Drawings of Scandinavian Plants 81–100

Chenopodium L.

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The drawings of the genus *Chenopodium* comprise 20 species occurring in Scandinavia. They represent indigenous as well as introduced species and only those which have been reported occasionally only have been omitted. Such species are: *C. aristatum* L. of sect. *Botryoides* C. A. MEY.; *C. anthelminticum* L. of sect. *Ambrina* BENTH. & HOOK.; *C. carinatum* R. BR., *C. cristatum* F. v. MUELL., *C. pumilio* R. BR. of sect. *Orthosporum* R. BR.; *C. acuminatum* WILLD., *C. giganteum* DON., *C. karoi* (MURR.) AELL., *C. missouriense* AELL. and *C. probstii* AELL. of sect. *Chenopodium*. These species are discussed in detail by AELLEN (1960). A survey of the sections and taxa dealt with is given in Table 1.

CHROMOSOME NUMBER

Most species within the genus *Chenopodium* are diploid and/or tetraploid with the basic number x=9. But in addition x=8 has been occasionally observed, e.g. in *C. capitatum* and *C. botrys*. Intraspecific variation is particularly pronounced in *C. opulifolium, C. strictum* and *C. album* (all having 2n=18, 36, 54), but also within *C. ficifolium* and *C. urbicum* (2n=18, 36), *C. capitatum* and *C. botrys* (2n=16, 18). The chromosome number seems to be of very little taxonomic significance.

MORPHOLOGICAL CHARACTERS

Several species are highly polymorphic and some particular characters such as habit, height, degree of branching and size of leaves show intraspecific variation. This high degree of variation is at least partly due to modification and consequently most vegetative characters are of limited taxonomical value. The most useful characters in the delimitation of taxa are: duration (annual v. perennial); type and degree of hairiness (glandular, yellowish hairs v. farinaceous on leaves, axis of inflorescence and perianth); the general appearance of lower leaves; type of inflorescence; appearance of perianth; position of the seed within the perianth (horizontal v. vertical); seed size; seed margin (obtuse v. acute); sculpturing of the testa (see below); shape of embryo (annular v. horseshoe-shaped).

SCULPTURING OF TESTA

In the delimitation of sections, subsections and species special attention has been paid to the sculpturing of the testa (cf. AELLEN 1960), a character which has been adopted in most modern floras. But, as was already pointed out by COLE (1961) and JÖRGENSEN (1973), it is not advisable to base taxonomy at higher levels on this character only. Ripe seeds are usually needed to be able to identify the pattern of sculpturing with certainty and, more-

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[1] ENGSTRAND is responsible for the drawings and GUSTAFSSON for the text.

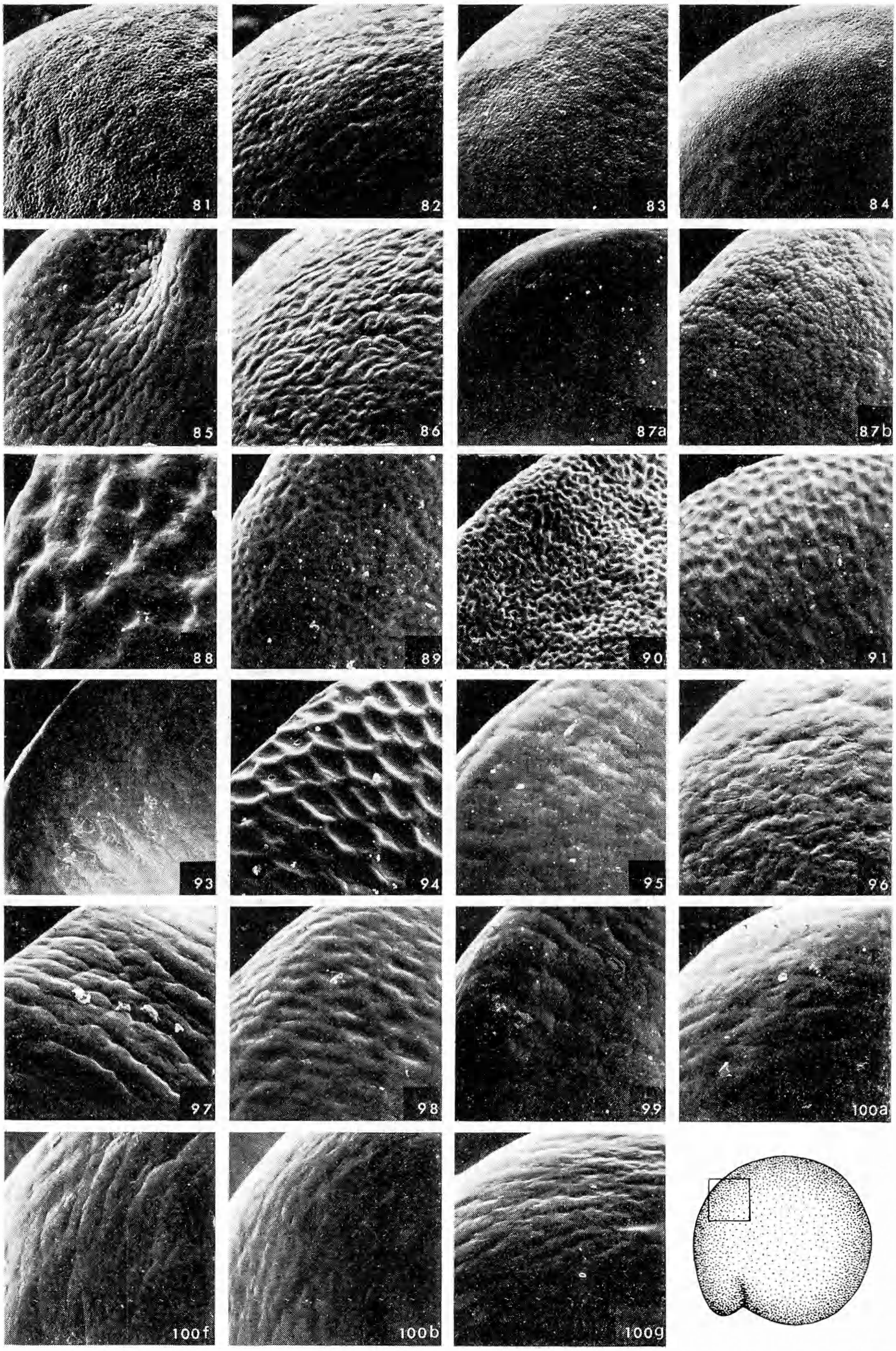
Table 1. A survey of taxa dealt with and their chromosome numbers.

