and of such with dwarf growth (STRESEMANN 1992, FECHTNER & FALKNER 1990) is mentioned within the species *A. arbustorum*. For taxonomic purposes, shell characters have exclusively been used up to now because distinctions of subspecies in land snails based on shell characters are preferable: anatomical differences are difficult to ascertain (MILDNER 1981, KLEMM 1974, EHRMANN 1910). SATTMANN & NEMESCHKAL (1993), for example, were unable to distinguish between three species of the genus Arianta (*A. arbustorum, A. chamaeleon, A. schmidti*) using various parameters of genitalia lengths.

The main purpose of the present study is to characterize *A. arbustorum* populations in the Ennstaler Alpen (Styria, Austria) by the morphometrics of seven shell characters. This characterization should be a basis for further ecological and population biological studies.

Material and Methods

A total of 1331 shells of *A. arbustorum* were recorded at 28 localities in the Ennstaler Alpen (Styria, Austria) (see Fig. 1). The localities are situated between 47° 31' and 47° 39' N and 14° 26' and 14° 41' E at altitudes between 574 m and 2260 m a. s. l. (see Tab. 1). All specimens of a single locality are considered to be members of one and the same population, and the terms "locality" and "population" are virtually synonymous. Measurements and estimations of the characters were exclusively carried out on adult specimens (comp. BOYCOTT 1919), i.e. only specimens with a fully developed lip were considered. All data were taken from living specimens with the exception of the localities Hochtor (No. 24), Buchau/Aichern (No. 25) and Gr. Buchstein (No. 28). Characters of the specimens were measured or estimated in the field and the specimens were then released at the collection site. Empty shells were also collected as far as they were available.

The following shell characters were measured or estimated:

Shell height (sh) and shell breadth (sb), in mm, were measured with a vernier caliper to the nearest 0.1 mm (shells oriented after KERNEY & CAMERON 1979, p. 14).

Shell shape (= height-breadth-ratio: hb) was calculated as hb = sh/sb. A low ratio indicates a flat shell shape and a high ratio indicates a globular shell shape. Height-breadth-ratio multiplied by 100 is equivalent to the shape index (GITTENBERGER 1991).

Degree of umbilication (du) was estimated by means of a rating scale (KOTHBAUER & al. 1991) with values between 0 and 10 (0 = umbilicus closed by reflected lip, i.e. not-umbilicated; 1 = umbilicus 10% open, i.e. visible; 2 = umbilicus 20% open; etc. up to 10 = umbilicus 100% open).

Umbilical width (uw), in mm, was estimated to the nearest 0.5 mm, by lining up a ruler against the largest breadth of the umbilicus opening.

Number of whorls (nw) was counted according to KERNEY & CAMERON (1979, p. 13), with an accuracy up to quarters of whorl.

Intensity of the brown band (bb) on the last whorl was estimated by means of a scale ranging from 0 to 3 (0 = unbanded, 1 = brown band faintly visible, 2 = brown band clearly visible and 3 = brown band distinctly marked).

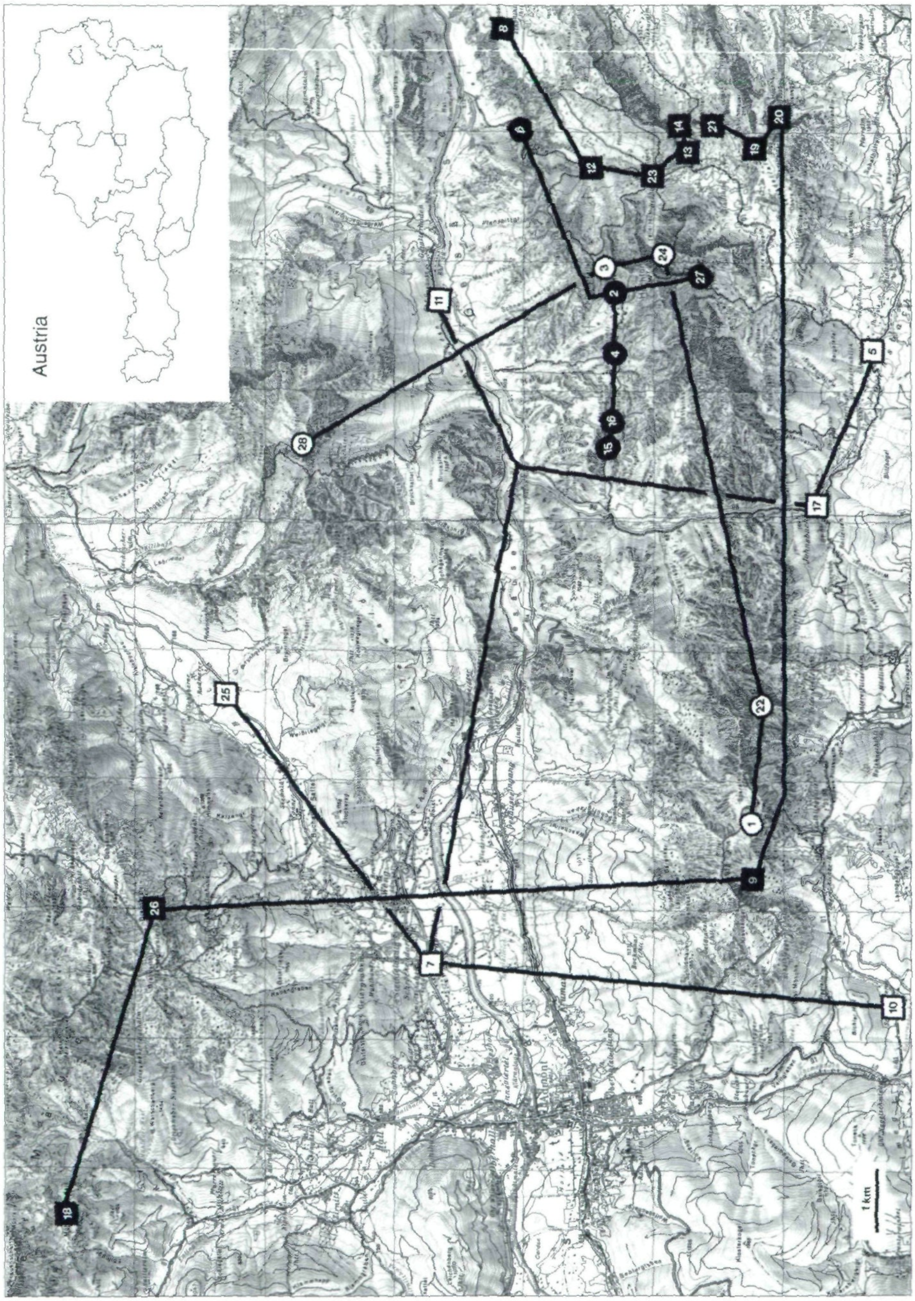


Fig. 1: *Arianta arbustorum* in the Ennstaler Alpen (Styria, Austria). Localities (distinguished by numbers) and groups. Groups (= clusters) are marked by symbols, corresponding to Tab. 7. Reproduction of details of the maps No. 99 and 100 from "Österreichische Karte 1 : 25.000 V" (with permission of the "Bundesamt für Eich- und Vermessungswesen - Landesaufnahme" in Wien, Zl. L 70 003/97 V).

Tab. 1: Localities and parameters. Units of measurement and estimation see Materials and methods. Localities: No., number of locality; name of locality (in parentheses: abbreviation of locality name); altitude; n, total number of shells (in parentheses: number of not-umbilicated shells). Shell parameters: sh, shell height; sb, shell breadth; hb, height-breadth-ratio; du, degree of umbilication; uw, umbilical width; nw, number of whorls; bb, intensity of brown band. Statistical parameters: av/med, averages of characters sh, sb, hb and medians of characters du, uw, nw, bb; min, minimum value; max, maximum value; ci, confidence intervals (p = 0.001).

