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The identity of *Pupa daliaca* WESTERLUND 1887, with notes on intraspecific variation in and ecology of *Vertigo ronnebyensis* (WESTERLUND 1871)

(Pulmonata: Pupillacea: Vertiginidae).

By

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With 10 figures and 4 tables.

Abstract: The syntype of *Pupa (Alaea) daliaca* WESTERLUND 1887 is shown to be a specimen of *Vertigo ronnebyensis* (WESTERLUND 1871) differing by the presence of only one apertural tooth (parietal) instead of the usual 3-4 teeth. Hence the name *P. daliaca* is a junior synonym of *V. ronnebyensis*. The intraspecific variation in shell morphology of *V. ronnebyensis* with regard to shell size, apertural denticulation and colour of the apertural teeth has been studied, using material from the province of Dalsland (SW Sweden).

The variation in size and, especially, in apertural denticulation was considerable, while the colour of the teeth was found to be rather stable. The ecology of the species is reviewed and discussed and a comparison with *Vertigo alpestris* ALDER is made. *V. ronnebyensis* has been found to have its ecological optimum in old, shady, mossrich mixed or coniferous woods of oligo- or mesotrophic type.

Kurzfassung: Der Syntypus von *Pupa (Alaea) daliaca* WESTERLUND 1887 ist untersucht worden, wobei sich herausstellte, daß es ein Exemplar von *Vertigo ronnebyensis* (WESTERLUND 1871) ist, welches sich durch das Vorhandensein von nur einem Zahn (parietal) in der Mündung, statt der gewöhnlichen 3-4 Zähne, unterscheidet. Folglich ist der Name *P. daliaca* als ein jüngeres Synonym von *V. ronnebyensis* zu betrachten. Die intraspezifische Variation der Morphologie des Gehäuses von *V. ronnebyensis* ist an Material von der Provinz Dalsland (SW Schweden) hinsichtlich Gehäusedimensionen, Bezahnung der Mündung und Farbe der Mündungszähne studiert worden. Die gefundene Variation in der Bezahnung, aber auch in der Größe, war bedeutend. Die Farbe der Mündungszähne war aber relativ konstant. Die Ökologie von *V. ronnebyensis* ist untersucht und mit der von *Vertigo alpestris* ALDER verglichen worden. *V. ronnebyensis* hat ihr ökologisches Optimum in alten, schattigen, moosreichen Misch- oder Nadelwäldern von oligo- oder mesotrophem Typ.

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Introduction.

Some years ago I started a study of the land mollusca of the province of Dalsland (SW Sweden). A survey of the literature is part of the project. In the works of the famous malacologist C. A. WESTERLUND I came across the name *Pupa (Alaea) daliaca* WESTERLUND 1887. Many of the species and varieties described by him have proved to have no taxonomic status as they were based on a single or a few aberrant specimens, whose characters fall within the range of variation of other well known species. Unfortunately the name *P. daliaca*, as well as many other WESTERLUND-names have just been ignored by taxonomists. That this is unsatisfactory can be seen clearly in the paper concerning the rediscovery of *Vertigo extima* (WESTERLUND) (WALDEN 1986).

The identity of *Pupa daliaca*.

The name *daliaca* is derived from the latinized name Dalia of the short form Dal of the province name – Dalsland. In the original description (WESTERLUND 1887) as well as in his later works (WESTERLUND 1897[1], 1904) the type locality is given only as: "Sweden, Dalsland". In 1897 he even states: "Suecia in Dalsland (locus specialis ignotus)". The only known material of the species is a sample in the WESTERLUND-collection in the Museum of Natural History, Göteborg (GNM). The label, which judging from both paper and handwriting must be the original one, contains what must be considered the locus typicus: "Suecia ad Ryr in prov. Dalsland". This is undoubtedly the Ryr peninsula in Lake Svanefjorden in parish Skållerud in the middle part of the province.

The sample consists of only one syntype (Fig. 1 A) on which WESTERLUND must have based his description. The most prominent characteristic of this specimen is the

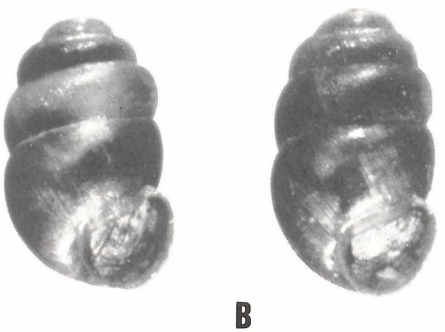


Fig. 1. – A) *Pupa (Alaea) daliaca* WESTERLUND, x 16. Sweden, Dalsland, parish Skållerud, Ryr peninsula. Syntype [Coll. C. A. WESTERLUND Nr. 2360, GNM]. — B) *Vertigo ronnebyensis* (WESTERLUND), × 16. Sweden, Dalsland, parish Skållerud, Ryr peninsula, 450 m WNW of Båtnäbba. Leg: T. VON PROSCHWITZ 22-VII-1983. Photo: H. BERG (GNM).

[1]) In this paper WESTERLUND describes a variety of *P. daliaca* – var. *darlecarlica* – found in two localities in the province of Dalarna. The description makes it probable that this is a 2-toothed form of *V. ronnebyensis*. This can, however, not be confirmed, as no material has been found in any museum.

presence of a single tooth (parietal) in the aperture. The measurements of the syntype are presented in Table 1. Its colour is dark yellowish-brown. The specimen agrees well in colour with, and falls well within the size range (studied in detail in next section, cf. Figs. 1 A-B, Table 1, Figs. 2-3) of *Vertigo ronnebyensis* (WESTERLUND) from the Ryr peninsula and from other parts of the province. The only difference is the presence of a single apertural tooth instead of the usual 3-4. The variation in apertural denticulation is, however, rather large in *V. ronnebyensis* (studied in detail in next section). Hence *P. daliaca* can be considered a junior synonym of *V. ronnebyensis* and the following added to the synonomy of this species:

1887 *Pupa (Alaea) daliaca* WESTERLUND, Fauna Paläarkt. Region Binnenconch., **3**: 130.
1897 *Pupa (Alaea) daliaca*, — WESTERLUND, Acta Soc. Fauna & Flora Fenn., **13**: 64.
1904 *Pupa (Vertigo) (Alaea) daliaca*, — WESTERLUND, Sveriges, Norges, Danmarks och Finlands Land- och Sötvattensmollusker. (Tillägg): 12.

