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Fen malacocenoses in Dovrefjell (S. Norway)

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The Malacofauna of 37 topogenous, soligenous and mixed fens in Dovrefjell consists of 18 snail species and 3 slugs, with 1—10 species per locality and 5—358 individuals per 10 l litter; at most localities single species dominate strongly. The number of species and individuals and the dominance structure of the malacocenoses depend on the fen type, litter pH and Ca content, and altitude. Two of the four records of *Vertigo parcedentata* (Al. Braun) are new.

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INTRODUCTION

Ecological studies on land malacocenoses, though numerous (see Andersen & Halvorsen 1984, Gärdenfors 1987, Drieczkowski 1988), rather unevenly cover various aspects of land snail ecology. Few papers deal with snail communities of open habitats, and still fewer contain data on those of fens (e.g. Nilsson 1968, 1987, Waldén 1971, Andersen & Halvorsen 1984).

The effects of calcium content and acidity of the substratum, important factors in mollusc ecology, are often considered (e.g. Valovirta 1968, Wäreborn 1970, 1982, see also Gärdenfors 1987), but the information on fen inhabitants pertains to requirements of particular species rather than to entire associations. Nilsson (1968, 1987) pointed to qualitative differences between malacocenoses of different fen types.

Vertical distribution limits of some land snails in S Norway were discussed by Solhøy (1969, 1976), though the effect of altitude on the community structure was not considered.

Samples taken in Dovrefjell enable at least some remarks on the above aspects of fen malacocenoses.

STUDY AREA

Dovrefjell is situated in S Norway (Fig. 1A). Its NE parts which consituted the study area, stretch between 62°00—62°30'N, and 9°00 — 10°09'E (Fig. 1B). The bedrock is Cambro-Silurian, of varied character: phyllite, gneiss, conglomerate rocks, mostly of high calcium content, and limestone (Holtedahl 1960). The altitude ranges from c. 800 m a.s.l. on valley bottoms to over 1600 m a.s.l. on summits.

According to meteorological stations at Kongsvoll (934 m a.s.l.) and Fokstua (974 m a.s.l.), the yearly precipitation is 473 mm. The snow-free period lasts usually from June to September. The mean temperature in July is 11°C, the mean monthly temperature exceeding zero from May to September.

The timberline runs between 900 and 1000 m a.s.l., reaching 1100 m a.s.l. along some of the valleys. Above it there is an alpine heathland. Below the timberline a rich birch forest is interspersed with a subalpine heath. The substratum is to a great extent moist, with extensive fens. Springs, streams and lakes are numerous.

In that area 37 fens situated at 800—1400 m a.s.l. (Fig. 1B) were selected for studies. Most were moderately to extremely rich calcareous fens. The pH of leaf litter ranged from 5.2 to 6.6, the calcium content from 3.5 to 14.6 mg/g. These factors were highly correlated ($r = 0.61$, $p<0.001$, $n = 37$). The altitude of the studied localities covered the upper distribution limit of nearly all mollusc species (Solhøy 1969, 1976, cf. also Tab. 4).

The fens, except one situated in the birch forest, were open. The vegetation consisted mostly of *Carex* spp., mosses and dwarf willows and birches *(Betula nana),* with numerous calciphilous plants indicative of a high *(Salix hastata, S. reticulata, S. myrsinites, Thalictrum alpinum, Equisetum scirpoide,*

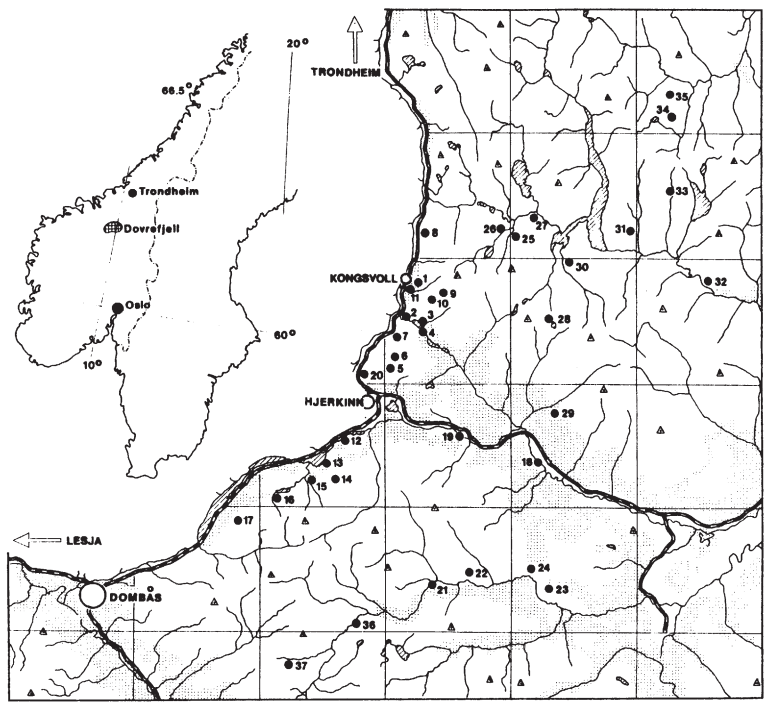

Fig. 1. The study area (A) and the studied localities (B). Black dots: localities; points in triangles: peaks above 1000 m a.s.l.; hatched fields: lakes; dotted areas: forest. Grid 5 km.