localities ⇩ parameters ⇨		sh	sb	hb	du	uw	nw	bb
No. 1	av/med	14.06	19.93	0.706	6	2.5	5.5	1
Kalbling (Kal)	min	12.9	18.1	0.640	0	0	5.0	0
1980 m	max	17.1	21.5	0.810	10	4	5.75	3
n = 50 (3)	ci	13.64 - 14.48	19.51 - 20.34	0.689 - 0.723	5 - 8	2 - 3	5.25 - 5.5	0 - 3
No. 2	av/med	13.66	22.61	0.605	9	3	5.25	3
Peternpfad (Pp)	min	12.1	20.0	0.533	3	2	5.0	0
1450 m	max	15.2	24.2	0.686	10	4	5.5	3
n = 42 (0)	ci	13.22 - 14.09	22.02 - 23.19	0.584 - 0.625	7 - 10	2.5 - 3.5	5 - 5.25	2 - 3
No. 3	av/med	13.21	20.01	0.660	10	3	5.25	0
Gamsgartl (Gg)	min	11.2	18.1	0.557	7	2	5.0	0
1780 m	max	15.3	21.8	0.763	10	4	5.5	3
n = 50 (0)	ci	12.79 - 13.63	19.57 - 20.44	0.642 - 0.679	9 - 10	2.5 - 3	5.25 - 5.25	0 - 0
No. 4	av/med	13.73	24.04	0.572	10	3	5.25	3
Haindlkar/Bachbett (HkBb)	min	11.7	20.8	0.494	8	2	4.75	0
1120 m	max	15.8	26.4	0.681	10	4.5	5.5	3
n = 50 (0)	ci	13.25 - 14.21	23.41 - 24.66	0.550 - 0.594	10 - 10	3 - 3.5	5 - 5.25	2 - 3
No. 5	av/med	16.25	20.06	0.810	0	0	5.25	2
Kölbl (Kö)	min	12.6	16.9	0.709	0	0	4.75	0
870 m	max	18.7	22.7	0.944	0	0	5.5	3
n = 50 (50)	ci	15.65 - 16.85	19.49 - 20.63	0.786 - 0.834	0 - 0	0 - 0	5 - 5.25	0 - 3
No. 6	av/med	14.45	23.54	0.614	8	3.5	5.25	3
Wasserfallweg (Wfw)	min	12.5	21.2	0.546	4	2	4.75	0
900 m	max	17.5	26.4	0.697	10	5	5.5	3
n = 49 (0)	ci	13.97 - 14.92	23.01 - 24.07	0.595 - 0.633	7 - 9	3 - 4	5 - 5.25	2 - 3
No. 7	av/med	17.06	20.42	0.836	0	0	5.25	1
Grabnerhof (Gh)	min	14.5	17.7	0.733	0	0	4.75	0
625 m	max	19.5	22.9	0.951	0	0	5.75	3
n = 52 (52)	ci	16.42 - 17.69	19.85 - 20.98	0.812 - 0.859	0 - 0	0 - 0	5.25 - 5.5	1 - 3
No. 8	av/med	15.92	21.17	0.753	3	2.5	5.25	2
Wolfbauernhochalm (Wbha)	min	13.3	18.6	0.663	0	0	4.75	0
1500 m	max	17.9	22.7	0.825	8	3.5	5.5	3
n = 41 (5)	ci	15.38 - 16.46	20.66 - 21.66	0.731 - 0.774	1 - 6	2 - 3	5.25 - 5.5	1 - 3
No. 9	av/med	16.52	22.36	0.739	4.5	2.5	5.5	2
Roßkar (Rk)	min	14.3	19.4	0.648	0	0	5.0	0
1700 m	max	18.7	24.6	0.857	9	3.5	5.75	3
n = 50 (6)	ci	15.99 - 17.04	21.75 - 22.97	0.717 - 0.760	2 - 6	2 - 3	5.25 - 5.5	0 - 3
No. 10	av/med	16.81	20.56	0.818	0	0	5.25	3
Schloß Kaiserau (SKai)	min	14.6	18.1	0.723	0	0	4.75	0
1127 m	max	18.7	22.2	0.931	0	0	5.5	3
n = 50 (50)	ci	16.31 - 17.31	20.08 - 21.04	0.796 - 0.840	0 - 0	0 - 0	5 - 5.25	3 - 3
No. 11	av/med	17.67	21.6	0.818	0	0	5.25	3
Gstatterboden (Gb)	min	14.7	18.8	0.703	0	0	4.75	0
574 m	max	20.3	23.9	0.979	0	0	5.5	3
n = 50 (50)	ci	16.99 - 18.35	21.06 - 22.15	0.790 - 0.846	0 - 0	0 - 0	5 - 5.5	1 - 3
No. 12	av/med	14.95	21.33	0.702	5	3	5.25	3
Ebnesangeralm (Eaa)	min	13.0	19.0	0.611	0	0	5.0	0
1500 m	max	17.3	23.3	0.874	8	4.5	5.75	3
n = 50 (6)	ci	14.42 - 15.46	20.83 - 21.81	0.678 - 0.725	2 - 6	2.5 - 3	5.25 - 5.5	2 - 3
No. 13	av/med	16.01	22.07	0.726	0	0	5.5	3
Gamsfriedhof (Gfh)	min	13.2	19.8	0.639	0	0	5.0	0
1700 m	max	18.4	24.7	0.811	8	4	5.75	3
n = 50 (26)	ci	15.44 - 16.57	21.49 - 22.64	0.703 - 0.748	0 - 5	0 - 3	5.25 - 5.5	3 - 3

Tab. 1 continued

localities ⇩ parameters ⇨		sh	sb	hb	du	uw	nw	bb
No. 14	av/med	16.08	21.75	0.740	3	3	5.5	3
Teufelsarsch (Ta)	min	14.4	20.1	0.653	0	0	5.0	0
1800 m	max	18.8	23.5	0.865	8	4	5.75	3
n = 50 (16)	ci	15.64 - 16.52	21.38 - 22.11	0.717 - 0.763	0 - 5	0 - 3.5	5.25 - 5.5	1 - 3
No. 15	av/med	13.95	23.64	0.590	7.5	2.75	4.75	3
Gseng (Gs)	min	12.2	21.6	0.521	5	2	4.5	0
1120 m	max	16.7	26.1	0.672	10	4	5.0	3
n = 50 (0)	ci	13.54 - 14.36	23.18 - 24.09	0.574 - 0.606	7 - 9	2.5 - 3	4.5 - 5	3 - 3
No. 16	av/med	13.26	22.38	0.593	8	2.5	4.75	3
Haindlkar/Gseng (HkGs)	min	11.6	19.7	0.510	3	1.5	4.5	1
1200 m	max	15.0	24.9	0.695	10	3.5	5.25	3
n = 50 (0)	ci	12.83 - 13.68	21.83 - 22.94	0.574 - 0.611	7 - 9	2.5 - 3	4.75 - 4.75	3 - 3
No. 17	av/med	17.24	21.28	0.811	0	0	5.0	3
Donner (Do)	min	14.7	19.9	0.710	0	0	4.75	0
750 m	max	21.2	24.0	0.913	0	0	5.5	3
n = 50 (50)	ci	16.66 - 17.81	20.81 - 21.74	0.787 - 0.834	0 - 0	0 - 0	5 - 5.25	0 - 3
No. 18	av/med	16.31	21.49	0.760	1	2	5.5	3
Liebl-Stadl (LiS)	min	14.6	19.5	0.714	0	0	5.0	0
1480 m	max	19.2	23.8	0.862	6	3.5	6.0	3
n = 50 (23)	ci	15.82 - 16.80	20.94 - 22.02	0.743 - 0.775	0 - 3	0 - 3	5.5 - 5.5	3 - 3
No. 19	av/med	14.78	20.11	0.735	2.5	2	5.5	3
Obere Stadlfeldalm (Osfa)	min	11.4	18.3	0.623	0	0	5.0	0
1980 m	max	17.7	22.5	0.832	9	3	5.75	3
n = 36 (4)	ci	13.95 - 15.61	19.41 - 20.81	0.703 - 0.766	1 - 6	1.5 - 2.5	5.25 - 5.5	0 - 3
No. 20	av/med	16.79	21.89	0.767	1	2	5.25	3
Glanegg-Luk´n (GlaL)	min	13.5	19.4	0.665	0	0	5.0	0
1800 m	max	19.5	24.1	0.854	10	3	6.0	3
n = 43 (20)	ci	16.15 - 17.43	21.22 - 22.55	0.743 - 0.791	0 - 3	0 - 2.5	5.25 - 5.5	3 - 3
No. 21	av/med	15.34	21.63	0.710	2.5	3	5.25	2.5
Rotofen (Ro)	min	13.5	19.6	0.644	0	0	5.0	0
1800 m	max	17.6	24.9	0.850	7	4.5	5.75	3
n = 50 (1)	ci	14.88 - 15.79	21.05 - 22.20	0.688 - 0.731	1 - 3	2.5 - 3.5	5.25 - 5.5	0 - 3
No. 22	av/med	15.15	23.05	0.658	8	3	5.25	0
Reichenstein (Res)	min	13.2	20.6	0.557	3	2	4.75	0
1940 m	max	17.4	24.9	0.753	10	4	5.75	3
n = 46 (0)	ci	14.57 - 15.73	22.46 - 23.63	0.636 - 0.679	6 - 9	3 - 3.5	5 - 5.5	0 - 2
No. 23	av/med	16.07	21.46	0.749	2	2.5	5.25	3
Heßhütte (Hh)	min	13.9	19.7	0.670	0	0	5.0	0
1695 m	max	18.5	24.5	0.841	8	4.5	5.5	3
n = 50 (2)	ci	15.46 - 16.67	20.90 - 22.01	0.729 - 0.768	1 - 3	2.5 - 3	5 - 5.5	1 - 3
No. 24	av/med	12.36	18.53	0.669	8	2.5	5.0	0
Hochtor (Ht)	min	10.6	16.8	0.606	4	1.5	4.75	0
2260 m	max	14.1	21.0	0.747	10	3.5	5.25	1
n = 50 (0)	ci	11.99 - 12.74	18.08 - 18.97	0.653 - 0.684	7 - 9	2 - 3	4.75 - 5.25	0 - 0
No. 25	av/med	18.14	20.38	0.890	1	1.25	5.5	0
Buchau/Aichern (BuAi)	min	16.4	17.5	0.770	0	0	4.75	0
830 m	max	20.2	22.4	0.995	5	4	5.75	3
n = 50 (24)	ci	17.62 - 18.65	19.88 - 20.88	0.859 - 0.919	0 - 2	0 - 2	5.25 - 5.5	0 - 3
No. 26	av/med	17.20	21.27	0.809	1	2.5	5.5	3
Grabnerstein (Grs)	min	14.7	18.2	0.711	0	0	5.0	0
1800 m	max	19.7	23.4	0.875	5	4	5.75	3
n = 50 (16)	ci	16.71 - 17.69	20.80 - 21.73	0.789 - 0.828	0 - 2	0 - 3	5.25 - 5.5	1 - 3
No. 27	av/med	15.20	23.62	0.644	7	3	5.25	3
Schneeloch (Sl)	min	13.0	20.3	0.584	3	2.5	5.0	0
1760 m	max	17.3	25.6	0.749	10	4.5	5.5	3
n = 42 (0)	ci	14.62 - 15.77	22.92 - 24.32	0.623 - 0.665	6 - 9	2.5 - 4	5 - 5.25	1 - 3
No. 28	av/med	13.93	19.90	0.701	6	2.5	5.25	0
Gr. Buchstein (GrBu)	min	12.3	18.5	0.624	1	1	5.0	0
2150 m	max	15.6	21.4	0.786	9	3.5	5.75	3
n = 50 (0)	ci	13.58 - 14.27	19.49 - 20.30	0.682 - 0.720	5 - 8	2.5 - 3	5.25 - 5.5	0 - 2