Bot. Not. volume	Section	Drawing no.	Species	Chromosome number
125: 283—286	*Eublitum*	81	*C. capitatum*	2n=16, 18.
		82	*C. foliosum*	2n=18.
126: 1—6	*Pseudoblitum*	83	*C. glaucum*	2n=18.
		84	*C. rubrum*	2n=36.
	Degenia	85	*C. botryodes*	2n=18.
126: 135—141	*Agathophyton*	86	*C. bonus-henricus*	2n=36.
	Botryoides	87	*C. botrys*	2n=16, 18.
	Chenopodium	88	*C. hybridum*	2n=18.
126: 273—276		89	*C. polyspermum*	2n=18.
		90	*C. murale*	2n=18.
126: 393—397		91	*C. ficifolium*	2n=18, 36
		92	*C. hircinum*	2n=18.
		93	*C. vulvaria*	2n=18.
127: 1—6		94	*C. berlandieri*	2n=36.
		95	*C. urbicum*	2n=18, 36
		96	*C. pratericola*	2n=18.
127: 159—164		97	*C. opulifolium*	2n=18, 36, 54.
		98	*C. suecicum*	2n=18.
		99	*C. strictum*	2n=18, 36, 54.
127: 291—296		100	*C. album*	2n=18, 36, 54.

over, the more or less closely attached pericarp has to be removed.

The testa structure of the Scandinavian species of *Chenopodium* is illustrated in Plate 1. The SEM photos have been taken with a Cambridge Stereoscan Mark II: A at the EM Laboratory at the Institute of Zoology, University of Lund, Sweden. The origins of the species examined are listed at the end of this paper. Unfortunately, seeds from only one or two specimens of each taxon have been investigated and consequently little information is available concerning the degree of intraspecific variation. The following results have been obtained: Species of sect. *Eublitum* (*C. capitatum* and *C. foliosum*), sect. *Pseudoblitum* (*C. glaucum* and *C. rubrum*), sect. *Degenia* (*C. botryodes*) and sect. *Agathophyton* (*C. bonus-henricus*) all have a more or less smooth testa, only some irregular furrows are visible. In sect. *Botryoides, C. botrys* has a smooth testa, while in *C. schraderianum* it is reticulate. But the material is too limited to permit of drawing certain conclusions. Sect. *Chenopodium* is very variable in this respect. The sculpturing of the testa of *C. hybridum* is formed by large, deep, orbicular pits, that of *C. suecicum* by rather large, shallow, oblong pits radially arranged, and that of *C. murale* by minute pits. *C. polyspermum* has a reticulate pattern of sculpturing, consisting of irregular ridges. Testa with hex-

Plate 1. SEM photos of seeds of Scandinavian *Chenopodium* species showing the testa structure within the framed area. The numbers of the photos correspond to the numbers of the drawings. — 81: *C. capitatum* (L.) Asch. — 82: *C. foliosum* (Moench.) Asch. — 83: *C. glaucum* L. — 84: *C. rubrum* L. — 85: *C. botryodes* Sm. — 86: *C. bonus-henricus* L. — 87 a: *C. botrys* L. — 87 b: *C. schraderianum* Roem. & Schult. — 88: *C. hybridum* L. — 89: *C. polyspermum* L. — 90: *C. murale* L. — 91: *C. ficifolium* Sm. — 93: *C. vulvaria* L. — 94: *C. berlandieri* Moq. ssp. *zschackei* (J. Murr.) Zobel. — 95: *C. urbicum* L. — 96: *C. pratericola* Rydb. — 97: *C. opulifolium* Schrad. — 98: *C. suecicum* J. Murr. — 99: *C. strictum* Roth. — 100 a: *C. album* L. ssp. *album*. — 100 f: ssp. *fallax* Aell. 100 b: ssp. *microphyllum* (Boenningh.) Sterner. — 100 g: ssp. *virgatum* (Thunb.) Blom. — All photos ×120.


81
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87a
87b
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95
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97
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100a
100f
100b
100g

Plate 1.

agonal pits are present in *C. ficifolium, C. hircinum* (not illustrated) and *C. berlandieri*. The hexagonal pits of *C. berlandieri* are rather large and regular in shape, forming a honeycomb-like pattern. In *C. ficifolium* and *C. hircinum* the pits are more irregular, somewhat oblong, smaller and not as distinct as in *C. berlandieri*. The testa of the other species (*C. vulvaria, C. urbicum, C. pratericola, C. opulifolium, C. strictum* and *C. album*) are smooth to irregularly furrowed. Thus, it seems likely that the testa of *C. hybridum, C. polyspermum, C. murale, C. ficifolium, C. hircinum, C. berlandieri* and *C. suecicum* respectively have a very distinct pattern of sculpturing, distinguishable from that of other species.