Carex dioica, C. capitata, C. capillaris, Drepanocladus revolvens, Campylium stellatum, Paludella squarrosa, Sphagnum warnstorfii) or very high *(Kobresia simpliciuscula, Carex saxatilis, C. atrofusca, Fissidens adianthoides, Lophozia rutheana, Ditrichum flexicaule, Catoscopium nigritum)* calcium content. Even in poorer fens there were «islands» where those calcium indicators could be found.

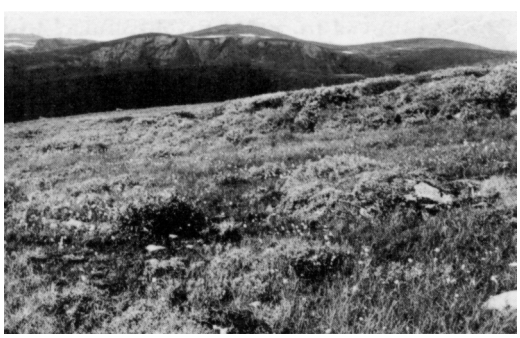

Fig. 2. The highest, sloping soligenous fen on the S slope of Knutshö (Loc. 9). Vegetation of *Betula nana, Salix phylicifolia, S. lapponum, Carex saxatilis, C. rostrata, C. norvegica, Paludella squarrosa, Cinclidium stygium, Drepanocladus revolvens, D. intermedius;* calcareous outcrops (right). A habitat of *V. arctica* (dominant), *C. columella & E. fulvus.* Photo author.

According to Nilsson's (1968, 1987) division, soligenous and topogenous fens could be distinguished, and, in addition, habitats of mixed character (Tab. 1). Thirteen soligenous fens were situated mostly on gentle slopes up to 5° (Figs. 2, 3), and in some of them (massif of Knutshöa) calcareous outcrops were scattered. Eleven topogenous fens were located on valley bottoms or close to them, below the timberline (Fig. 4). Thirteen fens were of mixed character (Figs. 5, 6), developed on the transition between flat, swampy topogenous and sloping soligenous fens.

MATERIAL AND METHODS

Samples were taken in August 1988. The permanently wet substratum rendered it impossible to use the square frame. Instead 10 l of ground cover (litter, mosses etc.) were taken at each locality. The litter was immediately sifted through a sieve of 10 mm mesh, then dried during 2—3 days, and sifted through a smaller (3 mm) mesh. Both the

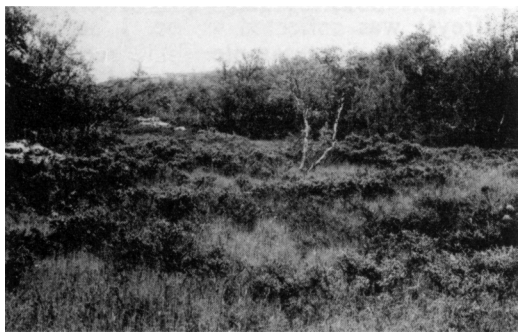

Fig. 3. A sloping rich soligenous fen above Kongsvoll (Loc. 11), close to the timberline; the only forest fen examined. Vegetation of *Betula nana, Salix myrsinites, Equisetum palustre, Parnassia palustris, Saussurea alpina, Deschampsia caespitosa, Polygonum viviparum, Carex capitata, C. nigra, C. dioica, Paludella squarrosa, Cinclidium stygium, Plagiomnium ellipticum;* calcareous outcrops (left). A. habitat of *O. elegans, C. lubrica, V. arctica, C. columella, P. pygmaeum* (dominant), *V. pellucida, N. petronella & E. fulvus.* Photo author.

Table 1. Characteristics of the studied fen types at Dovrefjell.

Fen type	Topogenous	Mixed/topog./solig./	Soligenous
Altitude:	880—1092	900—1100	900—1400
pH:	5.2 — 6.6	5.5 — 6.5	5.5 — 6.6
Ca/mg/g	3.5 —12.8	5.0 —14.6	4.7 —13.8
No. of fens:	11	13	13
Indicator plants:	*Carex lasiocarpa* *Carex aquatilis* *Menyanthes trifoliata*	*Saxifraga aizoides* *Parnassia palustris* *Tofieldia pusilla*	

resulting fractions were hand-sorted twice. Only living snails were taken into account, slugs and dead shells being omitted.

The litter pH was measured electrometrically on fresh litter in distilled water. The calcium content in litter was analysed using flame spectrophotometer, as total calcium per 1 g litter, each result being a mean of three measurements.

Species constituting 30% or more of a sample are referred to as dominants. Constancy is expressed as % localities at which a species was present. Dominance is % localities at which a species dominated.