Tab. 2: Measurement error statistics: the averages of measurement and estimation differences of all characters; SE = standard error; n for repeated measurement and estimation = 133 (i.e. 10% of all shells measured and estimated); confidence intervals p = 0.001; other abbreviations as in Tab. 1.

character	average	SE	confidence intervals
sh	0.20	0.014	0.16 - 0.25
sb	0.19	0.018	0.13 - 0.25
du	0.33	0.050	0.16 - 0.50
uw	0.20	0.029	0.11 - 0.30
nw	0.07	0.009	0.04 - 0.10
bb	0.10	0.026	0.01 - 0.18

Tab. 3: Pairwise character comparisons (above the diagonal) and matrix of Euclidean distances (below the diagonal) between localities. Localities (Lo) are marked by numbers (comp. Tab. 1). Below the diagonal: matrix of Euclidean distances calculated from z-transformed averages (sh, sb, hb) and z-transformed medians (du, uw, nw, bb). Above the diagonal: Pairwise comparisons of all characters of the analysed populations - only significant different characters (p = 0.001) are listed: shell height = 1, shell breadth = 2, height-breadth-ratio = 3, degree of umbilication = 4, umbilical width = 5, number of whorls = 6, intensity of brown band = 7. Shaded fields indicate missing significant character differences between populations.

Lo	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
1	-	2,3	1,3,4	2-4	1,3-5	2,3	1,3-5	1-3	1,2	1,3-5	1-5	2	1,2	1,2
2	3.279	-	2,3,7	2	1-5		1-5	1-4	1,3,4	1-5	1,3-5	1-4	1,3,4	1,3,4
3	2.077	3.271	-	2,3,7	1,3-5	1-3,7	1,3-5,7	1-4,7	1-4	1,3-5,7	1-5,7	1,2,4,7	1-4,7	1-4,7
4	4.213	1.167	4.067	-	1-5	3,4	1-5	1-4	1-4	1-5	1-5	1-4	1-4	1-4
5	3.645	5.129	4.965	5.908	-	1-5		2-5	2-5		1,2	1-5	2,3	2,3
6	3.722	1.010	3.835	1.058	5.323	-	1-5	1-4	1-4	1-5	1-5	2-4	1-4	1-4
7	3.921	5.584	5.121	6.277	1.075	5.676	-	3-5	2-5		2	1,3-5	2,3	2,3
8	2.366	3.206	3.480	4.015	2.541	3.197	2.797	-	2	3-5	1,3-5	3		
9	2.629	3.191	3.954	3.707	3.370	2.963	3.454	1.630	-	2-5	3-5	1		
10	4.131	5.119	5.506	5.836	0.995	5.226	1.706	2.670	3.333	-	2	1,3-5	2,3	2,3
11	4.555	5.208	5.877	5.769	1.702	5.155	1.950	2.830	3.191	0.957	-	1,3-5	1,3	1,3
12	2.455	2.065	3.302	3.020	3.543	2.192	4.040	1.415	2.066	3.508	3.705	-		1
13	3.806	4.385	5.369	4.887	2.344	4.425	2.837	2.833	2.656	2.067	2.013	3.305	-	
14	2.737	3.161	4.241	3.846	3.429	2.983	3.780	1.618	1.166	3.262	3.277	1.642	2.708	-
15	5.117	2.632	4.600	2.599	5.750	2.583	6.117	4.153	4.691	5.682	5.639	3.428	5.427	4.736
16	4.711	2.536	4.083	2.868	5.484	2.862	5.950	4.038	4.792	5.506	5.639	3.241	5.401	4.752
17	4.822	5.212	5.799	5.813	1.861	5.222	2.203	2.952	3.811	1.373	1.287	3.744	2.842	3.835
18	2.994	3.816	4.682	4.501	2.588	3.732	3.005	1.689	1.541	2.361	2.408	2.195	1.833	1.077
19	2.087	3.472	3.875	4.421	2.716	3.767	3.393	1.910	2.305	2.795	3.280	1.931	2.487	1.721
20	3.523	3.768	4.771	4.394	2.434	3.579	2.776	1.362	1.913	2.080	1.993	2.065	2.239	1.701
21	2.565	2.633	3.568	3.431	3.218	2.544	3.600	0.984	1.791	3.231	3.351	0.899	3.008	1.443
22	2.990	2.813	2.654	3.024	4.828	2.676	4.726	2.920	2.744	5.135	5.066	3.003	4.592	3.490
23	2.988	3.216	4.187	3.981	2.683	3.121	3.128	0.920	1.809	2.496	2.582	1.332	2.577	1.353
24	3.100	4.316	1.883	5.220	4.975	4.974	5.239	4.086	5.113	5.624	6.179	4.021	5.937	5.201
25	3.998	6.190	5.329	6.847	2.839	6.146	2.087	3.312	3.393	3.256	3.276	4.620	3.868	3.870
26	3.407	4.387	5.053	5.070	2.832	4.212	3.075	1.927	1.805	2.544	2.507	2.612	2.561	1.360
27	3.636	1.461	4.003	1.583	4.753	0.799	5.069	2.719	2.411	4.593	4.439	1.927	3.814	2.526
28	1.494	3.561	1.394	4.436	3.784	3.989	3.890	2.577	3.311	4.428	4.839	2.864	4.457	3.591

Averages and their confidence intervals (p = 0.001) were calculated for the characters sh, sb and hb. The median values and their confidence intervals (p = 0.001) were calculated for the characters du, uw, nw and bb (WERNER 1992). Averages, medians and confidence intervals were calculated by means of the program package STATGRAPHICS Plus vers. 7.0. To determine the measurement and estimation errors, 10% of the specimens of each locality were chosen at random for repeated measurements and estimations. The statistical analyses used here are similarity analyses (UPGMA and minimum spanning tree), character analysis and ordination technique (both PCA). The descriptive representation of data was done by means of diverse statistical methods. To minimize the chance of cases of random significance in a series of pairwise comparisons, a significance level of p = 0.001 was chosen (ZÖFEL 1992). Pairwise Euclidean distances between the populations (Tab. 3, below the diagonal) were calculated from the z-transformed averages (sh, sb, hb) and z-transformed medians (du, uw, nw, bb) to perform UPGMA (Unweighted Pair Group Method using Arithmetic averaging) and minimum spanning tree. A PCA (Principal Component Analysis) was based on the matrix of correlation between all characters over all populations (FLURY & RIEDWYL 1983, SNEATH & SOKAL 1973). All programs used are included in the program package SYN - TAX vers. 5.02. (© J. Podani, Scientia Publishing 1993, H - 1365 Budapest).