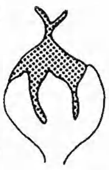
HYBRIDIZATION

The extent of hybridization and introgression in the genus *Chenopodium* is rather uncertain, as a number of suspected hybrids have been reported but their hybrid origin has rarely been proved. According to AELLEN (1960) it is true at least that hybridization between species native to Europe is rare, and hybrid derivatives occur only occasionally. But very little is known about reproductive isolation and interspecific crossing barriers within the genus. Moreover, the extent and nature of such barriers can hardly be tested by crossing experiments, as emasculation is very difficult to perform. The following hybrids have been reported from Scandinavia, but their status is uncertain: *C. album*×*C. berlandieri, C. album*×*C. borbasioides, C. album*×*C. ficifolium, C. album*×*C. hircinum, C. album*×*C. opulifolium, C. berlandieri*×*C. hircinum, C. berlandieri*×*C. suecicum, C. carinatum*×*C. cristatum, C. ficifolium*×*C. suecicum, C. hybridum*×*C. polyspermum* and *C. opulifolium*×*C. suecicum.*

KEY

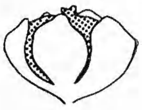
1\. Plant with yellow or amber-coloured glands or glandular hairs, not farinose .... Key A

Plant glabrous or whitely farinose, eglandular 2

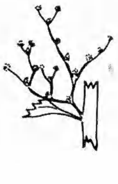


2\. Seeds mainly vertical, in terminal flowers sometimes horizontal (vertical seeds rarer in *C. glaucum*) .... Key B

All seeds horizontal .... Key C



KEY A



1\. Inflorescence composed of distinct, but sometimes small dichasial cymes 2

Inflorescence composed of small sessile clusters of flowers, not in distinct dichasial cymes 3

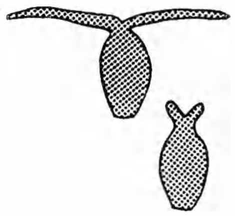
2\. Perianth lobes obtuse on the back, with sessile to shortly stalked glandular hairs. Seeds 0.5—0.8 mm in diameter .... 87. *C. botrys*

Perianth lobes with a conspicuous longitudinal keel on the back, with exclusively sessile glands. Seeds 0.7—0.8 mm in diameter .... 87. *C. schraderianum*

3\. Lower leaves mostly lanceolate, entire to dentate, rarely laciniate. Perianth lobes free to one half .... 87. *C. ambrosioides*

Lower leaves usually pinnatifid. Perianth lobes united near to apex, forming a net-veined sac entirely enclosing the seed 87. *C. multifidum*

KEY B

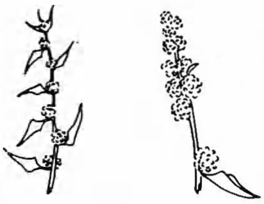


1. Perennial, with a thick and woody root. Stigmas long, more than 0.8 mm. Seeds exceeding 1.5 mm in diameter ...... 86. *C. bonus-henricus*

Annual, ± slender root. Stigmas short, less than 0.8 mm. Seeds less than 1.5 mm in diameter 2

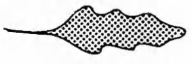
2. Flowers in dense berry-like, sessile cymes. Perianth red and fleshy at maturity 3

Cymes usually in branched panicles, not berry-like. Perianth not fleshy at maturity 4



3. Cymes all bracteate. Seeds 1.0—1.3 mm in diameter, obtuse in transection .... 82. *C. foliosum*

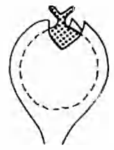
Upper cymes ebracteate. Seeds 0.8—1.0 mm in diameter, keeled in transection .... 81. *C. capitatum*



4. Lower leaves elliptical to lanceolate, sinuate to serrate, rarely subentire, conspicuously farinose and glaucous beneath .. 83. *C. glaucum*

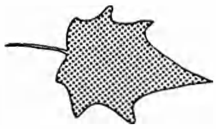
Lower leaves deltate to rhombic-ovate, dentate to entire, glabrous or sparsely farinose and green to red beneath 5

5. Perianth lobes of all flowers obtuse or scarcely keeled on the back, united at the most to one half .... 84. *C. rubrum*



Perianth lobes of lateral flowers distinctly keeled on the back, united almost to the apex, forming a sac entirely enclosing the seed (perianth lobes of terminal flowers united to at least one half) 85. *C. botryodes*

KEY C

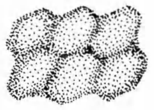


1. Lower leaves cordate to subtruncate at base, 3—5-angled. Seeds large, 1.5—2.0 mm in diameter .... 88. *C. hybridum*

Lower leaves not cordate at base, not 3—5-angled. Seeds less than 1.5 mm in diameter 2

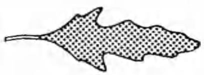
2. Surface of testa with large distinct pits forming honeycomb-like pattern 3