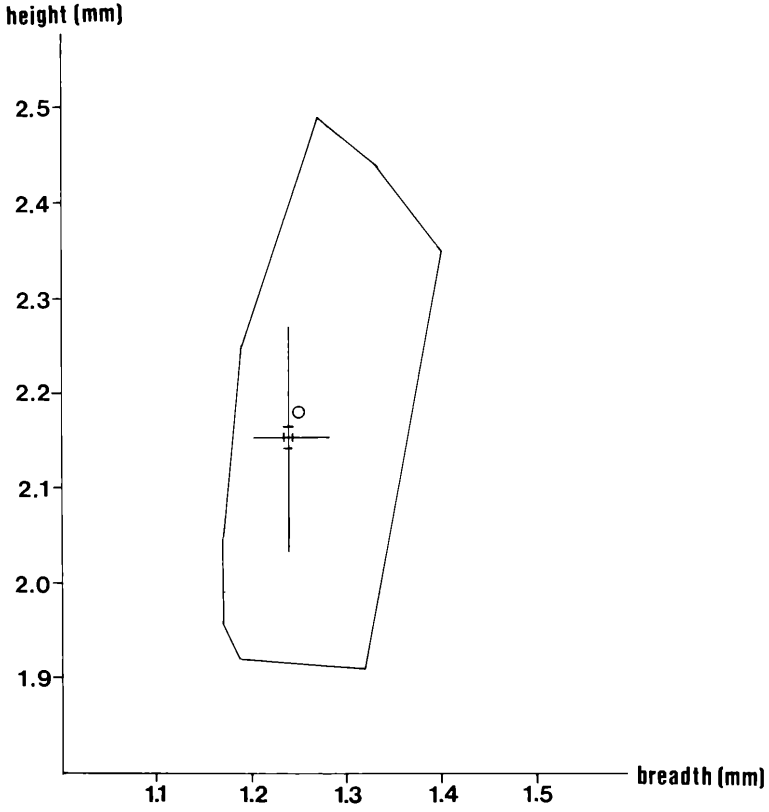


Fig. 2. Variation in height/breadth in 100 specimens of *V. ronnebyensis* from 24 localities in the province of Dalsland. The horizontal and vertical lines show standard deviation (S.D.) and cross at the mean. The bars indicate standard error (S.E.). ○ = Syntype of *P. daliaca*.

Table 1. Variation in the studied parameters (Number of whorls, height and breadth) in materials of *V. ronnebyensis* from the province of Dalsland compared to data given in the literature. Data of the syntype of *P. daliaca* is also given.

	Number of whorls		Height (mm)		Breadth (mm)	
	Range	$\bar{x}$	Range	$\bar{x}$	Range	$\bar{x}$
Sweden, Dalsland (100 Specimens)	4.5-5.2	4.9	1.19-2.49	2.15	1.17-1.40	1.24
Sweden, Dalsland, Härslätt (21 Specimens)	4.6-5.2	4.9	1.95-2.44	2.22	1.22-1.40	1.28
Sweden, Dalsland, Borekullen (23 specimens)	4.5-5.2	4.8	1.91-2.17	2.03	1.17-1.32	1.21
Sweden, the vicinity of Stockholm (WALDEN 1955)			1.95-2.50	2.17	1.20-1.30	
Sweden, Skåne (WALDEN 1955)			1.95-2.50	2.25	1.15-1.40	
EHRMANN (1933)	5-5.5		2.25-2.5		1.25-1.5	
KERNEY & CAMERON (1979)	5		2.2-2.4		1.2-1.4	
Pupa daliaca WESTERLUND Syntype	4.8		2.18		1.25	

Variation in shell morphology of *Vertigo ronnebyensis*.

When working with the identity of *P. daliaca* I decided to undertake further studies on the rather poorly known intraspecific variation in *V. ronnebyensis*. The material collected by myself in the province of Dalsland, together with samples from the same area in the collections of the GNM (Leg: H. LOHMANDER and H. W. WALDÉN) provided a solid basis for such studies.

A. Shell size and number of whorls.

100 adult specimens from 24 localities were measured with regard to height and breadth and the number of whorls was determined according to EHRMANN (1933). The results are presented in Figs. 2-3 and in Table 1, where they are compared to measurements and numbers of whorls given in the literature.

My figures for both the measurements and the number of whorls tend to be somewhat smaller than the figures given in the standard literature. The differences, however, are very slight. There are also differences in the measurements given in the standard literature. The figures given by KERNEY & CAMERON (1979) are smaller

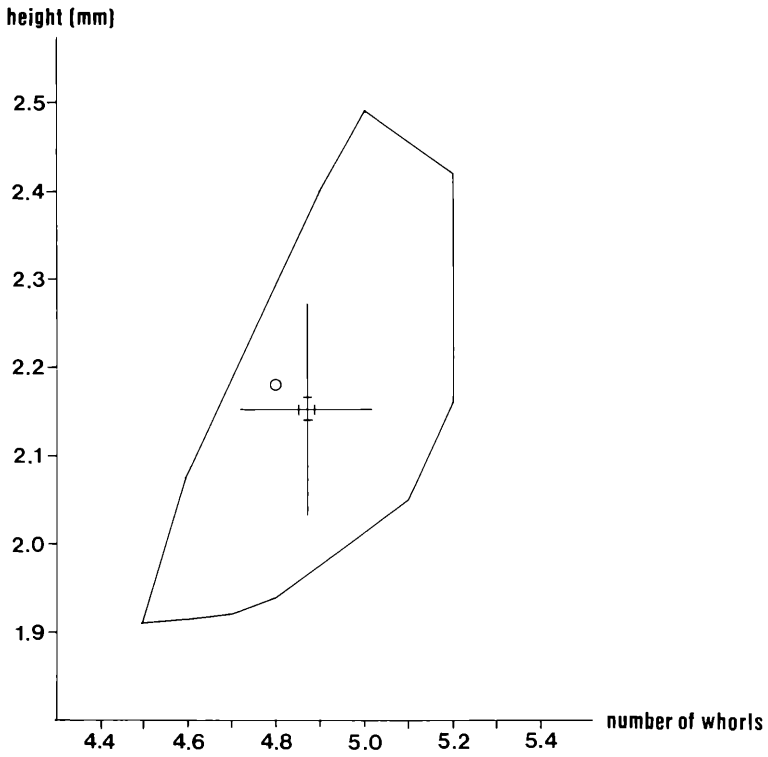


Fig. 3. Variation in height/number of whorls in 100 specimens of *V. ronnebyensis* from 24 localities in the province of Dalsland. Explanations: See text to Fig. 2.

than those given by EHRMANN (1933). Also the mean values of height and breadth are low in the Dalsland material; the height mean falling below the range given by both the cited authors. WALDÉN (1955) presented height and breadth measurements of material from the vicinity of Stockholm and the province of Skåne. Means are, however, only given for the height values. The lowest values for shell height in the Dalsland material are lower than the lowest corresponding values in these series. Compared to the values given in the standard literature, however, also the means of the Stockholm and Skåne series are low. The range is also wider in the Swedish material, especially in the Dalsland series, but to the largest extent falling within the range given in the standard literature.