Tab. 3 continued

Lo	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	2,3,6	2,3,6	1-5	1-4		1-4	1,2,4	1-3	1-4	1-3	1,3,4	1-4	1-3	
2		6	1-5	1,3,4,6	2-4	1,3,4	1,3,4	1,3	1-4	1-3,7	1-5	1-4	1	2,3
3	2,3,6,7	2,3,6,7	1-5	1-4,6-7	1,3,4	1-4,7	1-4	1,2	1-4,7	1,2	1,3-5	1-4,7	1,2,7	3,4
4	4	2,4,6	1-5	1-4,6	2-5	1-5	1-4	1,3,4	1-4	1-4,7	1-5	1-4	1,3,4	2-4
5	1-5	1-6	2	2,3,6	1,3-5	2	2-5	2-5	2-5	1-5	1,3	2	2-5	1,3-5
6		1,2,6	1-5	1-4,6	2-5	1-5	2-4	3	1-4	1-3,7	1-5	1-4		2,3
7	1-6	1-6		3	1,3-5	2,3	1-5	1-5	3-5	1-5,7			1-5	1,3-5
8	1-4,6	1-4,6	1,3-5					2,3		1-4,7	1,3	1,3	2,3	1-3
9	1-4,6	1,3,4,6	2-5		1,2		1	1,3		1-4	1-3	2,3	1,3	1,2
10	1-5	1-6		3,6	1,3-5	2,3	1-5	1-5,7	3-5	1-5,7	1,3		1-5	1,3-5,7
11	1-5	1,3-6		1,3	1-5		1,3-5	1-5	1,3-5	1-5,7	2,3		1-5	1-5
12	1-4,6	1-4,6	1,3-5	1,3	2	1,3		2	3	1,2,4,7	1,3,5	1,3	2,3	1,2
13	1-4,6	1,3,4,6	1,3		2			3,4,7		1-4,7	1-3	1,3	2-4	1,2,7
14	1-4,6	1,3,4,6	1,3		1,2			2-4		1-4,7	1-3	1,3	2-4	1,2
15	-	2	1-5	1-4,6	2-4,6	1-4,6	1-4,6	1,3,7	1-4	1-3,7	1-6	1-4,6	1,3	2,3,6,7
16	1.071	-	1-6	1,3,4,6	1-4,6	1,3,4,6	1,3,4,6	1,3,6,7	1,3,4,6	1-3,7	1-6	1-4,6	1,3,6	2,3,6,7
17	5.122	5.054	-	3,6	1,3-5		1,3-5	1-5	3-5	1-5	3		1-5	1-5
18	5.145	5.117	3.131	-	1,2		1,3	1-4,7		1-4,6,7	1-3	3	1-4,6	1-4,7
19	5.116	4.792	3.695	1.527	-	1,2	2	2,3,5	2	1-4	1,3	1,3	2,3	
20	4.418	4.480	2.248	1.307	2.310	-	1,3	1,3-5,7		1-4,7	1-3		1-4	1-4,7
21	3.662	3.607	4.310	1.833	1.977	1.579	-	2-4		1-4	1-3,5	1,3	2-4	1,2,4
22	3.734	3.872	5.152	3.996	4.089	3.831	2.896	-	2-4	1,2	1-5	1-4		1-3
23	4.085	4.041	2.743	1.347	1.861	0.798	0.916	3.522	-	1-4,7	1-3,5	1,3	2-4	1-4
24	4.929	4.150	5.781	5.414	4.424	5.303	4.236	4.041	4.732	-	1-4	1-4,7	1,2,7	1,2
25	7.162	7.086	3.914	3.367	3.915	3.533	4.148	4.817	3.800	5.872	-	3	1-5	1,3-5
26	5.619	5.627	3.264	0.950	2.104	1.493	2.240	4.343	1.639	5.785	3.042	-	1-4	1-4
27	2.684	3.028	4.558	3.174	3.450	2.922	2.151	2.579	2.580	5.098	5.581	3.641	-	1-3
28	4.701	4.243	4.778	3.796	3.090	3.862	2.848	2.624	3.362	2.021	4.191	4.151	3.925	-

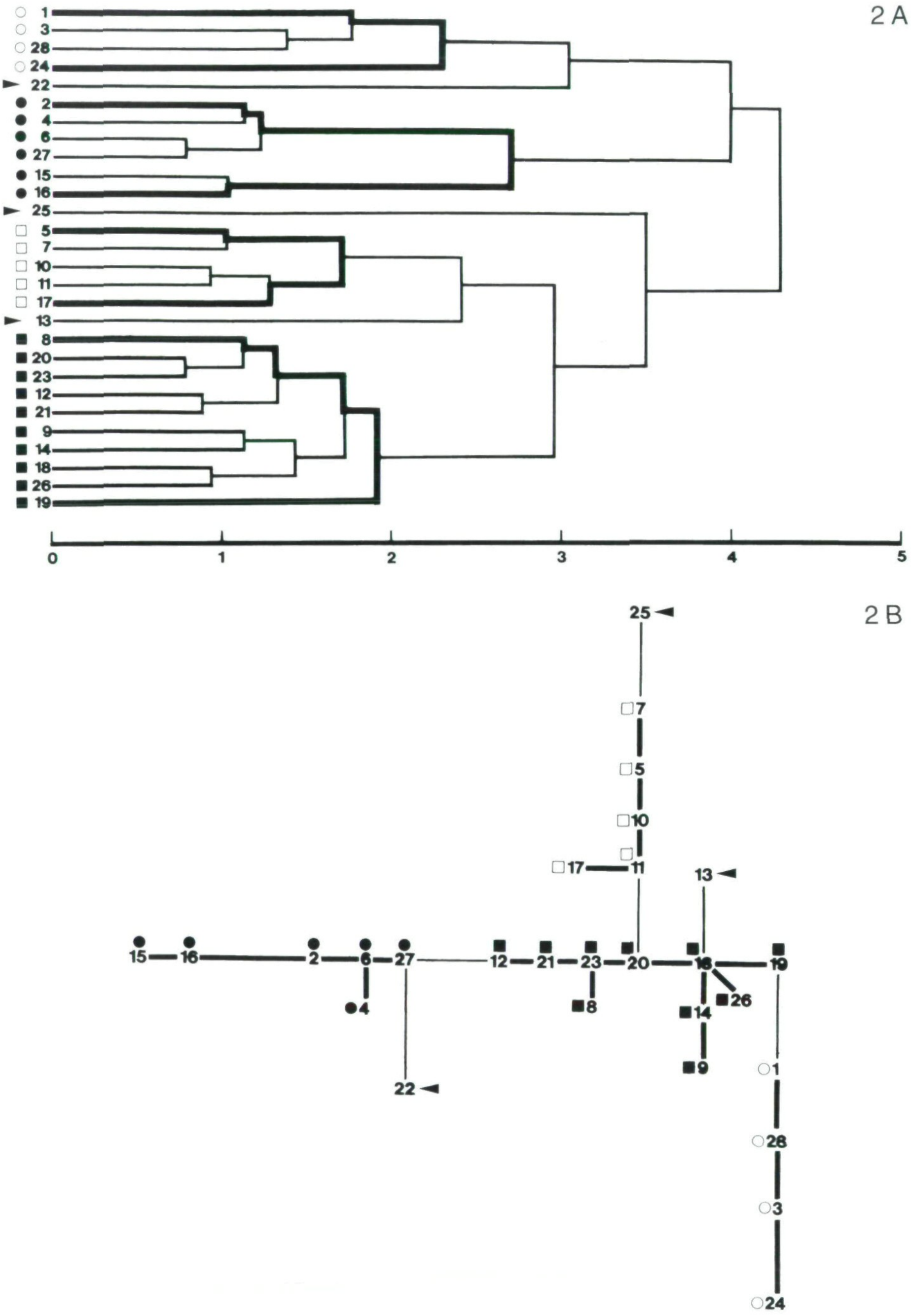


Fig. 2: A. UPGMA. B. Minimum spanning tree; branch lengths are proportional to distances. Both based on Euclidean distances (Tab. 3 - below the diagonal); for population numbers see Tab. 1. Clusters are marked by symbols (○ = high altitude group; ● = *Arianta arbustorum "styriaca"* group; □ = valley group; ■ = alpine pasture group) and additionally by thick lines. The assignment of three populations (No. 13, 22, 25) is ambiguous - these populations are marked by arrows.

Results

The averages, medians and confidence intervals (p = 0.001) of all shell characters of all populations investigated are shown in Tab. 1. The measurement error statistics are summarized in Tab. 2. Fig. 2 A and B show an UPGMA dendrogram and a minimum spanning tree. Both similarity analyses revealed, almost identically, four clusters. Only three populations (No. 13, 22, 25) could not be assigned unambiguously to a certain cluster (these populations are marked by arrows, see in Fig. 2 A and B, see also in Fig. 3 A and B). In the following, these clusters are considered as groups. With one exception, the groups were named by taking into consideration the altitudinal range and/or the habitat occupied by the respective populations. In the case of the *Arianta arbustorum* "*styriaca*" group, naming was done in accordance with the subspecies having the same name and being characterized by flat and umbilicated shells.

High altitude group (Fig. 4, No. 1 - 2):

Populations of this group had flat (hb = 0.66 - 0.71) and strongly umbilicated (uw = 6 - 10) shells without or with slight banding (bb = 0 - 1). Populations: No. 1, 3, 24, 28.