Surface of testa smooth or with sculpturing other than honeycomb-like 5

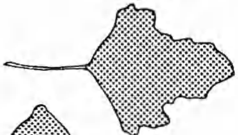


3. Lower leaves usually rhombic to ovate with a pair of prominent teeth below middle, or rarely 3-lobed with the midlobe broadly rounded. Testa with deep, large, regular hexagonal pits .... 94. *C. berlandieri*

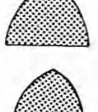
Lower leaves distinctly 3-lobed, with a distinct ± parallel-sided midlobe and large lateral lobes. Testa with shallower, smaller and radially elongated pits 4



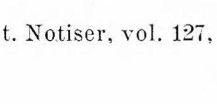
4. Lower leaves with an elongate midlobe, 2—3 times longer than the lateral lobes .... 91. *C. ficifolium*



Lower leaves with a short, broad midlobe as long as the lateral lobes .... 92. *C. hircinum*



5. Seeds with a distinctly keeled margin, surface of testa minutely and closely pitted. Margins of perianth lobes fringed ...... 90. *C. murale*

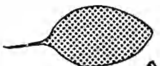


Seeds without a distinctly keeled margin, surface of testa smooth or with different types of sculpturing. Margins of perianth lobes entire .. 6

6. Axis of inflorescence and flowers glabrous or almost so 7

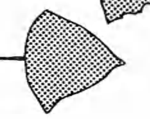
Axis of inflorescence and flowers white-farinose 8

7. Lower leaves ovate to suboblong, margins entire or rarely with two inconspicuous teeth, stem 4-angled .... 89. *C. polyspermum*



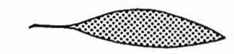
Lower leaves deltoid, dentate, stem not 4-angled .... 95. *C. urbicum*

8. Plant strongly farinose, smelling of decaying fish. Lower leaves ovate to broadly rhombic, entire or angled at the broadest part .... 93. *C. vulvaria*



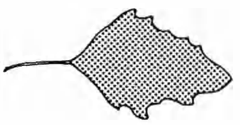
Plant ± farinose, not evil-smelling. Lower leaves of different shape, or ovate-rhombic with dentate to lobed margins 9

9. Plant greyish. Lower leaves narrowly elliptic to lanceolate, ± parallel-sided, only midvein and one pair of lateral veins distinct .... 96. *C. pratericola*



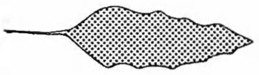
Plant usually greenish. Lower leaves with a midvein and several pairs of lateral veins arising above the base 10

10. Lower and middle leaves ± distinctly 3-lobed, as long as broad. Axis of inflorescence and flowers conspicuously grey-farinose (cf. *C. album* ssp. *album* var. *borbasii,* which has larger ± 3-lobed leaves, but moderately farinose inflorescence) .... 97. *C. opulifolium*



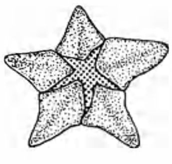
Lower and middle leaves usually ovate-rhombic to lanceolate, at least 1 1/2 times as long as broad. Axis of inflorescence and flowers moderately, rarely greyish, farinose 11

11. Lower leaves ovate to broadly oblong, with almost parallel margins, entire to sparsely toothed. Flowers in olive-green, pearl-like cymes, forming delicate, erect, spicate inflorescences (cf. *C. album* ssp. *microphyllum,* which has smaller, dentate to subentire, leaves, strongly farinose beneath and usually with convex margins) .. 99. *C. strictum*

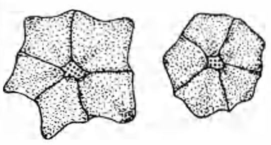


Lower leaves ovate-rhombic to lanceolate, margins usually convex and dentate, rarely entire, lowermost lateral teeth usually largest. Flowers in ± glaucous green cymes, forming a coarser often cymose inflorescence 12

12. Stem not red-striped. Lower leaves ovate to rhombic, often glaucous, margins dentate with acute, forward-pointing teeth. Perianth lobes sharply and narrowly keeled on the back. Margins of seeds usually obtuse, testa with radially situated shallow, gradually sloping, round—oblong pits .... 98. *C. suecicum*



Stem often red-striped. Leaves ovate-rhombic to lanceolate, mostly green, never glaucous, entire to dentate. Perianth lobes obtuse to somewhat keeled on the back. Margins of seeds usually acute, testa smooth, faintly furrowed or somewhat rugose .... 100. *C. album*



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COLE, M. J. 1961. Intraspecific relationship and specific variation of Chenopodium album L. in Britain. I. Taxonomic delimitation of the species. — Watsonia 5: 47—58.

JÖRGENSEN, P. M. 1973. The genus Chenopodium in Norway. — Norwegian Journ. Bot. 20: 303—319.

APPENDIX

Testa structure of the following specimens has been investigated (all preserved at LD):

