Variation and reproductive behaviour in some Swiss populations of Leontodon hispidus L.s.l. : a preliminary report

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Variation and reproductive behaviour in some Swiss populations of *Leontodon hispidus* L. s. l. — a preliminary report

by

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Contents

1. Introduction

The genus *Leontodon* covers a group of morphologically and genetically closely allied species. According to the taxonomical system of WIDDER (1931, 1975), *L. hispidus* L. belongs to the section *Leontodon* of the subgenus *Leontodon*, characterized by the nodding flower buds and a virtual absence of squamiform scapus leaves. Hairs, when present, are stellate, carrying 2 - 6 rays. The presence of a pappus with normally developed, partly feathery setae at all achenes, differentiates the section *Leontodon* from the section *Thrincia* (Roth) Bentham et Hooker. Main characters of *L. hispidus* are a more or less horizontal, knotted rhizome and a diploid somatic chromosome number 2n=14.

Early attempts to cope with the remarkable variation within the species, mainly by means of a straight description of the physiognomical variation, seem unsatisfactory (HEGI 1929).

Distinct karyotype descriptions of specimens from various European localities suggest some differentiation of chromosomes of *L. hispidus* (Table 8). A first contribution to the study of the relations between morphological, cytological and ecological variation was made by FINCH (1967).

Acknowledgements

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2. Material and methods

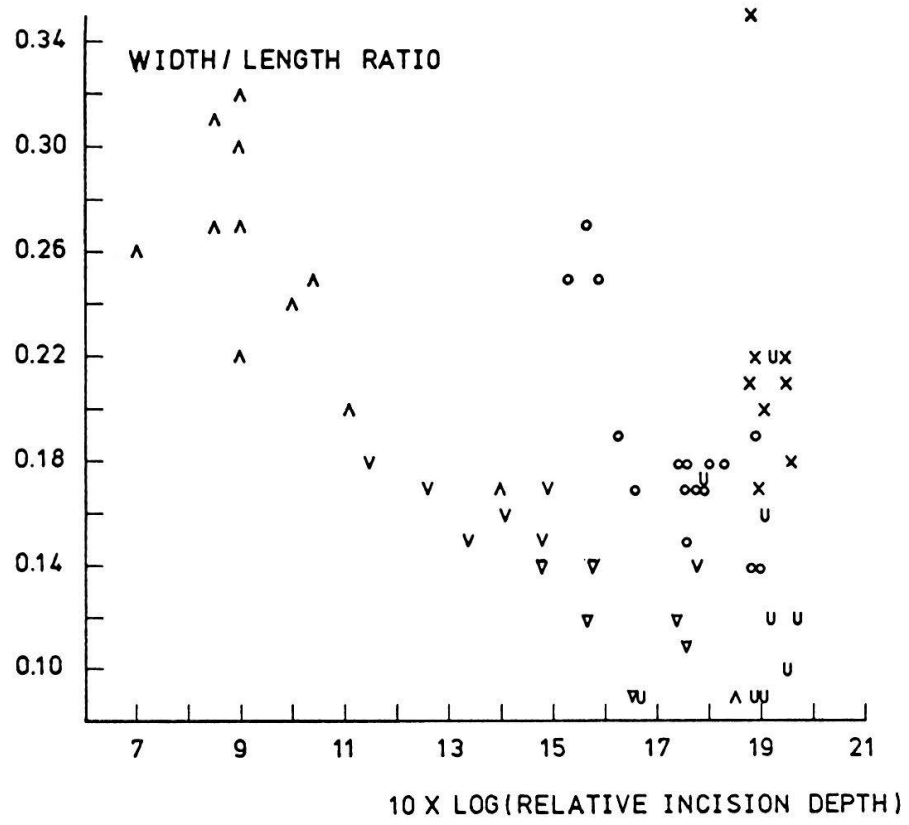
Populations from phytosociologically distinct vegetation units, sampled at various, mainly Swiss habitats were studied (Table 1). Part of the material was cultivated in a climatic chamber; the following conditions were applied: dry temperature at day 17°C, at night 10°C; day length 16 hrs.; light intensity 13000 Lux,relative air humidity 70 %. Methods used for morphological and cytological studies as well as those applied in experimental crosses are given in the respective chapters.

3. Morphology

3.1. *Leaf shape*

Leaf shape was described by means of the characters "width/length ratio", defined as the ratio of maximal leaf width to leaf length, "relative incision depth", defined as the ratio of isthmus width in the middle of the leaf, and "number of teeth", defined as one half of the total number of teeth per leaf. For each character, average values and standard deviations were determined from five leaves per individual.

For the assessment of the extent of phenotypical variation in leaf shape, samples from populations E and M were measured for the first time after a period of growth in a climatic chamber (see above) and, subsequently, after a period of growth in the garden. The characters "width/length ratio"



o grassland sample BOP (dry station)

u grassland sample BOP (wet station: var. glabr.)

∧ hyoseroides sample E

v hyoseroides sample FAL (exposed station)

∇ hyoseroides sample FAL (less exposed station)

x grassland sample M

Fig. 1. Leaf shape in wild samples

Table 1. Origin and code names of the investigated samples

Taxon (var.*)	Place of origin	Code name	Habitat	pH
glabratus	Hombrechtikon(CH) "Lutiker Riet"	LUT	wet hayland (*Molinietum*)	7.4(+)
	Schönenberg(ZH.-CH) "Hinterbergriet"	HB	wet hayland (*Molinietum*)	6.3(-)
	Boppelsen (CH) "Boppelser Riet"	BOP1	wet/dry hayland (*Mesobrometum,Molinietum*)	7.4(+)
hyoseroides	Zuerich (CH) "Entlisberg"	E	open molasse scree S.-exposed slope,70%	7.8(+)
	Zuerich(CH) "Fallätsche"	FAL	open molasse scree S.-exposed slope 80-90%	7.7(+)
	Wolfgang (CH)	WO	open serpentine scree	**
	Davos (CH) "Totalphorn"	TOT	open serpentine scree S.-exposition	7.1(-)
"*hysoreoides*-like"	Airolo (CH) Albinasca	AIR	mesic pasture, intensively grazed (*Trisetum,Poo-Pruneletum*)	4.5(-)
	Schilpario(I) "Passo di Campelli"	CA	mesic extensive pasture (*Nardetum, Seslerietum*)	5.5(+/-)
cf. *dubius*	Davos (CH) "Schiahorn"	SCHI	alpine meadow (on dolomite)	**
	Davos (CH) "Salezerhorn"	SAL	alpine meadow (on silicate)	
hispidus	Kirlovods (SU)	KIR		
	Pyatigorsk (SU)	PY		
	Zuerich-town(CH) "Kantonsschule"	M	lawn, cut frequently	(+)
	Zuerich-Hockler	HOE	mesic meadow (*Lolio-Cynosuretum*)	6.5(+)
	Stallikon(CH)	STAL	dry/wet hayland (*Mesobrometum*)	7.4(+)
	Boppelsen(CH)	BOP2	dry-mesic hayland (*Mesobrometum*)	
	Küttingen(CH)	TTMB	over 10 year old dry fallow land (*Tetragonolobus-Mesobrometum*)	8.0(+)
	Küttingen(CH)	TCMB	6 years old,dry follow land; S.E.-exp.slope, 50% (*Teucrio-Mesobrometum*)	7.8(+)
	Küttingen(CH)	ARRJ	(mesic,manures hayland 2-3 cuttings per year (*Arrhenatheretum*)	**

* according to HEGI(1929) (+) calcareous soil (-) not calcareous soil
** not measured

Table 2. Phenotypical variation in leaf shape: mean values for three leaf parameters, mean standard deviations and mean variation in time

Sample M (8 individuals)	N of teeth	Width/length ratio	Relative incision depth
climatic chamber	9.2 ± 1.5	0.21 ± 0.02	0.71 ± 0.06
garden	10.4 ± 0.9	0.21 ± 0.02	0.59 ± 0.06
mean variation in time (absolute values)	1.3	0.02	0.12
Sample E (10 individuals)	N of teeth	Width/length ratio	Relative incision depth
climatic chamber	8.0 ± 1.4	0.24 ± 0.04	0.11 ± 0.04
garden	8.0 ± 1.3	0.22 ± 0.03	0.17 ± 0.04
mean variation in time (absolute values)	1.4	0.03	0.06

and "number of teeth" were similar in samples E and M (table 2) so that variation ranges for both samples overlapped. On the other hand, the values for "relative incision depth" differed clearly and variation ranges were overlapping. The differences established at the 10^{-6}-level of significance with the T-test for unpaired data. Relatively high average values and standard deviations of "relative incision depth" were observed in some E-individuals, which were infected by mildew.