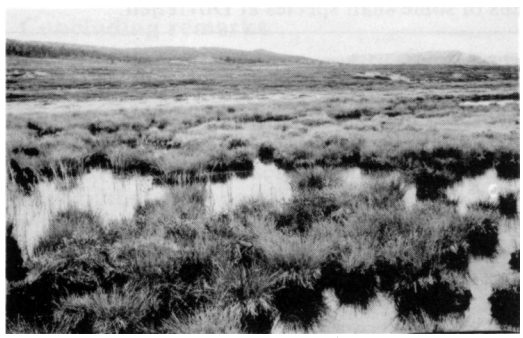

Fig. 4. A topogenous fen at Tollefshaugen, on the bottom of Grimsdalen (Loc. 23). Vegetation of *Carex nigra, C. panicea, Drepanocladus revolvens, Campylium stellatum, Scorpidium scorpioides.* A habitat of *O. elegans, V. lilljeborgi, V. geyeri* (dominant). *C. columella, P. pygmaeum, N. petronella, N. hammonis & E. fulvus.* Photo author.

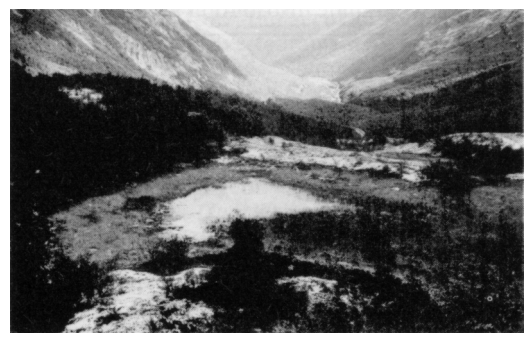

Fig. 5. A general view of a rich mixed fen at Tingsvaet (Loc. 8) Vegetation of *Betula nana, Salix lapponum, Scirpus caespitosus, Eriophorum angustifolium, Andromeda polyfolia, Paludella squarrosa, Philidium ciliare, Drepanocladus revolvens, D. badius.* A habitat of *C. lubrica, V. arctica, C. columella* (dominant). *P. pygmaeum, A. subfuscus, V. pellucida, N. petronella & E. fulvus.* Photo author.

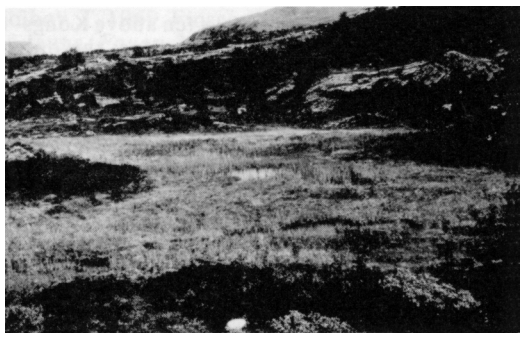

Fig. 6. A rich mixed fen at Grönbakken (Loc. 2). Vegetation of *Betula nana, Salix phylicifolia, Equisetum palustre, Eriophorum angustifolium, Carex nigra, C. panicea, C. dioica, Tomentypnum nitens, Paludella squarrosa, Campylium stellatum, Drepanocladus revolvens.* A habitat of *O. elegans, C. lubrica, V. lilljeborgi, V. genesii, C. columella* (dominant). *P. pygmaeum, N. petronella & E. alderi.* Photo author.

Statistical significance of differences between the soligenous and topogenous fens with respect to the presence of particular species was estimated using Chi square test with Yates' continuity factor.

RESULTS AND DISCUSSION

Characteristics of the fen malacocenoses

Twenty-one species were found in the studied fens, 17 of them being present in the quantitative samples (Appendix 2). *Vertigo substriata* (Jeffreys) was collected at loc. 1 but not found in the sieve sample. Slugs recorded were: *Arion subfuscus* (Draparnaud), *Deroceras laeve* (O. F. Müller) and *D. agreste* (Linnaeus). The number of species per locality ranged from 1 to 10, and the total density (number of individuals per 10 l litter) from 5 to 358 (Appendix 1). Seven species were common (constancy >40%), four rather common (constancy 20—40%) and six rare (constancy <10%) (Appendix 2).

In the studied malacocenoses, species restricted to fen habitats constituted 28.6% *(O. elegans, V. lilljeborgi, V. geyeri, V. genesii, E. alderi, V. parcedentata).* Zoogeographically, eight species (38.1%) were Arctic-Alpine, Boreo-Alpine or N European, the remaining being widely distributed (Tab. 2). Of constant components, four widely distributed species were euryoecious, two Arctic-Alpine species (*V. arctica. C. columella)* — rather euryoecious, and only two (N European *V. genesii* and Holarctic *O. elegans)* were restricted to fen habitats.

In all the malacocenoses single or at most two species dominated strongly (often >50% total density) (Appendix 1). Arctic-Alpine *C. columella* and *V. arctica* were the most frequent dominants, at 18 and 13 localities respectively. *O. elegans, V. lilljeborgi, V. geyeri, P. pygmaeum, V. pellucida* and *E. fulvus* dominated in one or at most in three sites (Appendix 2).

Table 2. Geographic distribution and restriction to fens of some snail species at Dovrefjell.