Arianta arbustorum "*styriaca*" group (Fig. 4, No. 3 - 4):

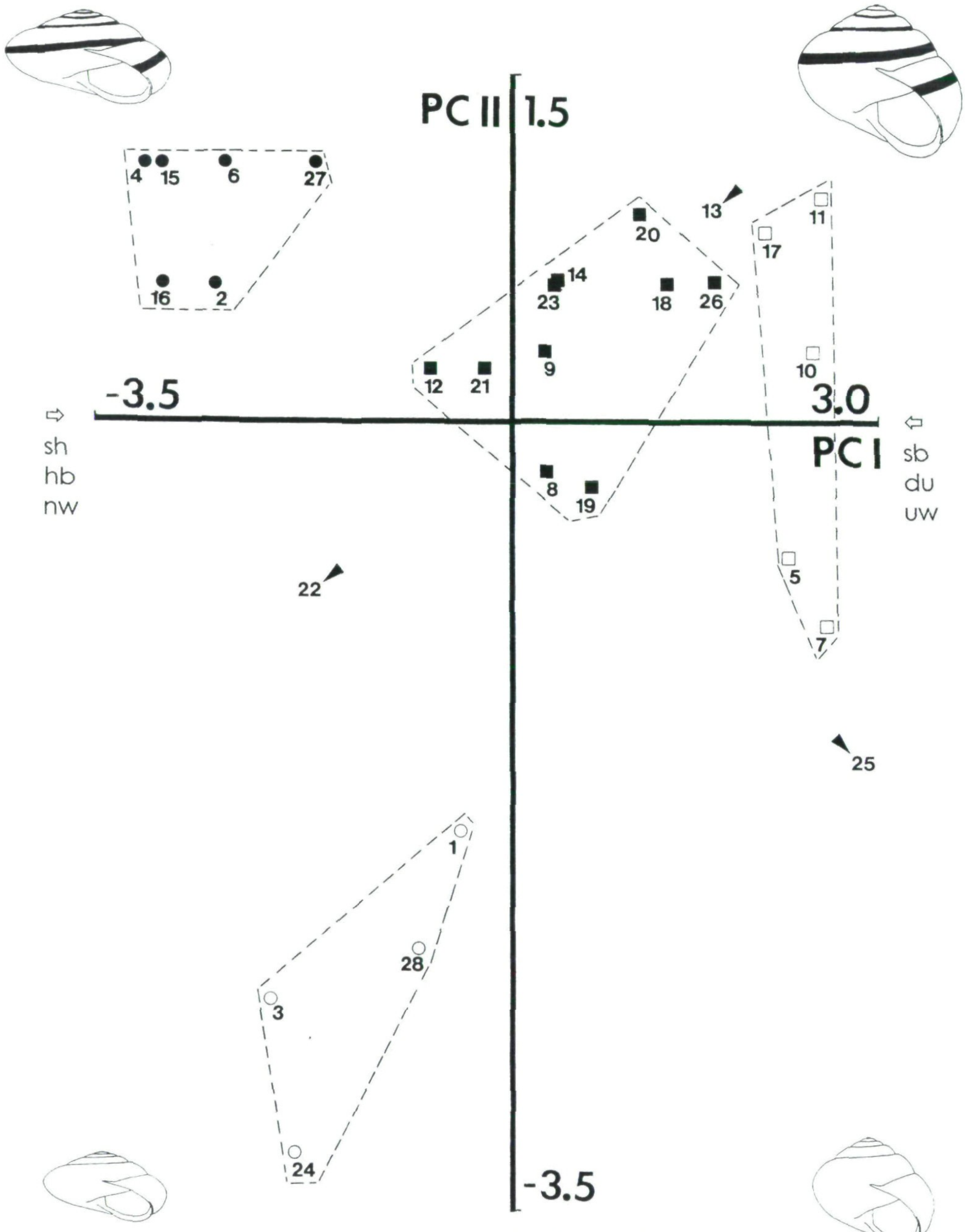
Populations of this group had extremly flat (hb = 0.57 - 0.64) and very strongly umbilicated (du = 7 - 10) shells with a very well - developed brown band (bb = 3). Populations: No. 2, 4, 6, 15, 16, 27.

Tab. 4: Principal Component Analysis (PCA): Eigenvalues and the weights (w) of the original characters in the Eigenvectors, Principal Components (PC) I - VII; tv, total variance in %; ctv, cumulative total variance in %; other abbreviations as in Tab. 1.

	PC I	PC II	PC III	PC IV	PC V	PC VI	PC VII
Eigenvalue	3.701	1.610	0.973	0.418	0.251	0.045	0.001
	w	w	w	w	w	w	w
sh	0.45978	0.25043	0.11131	-0.44450	0.27431	0.26039	-0.61070
sb	- 0.23553	0.62268	0.13395	-0.58099	-0.19997	-0.18319	0.35742
hb	0.50630	- 0.10210	0.01463	-0.09745	0.30999	0.36001	0.70557
du	- 0.49559	- 0.15063	0.08072	-0.16028	-0.17178	0.81791	-0.03185
uw	- 0.41240	- 0.02147	0.47766	0.04605	0.76263	-0.13096	0.02104
nw	0.24657	- 0.05950	0.85568	0.17732	-0.41476	0.00174	0.00253
bb	0.02012	0.71584	- 0.05094	0.62938	0.07445	0.28792	-0.00249
tv	52.87	23.00	13.91	5.98	3.59	0.64	0.01
ctv	52.87	75.87	89.78	95.76	99.35	99.99	100.00

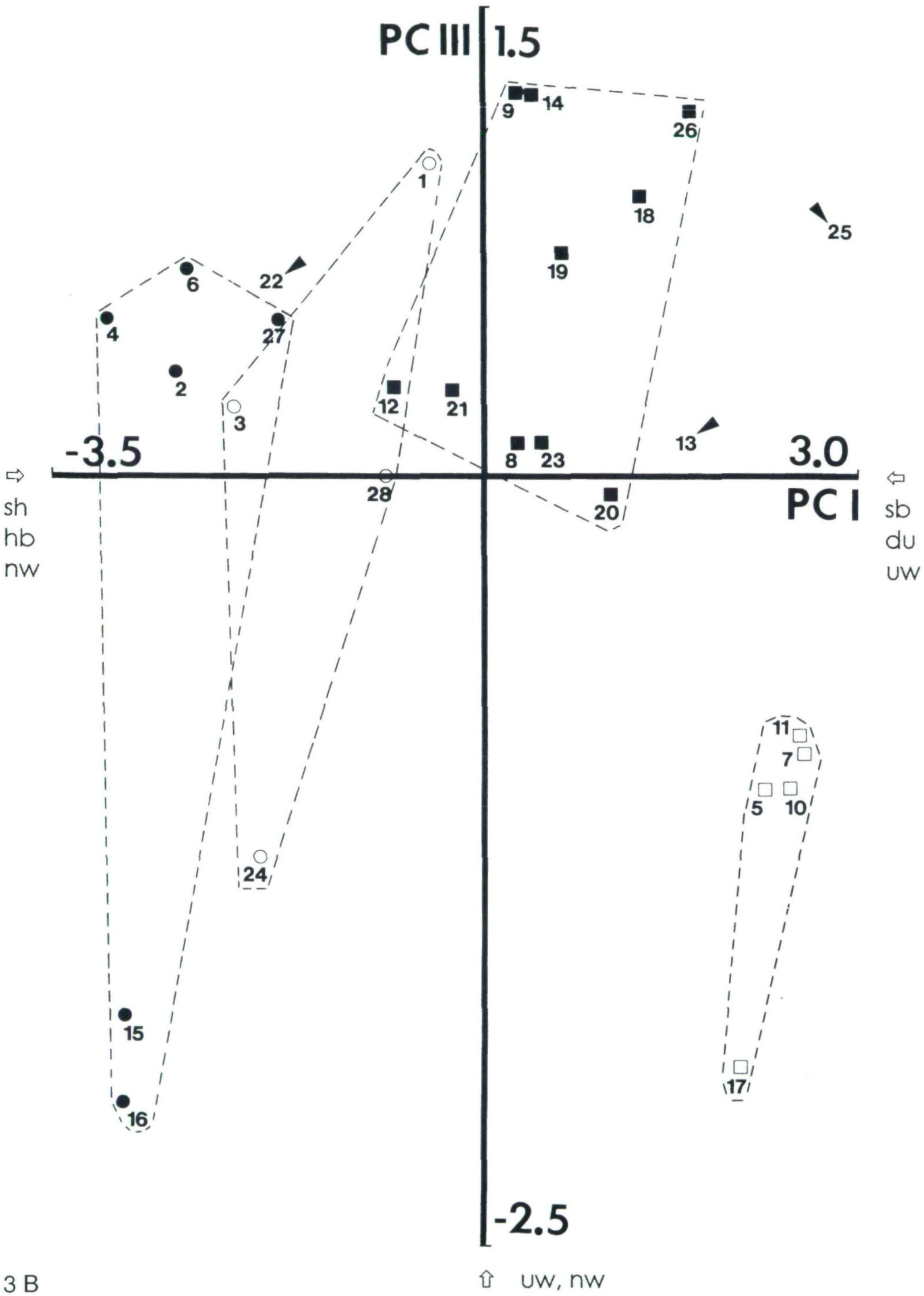
Tab. 5: Pairwise comparisons - number of significantly different characters. Number of significantly different characters obtained by comparisons of all characters of all populations (number of pairwise comparisons = 378) (comp. Tab. 3/above the diagonal).

number of significant different characters	number of incidents	number of incidents in %
0	49	12.96
1	27	7.14
2	61	16.14
3	57	15.08
4	88	23.29
5	82	21.69
6	14	3.70
7	-	-
total	378	100.00



3 A

Fig. 3: Ordination of populations (Principal Component Analysis, seven characters). A. Plot of Principal Components I vs. II. B. Plot of Principal Components I vs. III (for Eigenvalues and weights see Tab. 4). Population numbers and abbreviations see Tab. 1. Clusters are marked by symbols, corresponding to Fig. 2 A and B. The directions of increasing representation of the listed original characters on the principal axes are marked by arrows.