The range of variation in time and the range of momentary intrapopulational variation were comparable for both samples. Apparently, phenotypical variation in leaf shape equals or prevails over genetically fixed variation within the samples.

Differences in number of teeth among various population found in samples kept under controlled conditions fall within the range of phenotypical variation (table 3). It should be mentioned that the leaf shape of some FAL plants from less exposed places was closely similar to that of *glabratus* plants (fig. 1). With a single exception, the ratio width/length was similar for all investigated samples; the deviating sample FAL

Table 3. Leaf shape in cultivated samples; mean values and standard deviations over five leaves per individual (figures for wild samples M, E and FAL are given for comparison).

Sample	N of teeth	Width/lenght ratio	Relative incision depth	n. of invest. individuals
Samples kept in climatic chamber				
M	9.2 ± 1.5	0.21 ± 0.03	0.71 ± 0.11	8
BOP	8.2 ± 0.9	0.20 ± 0.03	0.40 ± 0.11	6
CA	9.6 ± 1.3	0.25 ± 0.04	0.24 ± 0.13	10
SCHI	9.7 ± 1.0	0.24 ± 0.08	0.58 ± 0.07	7
E	8.5 ± 1.5	0.25 ± 0.02	0.09 ± 0.04	9
WO	9.0 ± 1.8	0.22 ± 0.03	0.09 ± 0.02	5
PAR	9.5 ± 1.6	0.27 ± 0.04	0.10 ± 0.04	5
Wild samples				
M (27.10.75)	7.1 ± 1.1	0.22 ± 0.06	0.82 ± 0.06	8
E (26.10.75)	6.9 ± 0.9	0.26 ± 0.05	0.82 ± 0.06	11
FAL (4.11.75)	7.8 ± 1.4	0.14 ± 0.03	0.36 ± 0.15	13

of *L. hyoseroides* differed from all other samples, including the *hyseroides*-samples.

"Relative incision depth" was comparable in most of the *hyseroides*-samples (E, WO, TOT and PAR), but the sample FAL was aberrant again. Relative incision depth greatly contributes to the inter-populational differentiation of leaf shape (fig. 1); its apparent differentiation within the *hyseroides*-group suggests however that the character is of a minor taxonomical importance.

3.2. *Leaf thickness*

Leaf thickness of one leaf each per individual was measured by a transection in the middle of the leaf (table 4). The *hyseroides*-sample E apparently had thicker leaves than the grassland-sample M, when kept in the same environment, whereas hybrids between E and M appeared to be intermedi-

ate. Absolute values for both garden samples were similar. Average leaf thickness of samples E and M from the wild was smaller than that in the cultivated samples, but again differed significantly for both samples (table 7). However, broad overlappings occurred when both samples were kept under different conditions: potted individuals from both populations developed thicker leaves. This feature was so pronounced in the originally thin-leaved M-individuals that leaf thickness of these plants overlapped with the normal values for the *hyseroides*-plants.

Table 4. Leaf thickness in various cultures

Sample	Mean values and standard deviations (in mm)					
	Garden at the Institute	Number of plants	Garden at Höngger-berg	Number of plants	Pot cultures	Number of plants
E	0.50 ± 0.08	10	0.46 ± 0.04	4	0.61 ± 0.07	8
ExM/MxE					0.53 ± 0.06	12
M	0.30 ± 0.06	8	0.28 ± 0.06	5	0.44 ± 0.06	8

underlined: overlapping of samples E and M.

3.3. *Size of stomata*

Samples from populations E and M were kept under identical conditions during one winter season in a climatic chamber (see methods) and subsequently transferred in open soil, remaining there during one summer season. Part of the experimentally obtained F_1 -strains from both populations, including some hybrids, were potted and grown in open air. The length of the 5 larger, closed stomata at one leaf each per individual was measured (table 5). Size differences of stomatal cells between E- and M-individuals were significant under all conditions, significance levels ranging from 10^{-2} to 10^{-4} (T-test unpaired data). No significant change in stomatal size was observed in individuals kept in the climatic chamber and transferred to the garden. However, stomatal size of the potted samples from both populations was significantly higher than that of plants from the climatic chamber as well as these from the garden. Significance levels between the garden

and the potted plants were 10^{6}- and 10^{-3} for samples E and M, respectively. Because of absence of a strict genetical determination, stomatal length seems unsuitable as a diagnostic character. It indicates, however, different developmental responses of various populations of *L. hispidus* L. s. 1.

Table 5. Size of stomata

Sample	Mean values and standard deviations (in mm)					
	Climatic chamber	Number of plants	Garden	Number of plants	Pot cultures	Number of plants
E	0.042±0.002	10	0.042±0.002	10	0.047±0.002	8
ExM/MxE					0.045±0.003	12
M	0.035±0.003	8	0.037±0.001	8	0.044±0.002	8

3.4. *Number of involucral leaves*

The variation pattern seemed different in various samples (table 6). A low degree of individual variation was observed in sample E: in 14 individuals, 3 - 4 heads per individual were found and a deviation of more than 2 was noted only once. Total population variation appeared to be limited in populations E, M and BOP, whereas populations AIR and CA varied much more; in the latter populations a second modal value i.e. 21, apart from the normal one i.e. 13, occurred. A trend towards increase of the number of involucral leaves was also observed in the alpine sample SAL (table 7) and the Caucasic samples KIR and PY.

The number of involucral leaves might be related to the number of achenes per head: the average value of achene number amounted to 147 (14 heads) in CA-plants, whereas the average values for samples E, M and BOP were 58 (83 heads), 78 (93 heads) and 64 (58 heads), respectively. The intrapopulational variation in the number of achenes might be connected with the vitality of particular individuals.

Table 6. Variation in the number of involucral leaves.

Sample	Number of involucral leaves																	Number of plants	Number of heads
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24		
E	2	1	3	2	3	67	4	1		1								46	84
M				1	1	58	12	2	4	3	3	2	1	1				45	88
BOP			1		1	30		1	1									35	35
AIR						6			3	3	3	1	4	10				28	30
CA						8	6	8	7	2	1	3	3	6	1	2	1	27	48
KIR/PY							1				1		1	6			1	7	10

3.5. *Hairiness*

3.5.1. *Hair morphology*

Filiform hairs, which occur in all varieties of *L. hispidus* L. s. l., invariably consisted of a single cell row with one or a few enlarged terminal cells. On the other hand, complex stellate hairs were subject to both individual and populational variation manifesting itself in a surprising number of forms (fig. 2).

Hair morphology in *L. hispidus* was sometimes found to show congruencies with other species: for instance, bending hair rays which normally occur in *L. incanus* Schrank and in *L. taraxacoides* Mérat (PITTONI 1974) were also observed in an alpine population WO of *L. hyoseroides* (fig. 2).

Number of rays per hair was liable to a remarkable individual variation (fig. 2). However, modal ray numbers, i. e. the most frequently occurring number of hair rays per leaf, appeared to be fairly constant in given individuals. The modal ray number characterized as well the populations and no variation was observed in the offspring obtained from experimental crosses between populations with the same modal ray number. In contrast, variation in modal ray number was observed between 4 hybrids of a cross between plants from the northern grassland population M and the southern *hyseroides*-like grassland-population CA. The modal ray number of hairs was accordingly considered in the present study as a reliable character in hair morphology and was used for the description of populations (table 7).