Species	Restricted to fens	Arctic-Alpine/ Boreo-Alpine/ N European	Euryoecious/ rather euryoecious
O. elegans	X	/Holarctic/	—
V. lilljeborgi	X	X	—
V. parcedentata	X	X	—
V. geyeri	X	X	—
V. genesii	X	X	—
E. alderi	X	/Holarctic/	—
V. arctica	—	X	X
C. columella	—	X	X
Z. harpa	—	X	—
N. petronella	—	X	—
P. pygmaeum	—	/Holarctic/	X
V. pellucida	—	/Holarctic/	X
N. hammonis	—	/Palearctic/	X
E. fulvus	—	/Holarctic/	X

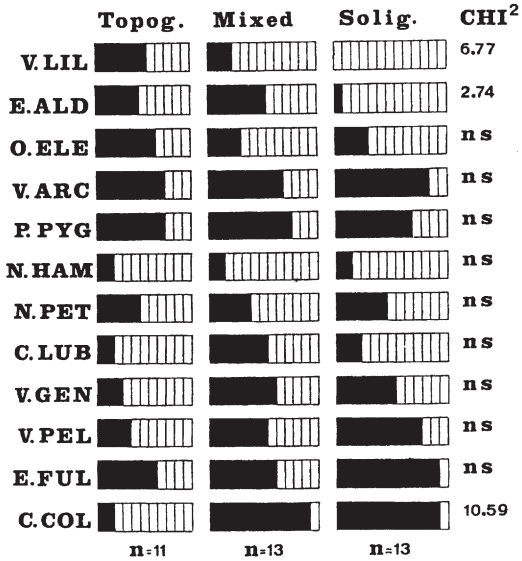

Fig. 7. Species distribution in the three types of fens. Black fields: species present, white fields: species absent. Species with less than 5 localities omitted.

Effect of fen type

The species composition of the malacocenoses inhabiting the three types of fens showed slight but constant differences (Fig. 7). Topogenous fens compared with soligenous or mixed habitats were characterized by the highest constancy of *V. lilljeborgi* and *E. alderi.* In soligenous fens *C. columella* was the most constant, *V. lilljeborgi* absent and *E. alderi* rare, the differences being statistically significant (Fig. 7). Though *V. genesii* and *V. pellucida* seemed rather to avoid topogenous fens, whereas *C. lubrica* showed a slight preference for mixed habitats, the differences were statistically not significant.

Most mixed and soligenous fens (15 of 26) were dominated by *C. columella,* six by *V. arctica,* and five by both those species or either species and *P. pygmaeum.* In topogenous fens the following species dominated: *V. lilljeborgi* (3 of 11 fens), *O. elegans* (2), and *V. arctica, V. geyeri, C. columella, P. pygmaeum* and *E. fulvus,* each in one fen.

The results indicate differences between the three fen types. Extreme and mean values of the number of species and total density for those habitats are presented in Table 3. The mixed fens appear on average to be the richest, both with respect to the number of species and individuals. The difference becomes still more pronounced when the poorest habitats are compared: pH<6, Ca content <8 mg/g, and altitude >1000 m a.s.l. (Tab. 3). Such differences can be partly explained in terms of the litter acidity and calcium content. However, the fact that the poorest of mixed fens harbour more species and individuals than the poorest fens of the other two types may be accounted for by the mosaic character of the former, their more varied topography and vegetation. Thus they may provide more places with locally favourable conditions than do topogenous and soligenous habitats.

Effect of litter acidity and calcium content

Both the number of species and the total density are correlated with the litter pH (Fig. 8A) and its Ca content (Fig. 8B), the correlation with the latter factor being more strict.

The increase in the total density with increasing pH and Ca content varies between species (cf. also Appendix 2). Though in most

Table 3. Number of species and total density in the studied types of fens. For poor fens only mean is given (see text).

Fen type:	Topogenous	Mixed / topog./solig./	Soligenous
No. of species	2—10	1—10	3—9
	5.6	6.7	6.3
Total density	5—236	5—356	14—358
	63.8	154.9	145.2
No. of fens	11	13	13
Poor fens:			
No. of species	3.0	4.3	3.0
Total density	33.0	104.0	37.5
No. of fens	3	4	2

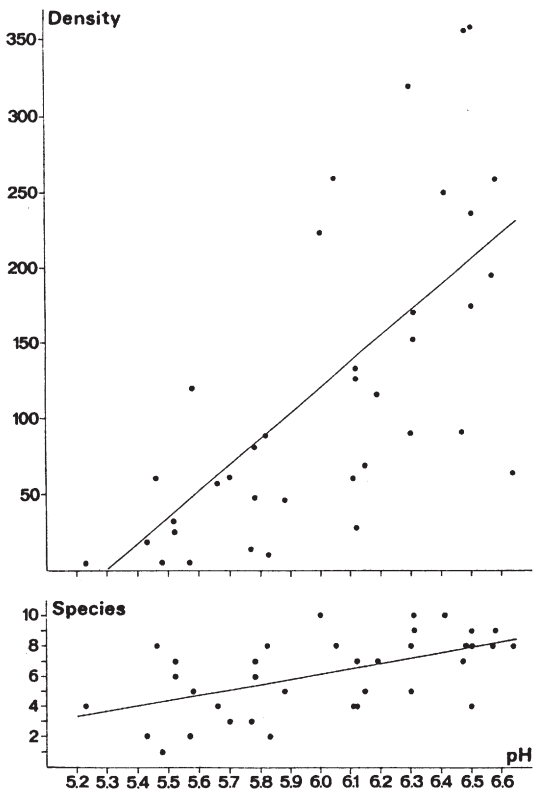

Fig. 8A. Total density (top) and number of species (bottom) in relation to litter pH. For total density r = 0.66, y = 170.7 x — 904; for species number r = 0.58, y = 3.58 x — 15.3; for both p = 0.001.