PC III
1.5
-2.5
PC I
-3.5
3.0
sh
hb
nw
sb
du
uw
uw, nw
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
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21
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25
26
27
28

3 B

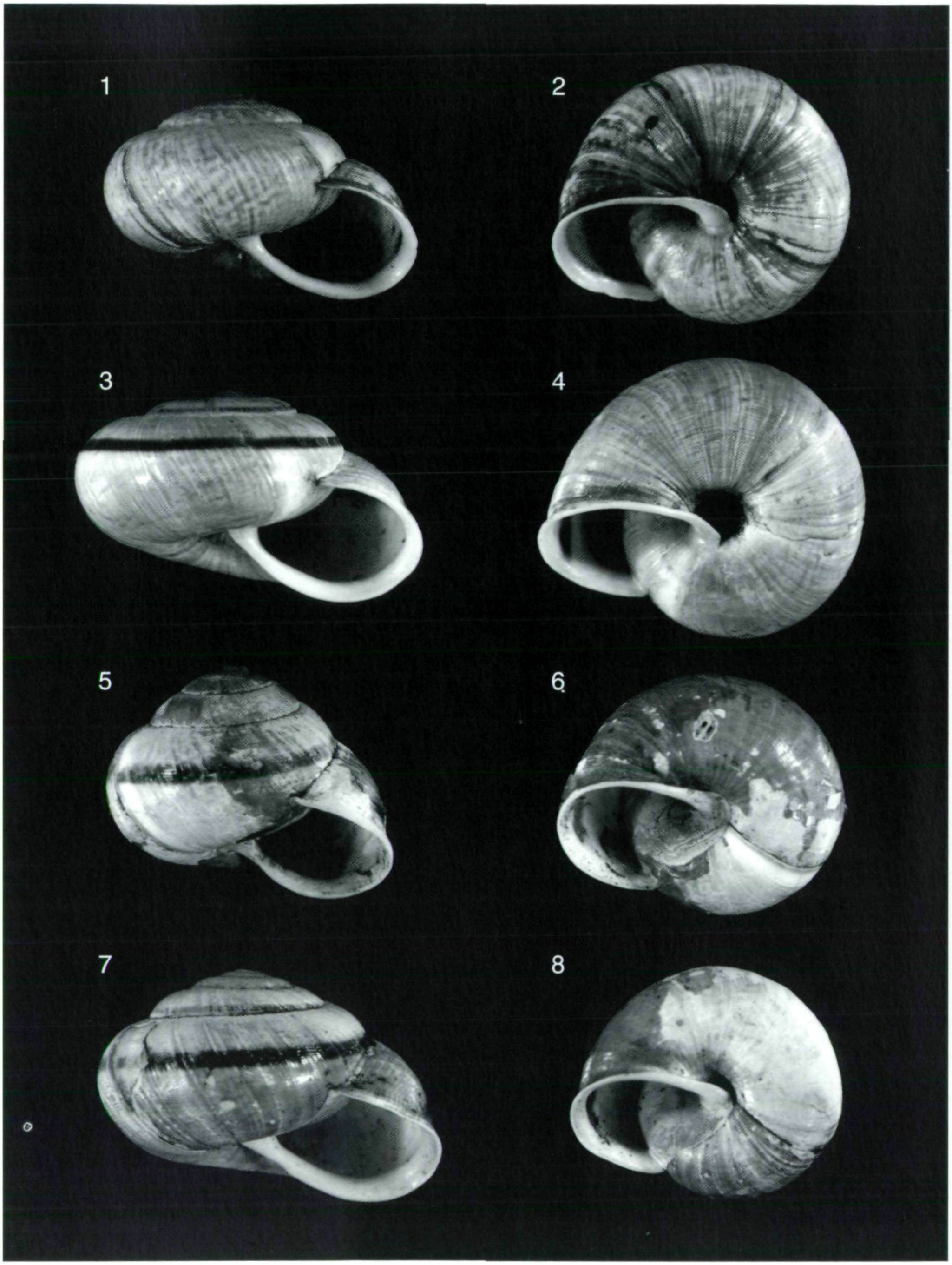

Fig. 4: Examples of shells from the various groups of *Arianta arbustorum*. No. 1 - 2: high altitude group (sh: 13.7, sb: 20.8), No. 3 - 4: *Arianta arbustorum* "*styriaca*" group (sh: 14.1, sb: 23.2), No. 5 - 6: valley group (sh: 17.0, sb: 20.3) and No. 7 - 8: alpine pasture group (sh: 14.9, sb: 21.8). Shells selected according to group averages and means in Tab. 7.

Valley group (Fig. 4, No. 5 - 6):

Populations of this group had the most globular shells (hb > 0.81), were not umbilicated (du = 0) but variable in banding (bb = 1 - 3). Populations: No. 5, 7, 10, 11, 17.

Alpine pasture group (Fig. 4, No. 7 - 8):

Populations of this group had globular (hb = 0.70 - 0.81), poorly umbilicated (du = 1 - 5) shells with a strongly expressed band (bb = 2 - 3). Populations: No. 8, 9, 12, 14, 18, 19, 20, 21, 23, 26.

A PCA was made in order to consider character intercorrelations. Eigenvalues and weights of the axes Principal Component I (PC I) to Principal Component VII (PC VII) of each character are listed in Tab. 4. The first two axes (PC I and II) of the PCA represent 75.87% of the total variance; the first three axes (PC I to PC III) represent 89.78% of total variance. In accordance with the variance (see Tab. 4), only the first three axes were used for ordination. PC I is primarily an axis of shell height and therefore, in connection with shell breadth, of shell shape (= height-breadth-ratio), degree of umbilication and umbilical width (see Fig. 3 A and B). PC II is mainly an axis of the intensity of the brown band and shell breadth (see Fig. 3 A), and PC III is mainly an axis of the number of whorls and umbilical width (see Fig 3 B). The clusters of the UPGMA and the minimum spanning tree are also reflected in the character space (Fig. 3 A and B). The plot PC I/PC II (Fig. 3 A) clearly separates the four different clusters (= groups). In the plot of PC I/PC III (Fig. 3 B), three clusters widely overlap. The results of the pairwise comparisons are shown in Tables 5 and 6. Based on pairwise comparison of all characters, the populations differ significantly in 44.98% of the cases in four or five characters. This means that nearly half of the differences between the populations are very distinct. In comparison, only 23.28% of the differences are due to one or two characters (see Tab. 5). The characters with the greatest numbers of significant differences are height-breadth-ratio (75.40%), shell height (64.02%), shell breadth (61.38%) and degree of umbilication (54.76%). The high variability of the height-breadth-ratio, which leads to a considerable number of significant differences and therefore can be used for a rough distinction of different populations (see Tab. 7), is confirmed by the PCA (PC I is mainly an axis of shell shape). The characters umbilical width, number of whorls and intensity of the brown band are responsible for fewer cases of significant differences (see Tab. 6). These characters, however, are useful for a more detailed distinction than by the height-breadth-ratio alone.

Tab. 6. Pairwise comparisons - number of significant pairwise differences. Significant pairwise differences of each character in relation to the total number of significant differences between the characters (n = 1164) and in relation to the number of theoretically possibly significant differences of each character (n = 378) (comp. Tab. 3/above the diagonal). Abbreviations as in Tab. 1.

character	number of significant pairwise differences	significant pairwise differences in % (n = 1164)	significant pairwise differences in % (n = 378)
hb	285	24.49	75.40
sh	242	20.79	64.02
sb	232	19.93	61.38
du	207	17.78	54.76
uw	103	8.85	27.25
nw	49	4.21	12.96
bb	46	3.95	12.17
	1164	100.00	

Discussion

KOTHBAUER & al. (1991) showed that the separation of *Arianta a. styriaca* individuals within the species *A. arbustorum* based on shell characters alone is not feasible. Similarly, individuals of another subspecies of *A. arbustorum*, *Arianta a. alpicola*, are not separable by shell shape within the species (NEMESCHKAL & KOTHBAUER 1988). Comparing populations, BISENBERGER (1993) showed that different species of the genus *Arianta* [*A. arbustorum* (LINNAEUS, 1758), *A. chamaeleon* (L. PFEIFFER, 1842), *A. schmidti* (ROSSMÄSSLER, 1836)] are clearly separable by different banding modes.