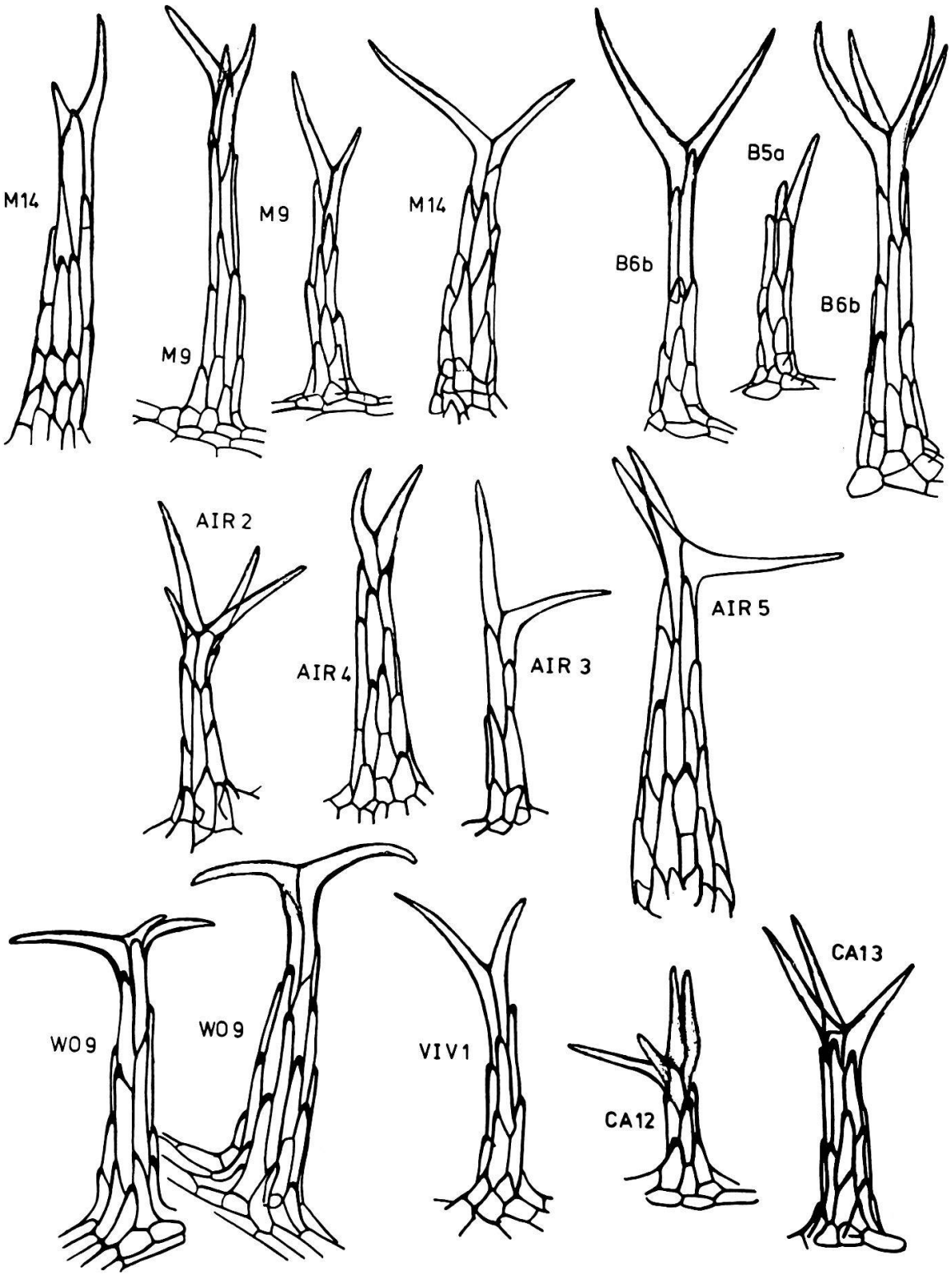


Fig. 2. Various forms of stellate hairs in *Leontodon hispidus* L. s. l.

Table 7. Interpopulational differentiation of some morphological characters.

Sample	Modal value of ray number	Hair length (mm)	Mean leaf thickness	Mean number of involucral leaves
LUT(7)	2	0.5 - 0.7	0.39	13.4
HB(3)	2	0.4 - 0.6	0.27	12.8
STAL(2)	2	0.5 - 0.5	0.32	14.3
BOP(5)	2	0.4 - 0.5	0.33	12.9
M	2	0.4 - 0.6	0.23	13.1
HOE	2	0.4 - 0.9	0.25	13.0
ARRJ	3 - 2	0.4 - 0.7	0.26	13.7
TTMB	2	0.5 - 1.0	0.25	12.9
TCMB	2 - 3	0.4 - 0.8	0.29	12.6
AIR	3	0.3 - 0.6	0.26 !	17.4
SAL	3	0.4 - 1.0	0.36	16.0
SCHI	3 - 2	0.4 - 0.7	0.39	13.1
FAL	-	-	0.40	12.1
TOT(2)	2	0.6 - 0.6	0.46	13.0

Note: Numbers of haired individuals in populations with less than 50 % haired individuals are given in brackets. Samples ARRJ, TTMB, TCMB consisted of 10 individuals, all other samples consisted of 20 individuals.

The following values of modal ray number were observed:

MRN = 1 occurring solely in experimentally obtained hybrids (CA x M and E x M).

MRN = 2, mainly found in the grassland populations from the Swiss Plateau; it occurred as well in some *hyseroides*-populations TOT and WO, where a few individuals were sparsely haired.

MRN = 3 was found in the grassland population TTMB, TCMB and ARRJ (the Jura of Aargau), AIR (central Alps) and also in the Alpine population SCHI and SAL (table 7).

The obtained results suggest that the "modal ray number" might be geographically differentiated. It should be mentioned, however, that similar values occur in otherwise physiognomical distinct populations, inhabiting distant areas: the investigated Jura populations on the one hand and the Alpine populations on the other hand, all have a congruent range of modal values with a highest value of 3. Though it may serve as an indication of

regionally occurring gene exchange, the modal number of rays seems to be of rather limited taxonomic value.

3.5.2. *Length of hairs*

Average hair length was measured in the middle leaf part of each two leaves per individual (table 7). All investigated populations, both with a strongly varying leaf shape as well as those with relatively constant leaf shape, showed a wide range of hair length. Consequently, hair length seems to be of a limited adaptive significance. It should be noted that a very dense and remarkable short indument (0.3 mm) was typical for some individuals in population CA; such induments seem far less variable than less dense and longer haired induments.

3.5.3. *Density of hairs*

The populations of *L. hyseroides* from Entlisberg and Fallätsche were both completely glabrous. On the other hand, some sparsely haired individuals, probably resulting from a gene exchange, occurred in the samples TOT and WO. Other investigated populations either consisted of both hairless as well as haired individuals or were completely haired (PY, KIR). Some haired individuals were found in the *glabratus*-populations LUT and HB and in the populations STAL and BOP. On the other hand, the populations M, HOE, AIR, SCHI, SAL and all three Jura populations (TTMB, TCMB and ARRJ) consisted of more than 50 % of haired individuals.

In 3 out of 4 sparsely haired F_1-individuals from a hybridization between a *hyoseroides*- and a grassland-parent a temporal variation in presence/absence of leaf hairs was observed: formerly haired individuals turned glabrous. Such kind of variation was further noticed in 2 sparsely haired individuals from the heterogeneous population BOP.