C. capitatum: Sw. Stockholm, Södermalm. 1853. FR. BJÖRNSTRÖM.

C. foliosum: Sw. Skåne, Hörby. August 1924. H. NILSSON.

C. glaucum: Sw. Öland, Borgholm. 11.9. 1917. O. STERNVALL.

C. rubrum: Sw. Skåne, Glimåkra, Hörninge. 25.9.1951. T. NORLINDH.

C. botryodes: Denm. Fyn, Oxemose at Hofmansgave. August 1893. MÖLLER.

C. bonus-henricus: Sw. Öland, Vannborga. 17.7.1942. S. NORDENSTAM.

C. botrys: Sw. Stockholm, Beckholmen. 14.8. 1882. H. O. JUEL.

C. schraderianum: Denm. Sjælland, Snedinge. 1879. P. NIELSEN.

C. hybridum: Sw. Skåne, Malmö. 15.8.1931. G. NORRMAN.

C. polyspermum: Sw. Skåne, Lund. 16.8. 1905. E. RUNDKVIST.

C. murale: Sw. Skåne, Furulund. 29.9.1921. C. BLOM.

C. ficifolium: Sw. Skåne, Lund. 25.8.1928. F. H. ANDER.

C. vulvaria: Sw. Blekinge, Karlshamn. August 1905. Y. T. E. SVANLUND.

C. berlandieri ssp. *zschackei*: Schweitz, Basel, Strassenzug in Kleinhörningen. 24.9.1932. P. AELLEN.

C. urbicum: Sw. Skåne, Glimåkra, Färeköp. T. PERSSON.

C. pratericola: Sw. Skåne, Hälsingborg. 7.10. 1940. TH. LANGE.

C. opulifolium: Sw. Bohuslän, Nödinge, Bohus station. 10.9.1935. H. FRIES.

C. suecicum: Sw. Skåne, Lund. 30.8.1946. H. NILSSON.

C. strictum: Sw. Skåne, Malmö. 10.9.1922. C. BLOM.

C. album ssp. *album*: Sw. Göteborg, Backa nära Brunnsbo. 6.9.1948. C. BLOM.

C. album ssp. *fallax*: Sw. Göteborg, Gullbergs gärde. 6.9.1929. C. BLOM.

C. album ssp. *microphyllum*: Sw. Öland, Borgholm. 14.9.1917. O. STERNVALL.

C. album ssp. *microphyllum*: Sw. Gotland, Katthammarsvik. 25.8.1930. E. TH. FRIES.

C. album ssp. *virgatum*: Sw. Göteborg, Frölundaborg. 5.9.1932. C. BLOM.

Karyotypes and DNA Content in Species of Ranunculus L. and Related Genera

Dietrich Goepfert

GOEPFERT, D. 1974 12 30. Karyotypes and DNA content in species of Ranunculus L. and related genera. — Bot. Notiser 127: 464—489. Lund. ISSN 0006-8195.

Variation in chromosome number, karyotype composition, and nuclear DNA content as determined by cytophotometry, is analyzed in 18 subdivisions of the genus *Ranunculus* L., and in species of two related genera, *Ceratocephalus* PERS. and *Trautvetteria* FISCH. & MEY.

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INTRODUCTION

Ranunculus L. is a genus of herbaceous perennials and annuals from both hemispheres which is generally regarded as fairly highly derived. TAMURA (e.g., 1962a) considers it to be more derived than *Caltha* L., *Trollius* L., as well as *Callianthemum* C. A. M. The genus is large; recent regional accounts deal with some 240 species and recognize 26 distinct subgenera or sections (BENSON 1940, 1942, 1948, 1954; DAVIS 1960, 1965; FISHER 1965; LOURTEIG 1952, 1956; MAIRE 1964; OHWI 1965; OVCZINNIKOV 1937; TUTIN 1964). The world-wide account of DE CANDOLLE (1824) treats 159 species and classifies them in five sections.

FLOVIK (1936), COONEN (1939), NEVES (1944 a, 1944 b), GREGSON (1965), KURITA (1957—1966), KAPOOR and LÖVE (1970), and other authors, have demonstrated variation in chromosome number, karyotype proportions, and chromosome size, among species from the whole genus. LÖVE and LÖVE (1961 b) and KAPOOR and LÖVE (1970) suspect on cytotaxonomic grounds that a number of the commonly recognized subdivisions of *Ranunculus* may be better treated as distinct genera. The present study analyzes karyotype variation in species of 18 subdivisions of *Ranunculus*, and in two related genera, *Ceratocephalus* and *Trautvetteria*.

MATERIAL AND METHODS

Field collections and botanic garden accessions of some 100 species were established in greenhouses for cytological study. Vouchers are available in TRT. A representative selection of vouchers has been determined or verified by B. BOIVIN (North American material) and T. G. TUTIN (European material). Somatic chromosomes were drawn and measured at ×5,000 from Feulgen-stained root-tip squash preparations using colchicine pre-treatment (.15 %, 60 min.). Raw data for a total of 15,000 chromosomes were subjected to combinatorial karyotype analysis by an automated procedure (unpubl.) which employed (i) centromere position, (ii) chromosome length relative to total complement length, as primitive parameters. Diploid complements were treated as "2n" sets, polyploids, as *combinations* of 2n sets. Centromere position, i.e., chromosome arm ratio, is used for karyotype characterizations in the text; chromosomes are referred to as metacentrics (1.0—1.34), submetacentrics (1.35—1.99), and acrocentrics to facilitate karyotype description, however, this classification system played no role in the actual karyotype analysis.

Relative nuclear DNA content was determined by cytophotometry using the two-wavelength method and conversion tables of MENDELSOHN (1958), and the techniques of ROTH-

FELS et al. (1966). DNA content of any unknown sample was determined relative to that of a laboratory standard, an accession of *Anemone virginiana* L. with 4 C DNA content of 2.1×10^{-11} g.

Chromosome size comparisons between species were standardized using "plots" of DNA values on geometric scales. The following descriptive terms were adopted in the text: *large chromosomes,* 2n DNA values exceeding .8, *medium* .4, *small* .2, and *very small,* .1.