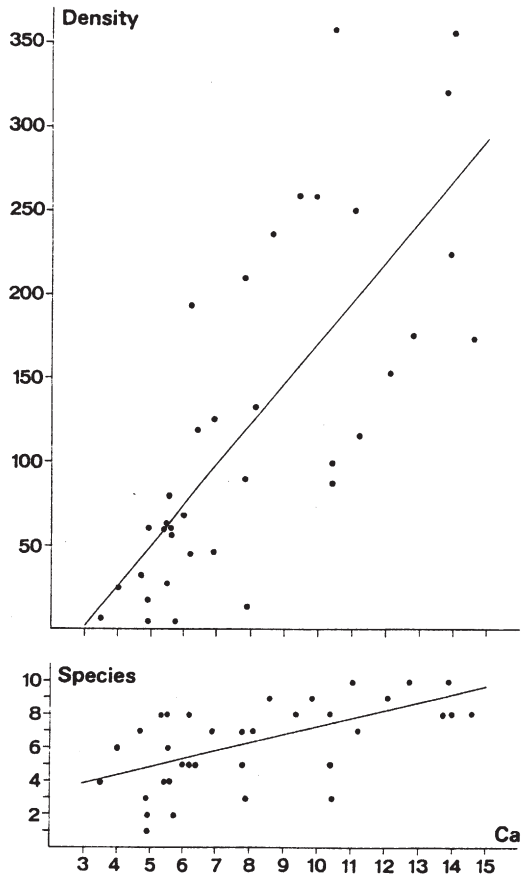

Fig. 8B. Total density (top) and number of species (bottom) in relation to Ca level (mg/g). For total density r = 0.74, y = 23.79 x — 67.95; for species number r = 0.80, y = 0.48 x + 2.37; for both p = 0.001.

cases the abundance was lower in poorer habitats, such species as *O. elegans, V. lilljeborgi, N. petronella* and *E. alderi* attained fairly high abundance of both rather low (pH 5.5—5.7, Ca 5—6 mg/g) and very high (pH c. 6.5, Ca c. 14 mg/g) values of pH and Ca content. *C. lubrica* and *N. hammonis* both reached their highest density at pH c. 6.5 and Ca level c. 14 mg/g. For species with numerous records it was possible to determine an optimum range of pH and Ca content at which they reached their highest densities. *V. genesii* and *C. columella* are typically calciphilous (pH>6.5, Ca>11 mg/g). *V. arctica* is more tolerant (Appendices 1, 2). The abundance of *P. pygmaeum, V. pellucida* and *E. fulvus* seems to depend on factors other than the acidity and calcium content in the litter.

The dominance structure of snail communities in particular fen types was partly dependent on the litter pH and Ca content. This was especially clear in topogenous fens — those of low pH and Ca level were dominated by *V. lilljeborgi, O. elegans, V. arctica* and *E. fulvus.* In the fens of higher values of both factors *V. geyeri, P. pygmaeum* and *C. columella* were the dominants. The dependence is also apparent from the comparison of habitats in which the two most common dominants formed a majority. Most (11 of 18) fens dominated by calciphilous *C. columella* had pH>6 and Ca content >10 mg/g (Appendix

1). All sites at which *V. arctica,* preferring a lower pH and Ca content, was dominant (13 fens) had Ca content <8 mg/g, and all, except one, had pH<6.

Numerous authors (e.g. Burch 1955, Valovirta 1968; Wäreborn 1970, 1982, Waldén 1981, Andersen & Halvorsen 1984) found a strong positive correlation between the pH of soil or litter on one hand, and the number of species and/or individuals on the other. According to Burch (1955) and Voelker (1955) pH itself within a certain range has no effect on land snails and should be viewed not as a decisive factor, but as an indicator of e.g. calcium level which is an actual critical factor for land snails (Waldén 1981). The fact that the number of species and individuals in the studied fens is better correlated with the calcium than with the litter pH confirms the suggestion.

Valovirta (1968), when studying effects of the soil and litter acidity on snails in hyperite hills in Finland, found differences between species in their preferred pH ranges. His results, considering differences in habitats and species composition between the two areas, agree well with those obtained in Dovrefjell.

The fact that soligenous and mixed fens were on an average richer in species and individuals than topogenous habitats may be partly explained in terms of Ca content and litter pH. The mean Ca level of the litter in soligenous and mixed fens was 9.1 mg/g, in topogenous, 6.5 mg/g. The mean pH value for the former group of fens was 6.1, for the latter 5.9. The differences in pH in most cases may be accounted for by the so called slope effect (Valovirta 1968): calcium of the bedrock is more readily extracted by running water on sloping ground, resulting in turn in the litter pH being higher on sloping than on level ground. The studied soligenous and mixed fens were situated wholly or partly on slopes, topogenous on flat valley bottoms.