Leaf hairs were partly very coarse; coarser hairs occurred in the median part of the involucral leaves, and most frequently had fewer rays. The indument of the marginal part of the involucral leaves was less dense than that of the leaves. Hairs were irregularly distributed over the involucral leaves. Their presence/absence was controlled at 4 inflorescences

per individual pf each 4 F_1-individuals from 8 crosses (viz. 2 crosses E x E, 2 crosses CA x CA, 2 crosses M x M and 2 crosses E x M: all 8 individuals from reciprocal *hyseroides*-crosses E x E were hairless; all 8 individuals from reciprocal intrapopulational grassland-crosses M x M were constant in the presence of hairs; their leaves had a dense indument whereas those of their parents were intermediate to densely haired. The hairiness apparently is a character with expression varying in different parts of an individual, all 8 plants from crosses CA x CA showed a constant absence of involucral hairs whereas their leaves sometimes were sparsely haired (parents totally glabrous!). All 8 individuals obtained from interpopulational crosses E x M invariably had glabrous leaves; rosette leaves were also glabrous except for a single sparsely haired individual.

3.6. *The seed*

The following seed characters were studied: seed length, number of ribs, number of long setae and colour of the seed coat. Seed length without pappus was measured in samples M and E. Individual variation between different fruit heads was investigated in 10 seeds per head for 5 plants from the former sample, whereas the latter one was studied in 13 individuals. Variation between various fruit heads most frequently proved to be nearly the same as that within a single head. Individual variation within either population was well-marked, the respective average values being 5.9 mm ± 0.5 mm for sample E (17 individuals) and 5.7 mm ± 0.8 mm for sample M (16 individuals). It should be noted that variation within the population M is partly due to a local polyploid differentiation: the longest seeds in sample M were found in autotriploids, whereas the sample E consisted solely of diploids. The ranges of variation in seed length overlapped for both samples.

The number of seed ribs was counted in 24 heads from 11 E-individuals and in 34 heads from 13 M-individuals (1 seed per head). The number of ribs was always 5; in some individuals ribs were not clearly visible.

The variation ranges of the number of long pappus setae overlapped largely in samples E and M. Lowest values were found in sample M (11), highest values in sample E (18), whereas interpopulational hybrids were intermediate.

Seed coats were mostly darker in E- than in M-plants. Transversal ribbing of the coat sometimes seemed deeper in E- than in M-individuals.

4. Cytology

4.1. *Somatic chromosome numbers*

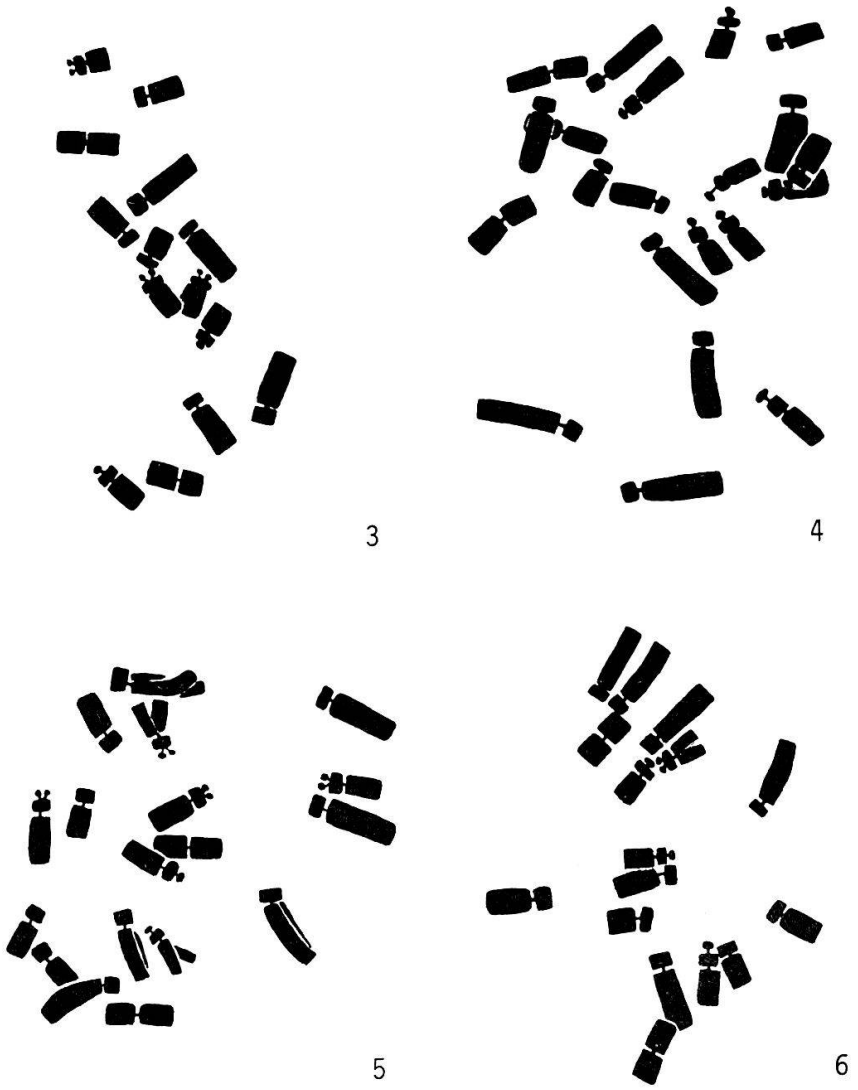
Somatic chromosome numbers of *L. hispidus* L. s. 1. were previously reported from various parts of Europe (table 8). The incidental occurrence of triploids seems to constitute the main variation in chromosome number. Triploid plants were found in larger samples; the finding of triploids might therefore be related to sample size.

The present counts were performed on root tips of germinating seeds and potted plants. Fresh root tips were collected at noon and pretreated over 1.5 hrs in 0.05 per cent aqueous colchicine at room temperature (± 20°C). They were subsequently transferred to 3 : 1 acetic alcohol and, after overnight fixation, kept in lacto-propionic orceine until further processing. The root tips were gently cooked for 2 - 2.5 min. and squashed in a fresh drop of the lacto-propionic orceine. Squashes were made permanent by removing the cover slide in butyl alcohol; then object slide and cover slide were processed in xylol and embedded in caedax. Loss of material could be avoided by covering the cover slide with a thin layer of albumen-glycerine and heating it over a flame.

The chromosome numbers found in the course of the present study are in agreement with previous data (table 8): most of the studied plants represented the diploid level (2n=14, fig. 3) and only in a single sample some autotriploids were found (2n=21,fig.4).In addition, some aneuploids (2n=16, 18, figs 5 - 6) were found in the offspring of the triploids.

Table 8. Somatic chromosome numbers in *L. hispidus* L. s. l.

Place of origin	2n	Author(s)	Remarks
Great Britain	14	ELLIOT 1950	Deviating karyotype.
	14	FINCH 1967	58 plants in samples from 8 counties;
	21		1 sample (14 plants) with triploid.
	14	ROUSI 1973	
	14	EDMONDS et al. 1974	
Netherlands	14	GADELLA and KLIPHUIS 1968	
France	14	GUINOCHET and LOGEOIS 1962	Deviating karyotype in material from the Maritime Alps.
	14	GADELLA and KLIPHUIS 1970	
	14	ROUSI 1973	var. *glabratus* (Koch) Bischoff
Portugal	14	FERNANDES and QUEIROS 1971	
GERMANY	14	TISCHLER 1934	
	14	ROHWEDER 1937	
	14	FINCH 1967	
Switzerland	14	FINCH 1967	9 individuals
	14	present study	*L. hispidus* L.s.str.: 1 sample(39 plants) with 2 triploids; 2 samples(12 and 5 plants) without triploids.
	14		*L. hyoseroides* Welwitsch: 3 samples(5, 6 and 15 plants) without triploids.
Austria	14	FINCH 1967	
	14	NILSSON and LARSEN 1971	
	14	PITTONI 1974	var. *glabratus* (Koch) Bischoff and var. *hispidus*
Poland	14	SKALINSKA et al. 1964	var. *glabratus* (Koch) Bischoff from the High Tatra with deviating karyotype.
USSR	14	ROUSI 1973	*L. danubialis* Jacq.
Czechoslo-	14	FINCH 1967	
vakia	14	ROUSI 1973	
Italy	14	PITTONI 1974	var. *hispidus*, var. *hyoseroides* (Welw.) Beck and var. *pseudocrispus* Sch.-Bip.
Yugoslavia	14	PITTONI 1974	var. *glabratus* (Koch) Bischoff
Rumania	14	ROUSI 1973	
Bulgaria	14	KUZMANOV and GEORGIEVA 1976	
Sweden	14	BERGMAN 1935	Deviating karyotype.
	14	STEBBINS et al. 1953	
Finland	14	FINCH 1967	
	14	PITTONI 1974	



Figs. 3 - 6. *Leontodon hispidus* s. l.: root-tip metaphases.
3. A normal diploid (2n=14). 4. An autotriploid (2n=21).
5, 6. Aneuploid plants (2n=18, 2n=16). (c.) 1500 x.