OBSERVATIONS

Table 1 gives information on ploidy, DNA content, complement length (CL), and relative chromosome length in percent of diploid complement length, for the species studied. Except for DNA content, the data represent single cells arbitrarily selected from several studied in each population and species. DNA values, however, represent replicate determinations, using three samples per population, 10 2 C and 10 4 C nuclei per sample, and generally pooled over two or three populations per species. Standard errors of the mean reflect what is, very largely, interpreted here as random experimental variation "between samples".

Chromosome numbers and provenances of the materials used are given in the text. The classification system of TUTIN (1964) was followed throughout, with some modifications, however, to accomodate non-European taxa. For reasons explained in the text, some of the subdivisions were broken into smaller units.

Ranunculus L.

Ranunculus subgenus **Ranunculus**

SECTION RANUNCULUS
SPECIES BASED ON x=7

R. velutinus TEN., 2n=14, 5 pops.; *R. constantinopolitanus* (DC.) D'URV., 2n=42, 3 pops.; *R. lanuginosus* L., 2n=28, 2 pops.; *R. sericeus* BKS. & SOL., 2n=14, Copenhagen BG; *R. baldshuanicus* RGL., 2n=14, 2 pops.; *R. acris* L., 2n=14, 15 pops. (Eur. BG); Ontario: Brooklin, 5 Oct. 1968; Toronto, 2 Oct. 1968; — ssp. *granatensis* (BOISS.) NYM., 2n=28, 2 pops.; — ssp. *strigulosus* (SCHUR) HYL., 2n=28, 1 pop.; *R. serbicus* VIS., 2n=28, 7 pops.; *R. laetus* WALL., 2n=28, LLOYD BG, Darjeeling (P. SARKAR 1971); *R. uncinatus* D. DON, 2n=28; British Columbia: Queen Charlotte Is, Moresby I, J. A. CALDER and R. A. TAYLOR 36259, 24 July 1964; Needles, C. & M. HEIMBURGER 2413, 20 Aug. 1967; McIntyre L, C&MH 2412, 24 Aug. 1967; Manning Park, C&MH 6675, 23 July 1972; Alberta: Coleman, C&MH, 16 Aug. 1967; *R. occidentalis* NUTT., 2n=28; British Columbia: Queen Charlotte Is, P. J. SCOTT 74, 8 June 1971; *R. californicus* BENTH., 2n=28; California: Sta. Inez Mts, Schofield Park, D. EMERY, Santa Barbara BG.

While most *Ranunculi* have chromosome numbers based on x=8, a second base number, x=7, characterizes some of the species of section *Echinella* (see below), and some of the species of section *Ranunculus.*

The species studied here are representative of the x=7 series, involving the *R. acris, R. sericeus,* and *R. velutinus* groups in Eurasia, and the *R. uncinatus* - *R. occidentalis* complexes in western North America. Species from these groups have very similar karyotypes, an observation easily verified from Table 1 if values for relative chromosome length in percent of CL, and corresponding centromere positions, are compared by reading the table vertically rather than horizontally. Fig. 1 illustrates the karyotype of *R. acris.* Similar karyotypes are seen in illustrations for *R. acris* by GREGSON (1965) or KURITA (1957 a). The karyotypes of *R. japonicus* THUNB. and *R. yakushimensis* (MAK.) MAS., as illustrated by KURITA (1957 a), show the same pattern.

Old World and New World members of the x=7 series differ in chromosome size. This is evident in DNA values, and it is reflected also in diploid complement length, as shown in Table 1. The European species studied are all in the medium size range, e.g., *R. acris* (DNA .525) in the lower medium range, *R. velutinus* (.649) in the upper medium range. North Ame-

Table 1. Relative amounts of nuclear DNA in terms of *Anemone virginiana* L. (=1.0), typical diploid complement lengths (CL) in μ, typical relative chromosome lengths (RCL) and corresponding centromere positions in the same cell, in species of *Ranunculus, Ceratocephalus,* and *Trautvetteria.* Information for three species marked with an asterisk (*) determined from karyotype illustrations of GREGSON (1965).