One possible explanation of the differences is that the figures given in the literature are based on small sample sizes and hence, part of the variation has been overlooked. The statement given by EHRMANN (1933), that the German specimens are not as big as the Swedish ones is contradicted by the present results, which indicate a wide size range in the Swedish populations.

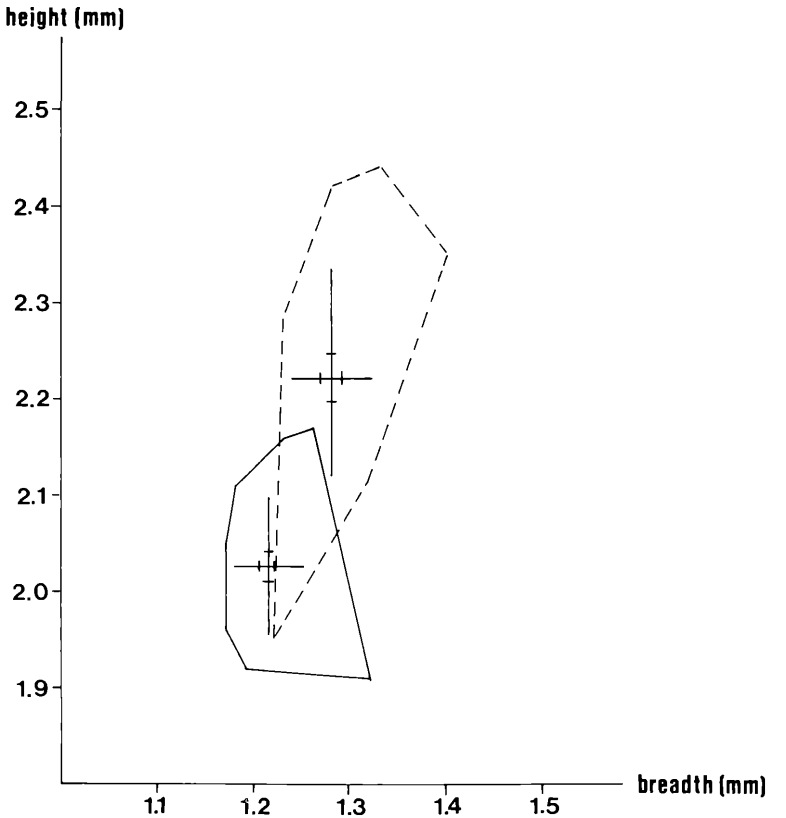


Fig. 4. Variation in height/breadth in two populations of *V. ronnebyensis* from the province of Dalsland. —— = Ör, Borekullen (n = 23), = Rännelanda, Härslätt (n = 21).

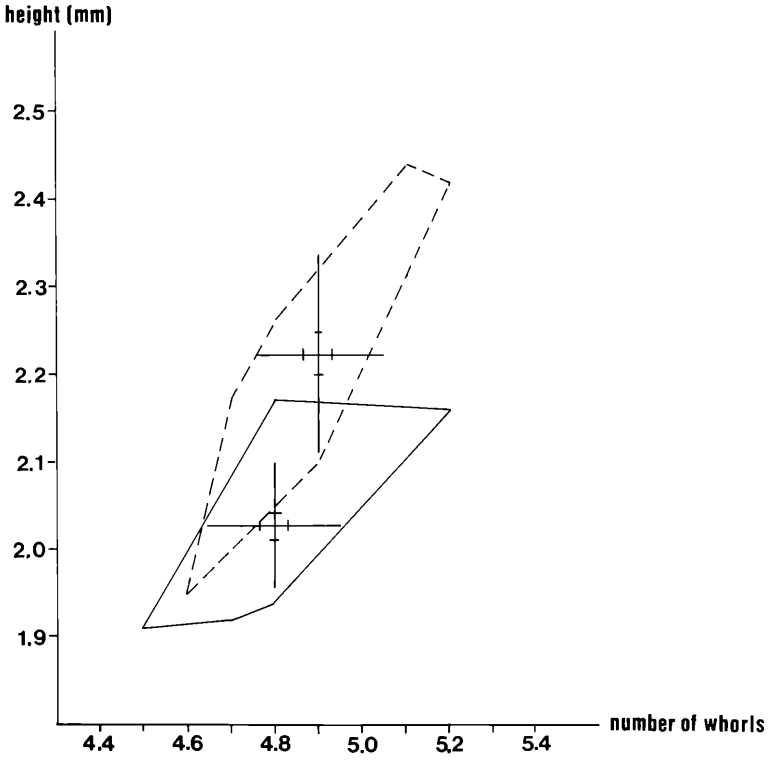


Fig. 5. Variation in height/number of whorls in two populations of *V. ronnebyensis* from the province of Dalsland. Explanations: See text to Fig. 4.

To study the variation between and within single populations, the two samples with the largest number of specimens — Härslätt and Borekullen — were treated statistically. The results are presented in Figs. 4-5 and in Table 1. There exists a rather large variation in characters both between and within the populations. The differences between the two populations in height and breadth show strong significance ($p < 0{\cdot}1\%$) and in number of whorls a probable significance ($p < 5\%$) when t-tested.

It is impossible to say if any environmental factor in the habitats is responsible for the differences, or if the populations are isolated enough to allow genetic drift. Size differences within the distribution range (macrogeographic differences) have been shown to exist in several land mollusc species (cf. Proschwitz 1985) but the underlying reasons are still poorly understood in most cases.

B. Apertural denticulation.

The most important character given in the description of *P. daliaca* is the apertural denticulation. This is considered an important character in species discrimination within the genus *Vertigo*, but is often rather variable. The form and

presence of some characteristic teeth, however, remain fairly stable. All available material from the province — 372 adult specimens from 77 localities — was studied with respect to this character. Earlier the variation in apertural denticulation seems to have been studied closely only in one of the European species in the genus — *Vertigo moulinsiana* DUPUY (BONDESEN 1966).

The terminology used for the teeth follows EHRMANN (1933). In the literature the aperture is described as having 3-4 teeth; columellar, parietal, lower palatal and occasionally an upper palatal. The shape of the teeth is different; the parietal is normally lamella-like the palatals are tuberculate (occasionally the lower palatal can have lamella form), the columellar also has tuberculate shape but rises from the end or near the end of a low, longish callus on the columellar wall. The other teeth rise directly from the walls. In this study the status of the separate teeth was estimated according ot a 4-degree scale; 0 – absent, 1 – indicated, weak, 2 – intermediate, 3 – prominent. The results for each separate tooth are presented in Table 2.