4.2. *Chromosome morphology*

For the study of chromosome morphology, drawings of 8 metaphases per individual at comparable stages of contraction were made with the aid of a camera lucida at 2975 x magnification. The choice of metaphases was based on the long arm length of the metacentric chromosomes, the criterion of choice ranging within 0.5 mm on drawing paper (about 0.17 µm).

Chromosome complements of *L. hispidus* L. were previously described by BERGMAN (1935), ELLIOT (1950), GUINOCHET and LOGEOIS (1962), SKALINSKA et al. (1964), FINCH (1967), FERNANDES and QUEIROS (1971) and ROUSI (1973). The descriptions of BERGMAN (1935) as well as SKALINSKA et al. (1964) remain isolated. ELLIOT (1950) as well as GUINOCHET and LOGEOIS (1962) mentioned two pairs of metacentric chromosomes, whereas only one metacentric or submetacentric pair was reported in the works of FINCH (1967), FERNANDES and QUEIROS (1971) and ROUSI (1973). Satellites restricted to the subacrocentric pairs were reported in all later studies.

The best document study is that of FINCH (1967); apart from the metacentric pair "C" he distinguished for the first time two longer subacrocentric pairs named "A" and "B", and for shorter ones, viz. "D", "E", "F" and "G", satellites being confined to the latter group. FINCH mentioned a variation in satellite visibility and size. His observations were later confirmed by ROUSI (1973).

In the present study, the karyotypes of four plants from the grassland-population M are compared with those of five plants from the *hyoseroides*-population E (table 9, fig. 7). The differences between both samples are small in relation to the interindividual variation. The general idiograms (fig. 7) are in agreement with the results of FINCH. The two pairs of longer subacrocentric chromosomes (A and B), on the one hand, and the three shortest pairs of the four SAT-pairs (E, F and G), on the other hand, appeared to be undistinguishable from each other. FINCH's values, as derived from his diagram, don't considerably exceed the range of interindividual variation in samples E and M. In the present material satellites were not always visible, variation occurring within single root tips. However, satel-

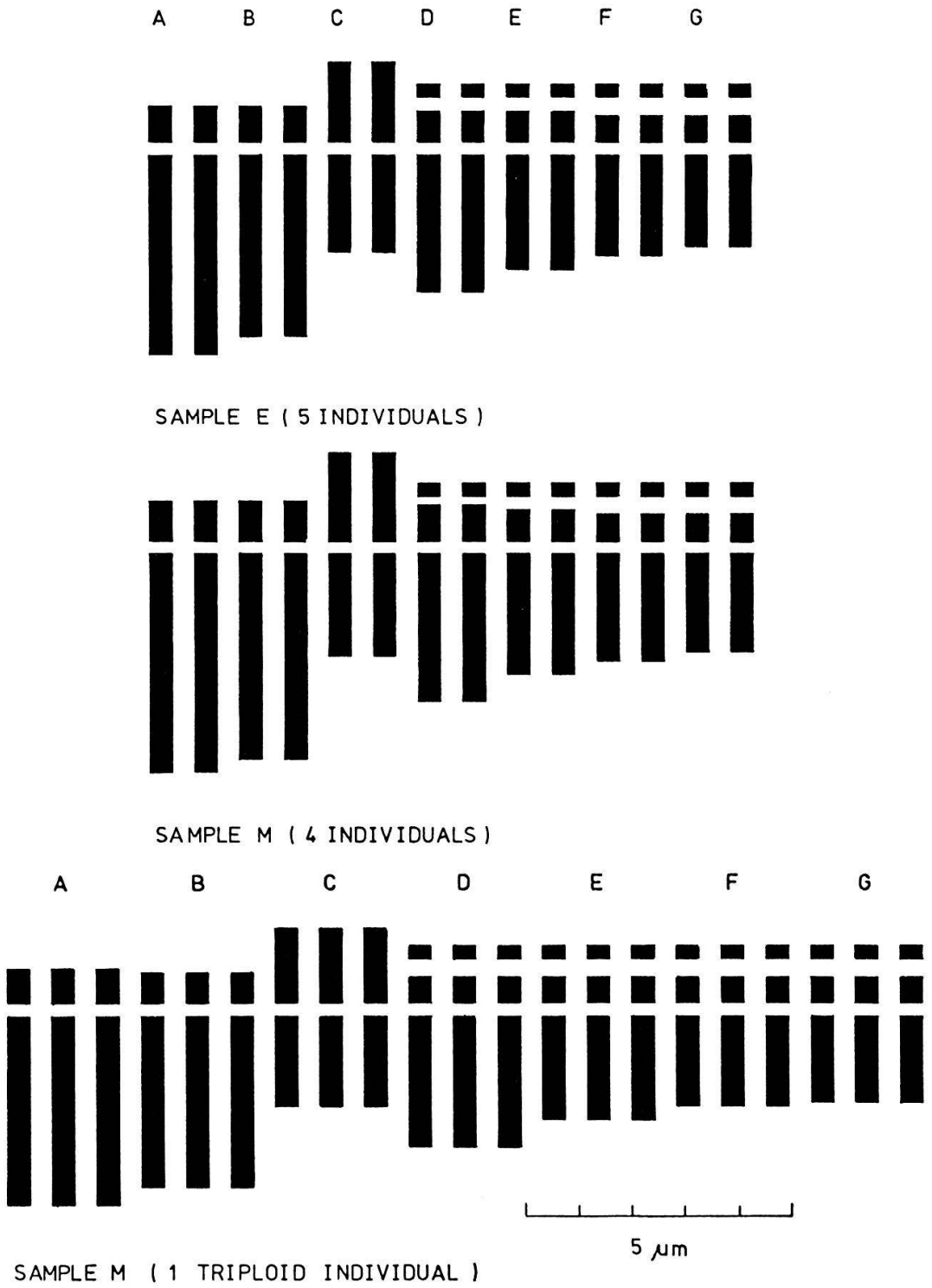


Fig. 7. Chromosome complements in *Leontodon hispidus* s. l.