Ploidy/Species [1]		DNA	CL	RCL in % of CL								Centromere Position							
Ranunculus subgenus *Ranunculus*																			
Section *Ranunculus* (x=7): Haploid sets of *4* acro- *0* submeta- *3* metacentrics (type 4-0-3)																			
2n	*velutinus*	.649 ± .031	77	—	11	11	13	12	14	19	20	—	5.9	4.2	3.2	2.8	1.2	1.1	1.1
6n	*constantinopolitanus*	1.361 ± .053	71	—	11	11	12	12	17	18	19	—	4.9	3.6	2.8	2.6	1.2	1.1	1.1
			63	—	11	12	11	13	15	18	20	—	4.4	3.9	2.9	2.6	1.3	1.1	1.1
			53	—	11	12	12	14	14	16	19	—	6.8	3.6	3.1	2.3	1.3	1.1	1.1
4n	*lanuginosus*	1.056 ± .044	71	—	11	11	13	12	15	17	22	—	6.1	3.5	2.9	2.5	1.2	1.2	1.1
			58	—	11	12	13	14	14	16	19	—	5.2	2.8	2.7	2.4	1.3	1.2	1.1
2n	*acris* ssp. *acris*	.525 ± .006	69	—	11	11	12	12	14	18	20	—	4.3	3.7	2.6	2.3	1.2	1.1	1.1
	ssp. *borealis*	.501 ± .017	62	—	11	12	12	12	14	17	21	—	4.5	3.5	3.2	2.3	1.3	1.1	1.1
4n	ssp. *granatensis*	.874 ± .109	73	—	12	9	11	12	17	18	19	—	3.6	3.6	2.8	2.4	1.0	1.2	1.2
			56	—	12	11	12	14	15	16	20	—	3.9	3.5	3.0	2.6	1.2	1.2	1.1
	ssp. *strigulosus*		70	—	10	11	12	12	17	19	20	—	7.9	3.9	3.1	2.8	1.1	1.1	1.2
			58	—	11	12	13	13	14	18	21	—	6.2	4.6	3.6	2.8	1.3	1.3	1.1
	serbicus	.948 ± .022	73	—	11	10	12	12	16	19	20	—	5.3	3.9	3.1	2.6	1.2	1.1	1.1
			60	—	11	11	12	13	13	17	22	—	5.3	3.9	3.1	2.6	1.2	1.1	1.1
2n	*sericeus*	.437 ± .024	62	—	11	12	11	13	14	18	20	—	5.0	3.9	3.6	3.1	1.2	1.1	1.1
4n	*uncinatus*	.698 ± .018	56	—	12	11	12	12	15	18	21	—	4.9	3.6	3.0	2.4	1.2	1.2	1.1
			42	—	12	11	12	13	13	17	22	—	5.0	3.8	3.1	2.5	1.2	1.3	1.1
	occidentalis		45	—	11	10	10	15	13	16	24	—	4.0	3.3	3.2	2.5	1.1	1.2	1.1
			37	—	11	10	12	14	14	15	26	—	4.3	3.6	2.5	3.1	1.0	1.9	1.1
	californicus	.795 ± .035	43	—	11	11	13	11	17	17	19	—	3.4	3.4	3.1	2.8	1.1	1.1	1.2
			34	—	13	14	15	10	12	15	20	—	6.3	3.4	3.3	2.6	1.2	1.2	1.1
Section *Ranunculus* (x=8)/*Rhizomatosi*: Haploid sets of type 5-0-3																			
2n	*cappadocicus*	.759 ± .029	74	10	11	11	11	12	13	14	16	8.7	5.6	4.1	3.3	2.6	1.2	1.1	1.1
	oreophilus	.481 ± .011	53	10	11	12	11	12	13	14	16	7.6	5.7	3.9	3.3	2.8	1.1	1.2	1.2
	grenierianus	.641 ± .030	60	10	10	11	12	13	14	14	16	5.7	4.7	4.0	3.0	2.5	1.1	1.1	1.1
	gouanii	.704 ± .020	73	10	10	11	12	13	14	14	15	6.9	4.9	3.9	2.9	2.5	1.1	1.1	1.1
4n	*montanus*	1.093 ± .023	70	10	10	11	12	13	13	15	16	6.5	4.8	3.6	2.8	2.3	1.1	1.1	1.1
			63	10	11	11	12	13	14	14	16	7.2	5.1	3.9	3.0	2.5	1.1	1.1	1.1
	recurvatus	.992 ± .031	63	10	11	11	12	13	13	13	16	8.0	4.8	3.6	3.1	2.6	1.2	1.1	1.1
			55	10	11	11	12	13	12	14	16	7.8	4.5	3.8	3.1	2.7	1.3	1.2	1.1
Section *Ranunculus* (x=8)/*Praemorsi,* northern range: Haploid sets of type 5-2-1																			
2n	*polyanthemos*	.698 ± .026	81	11	11	12	12	12	13	14	15	9.9	6.0	4.5	3.8	2.9	1.8	1.5	1.1
	nemorosus	.684 ± .026	82	11	11	12	12	13	13	13	15	9.6	5.7	4.8	4.0	3.4	1.9	1.6	1.1
4n	*repens*	1.074 ± .033	81	11	11	11	12	11	11	13	16	9.9	9.0	5.4	3.5	3.3	1.4	1.8	1.0
			70	11	11	11	13	14	12	13	13	9.9	8.3	6.1	3.5	2.9	1.4	2.0	1.2
2n	*bulbosus* s.l.	.600 ± .012	82	11	11	11	12	12	13	13	15	9.9	7.1	4.8	3.9	3.7	1.9	1.6	1.2
	ssp. *gallecicus*		80	11	11	12	12	12	13	13	15	9.9	6.5	4.6	3.8	3.6	1.6	1.8	1.1
	pratensis	.745 ± .058	77	11	12	12	11	11	13	14	15	9.9	6.4	5.3	4.3	3.8	1.7	1.5	1.3
	**neapolitanus*		82	12	10	9	11	13	14	15	15	9.9	9.5	5.7	4.9	4.1	1.6	1.4	1.1
	macrophyllus	.706 ± .060	78	12	12	12	11	13	13	13	14	9.2	7.4	4.8	4.2	3.8	1.6	1.6	1.3
	quelpaertensis		60	11	12	11	12	13	13	13	14	7.8	4.4	3.7	3.5	2.9	1.9	1.6	1.1
	chinensis	.623 ± .050	66	12	12	12	12	12	13	13	14	7.7	5.8	4.0	3.7	3.1	1.5	1.5	1.3
	pensylvanicus	.504 ± .014	58	11	12	12	12	13	12	13	15	9.0	4.6	4.3	3.5	3.0	1.9	1.6	1.1
6n	*macounii*	1.459 ± .059	64	10	12	13	12	11	11	14	16	4.1	4.0	3.4	3.2	2.7	1.6	1.4	1.1
			51	11	13	13	11	12	12	13	14	4.5	3.9	3.5	3.2	2.7	1.5	1.4	1.1
			48	11	12	12	11	13	12	13	15	7.9	3.8	3.8	3.5	2.8	1.6	1.4	1.1

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[1] Chromosome number in text.