This study shows that *A. arbustorum* populations can be characterized and discriminated by shell characters (see also BISENBERGER 1993). It also shows a classification (= grouping) using similarity analyses (UPGMA and minimum spanning tree) is possible, although there are three populations (No. 13, 22, 25) which cannot be unequivocally assigned to a certain group since they cluster to different groups in the two similarity analyses. In the case of population No. 13, the definitive assignment to the alpine pasture group is supported by the PCA (Fig. 3 B). A definitive assignment of population No. 22 is feasible by comparing the intensity of the brown band with that of populations of two other possible groups (high altitude group and *Arianta arbustorum "styriaca"* group). Therefore, in accordance with the UPGMA, the population in question is ascribed to the high altitude group. In population No. 25, the PCA fails to clarify the situation, either. Considering the significance of shell shape in distinguishing different populations, this population is assigned to the valley group. The result after allocating these three populations is given in Fig. 1, 5 and Tab. 7.

A distinction between different groups of populations by means of shell height and shell breadth is possible, for example, within *Rupestrella dupotetii* (TERVER, 1839) from clearly separated ranges in Morocco and Algeria (HOLYOAK & SEDDON 1986). Another example for the appearance of morphologically distinct forms within land snails is *Luchuphaedusa (Oophaedusa) ophidoon* (PILSBRY, 1905) from Shimo-Koshiki Island, Japan (UESHIMA 1993).

Shell characters are of varying advantage to distinguish different groups of *A. arbustorum* (see Tab. 7). Shell height and shell breadth are variable and the ranges of these characters widely overlap in the groups. The number of whorls lies between 5.0 and 5.5 (with the exception of populations No. 15 and 16). The intensity of the brown band is predominately suited to separate the high altitude group from the remaining groups. Umbilical width only separates the not - umbilicated valley group (with the exception of population No. 25) from all, more or less, umbilicated groups (with the exception of population No. 13). The degree of umbilication can be mainly used to distinguish between the strongly umbilicated groups (high altitude group and *Arianta arbustorum "styriaca"* group) and the not-umbilicated valley group (with the exception of population No. 25) as well as the weakly umbilicated alpine pasture group. Shell shape is the most suitable character to distinguish the different *A. arbustorum* groups. Each group of populations comprises a certain range, there being practically no overlapping between the ranges with the exception of the high altitude group (No. 1) and the alpine pasture group (No. 12). This circumstance favours a distinction of different groups of *A. arbustorum* on the basis of shell shape. The usefulness of shell shape is confirmed by comparing different populations from Austria and Switzerland (BAMINGER in prep.).

Concerning the altitudes of the different localities (Fig. 5), the valley group is characterized by sites well below 1000 m altitude, with one exception (No. 10). The habitats of this group are meadows, brush along fences, brook embankments or undergrowth of stinging-nettle (*Urtica dioica*). All of these habitats are characterized by dense vegetation (see also CAMERON & PALLES-CLARK 1971, CAIN & al. 1969, STRATTON 1954). Population No. 10 was recorded in an area which has been used agriculturally for centuries. Therefore, it is likely that this population descends from individuals from a lower-altitude population accidently brought into this area (through cattle or passive transport by man; see also HONEK 1995). The populations attributed to the valley group are nominotypical *Arianta a. arbustorum*.

All populations of the alpine pasture group inhabit altitudes between 1500 and 2000 m. The areas of these populations were formerly (No. 8, 9, 12, 14, 19, 26) or are currently (No. 13, 18, 20, 21, 23) used as alpine pastures. These pastures are partly covered with rocks in some cases. Snails from pastures that are in current use live either in places where they are protected from grazing cattle by rocks, or on plants on which cattle do not feed (see also ZHUBER-OKROG 1995, BAUR 1993, CAMERON 1969).

The high altitude group is located between 1780 and 2260 m altitude in sparsely vegetated, rocky areas with grass. The altitudinal range of this group overlaps with that of the alpine pasture group, but the habitat types differ especially with regard to plant communities and plant covering. Populations of the high altitude group mainly live on alpine lawn, whereas those of the alpine pasture group inhabit alpine meadows. In general, the plant cover of the latter has a higher density and the proportion of plants to stones and scree is larger.

The three groups discussed above seem to represent so-called ecomorphological units or eco-phenotypes. Already MELL (1937) noticed certain common traits in *A. arbustorum* from ecologically uniform areas. He distinguished six ecological races based on the colour of the shell and the soft body. The traits are generally characteristic for the ecological races, but single specimens deviate frequently. A correlation between morphs and habitats was shown by ARTER (1990) for *A. arbustorum* populations along a contour line at an altitude of 2000 m (± 100 m) in Switzerland. CAIN & SHEPPARD (1950) state that *Cepea nemoralis* colonies living in the same type of ecological habitat tend to resemble one another, whereas those from different habitats tend to differ with regard to colour and banding pattern. CHIBA (1996) reported a clear relationship between shell form, size, weight and habitat in *Mandarina hahajimana*, an endemic land snail of the Bonin Islands ("... Populations with similar habitat preference have similar shell morphology. The remarkable divergence in shell morphology of *M. hahajimana* results from its habitat differences...").

The altitudinal range (900 - 1760 m altitude) of the *Arianta arbustorum* "*styriaca*" group overlaps with that of the valley group as well as with that of the alpine pasture group. Its habitat is usually scree slopes, as in *A. schmidti* (BISENBERGER & BAUMGARTNER 1996), or rock faces with very little vegetation (mainly grass), whereas populations of the two latter groups inhabit dense vegetation without or with few stones. Populations of the *Arianta arbustorum* "*styriaca*" group are located close to each other.

Individuals from populations belonging to the *Arianta arbustorum* "*styriaca*" group are characterized by very flat shells compared with members of the other groups. Because

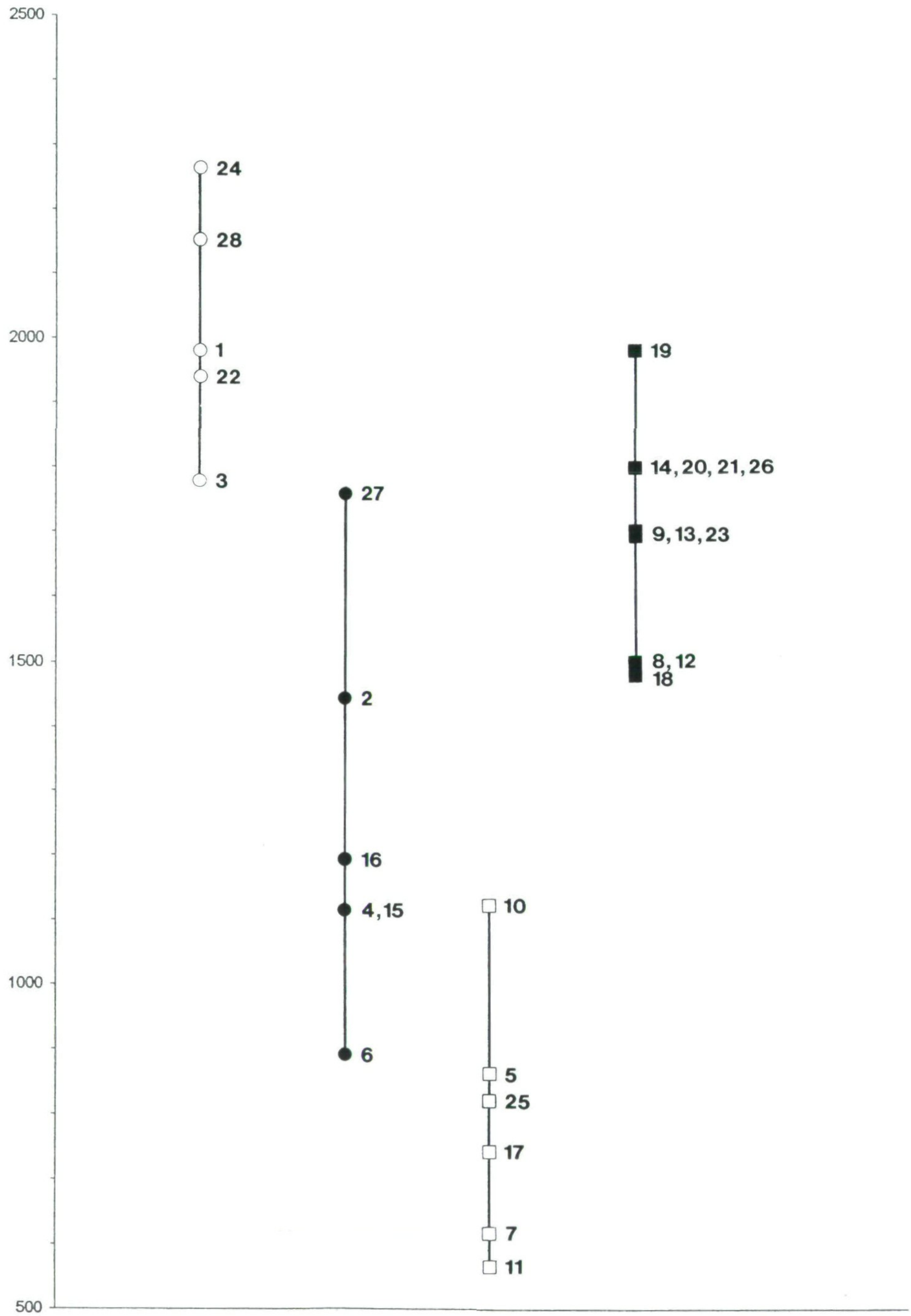

Fig. 5: Altitudes of *Arianta arbustorum* populations. Population altitudes (on the y - axis) and numbers see Tab. 1. Clusters are marked by symbols, corresponding to Tab. 7.