Table 9. Chromosome morphology

Mean arm length (sa = short arms; la = long arms) and standard deviations in units of 0.336 µm			
Chromosome pair		Complement E (5 individuals)	Complement M (4 individuals
A	s.a.	2.05 ± 0.23	2.27 ± 0.32
	l.a.	11.14 ± 0.44	12.27 ± 0.49
B	s.a.	1.97 ± 0.20	2.15 ± 0.32
	l.a.	10.37 ± 0.42	11.43 ± 0.46
C	s.a.	4.60 ± 0.33	5.00 ± 0.36
	l.a.	5.38 ± 0.32	5.87 ± 0.41
D	s.a.	1.84 ± 0.21	1.94 ± 0.24
	l.a.	7.73 ± 0.51	8.34 ± 0.45
E	s.a.	1.73 ± 0.22	1.70 ± 0.24
	l.a.	6.42 ± 0.36	6.78 ± 0.43
F	s.a.	1.58 ± 0.22	1.62 ± 0.20
	l.a.	5.73 ± 0.30	5.96 ± 0.28
G	s.a.	1.60 ± 0.20	1.60 ± 0.18
	l.a.	5.18 ± 0.30	5.44.± 0.28

Relative arm length (length arm/total karyotype length)					Ratio short arm/long arm		
Chromosome pair		E	M	Data of FINCH (1967)*	E	M	Data of FINCH (1967)*
A	s.a.	1.5	1.6	1.6	0.18	0.19	0.21
	l.a.	8.3	8.5	7.9			
B	s.a.	1.5	1.5	1.6	0.19	0.19	0.21
	l.a.	7.7	7.9	7.8			
C	s.a.	3.4	3.5	3.5	0.86	0.85	0.83
	l.a	4.0	4.1	4.2			
D	s.a.	1.4	1.4	1.5	0.24	0.23	0.26
	l.a.	5.8.	5.8	5.9			
E	s.a.	1.3	1.2	1.3	0.27	0.25	0.29
	l.a.	4.8	4.7	4.5			
F	s.a.	1.2	1.1	1.2	0.28	0.27	0.28
	l.a.	4.3	4.1	4.1			
G	s.a.	1.2	1.1	1.0	0.31	0.29	0.25
	l.a.	3.9	3.8	3.8			

* FINCH's data are derived from his general idiogram

lite frequencies were similar for both investigated samples (table 10). In agreement with FINCH's observation, satellites were confined to the four shorter subacrocentric pairs (D, E, F and G). They seem to be more frequent in the shorter pairs. The varying visibility of satellites might be attributed to the preparation technique.

The variation range of short arms of the SAT-chromosomes was about as large as their own size, viz. 1.5 - 2.0 mm on the drawings, corresponding with 0.50 - 0.67 µm. This variation was remarkably related to the variation in satellite visibility (satellited arms are generally shorter). In table 9 the average short arm length of SAT-chromosomes is based only on satellited short arms. The variation in longer arms might be attributed to interindividual differences in the metaphase contraction stage.

Arm ratios proved to be rather unreliable for homologue identification because of the small dimensions of the short arms. The two pairs of longer subacrocentric chromosomes (A and B) as well as the four pairs of shorter subacrocentric SAT-chromosomes (D, E, F and G) accordingly appeared to be indistinguishable. The increase of the ratio: short/long arm from the longer to the shorter SAT-pairs was related to the progressive length decrease of the long arm. Since the variation ranges of long arm length were overlapping, the three shortest SAT-pairs might be identical in morphology. In contrast, the long arm length distribution of the longest SAT-pair suggest its distinct morphology.

None of the data obtained in the present study give some indications for discontinuous variation in chromosome morphology within or between samples E and M. A superficial check on populations M, BOP, TOT and SCHI by means of the single metaphase drawings from 12, 12, 11 and 5 individuals respectively, did not reveal any remarkable deviation either: a general chromosome morphology in the *hyoseroides* variety might be identical with that of the grassland varieties. Deviating earlier descriptions might represent rare exceptions without ecological significance.

Table 10. Percentage occurrence of satellites

Chromosome	Sample E	Sample M
D	44	35
E	50	49
F	69	70
G	70	69

5. Reproductive behaviour

5.1. *Seed setting*

Plants from populations M, BO, CA, E, WO and PAR were submitted to selfings and crosses in order to gain insight into their breeding behaviour and to check on the possible sterility barriers. Five plants each from the populations E and M were left in the garden for an open pollination.

Forced crosses and both free as well as forced selfings were carried out in the greenhouse and climatic chamber. Selfed flowers were isolated with aseptic gauze bags. Cross-populations were performed by brushing reciprocally two flower heads each 24 hrs at noon over the whole or pratically the whole period (up to maximal 5 days) of flowering. The flower heads were subsequently isolated. A practical problem with some influence on the seed setting percentage was raised by the fact that two flower heads, which one decided to cross, did not always open and wither on the same day. As a result, the achenes in the centre of the delayed flower head were sometimes not pollinized by the partner flower head giving rise to a centered spot of empty seeds.

The flowering period in the garden ranged from two up to eight days, varying between three and six days for most of the plants. The shorter flowering periods coincided with sunny weather, whereas cool, cloudy or rainy days coincided with the longer periods. Most flower heads with a seed set-

ting higher than 50 % flowered on either sunny, or lightly clouded, periodically sunny days, whereas heads with lower seed output flowered on cloudy, cool or rainy days. Apart from diminutive *Staphylinidae*, the predominant insect-visitors were syrphid flies. The shortest seed ripening period with the garden plants was 21 days. It corresponded to the average duration of the ripening period in the greenhouse. The seed output from open pollinations was generally lower than that resulting from the forced crosses. Average seed setting of 4 individuals each from populations E and M amounted to 38 and 50, respectively. The average values were taken from the average values per individual.

In general, free-selfed flower heads did not develop and their distinct shrinking began about nine days after the opening of the flower head, the processus being completed in about 15 days.

Most of the ripened fruit heads developing after cross-pollination (30 against 39, 77 %) opened in the period of 18 - 22 days after the first day of flowering.All fruit heads except one opened in the period of 16 - 24 days.

The average seed setting of forced crosses was of 52.8 % for 30 E-heads and of 54.9 % for 28 M-heads. The average seed setting of free selfings was nil for 21 E-heads and of 2.0 % for 31 M-heads; the relatively high value for sample M is due to a self-compatible individual with seed output of 30 %, obtained from free selfings. Average seed setting in forced selfings between various heads of the same individual was of 5.8 % for 28 E-heads and 18.9 % for 26 M-heads. The relatively high seed setting percentages of forced selfings result from the behaviour of three E- and four M-individuals with a nil seed setting in free selfings and average seed settings of 19.2 % and 29.6 %, respectively, in forced selfings. The highest seed setting observed in forced selfings, with an average value of 89 % (!, 4 heads), occurred in an apparently self-compatible M-individual.

Seed setting percentages of the intrapopulation crosses in population samples BOP, CA, WO and PAR range from nil (7 heads) to 91 % over a total of 30 heads. In these populations the average seed setting resulting from free selfings (28 heads) was of 0.8 %, whereas the average seed setting

Table 11. Seed output and development of seedlings.
A = Selfings; B = Intrapopulational crosses; C = Interpopulational crosses.

	Cross	Seed setting %	Age of seeds (months)	Germination %	Number of seeds	Seedling viability %	Number of seedlings %	Fertility %
A	E 10 (4 heads)	32	8	100	42	88	31	28
	M 11 (4 heads)	89	8	24	42	100	8	21
B	M20xM14	81	8	77	26	100	14	60
	scar.			70	10			
	M24xM29	56	8	85	26	89	18	39
	scar.			70	10			
	M29xM24	64	8	70	10	44	9	24
	scar.			100	10			
	E22xE4	59	3	100	26	100	17	56
	scar.			90	10			
	E25xE10	67	3	95	21	100	16	65
	scar.			100	10			
	E26xE15	62	3	100	21	90	10	53
	scar.			90	10			
	E13xE14	55	3	100	21	94	18	50
	E14xE13	49		100	21	100	18	
	BOP5xBOP6	26		71	21	100	14	18
	BOP6xBOP5	36		47	17	100	9	
	CA2xCA4	53	3	90	21	100	18	49
	CA4xCA2	80		57	21	100	12	
	PAR7xPAR8	62		76	21	100	14	44
	PAR8xPAR7	79		48	21	100	11	
C	M7xE13	91	8	96	26	100	18	89
	scar.			100	10			
	M11xE18	96	8	69	26	75	12	57
	scar.			90	10			
	E19xM19	58	8	100	25	100	13	58
	scar.			100	10			
	E14xBOP5	62	3	90	21	100	17	41
	BOP5xE14*	25		100	21	100	17	
	CA3xE3	16	3	100	21	94	18	15
	M9xBOP6	67	3	85	20	94	16	25
	BOP6xM9*	24		29	17	100	5	
	M4xCA4	94	3	86	21	100	17	62
	CA4xM4	79		57	21	100	12	
	BOP5xCA5	78	3	57	21	100	12	39
	CA5xBOP5	36		81	21	100	17	
	Mean fertility (%) in intrapopulation crosses (14 cross combinations of which 8 reciprocal)							46
	Mean fertility (%) in interpopulation crosses (12 cross combinations of which 8 reciprocal)							48

* = very small seeds
scar. = scarificated seeds

in forced selfings (30 heads) was of 2.2 %. The residual percentage in free selfings mainly resulted from a self-compatible individual with a seed setting of 20 %. This individual produced as well 32 % of seeds in the forced selfings which represent the highest percentage obtained in these experiments.