Effect of altitude

Three groups of species could be distinguished with respect to vertical distribution (Tab. 4). The first comprises species which have distinct lower limits to their vertical range (c. 900 m a.s.l.). *V. arctica, C. columella* and *V. genesii* have an altitude optimum (>1000 m a.s.l.) at which they attain their highest abun-

Table 4. The highest records of species found in Dovrefjell compared with their previous highest records in S Norway. Hardangervidda — Solhøy, 1969; various sites in S Norway — Waldén, personal communication.

Species	Dovrefjell	Hardangervidda	Various sites, S Norway
C. arctica	1400	1470	—
C. columella	1400	1470	1460
V. parcedentata	1210	—	—
V. genesii	1210	—	770
E. fulvus	1400	1470	1450
Z. harpa	1250	780	1250
C. lubrica	1210	1000	1200
P. pygmaeum	1210	1300	1300
A. subfuscus	1210	1470	—
V. pellucida	1210	1470	—
N. petronella	1210	1260	1200
E. alderi	1169	—	—
A. arbustorum	1169	1470	—
V. substriata	1100	270	—
P. muscorum	1100	—	—
O. elegans	1050	—	—
V. lilljeborgi	1000	250	990
N. hammonis	1000	1100	1050
D. agreste	950	270	—
D. laeve	950	1250	—
V. geyeri	880	—	410

dance. The second group appeared in most of the studied vertical range, though often with quite a modest abundance. The third group comprises species limited to lower altitudes.

The altitude preferences of the first group are reflected by the dominance structure of the malacocenoses in sites situated above 1000 m a.s.l. (Appendix 1). At 19 (95%) of 20 such localities *V. arctica* and/or *C. columella* dominated. The dependence of the dominance structure on altitude was less pronounced at localities situated below 1000 m a.s.l. Six of 17 such sites were dominated by species of the third group *(O. elegans, V. lilljeborgi, V. geyeri),* two by a member of the second *(P. pygmaeum),* the remaining nine localitites being dominated by *C. columella.*

The first and second groups (14 species) exceeded the timberline, the third did not. Of the former *V. substriata, Z. harpa* and *C. lubrica* were listed by Solhøy (1969, 1976) as not exceeding the timberline on Hardangervidda. Of species listed by that author from above the timberline *N. hammonis* and *D. laeve* were found only below it in Dovrefjell.

Since Dovrefjell is situated farther to the north-east than Hardangervidda, it could be expected that some species might reach lower altitudes in the former area. Likewise, the number of species exceeding the timberline should be lower in Dovrefjell. The actual situation was the opposite (14 species in Dovrefjell compared with 12 listed by Solhøy 1976).

The records of *V. substriata, V. geyeri, V. genesii, D. agreste* and *E. alderi* from Dovrefjell considerably extended their vertical distribution in S Scandinavia (Tab. 4). There are no data on the vertical range of *E. alderi* in S Norway. The species was found at 560 m a.s.l. in Abisko (N Sweden) (Nilsson 1968), at 850 m a.s.l. in Lycksele Lappmark (Waldén 1971), and at 690 m a.s.l. in Ammarnäs, N Sweden (Proschwitz 1985), so its occurrence at 1169 m a.s.l. would be the highest known, even though farther to the south.

Notes on Vertigo parcedentata

As nearly all previously published data on *V. parcedentata* Al Braun) (Ložek 1964, Waldén 1986, Stworzewicz 1989) pertain to subfossil associations, its habitats and requirements merit a more detailed description. The species as subfossil is a characteristic component of loess faunae in entire Europa, and in C Europe it indicates cool climatic phases (Ložek 1964, Stworzewicz 1989). Until not long ago it was regarded as extinct since the end of Weichselian (Waldén 1986), but was then found alive in Dovrefjell (Waldén 1986, Nilsson 1987).

At two of the present localities (W. Knutshöa 1, Grosmyra 7) it was previously found by Nilsson (1987 and personal communication), the other two (S Hjerkinnhöi 5, Flåmsaetrin 30) are new records. All the sites are situated at 990—1210 m a.s.l., the litter pH ranges from 5.9 to 6.5, the calcium content from 7.5 to 14.0 mg/g (Appendix 1). All are open fens of soligenous (locs 1, 5) or mixed (7, 30) character, from sloping at 5°—10° (1, 5) to nearly flat (7, 30). These facts allow one to characterize the species provisionally as an Arctic-Alpine calciphile inhabiting rich to

Table 5. Vegetation at localities of *V. parcedentata* in Dovrefjell.