The upper palatal is absent in most cases, when present it is often weakly developed. The presence of the other three teeth is much more stable. When present the lower palatal is prominently or intermediately developed in most cases. The same trend is even more pronounced for the parietal. The columellar is the most regular of the teeth. Its degree of development is, however, approximately equally distributed amongst the three classes. Some irregularities were also found. A small angular tooth, mentioned by EHRMANN (1933) as very rare, was found in 55 specimens (14.8%). A small infracolumellar was found in 1 specimen. Rare aberrations noted, were a two-parted columellar in 1 specimen and a two-parted lower palatal in 2 specimens.

The data were then sorted by help of a computer program, in order to look at the combinations of present and absent teeth. The results are presented in Table 3. The most conspicuous fact is that in individuals with one tooth absent, this was always the upper palatal. The other three teeth were never absent alone. The 3-teeth pattern was the most common in the material. 4-toothed specimens were also common. Combinations of 2-teeth present were less frequent. It should be noted that only four of the possible six combinations were found and that two of these were very rare. Not surprisingly, the two most common combinations of 2-teeth both involved loss of the upper palatal. 1-toothed specimens were rare. Two of the four possible types were found and only one individual showed "the *Pupa daliaca* – combination" (only parietal present). A completely toothless aperture was found in only one case.

The results show that the teeth disappear in the following order: upper palatal (often missing) – lower palatal – parietal (both seldom missing) – columellar (very rarely missing). If the 228 specimens without the upper palatal are treated separately it is obvious that the absence does not have to be combined with a loss or even a weaker development of the other teeth, but it is notable that in only one case was the upper palatal present when any other tooth was absent.

The intra-populational variation was also studied, with special reference to the upper palatal. Of the 77 studied populations all specimens lacked it in 34 cases (44·1%), some specimens lacked it in 24 cases (31·2%) and it was present in all specimens in 19 cases (24·7%). If the status of each tooth is estimated according to the 4-degree scale the variation and the found combinations in some populations are considerable. In the two populations studied in the previous section (Borekullen: n

Table 2. Status of the apertural teeth in *V. ronnebyensis*. Material from the province of Dalsland (n 372). Explanations: See text.

	Tooth	Number		%	
	columellar				
State:	0	3		0.8	
	1	117		31.5	
	2	128	362	34.4	99.2
	3	124		33.3	
	parietal				
	0	26		7.0	
	1	10		2.7	
	2	23	346	6.2	93.0
	3	313		84.1	
	upper palatal				
	0	228		61.3	
	1	107		28.8	
	2	29	164	7.8	38.7
	3	8		2.1	
	lower palatal				
	0	40		10.7	
	1	45		12.1	
	2	84	332	22.6	89.3
	3	203		54.6	

= 23 and Härslätt: n = 21) the number of found combinations was 13 and 10. The accessorical angular was found in 18 of the populations (23·4%).

The presence and state of the apertural teeth in the Pupillacea is undoubtedly genetically regulated. However, it seems possible that at least the degree of development (state) of the teeth may be influenced by environmental factors. That the underlying genetic mechanisms may be complicated is indicated by the fact that in *V. ronnebyensis* three of the teeth are never absent alone and that not all possible combinations of losses are found (cf. inheritance of colour and banding patterns in the *Cepaea*-species). Crossing experiments and heritability analysis may reveal the mechanisms in the future. An extended analysis should also include detailed studies of intra- and inter-populational differences in denticulation.

Such differences were studied in three Danish populations of *V. moulinsiana* by Bondesen (1966), with statistical analysis by Jørgensen (1966). The studied populations differ significantly and this is, according to Bondesen (1966), most probably due to random genetic drift within the small isolated populations of this

Table 3. Combinations of presence / absence of the apertural teeth in *V. ronnebyensis*. Material from the province of Dalsland (n = 372).

Tooth:	columellar	parietal	upper palatal	lower palatal	Number		%	
State:								
I. Four teeth present.	1	1	1	1	143		32.4	
II. Three teeth present.	1	1	0	1	170		45.7	
	(3 other possible combinations not present in the material)							
III. Two teeth present.	0	1	0	1	1		0.3	
	1	0	0	1	18		4.8	
	1	0	1	0	1	51	0.3	13.7
	1	1	0	0	31		8.3	
	(2 other possible combinations not present in the material)							
IV. One tooth present.	1	0	0	0	6		1.6	
	0	1	0	0	1	7	0.3	1.9
	(2 other possible combinations not present in the material)							
V. No tooth present.	0	0	0	0	1		0.3	

Table 4. Colour of the apertural teeth in *V. ronnebyensis*. Material from the province of Dalsland.

Tooth:		columellar (n=369)		parietal (n=346)		upper palatal (n=164)		lower palatal (n=332)		angular (n=55)	
		Number	%	Number	%	Number	%	Number	%	Number	%
Colour:	brown	362	98.1	1	0.3	7	4.3	4	1.2	45	81.8
	white	7	1.9	345	99.7	157	95.7	328	98.8	10	18.2

species on the edge of its distribution. He found it very difficult to pinpoint any microgeographic environmental factor(s), responsible for the differences. The situation is somewhat different for *V. ronnebyensis* in the high boreal region of Scandinavia, as the species is common in coniferous forests in this area. Also in this species inter-populational differences are indicated in the present study, but it is difficult to say whether the populations are small and isolated enough to allow genetic drift. Further studies of material from different areas, laboratory experiments and comparison with other *Vertigo*-species are necessary to clarify this complex of problems.

C. Colour of the apertural teeth.

On the material used in the previous section also the colour of the teeth was studied. The results are presented in Table 4. The tooth colour is a stable character, at least for the four large teeth. The parietal, lower and upper palatal are normally white, very seldom brown. For the columellar the reverse is normal. In the columellar it is, however, the proximal part of the tooth and the callus on which it is situated, which are dark brown. The distal part is usually very light brown or white, but when the basal parts are dark this gives the entire tooth a brown appearance. Only completely white teeth have been classified as such. The other teeth are always uniformly coloured. In the accessorical angular the colour seems somewhat less fixed, the individuals having brown colour dominating in an approximately 4:1 ratio. In no case more than one aberration in tooth colour was found in the same specimen. The stable conditions makes it probable that the character is basically regulated by genetic factors.

The ecology of *Vertigo ronnebyensis*.

The total distribution of *V. ronnebyensis* is N. Europe with scattered localities in Eastern Germany and Poland. Within the Nordic countries it shows an eastern-continental type of distribution. It is absent or rare in the southern and western coastal areas of Norway and Sweden and is also missing in large parts of the Scandinavian Alps (cf. distribution map in KERNEY, CAMERON & JUNGBLUTH 1983).