The highest seed setting of the interpopulation crosses (26 heads) was of 94 %, the average value percentage amounting to 48 %.

It can be concluded that the investigated population samples are mainly outcrossing and panmixous. The more intensively investigated populations E and M show a comparable reproductive behaviour. The results of the present experiments agree with the data of ROUSI (1973), who found no seed setting after free selfings and concluded that autonomous apomixis might be ruled out. The major part of this material was self-incompatible. The average seed setting upon crossing was relatively low, which ROUSI mainly contributed to incompatible cross combinations.

5.2. *Seed germination*

Three-and eight-month-old seeds from various experiments were water-soaked over 12 hrs and transferred onto wet blotting paper in Petri-dishes. The Petri-dishes were left in the dark at room temperature (+/- 20°C).

First germinations occurred in about four days after soaking of the seeds; most seeds germinated within 10 days after water soak-up. In general, germination was good (table 11), seeds which were scarificated by partial dissection of the seed coat, behaving similarly to the unscarificated ones. The age of the seeds did not seem to have any noticeable effect on germination.

Over-all germination percentages of the interpopulation crosses were somewhat higher than those of the intrapopulation crosses (85 vs. 81 %, table 11). Only one interpopulation cross showed a relatively low germination (29 %). Seeds from this cross were markedly small. The reciprocal cross combination had a higher seed setting (67 %), a normal seed size and germination. The germination percentages of the two investigated selfings differed

strikingly (table 11). The individual M 11 appeared to be more self-incompatible than could be expected on account of seed setting percentages, the average of two reciprocal selfings being 89 % (4 heads).On the contrary, the other self-compatible individual, viz. E 10, in which seed setting was considerably lower (32 %), showed a germination percentage of 100 %.

5.3. *Development of seedlings*

To check on seedling viability, up to 18 germinated seeds per strain were planted in soil and grown in a climatic chamber (dry temperature at day: 17°C, at night 10°C; day length 16 hrs.; 13'000 Lux., relative air humidity 70 %).

Seedling viability, defined as the percentage of germinated seeds which developed further, was very high in nearly all crosses, its average being 95 % (table 11).

Up to 10 seedlings that germinated within a four-day-interval, were potted separately and grown in the climatic chamber. The rate of development was expressed by the duration of the period from germination, +/- two days, until the stage of five leaves was reached. The offspring of various grassland populations obtained from both intra- and interpopulational crosses showed the shorter duration of development (42 days or less) than the offspring of *L. hyoseroides* (43 days or more). Exceptionally slow development was observed in the seedlings originating from a cross between M 29 and M 24 as well as the selfing M 11. All seedlings from selfing M 11 had wrinkled leaves,which did not unfold entirely. It seems plausible, that the relatively slow development of *L. hyoseroides* might be related to its longer leaves: the average length of the longest leaf per seedling in the five-leaf-stage was between 37 and 58 mm for 4 M-strains, between 75 and 108 mm for 6 E-strains and between 41 and 70 mm for 6 E x M-strains. The *L. hyoseroides* sample PAR 670 mm) corresponded roughly to the sample E, whereas the grassland strains from samples BOP and CA again had shorter leaves of 60 and 49 mm, respectively.

The obtained data indicate that growth rate of seedlings is not im-

Table 12. Pollen size variation in parents and F_1-plants (values of pollen size in arbitrary units*; 50 - 80 grains measured in each sample).
A = Parents; B = Selfings; C = Intrapopulational crosses; D = Interpopulational crosses.

		3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5
A	E 10			3.7	40.7	48.1	7.4											
	E 13			1.9	23.1	71.2	3.8											
	E 14								76.5	23.5								
	E 19					3.8	1.9	11.5	67.3	15.4								
	M 4					1.9	3.8	21.2	69.2	3.8								
	M 7				1.9		3.8	11.3	75.5	7.5								
	M 9							11.7	68.5	20.4								
	M 11				29.4	54.9	13.7			2.0								
	M 19							9.6	65.4	23.1	1.9							
	BOP 5							2.0	82.4	15.7								
	CA 4							13.5	86.5									
B	E 10 S_1	1.4	4.1	6.8	8.2	12.3	41.1	12.3	5.5	1.4	4.1			1.4	1.4			
	E 10 S_2			3.8		1.9	37.7	23.1	9.6			3.8						
	M 11 S_1			3.0	13.4	3.0	9.0	14.9	40.3	1.5		1.5		1.5	3.0	3.0		6.0
	M 11 S_2			2.5	8.8	1.3	11.3	25.0	27.5	6.3	2.5	3.8		10.0				1.3
C	E 13 x E 14		1.9				35.2	50.0	73.0									
	E 25 x E 15			4.6	15.4	9.2	10.8	7.7	6.2	16.9	18.5	7.7		3.1				
	BOP6 x BOP5			3.6		5.4	53.6	30.4	7.1									
D	M 11 x E 18(1)			8.5	5.1	15.3	20.3	25.4	23.7	1.7								
	M 11 x E 18(2)			1.9	1.9	1.9	11.3	41.5	32.1	9.4								
	M 11 x E 18(3)			3.4	16.9	15.3	20.3	27.1	16.9									
	M 7 x E 13				5.1	3.4	42.4	40.7	6.8	1.7								
	M 19 x M 19			1.6	9.7	9.7	16.1	21.0	32.3	6.5								
	E 14 x BOP 5				4.0		14.0	50.0	30.0	2.0								
	BOP 5 x E 14				1.8	1.8	1.8	14.3	62.5	14.3	1.8			1.8				
	M 4 x CA 4			1.9	3.8	1.9	9.4	28.3	52.8	1.9								
	CA 4 x M 4			3.3	11.5	8.2	21.3	21.3	29.5	4.9								
	M 9 x BOP 6			4.3	5.7	5.7	8.6	7.1	38.6	25.7	4.3							

* 1,0 = 4,2 mm

peded by hybridizations. Checks performed on both seed germination and seedling development show that, in general, seed setting percentages can be used as a good measure for fertility.

6. Effect of hybridizations on pollen fertility

Pollen development was studied on three levels: a) intraindividual variation; b) variation between the individuals of a given strain and c) variation between strains. The results of measurements are presented in table 12.

a) The differences in the percentage of a well-developed pollen between two flower heads each per individual, determined for 25 individuals, ranged from 0 to 32 %, their average being 8.2 %.

b) Variation between the individuals of a strain. Percentages of well developed pollen were determined in each 4 - 6 individuals from 25 strains. The maximal difference between these percentages per strain ranged from 0 to 97 %, its average being 27 %; this wide range of variation within a given strain indicates that pollen development can be influenced by recombination factors. It should be added that the extent of variation was similar in hybrids between various populations as well as intrapopulation crosses.

c) Variation between various strains. Average percentages of well-developed pollen for the various hybridogenous strains, the strains from intrapopulation crosses and those from selfings ranged from 76 to 99 %, from 69 to more than 99 % and from 81 to 91 %, respectively. Apparently there is no decrease in percentage of well-developed pollen in both hybrids and offspring from selfings. Clumping and translucent pollen was observed only in a single hybrid cross.