Vegetation	Locality:	1	5	7	30
Shrubs:					
Betula nana		X	X	X	X
Salix myrsinites		X	—	X	X
S. phylicifolia		—	X	—	—
S. arbuscula		X	—	—	—
Herbaceous plants:					
Parnassia palustris		X	X	X	X
Thalictrum alpinum		X	X	X	X
Saxifraga aizoides		X	X	—	—
Eriophorum angustifolium		—	X	X	—
E. scheuchzeri		—	X	—	—
Andromeda polyfolia		X	—	—	—
Deschampsia caespitosa		X	—	—	—
Equisetum palustre		X	—	—	X
E. hyemale		X	—	—	—
E. variegatum		X	—	—	—
Carex dioica		X	—	X	—
C. capillaris		X	—	—	—
C. saxatilis		—	X	—	—
C. vaginata		—	X	—	—
C. atrofusca		—	—	X	—
C. cardorhyza		—	—	—	X
Mosses:					
Sphagnum warnstorfii		X	X	X	X
Tomentypnum nitens		X	X	X	X
Drepanocladus revolvens		X	X	X	X
Campylium stellatum		X	X	X	X
Paludella squarrosa		X	X	X	X
Ditrichum flexicaule		X	X	—	—
Fissidens adianthoides		—	X	—	—
Catoscopium nigritum		—	—	X	—

Table 6. Accompanying species of *Vertigo parcedentata.*

Species	Locality: 1	5	7	30
V. genesii	X	X	X	X
C. columella	X	X	X	X
V. arctica	X	X	—	X
V. pellucida	X	X	—	X
P. pygmaeum	X	X	X	—
N. petronella	X	X	—	—
E. fulvus	X	X	—	—
C. lubrica	—	X	X	—
E. alderi	—	—	X	X
O. elegans	—	—	X	—
V. substriata	X	—	—	—
V. lilljeborgi	—	—	X	—

extremely rich open fens of soligenous or mixed type. The number of localities (4) and specimens (c. 20) suggests that the species is rare. Vegetation at the four localities varies, the common character being many plants indicative of rich conditions, and a luxuriant moss cover (Tab. 5). In all the sites *V. parcedentata* was accompanied by *V. genesii* and *C. columella* (for other accompanying species see Tab. 6). At localities 5, 7 and 30 *V. parcedentata* was found only in the samples, at loc. 1 also in the field. The individuals collected in August 1987 and August 1988 were found among birch (*Betula nana)* litter, at the base of drier hummocks or elevated calcareous outcrops.

Concluding remarks

The type of fen, leaf litter acidity and calcium content, and altitude have an effect on the number of species, their abundance and the composition and dominance structure of the studied malacocenoses. The degree to which each of these and possibly other factors influence the qualitative and quantitative characteristics of the fen malacocenoses requires more extensive studies.

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SAMMENDRAG

Sneglefaunaen i Dovrefjell

Sneglefaunaen i 37 gjengroingsmyrer, bakkemyrer og blandingsmyrer (ultraoligotrofe, meso-/eutrofe) i Dovrefjell består av 18 sneglearter og 3 nakensneglearter, med 1—10 arter pr. lokalitet og 5—358 individer pr. 10 l strø. På de fleste lokaliteter dominerte enkeltarter sterkt. Antall arter og individer og dominans-strukturen av landsnegler avhenger av myrtype, pH og Ca-innhold, og høyde. To av fire registreringer av *Vertigo parcedentata* (Al. Braun) er på nye lokaliteter.

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Appendix. 1. Characteristics of the studied localities.