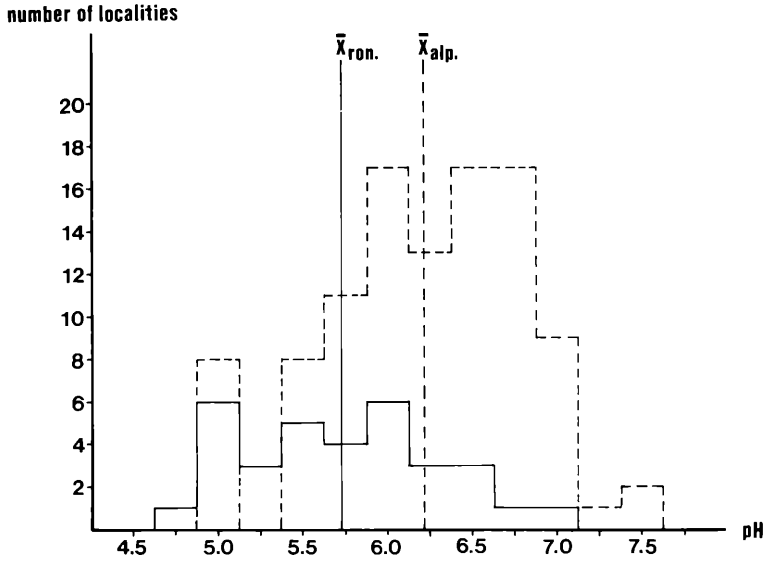


Fig. 6. Distribution of localities for *V. ronnebyensis* (n = 33) and *V. alpestris* (n = 103) in the province of Dalsland at different pH-intervalls. $\bar{x} \pm$ S.D.; *V. ronnebyensis:* 5·73 ± 0·58, *V. alpestris:* 6·22 ± 0·59.

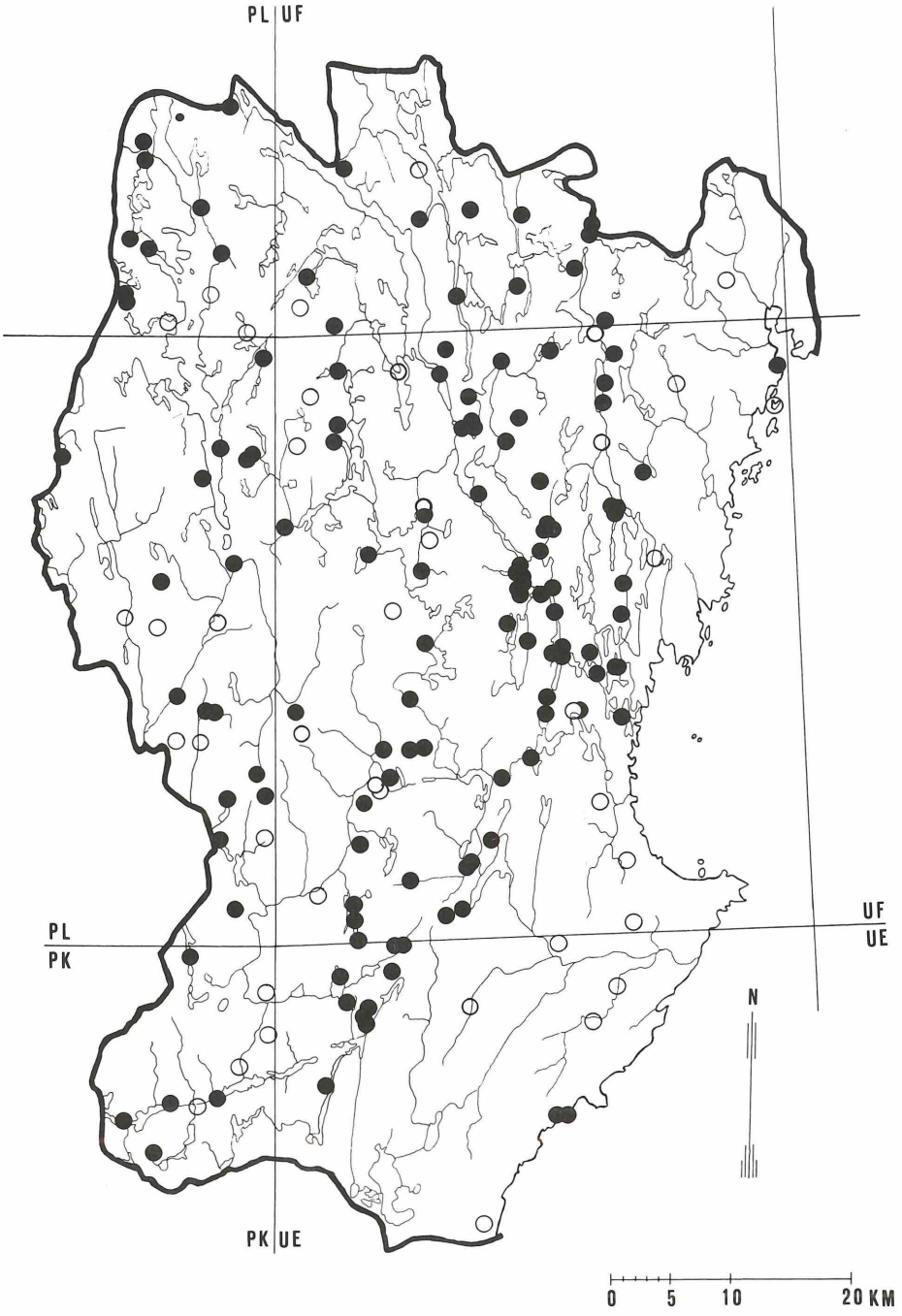


Fig. 7. Distribution of *V. alpestris* in the province of Dalsland. ● = Occurrences in natural habitats. ○ = Occurrences in man-made habitats.