Noticeable differences in the size variation of the well-developed pollen were observed in various individuals (tables 12, 13). It is interesting to note that wide variation ranges appeared to occur more frequently

Table 13. Percentage of sound-looking pollen grains and mean values of pollen diameter with standard deviations (arbitrary units).

Parents	%	Mean Ø and stand. dev.	F_1-plants	%	Mean Ø and stand. dev.
E 13*	78	5.63 ± 0.27	E 13 x E 14	97	6.59 ± 0.46
E 14	96	7.37 ± 0.21			
	87	6.50 ± 0.24		97	6.59 ± 0.46
E 14	96	7.37 ± 0.21	E 14 x B 5b	95	6.79 ± 0.47
BOP5	99	7.32 ± 0.20	BOP5 x E 14	98	7.22 ± 0.54
	98	7.35 ± 0.33		97	7.01 ± 0.51
E 19	91	7.19 ± 0.42	E 19 x M 19	89	6.70 ± 0.88
M 19	97	7.34 ± 0.31			
	94	7.27 ± 0.37		89	6.70 ± 0.88
M 4	93	7.10 ± 0.35	M 4 x CA 4	76	6.87 ± 0.59
CA 4	>99	7.18 ± 0.17	CA 4 x M 4	93	6.52 ± 0.78
	96	7.14 ± 0.26		85	6.70 ± 0.69
M 9	98	7.30 ± 0.28	M 9 x BOP6	78	6.99 ± 0.88
BOP6		not measured			
	98	7.30 ± 0.28		78	6.99 ± 0.88
E 10*	98	5.55 ± 0.34	E 10 S_1,5	81	6.20 ± 1.05
E 13*	78	5.63 ± 0.27	E 10 S_2,1	91	6.49 ± 0.66
M 11*	>99	5.71 ± 0.43	M 11 S_1,1	81	7.16 ± 1.57
			M 11 S_2,3	90	7.12 ± 1.20
	92	5.63 ± 0.35			

* abnormally small-sized flower heads

individuals obtained from selfings and interpopulational hybridizations than those obtained from intrapopulation crosses. Small-sized pollen grains were most frequently found both in the self-compatible individuals as well as in their offspring, whereas the finds of abnormally large-sized pollen grains were mainly restricted to the latter ones. Incidentally, the lowest modal values of pollen size were observed in three individuals with small heads. Two of these were self-compatible plants (table 12).

7. Discussion

Leontodon hispidus L. s. l. is a remarkably variable taxon. The over-all picture of variation shows a wide intrapopulational variation and large interpopulational overlappings, apparently due both to genotypical as well as phenotypical factors. As a result, taxonomical treatment of the group is very difficult and some diagnostic characters that were formerly used, do not appear to be reliable.

No differentiation could be observed between the few investigated grassland populations of the Swiss Plateau, belonging to plant communities such as Molinion, Arrhenatherion and Bromion. *L. hispidus* var. *glabratus* (Koch) Bischoff is exemplary: apart from its glabrousness the taxon is not well-defined. Hairless plants corresponding to this taxon occur side by side with hairy individuals. The long, dentate leaves, which characterized the investigated material, tended to lose their typical shape under culture conditions. Some more characters, e.g. hair density and hair length occured in haired grassland populations. However, the range of variation within the grassland samples was so wide that large overlappings occurred between them. Slight interpopulational, possibly geographical, differentiation was observed only in modal ray number of hairs.

More distinct interpopulational differentiation was found in the thickness of leaves. Differences between both wild and cultivated samples corresponded to the *L. hyoseroides* samples on the one hand (thick leaves)

and the grassland samples on the other hand (thin leaves). In some thick leaves a double layer of palissade parenchym was observed. However, this character is not of absolute validity, high degree of phenotypical variation being observed.

The investigated populations of *L. hyoseroides* inhabit scree habitats, often characterized by extreme or extremely changing microclimatic factors, viz. heat, including radiation and drought (FABIJANOWSKI 1950; DUVIGNEAUD et al. 1970). The thick leaves of *L. hyoseroides* might therefore have an adaptive value for such open stations, whereas the thin, drought-sensitive leaves occurring in the grassland forms might be adaptive for the relatively temperate microclimate of more closed vegetations. Hairiness might have a similar adaptive background; this problem, however, requires a detailed eco-physiological investigation.

Cytological differentiation in *L. hispidus* L. s. l. apparently is limited. The occurrence of autotriploids seems to be incidental (FINCH 1967; the present study). The triploids studied in the course of the present investigation produced abnormally long seeds. It should be noted that no other morphological differences were observed. Remarkably divergent karyotypes were reported by BERGMAN (1935), ELLIOT (1950), GUINOCHET and LOGEOIS (1962) and SKALINSKA et al. (1964). On the other hand, FINCH (1967) reported that variation in this material was too rare to constitute polymorphism. The results of the present investigation stay in agreement with FINCH's observations, for no significant distinctions were revealed between the diploid karyotypes of a *hyoseroides* and a grassland sample.

The described patterns of variation suggest that ecological-morphological differentiation in *L. hispidus* L. s. l. is rather unadvanced. The species is predominately outcrossing (ROUSI 1973; the present study). Observations on experimental hybrids suggest that the intrapopulational variation might be due, at least partly, to a continuous gene exchange between populations, in particular those from anthropogenous habitats, which are ecologically not well-isolated.

The present state of knowledge of the *L. hispidus* group lacks a sufficient geographical scope. The present study had a preliminary character and was confined to a few small population samples, mostly from anthropo-

genous habitats. A clear insight into the taxonomical rank of taxa like *hyseroides* or *pseudocrispus* might only be obtained by more intensive ecological and genetical investigations. Numerous morphological characters of the *L. hispidus* group overlap with related species of the genus *Leontodon*. Some experimental data indicate that the genetical differences between various species are not sharply defined even when divergences in chromosome morphology are distinct (FINCH 1967); further studies in this subject are required.

Summary

The present study deals with variation on some Swiss population samples of *L. hispidus* L. s. l. from various habitats. The samples appeared to be closely similar in morphology and highly variable. Plants from scree habitats, identificated as *L. hyoseroides* Welwitsch were, by their thicker leaves, mostly well-distinguishable from individuals growing in anthropogenous grassland habitats. No distinction could be observed between the karyotype of a grassland variety of *L. hispidus* L. and that of *L. hyoseroides* Welwitsch. The investigated material was predominantly outcrossing and panmixous.

The present observations suggest that ecological-morphological differentiation in *L. hispidus* L. s. l. is rather unadvanced, no pronounced barriers to gene exchange occurring in the studied material.

Zusammenfassung

Die morphologische und zytologische Variationsbreite einiger schweizerischer Populationen von *Leontodon hispidus* s.l. aus verschiedenen Pflanzengesellschaften wurden untersucht. Die Variationen innerhalb der Populationen erwiesen sich als sehr gross, während die Unterschiede zwischen den Populationen oft gering waren. Pflanzen von Schuttgesellschaften, die morphologisch mit *L. hyoseroides* Welwitsch übereinstimmen, konnten vor allem durch die dickeren Blätter von Pflanzen aus bewirtschafteten Wiesen und Weiden abgetrennt werden. Der Karyotyp dieser Pflanzen lässt sich indessen nicht unterscheiden. Die untersuchten Pflanzen waren vorwiegend fremdbestäubend. Die vorliegenden Beobachtungen deuten an, dass die ökologisch-morphologische Differenzierung innerhalb von *L. hispidus* s.l. noch nicht sehr weit fortgeschritten ist. Es konnten keine Genaustauschbarrieren im untersuchten Material festgestellt werden.

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