Locality N°	Locality Name	Fen type	pH	Ca	Altitude	Number of species	Total density	Dominant species /%/
1.	W Knutshöa	soligenous	6.3	13.8	1100	8	320	C. columella /45.31/
2.	Grönbakken	mixed	6.5	14.6	920	8	174	C. columella /53.74/
3.	Gåvålisaetra	soligenous	6.5	10.5	940	4	358	C. columella /70.59/
4.	Fisktjin	mixed	6.2	11.2	940	7	116	C. columella /46.55/
5.	S Hjerkinnhöi	soligenous	6.3	12.1	1210	9	152	C. columella /46.05/
6.	N Hjerkinnhöi	soligenous	6.5	7.8	1100	7	90	C. columella /48.89/
7.	Grosmyra	mixed	6.5	14.0	990	8	356	C. columella /58.99/
8.	Tingsvaet	mixed	5.8	10.4	970	8	89	C. columella /38.89/
9.	Knutshöa S upper	soligenous	5.8	7.9	1400	3	14	V. arctica /71.43/
10.	Knutshöa S lower	soligenous	6.3	10.4	1250	5	90	C. columella /46.74/
11.	Kongsvoll forest	soligenous	6.0	9.4	1000	8	259	P. pygmaeum /60.62/
12.	Hegglingen	topogenous	6.1	5.5	900	4	28	O. elegans /64.29/
13.	Avsjöen	topogenous	5.2	3.5	930	4	7	V. lilljeborgi /42.86/
14.	Skridubekken	soligenous	5.7	4.9	1200	3	61	V. arctica /85.25/
15.	Avsjösaetri	mixed	5.5	5.0	1020	1	5	V. arctica /100/
16.	Haukskardtjin	topogenous	5.4	5.0	1092	2	18	V. arctica /83.33/
17.	Haukskardmyrin	topogenous	5.6	5.8	1050	2	5	V. arctica /80.00/
18.	Lalen	topogenous	5.8	6.9	800	7	47	O. elegans /76.60/
19.	Bergseng	topogenous	5.5	4.0	850	6	25	V. lilljeborgi /48.00/
20.	Hjerkinn	soligenous	5.5	5.4	950	8	60	C. columella /30.00/
21.	Grimsdalshytta	soligenous	6.6	9.9	950	9	259	C. columella /67.95/
22.	Tverrlisaetri	mixed	6.0	13.9	920	10	223	C. columella /43.95/
23.	Tollefshaugen	topogenous	6.6	7.5	880	8	63	V. geyeri /34.92/
24.	Mesaetri	topogenous	6.5	8.6	880	9	236	P. pygmaeum /39.83/
25.	Hreidslågåbkn	mixed	6.1	6.0	1060	5	69	V. arctica /36.23/ V. pellucida /34.78/
26.	Bekkelaegret	topogenous	5.9	6.2	1100	5	46	E. fulvus /39.13/ V. arctica /32.61/
27.	Elgsjöbekken	soligenous	6.1	8.1	1081	7	133	C. columella /53.38/
28.	Råtåsjöen	mixed	6.1	6.9	1169	7	126	V. arctica /56.35/
29.	Furuhovde	topogenous	5.7	5.6	920	4	57	V. lilljeborgi /57.89/
30.	Flåmsaetrin	mixed	5.9	7.5	1060	6	81	V. arctica /39.51/ C. columella /34.57/
31.	Dölbekken	mixed	6.6	6.2	1000	8	194	C. columella /69.59/
32.	Svesaetra	soligenous	5.5	4.7	980	7	32	P. pygmaeum /40.63/ V. arctica /31.25/
33.	Marsjötangen	topogenous	6.3	12.8	980	10	170	C. columella /32.35/
34.	Såtålii	soligenous	6.1	5.6	1030	4	60	V. arctica /55.00/ C. columella /41.67/
35.	Såtålbekken	mixed	6.4	11.1	1000	10	250	C. columella /54.80/
36.	Verkenssaetri	mixed	5.6	6.4	1100	5	120	V. arctica /59.17/
37.	Vegaskilet	mixed	5.8	7.8	1100	5	210	V. arctica /60.48/

Appendix 2. Species list with some ecological characteristics. Localities at which a species dominated underlined. For density both range and mean are given.

Species	Localities	Constancy	Density	Dominance	pH	Ca
Vertigo arctica /Wallenberg/	1,5,6,8,9,10-12,14-17,18-20, 22,25,26,27,28,29,30,31,32, 33,34,35,36,37	75.7	1-127 21.9	29.7	5.5-6.5	4.0-13.9
Columella columella /Martens/	1-8,9,10,11,20-22,23-25,27, 28,30,31,32,33-35,36,37	73.0	2-252 66.2	48.7	5.5-6.6	4.7-14.6
Punctum pygmaeum /Draparnaud/	1,2,4-8,10,11,13,18-23,24, 25-29,31,32,33,35,37	73.0	1-157 24.6	8.1	5.2-6.6	3.5-14.6
Euconulus fulvus /O. F. Müller/	1,4-6,8-11,14,16,18-25,26, 27,28,32-37	73.0	1-53 15.2	2.7	5.4-6.6	4.0-13.9
Vitrina pellucida /O. F. Müller/	1,5,6,8,11,13,14,20,21,24, 25,26-28,30-33,35,37	54.0	1-24 5.0	2.7	5.2-6.6	3.5-13.8
Vertigo genesii /Gredler/	1,7,18,20-22,24,27,30,31,33, 35,36	48.7	1-101 23.7	---	6.0-6.6	7.5-13.8
Nesovitrea petronella /L. Pfeiffer/	1,2,4-6,8,11,18,19,21,23,26, 27,31,33,35	46.0	1-28 5.7	---	5.5-6.6	4.0-14.6
Oxyloma elegans /Risso/	2-4,7,11,12,13,17,18,19-23, 32,33	43.2	1-30 6.9	5.4	5.2-6.6	3.5-14.6
Euconulus alderi /Gray/	2,7,12,18,22,24,28-31,33-35	35.1	1-16 5.3	---	5.7-6.5	5.5-13.9
Cochlicopa lubrica /O. F. Müller/	2,4,5,7,8,11,21,22,24,31,33, 35	32.4	1-17 6.0	---	5.8-6.6	6.2-14.6
Vertigo lilljeborgi /Westerlund/	2,7,12,13,19,22-24,29,31	27.0	3-45 15.9	5.4	5.2-6.6	3.5-14.6
Vertigo parcedentata /Al. Braun/	1,5,7,30	10.8	1-8 3.0	---	5.9-6.5	7.5-14.0
Pupilla muscorum /Linnaeus/	21,36	5.4	1-3 2.0	---	5.6-6.6	6.4-9.9
Vertigo geyeri Lindholm	23	2.7	22	2.7	6.6	7.5
Zoogenetes harpa /Say/	10	2.7	4	---	6.3	10.4
Arianta arbustorum /Linnaeus/	28	2.7	2	---	6.1	6.9