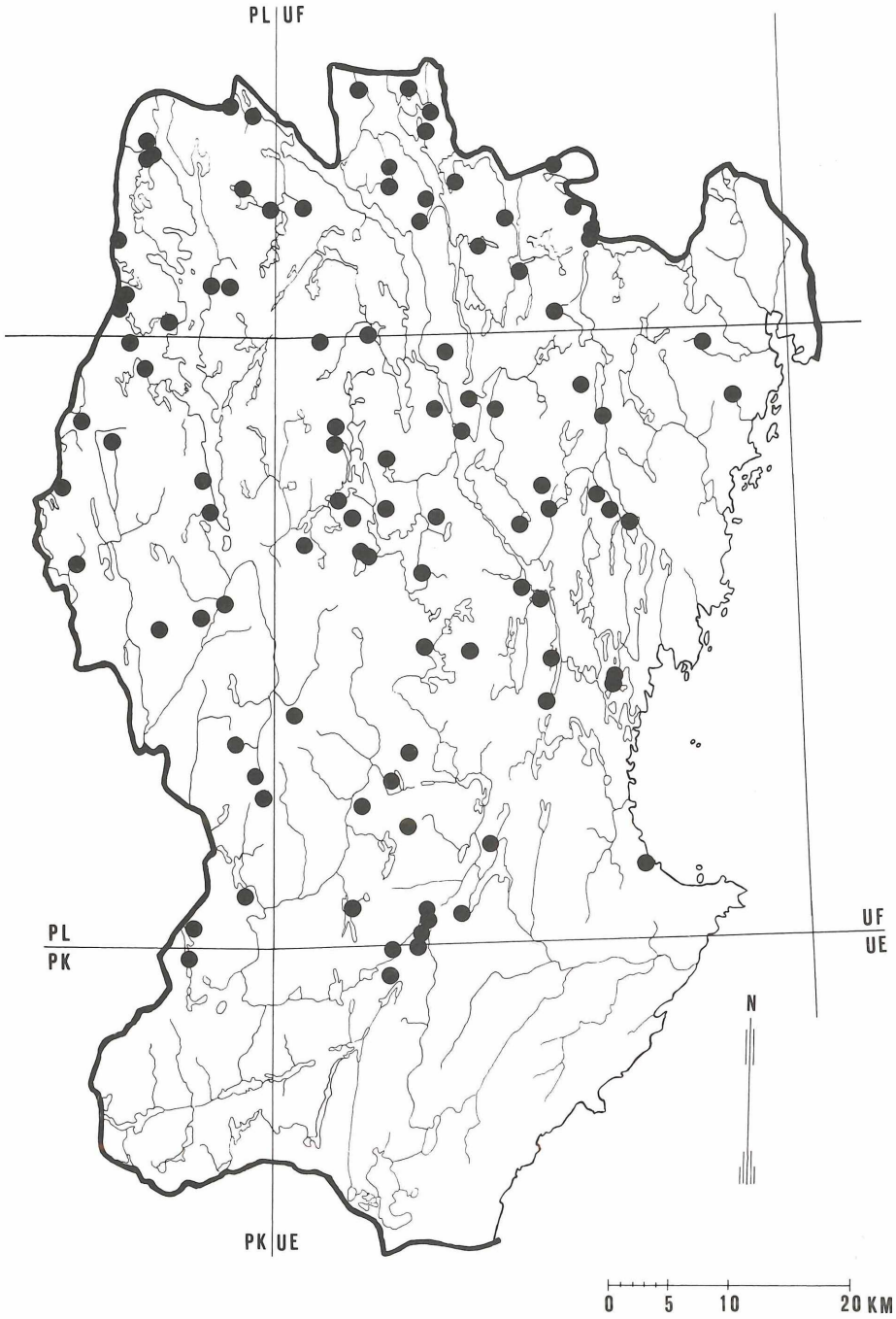


Fig. 8. Distribution of *V. ronnebyensis* in the province of Dalsland. ● = Occurrences in natural habitats.

The information in the literature on its ecology, is rather scarce and scattered (cf. LOHMANDER 1953, LUNDGREN 1954, WALDÉN 1955, 1966, 1969 and WÄREBORN 1969) and in some cases obscured due to the, at that time, unclear relationship between *V. ronnebyensis* and *Vertigo modesta arctica* (WALLENBERG).

In the province of Dalsland characteristic habitats for *V. ronnebyensis* are old, shady, moss-rich meso- or oligotrophic mixed or coniferous forests with *Vaccinium myrtillus* and *V. vitis-idaea*. Here the species seems to have its ecological optimum. When occurring in eutrophic woods it is often found in low numbers and associated with "oligotrophic islets" with *Vaccinium*-species on which it is often found feeding on the leaves. This is in good accordance with the information which can be compiled from the literature cited above. On the southern-southeastern edge of its distribution it may, however, prefer more eutrophic woods (cf. WALDÉN 1969).

To study the ecology of *V. ronnebyensis* further, it was compared to the closely related *Vertigo alpestris* ALDER, which is common in the province. *V. alpestris* has been found in 169 and *V. ronnebyensis* in 99 of 877 localities examined. In 36 sites the species co-occurred. The localities were divided into one group with habitats of predominantly oligotrophic character and one group with habitats of predominantly eutrophic character. The division was based on the character of the vegetation. The distribution of the records between the oligotrophic and eutrophic groups were: 61 (61·6%) – 38 (38·4%) in *V. ronnebyensis* and 21 (12·4%) – 148 (87·6%) in *V. alpestris*. A χ^2-test showed a strongly significant difference in habitat preference between the species ($p < 0{\cdot}01\%$).

This difference was studied further by help of pH-measurements of the ground litter. In localities investigated in the 1960s, 70s and 80s, in which sifting samples were taken, the pH of the litter has been measured colorimetrically using a S. K. P. Soil Tester, Weibul Ltd. Two pH-tests were made per sample and a four step scale was used within each full pH-step (eg. 5·0, 5·25, 5·5, 5·75 etc.). If the results differed the lower value was always used in statistical calculations. The allotment of the localities, in which *V. ronnebyensis* (n = 33) and *V. alpestris* (n = 103) has been found, on different pH-intervals is presented in Fig. 6. In 19 of the localities the species co-existed. The pH-range is wide in both species, but the difference between the means of *V. ronnebyensis* ($\bar{x} = 5{\cdot}73$) and *V. alpestris* ($\bar{x} = 6{\cdot}22$) was shown to be statistically significant when t-tested ($p < 0{\cdot}1\%$). This corroborates the results of the χ^2-test in the previous section and the general field impression.

If another aspect of habitat selection is considered, typical localities of *V. alpestris* are taluses, boulder-slopes, screes (both of open type and in closed woodlands) and also man-made "boulder-habitats" i.e. old walls and mounds of stones. Only in 3 localities (1·8%) it was not associated with boulders or stones. 36 (21·3%) of the "boulder-habitats" were of man-made type. The same strong association is not found in *V. ronnebyensis*, even if 78 (78·8%) of the records were made in taluses or boulder-slopes and 21 (21·2%) in flat woodlands. A χ^2-test showed a strongly significant difference ($p < 0{\cdot}01\%$) between the species in this aspect of habitat selection. It seems probable that *V. alpestris* can tolerate oligotrophic conditions, if the habitat is of "boulder-type" (cf. range in Fig. 6). Of greater importance to *V. ronnebyensis*, than the presence of boulders, seems to be the type of woodland (old, mossy, mixed or coniferous, oligotrophic type). It is also striking that *V. ronnebyensis* is never found in any type of strongly man-influenced or man-made habitat – it can be classified as antropophobe.