of this group´s distinct shell shape and narrow geographical distribution, its members propably represent a geographical subspecies.

GITTENBERGER (1991) regards the flat shells as the plesiomorphic condition in the present polymorphic *A. arbustorum*. Outgroup comparisons led him to conclude "...that the species ancestral to *Arianta* most probably occurred in a montane habitat and had a depressed shell (shape index below 72) with an open umbilicus, comparable to that of, for example, *A. chamaeleon* and nearly all *Chilostoma* species...". His argument is thus a phylogenetic one. According to Gittenberger's hypothesis, the change from depressed shells with an open umbilicus to more globular shells with a closed umbilicus in *A. arbustorum* took place during the conquest of valleys and lowland, whereas the montane populations did not or only minimally changed conchologically. In contrast, *Helicigona lapicida*, another widespread species of the subfamily *Ariantinae*, living both on rocks and in lowland regions (woods and hedge rows), retained the flattened shape and the large umbilicus.

Tab. 7: Localities arranged corresponding to Fig. 1. Clusters are marked by symbols: ○ = high altitude group; ● = *Arianta arbustorum "styriaca"* group; □ = valley group; ■ = alpine pasture group. no. = locality number, other abbreviations see Tab. 1. Averages for sh, sb, hb; medians for du, uw, nw, bb.

	no.	locality name (abbrev.)	altitude	sh	sb	hb	du	uw	nw	bb
○	1	Kalbling (Kal)	1980 m	14.06	19.93	0.7064	6	2.5	5.5	1
○	3	Gamsgartl (Gg)	1780 m	13.21	20.01	0.6604	10	3	5.25	0
○	28	Gr. Buchstein (GrBu)	2150 m	13.93	19.90	0.7010	6	2.5	5.25	0
○	24	Hochtor (Ht)	2260 m	12.36	18.53	0.6687	8	2.5	5	0
○	22	Reichenstein (Res)	1940 m	15.15	23.05	0.6576	8	3	5.25	0
		group averages/medians		13.74	20.28	0.6788	8	2.5	5.25	0
●	2	Peternpfad (Pp)	1450 m	13.66	22.61	0.6048	9	3	5.25	3
●	4	Haindlkar/Bachbett (HkBb)	1120 m	13.73	24.04	0.5722	10	3	5.25	3
●	6	Wasserfallweg (Wfw)	900 m	14.45	23.54	0.6142	8	3.5	5.25	3
●	27	Schneeloch (Sl)	1760 m	15.20	23.62	0.6443	7	3	5.25	3
●	15	Gseng (Gs)	1120 m	13.95	23.64	0.5904	7.5	2.75	4.75	3
●	16	Haindlkar/Gseng (HkGs)	1200 m	13.26	22.38	0.5927	8	2.5	4.75	3
		group averages/medians		14.04	23.30	0.6031	8	3	5.25	3
□	5	Kölbl (Kö)	870 m	16.25	20.06	0.8103	0	0	5.25	2
□	7	Grabnerhof (Gh)	625 m	17.06	20.42	0.8357	0	0	5.25	1
□	10	Schloß Kaiserau (SKai)	1127 m	16.81	20.56	0.8183	0	0	5.25	3
□	11	Gstatterboden (Gb)	574 m	17.67	21.60	0.8183	0	0	5.25	3
□	17	Donner (Do)	750 m	17.24	21.28	0.8106	0	0	5	3
□	25	Buchau/Aichern (BuAi)	830 m	18.14	20.38	0.8896	1	1.25	5.5	0
		group averages/medians		17.19	20.72	0.8305	0	0	5.25	2.5
■	8	Wolfbauernhochalm (Wbha)	1500 m	15.92	21.17	0.7525	3	2.5	5.25	2
■	20	Glanegg-Luk´n (GlaL)	1800 m	16.79	21.89	0.7670	1	2	5.25	3
■	23	Heßhütte (Hh)	1695 m	16.07	21.46	0.7485	2	2.5	5.25	3
■	12	Ebnesangeralm (Eaa)	1500 m	14.95	21.33	0.7018	5	3	5.25	3
■	21	Rotofen (Ro)	1800 m	15.34	21.63	0.7101	2.5	3	5.25	2.5
■	9	Roßkar (Rk)	1700 m	16.52	22.36	0.7387	4.5	2.5	5.5	2
■	14	Teufelsarsch (Ta)	1800 m	16.08	21.75	0.7401	3	3	5.5	3
■	18	Liebl-Stadl (LiS)	1480 m	16.31	21.49	0.7592	1	2	5.5	3
■	26	Grabnerstein (Grs)	1800 m	17.20	21.27	0.8088	1	2.5	5.5	3
■	19	Obere Stadlfeldalm (Osfa)	1980 m	14.78	20.11	0.7346	2.5	2	5.5	3
■	13	Gamsfriedhof (Gfh)	1700 m	16.08	22.07	0.7258	0	0	5.5	3
		group averages/medians		14.54	21.50	0.7443	2.5	2.5	5.5	3

However, due to the very restricted area of this very flat *Arianta a. styriaca* and its total absence in the fossil record up to now - all reported fossil *A. arbustorum* are globular - the present author favours an alternative scenario as to the origin of *Arianta a. styriaca*.

These very flat shells developed can be seen as a good adaptation to the given environmental conditions (areas with scree, rocks and rock-faces) (see also LEDERGERBER & al. 1997, CHIBA 1996). There are several benefits in having flat shells, most of all it is advantageous during extreme weather conditions: these snails can survive winter better in fissures or, conversely, hot days in cooler places like crevices (to reduce water loss; see also KLEIN-ROLLAIS & DAGUZAN 1990). Other snail species inhabiting rock faces and having such "advantageous" flat shells include *Chilostoma* spp. and *Helicigona lapicida*. *A. schmidtii* with "...the most-strongly depressed shells measured in *Arianta*..." also lives in "...most extreme, rocky, montane habitat, with hardly any vegetation..." (GITTENBERGER 1991).

During the Pleistocene glaciations the ancestral form of the present polymorphic *A. arbustorum*, hypothesized to be globular with an closed umbilicus by the author, mostly are assumed to have been pushed back to regions free of ice, i.e. lowland regions. The remaining populations in Pleistocene refugia like nunatakr - sites seasonally free of ice within the otherwise closed ice-cover (comp. GITTENBERGER 1991, VAN HUSEN 1987, ANT 1966), were geographically strictly separated from conspecific individuals persisting in the lowland. During this time of separation, directional selection gave rise to individuals with flat shells. Populations of the *Arianta arbustorum "styriaca"* group are considered to descend from these individuals.

The conservation of the acquired flat shells may be due to a) a persistent geographical isolation up to the present, enhanced by a high site fidelity of the populations of the *Arianta arbustorum "styriaca"* group (KLEEWEIN 1996) combined with a reduced probability for passive dispersal (downhill rolling on mountain slopes) of flat-shelled individuals (BAUR & al. 1997) and/or b) differences in the mating behaviour (BAUMGARTNER 1997).

The earliest findings of *A. arbustorum* are from the Pliocene (LOZEK 1964, WENZ 1923, BOETTGER & WENZ 1921, BAILY 1858). Fossil shells were found in loess deposits (LOZEK 1964) and in caves (FRANK 1995) due to the favourable conditions for fossilisation at these sites. They are all globular, although of different size. GITTENBERGER (1991) mentioned the possibility of a globular ancestor too, but refused it for several reasons like e.g. Dollo's rule. However, the lack of fossils is certainly not an adequate argument to reject Gittenberger's approach.

These two alternative hypotheses could be tested with a phylogenetic analysis based on non-morphological characters, i.e. molecular data.

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