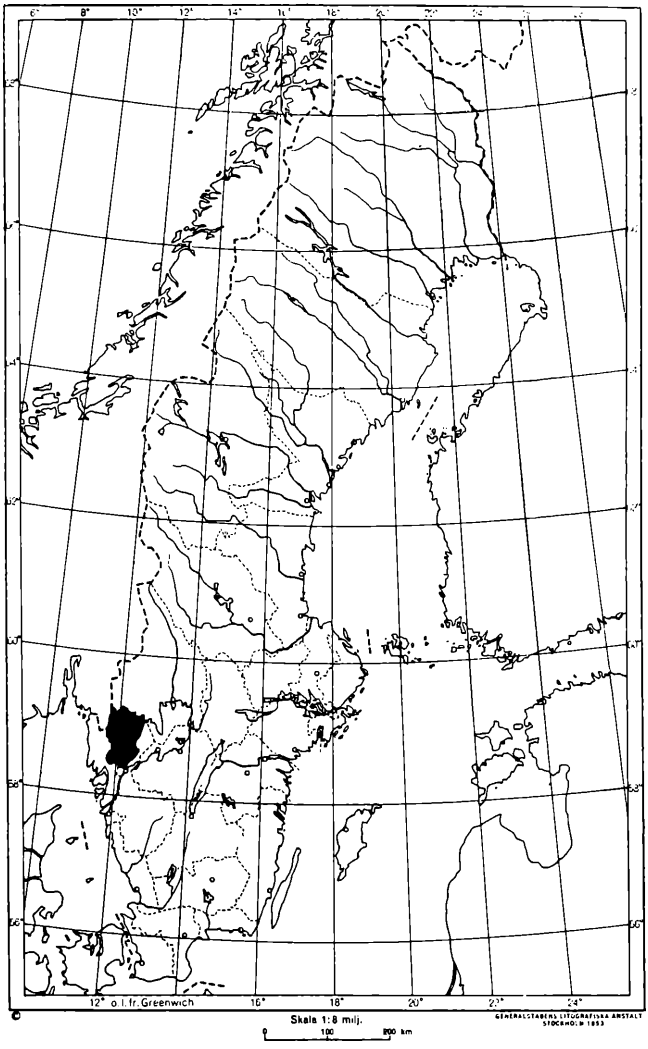
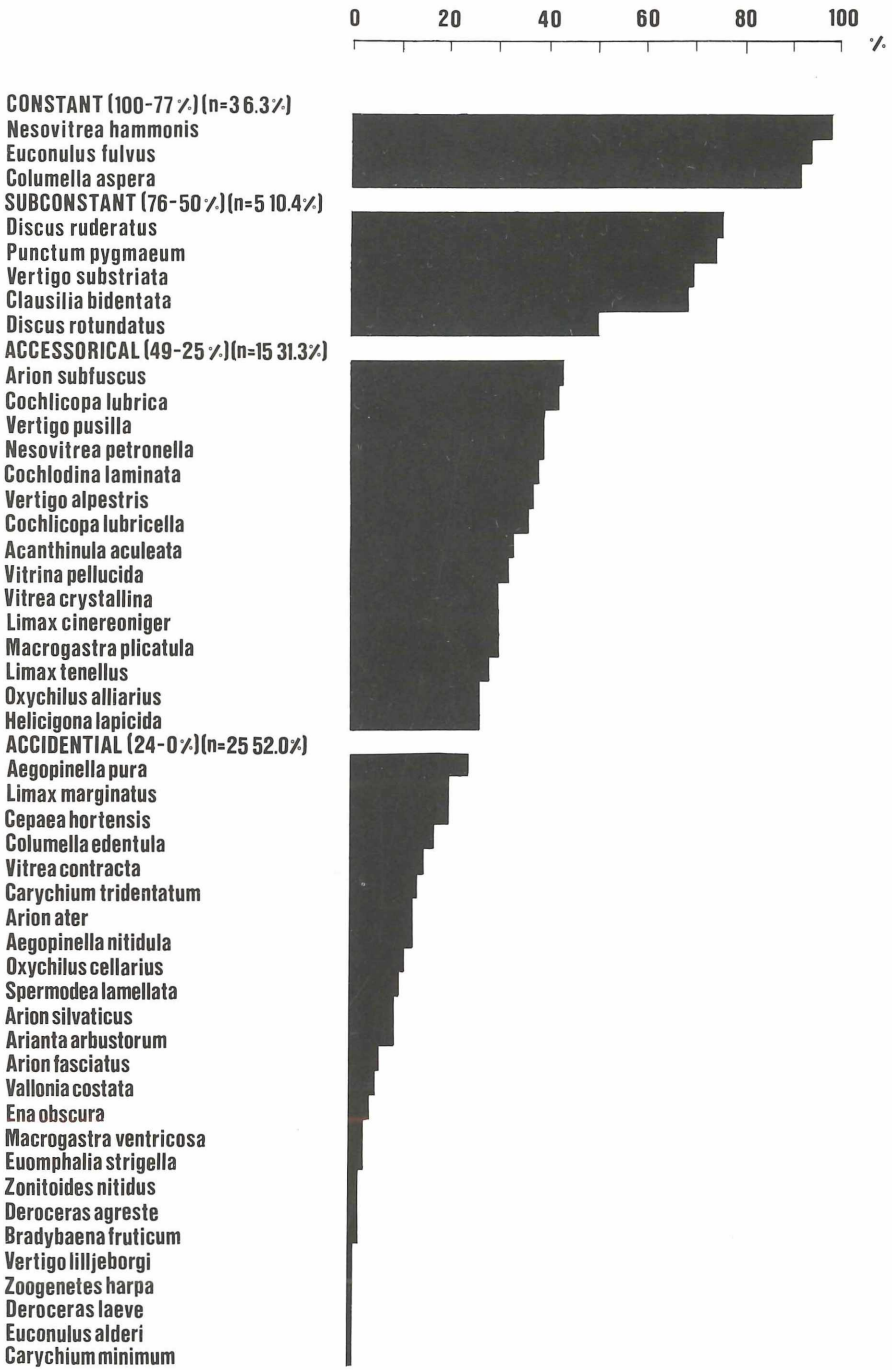


Fig. 9. The location of the province of Dalsland.

The difference in ecology between the species is reflected also in their patterns of distribution in the province (Figs. 7-8). Both have the main part of their distribution in the northern and western parts, which are strongly dominated by woodlands. *V. alpestris* (Fig. 7) has extended its distribution by colonizing walls and mounds of stones in all parts of the province, including the highly cultivated eastern areas. No such pattern is found in *V. ronnebyensis* (Fig. 8).


0
20
40
60
80
100
%
CONSTANT (100-77 %) (n=3 6.3%)
Nesovitrea hammonis
Euconulus fulvus
Columella aspera
SUBCONSTANT (76-50 %) (n=5 10.4%)
Discus ruderatus
Punctum pygmaeum
Vertigo substriata
Clausilia bidentata
Discus rotundatus
ACCESSORICAL (49-25 %) (n=15 31.3%)
Arion subfuscus
Cochlicopa lubrica
Vertigo pusilla
Nesovitrea petronella
Cochlodina laminata
Vertigo alpestris
Cochlicopa lubricella
Acanthinula aculeata
Vitrina pellucida
Vitrea crystallina
Limax cinereoniger
Macrogastra plicatula
Limax tenellus
Oxychilus alliarius
Helicigona lapicida
ACCIDENTIAL (24-0 %) (n=25 52.0%)
Aegopinella pura
Limax marginatus
Cepaea hortensis
Columella edentula
Vitrea contracta
Carychium tridentatum
Arion ater
Aegopinella nitidula
Oxychilus cellarius
Spermodea lamellata
Arion silvaticus
Arianta arbustorum
Arion fasciatus
Vallonia costata
Ena obscura
Macrogastra ventricosa
Euomphalia strigella
Zonitoides nitidus
Deroceras agreste
Bradybaena fruticum
Vertigo lilljeborgi
Zoogenetes harpa
Deroceras laeve
Euconulus alderi
Carychium minimum

Finally the synecological relations of other mollusc species to *V. ronnebyensis* was studied, using constancy figures for the associated species in the 99 localities. The results are shown graphically in Fig. 9. 48 of the 73 taxa of land mollusca found in the province have been recorded together with *V. ronnebyensis*. The species are divided into four groups according to frequency; Constant (100-77%), Subconstant (76-50%), Accessorical (49-25%) and Accidential (24-0%) – following TISCHLER (1949). In the constant group (n = 3) are found the two very eurytopic species *Nesovitrea hammonis* (STRÖM) and *Euconulus fulvus* (MÜLLER) and the common woodland species *Columella aspera* WALDÉN, the latter typical for oligotrophic woods and often found together with *V. ronnebyensis* on *Vaccinium* leaves[2]. In the subconstant group (n = 5) also are found predominantly eurytopic, wide-spread woodland species [*Vertigo substriata* (JEFFREYS), *Discus ruderatus* (FÉRUSSAC), *Punctum pygmaeum* (DRAPARNAUD) and *Clausilia bidentata* (STRÖM)].

In the accessorical group (n = 15) more eurytopic woodland species are found and in the accidental group (n = 25) are grouped rare woodland species with special ecological demands or a limited distribution in the province [e.g. *Ena obscura* (MÜLLER), *Macrogastra ventricosa* (DRAPARNAUD), *Spermodea lamellata* (JEFFREYS)] in which habitats *V. ronnebyensis* only occurs in oligotrophic islets – or species usually occurring in other kinds of habitats and hence found only in randzones [e.g. *Deroceras agreste* (MÜLLER), *Vertigo lilljeborgi* (WESTERLUND), *Euconulus alderi* (GREY)].

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References.

BONDESEN, P. (1966): Population studies of *Vertigo moulinsiana* DUPUY in Denmark. — Natura Jutlandica, **12**: 240-251.

EHRMANN, P. (1933): Mollusca. — In: BROHMER, P., EHRMANN, P. & ULMER, G.: Die Tierwelt Mitteleuropas, **2** (1): 264 pp. Leipzig.

JØRGENSEN, F. A. (1966): Statistical analysis of dr. phil. P. BONDESEN's data on the dental armament in three Danish populations of *Vertigo moulinsiana*. — Natura Jutlandica, **12**: 252-257.

[2]) In large parts of northern and central Sweden *Zoogenetes harpa* (SAY) is regularly found in the same type of habitats as *V. ronnebyensis*, also feeding on *Vaccinium*-leaves. In the province of Dalsland this species is, however, on the southern edge of its distribution and very rare.

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Fig. 10. Constancy figures for species associated to *V. ronnebyensis* shown graphically. Material from 99 localities in the province of Dalsland.

KERNEY, M. P. & CAMERON, R. A. D. (1979): A Field Guide to the Land Snails of Britain and North-West Europe. — 288 pp. London.

KERNEY, M. P., CAMERON, R. A. D. & JUNGBLUTH, J. H. (1983): Die Landschnecken Nord- und Mitteleuropas. — 384 pp. Hamburg and Berlin.

LOHMANDER, H. (1953): Faunistiskt fältarbete 1951 och 1952 (södra Småland, östra och mellersta delen). — Göteb. Mus. Årstryck: 31-83.

LUNDGREN, G. (1954): The land mollusca of Värmland and remarks on their ecology. — Ark. Zool., (2) **6** (22): 443-484.

PROSCHWITZ, T. von (1985): Intraspecific variation in *Nesovitrea hammonis* (STRÖM) (Pulmonata: Zonitidae) in Sweden, with special reference to colour dimorphism. — J. Conch., **32:** 49-61.

TISCHLER, W. (1949): Grundzüge der terrestrischen Tierökologie. — 220 pp. Braunschweig.

WALDÉN, H. W. (1955): The land Gastropoda of the vicinity of Stockholm. — Ark. Zool., (2) **7** (21): 391-448.

— — — (1966): Einige Bemerkungen zum Ergänzungsband zu EHRMANN's „Mollusca", in „Die Tierwelt Mitteleuropas" — Arch. Moll., **95:** 49-68.

— — — (1969): En översikt över Hallands landmolluskfauna — Fauna och flora, **64:** 141-188.

— — — (1986): Über Variation, Verbreitung und Ökologie von *Vertigo extima,* einer für Europa neuen und bisher als selbständiges Taxon übersehenen Art. — Arch. Moll., **117:** 39-59.

WÄREBORN, I. (1969): Land molluscs and their environments in an oligotrophic area in southern Sweden. — Oikos, **20:** 461-479.

WESTERLUND, C. A. (1887): Fauna der in der Paläarktischen Region lebenden Binnenconchylien. III. Gen. *Buliminus, Sesteria, Pupa, Stenogyra* & *Cionella.* — 1-181, 1-15. Lund.

— — — (1897): Synopsis Molluscorum Extramarinorum Scandinaviae (Sueciae, Norwegiae, Daniae & Fenniae). — Acta. Soc. Fauna & Flora Fenn., **13:** 1-138.

— — — (1904): Sveriges, Norges, Danmarks och Finlands Land- och Sötvattensmollusker. Exkursionsfauna. Tillägg. — 48 pp. Stockholm.