Ploidy/Species		DNA	CL	RCL in % of CL								Centromere Position							
Section *Ranunculus* (x=8)/*Praemorsi,* southern range: Haploid sets of type 6-1-1																			
2n	*hirtus*	.514±.023	53	12	11	13	13	13	13	13	13	5.9	4.6	4.0	3.7	3.3	2.8	1.5	1.2
	lappaceus		53	12	12	12	12	12	13	13	14	7.3	5.4	4.2	3.6	3.2	2.0	1.6	1.2
	graniticola		49	12	11	12	11	13	13	13	14	5.5	4.5	3.7	3.2	3.0	2.2	1.7	1.1
4n	*hispidus*	1.135±.064	64	13	11	12	12	12	12	14	14	6.5	4.7	4.3	4.0	3.7	2.1	1.5	1.1
			54	13	12	13	11	14	13	12	12	8.3	5.4	4.4	4.0	4.0	2.9	2.1	1.0
	fascicularis	1.229±.066	60	12	13	11	14	12	12	12	14	8.3	4.7	4.1	3.6	3.2	2.7	1.6	1.1
			53	14	12	10	14	12	13	12	14	6.3	4.2	3.7	3.5	3.3	2.6	1.5	1.1
8n	*septentrionalis*	1.879±.059	67	12	13	11	12	12	14	12	15	7.3	4.9	4.5	3.4	3.5	2.3	1.4	1.1
			59	11	12	10	12	12	14	13	15	7.4	4.9	4.6	4.4	2.9	2.6	1.5	1.1
			54	12	13	10	12	12	14	12	16	6.1	4.7	4.3	3.5	3.2	3.1	1.6	1.2
			47	8	15	10	12	14	13	11	17	6.6	4.7	3.9	3.7	3.3	2.4	1.8	1.1
	geoides	2.085	61	11	14	13	13	12	11	12	12	8.3	4.3	3.8	3.8	3.2	2.9	1.6	1.0
			58	12	13	13	13	12	12	11	13	4.8	4.5	3.8	3.6	3.4	2.7	1.5	1.0
			55	2	13	13	13	12	12	12	13	9.7	4.6	4.1	3.7	3.3	2.9	1.6	1.1
			51	12	14	12	13	12	12	11	13	8.2	4.7	3.9	3.8	3.0	2.7	1.7	1.1
Section *Ranunculus* (x=8)/*Annuals*: Haploid sets of types 6-1-1 and 5-1-2																			
2n	*sardous*	.429±.013	65	11	11	11	12	12	13	14	16	9.9	4.6	3.9	3.2	2.9	1.9	1.2	1.1
6n	*trilobus*	.975±.048	59	10	10	12	11	13	13	15	16	6.6	4.4	3.6	2.9	2.8	1.6	1.3	1.1
			55	10	10	11	11	13	13	15	16	6.0	4.8	3.5	3.5	2.8	1.6	1.3	1.0
			49	11	10	11	12	13	11	14	17	3.4	4.5	4.3	3.3	2.6	2.3	1.6	1.0
4n	*marginatus*	.757±.024	58	11	12	11	11	14	12	13	16	9.9	5.2	3.8	3.6	3.4	2.8	1.7	1.0
			50	12	12	11	12	12	12	13	16	5.5	4.6	3.8	3.7	3.4	2.8	1.7	1.1
6n	*muricatus*	1.036±.055	71	10	11	11	13	13	13	13	15	8.8	4.7	3.8	2.8	2.5	2.3	1.8	1.1
			63	10	12	11	11	13	13	14	15	8.2	5.5	4.2	3.4	3.0	2.6	1.6	1.0
			58	10	12	10	12	13	14	12	15	9.9	4.0	5.0	3.5	2.8	2.6	1.2	1.1
Section *Ranunculastrum* (x=8)/*Xiphocoma*: Haploid sets of type 5-0-3																			
2n	*psilostachys*	.554±.031	67	10	10	12	12	13	13	14	16	9.9	4.8	3.3	2.8	2.1	1.2	1.1	1.1
	oxyspermus	.605±.083	62	10	11	11	12	13	13	14	16	6.7	4.3	4.0	2.7	2.3	1.1	1.1	1.1
4n	*illyricus*	.819±.053	67	10	10	11	12	12	13	15	15	5.7	4.2	3.0	2.5	2.2	1.1	1.1	1.1
			60	9	10	11	13	13	13	14	15	7.0	4.3	3.4	2.6	2.0	1.2	1.1	1.1
	monspeliacus	1.050±.041	66	10	12	11	12	12	12	13	15	7.5	4.5	3.3	2.6	2.2	1.0	1.1	1.1
			55	9	11	13	13	12	12	13	16	6.3	4.2	3.2	2.7	2.3	1.1	1.0	1.0
Section *Ranunculastrum* (x=8)/*Pterocarpa*: Haploid sets of type 5-0-3																			
2n	*pedatus*	.470±.010	64	10	10	12	12	13	14	15	16	7.6	4.9	3.0	2.8	2.5	1.2	1.1	1.1
	severtsovii		58	10	10	11	12	13	14	14	16	7.1	4.5	3.2	2.7	2.4	1.2	1.2	1.1
	gregarius	.556±.037	64	10	11	12	11	12	13	14	16	7.1	4.9	3.2	2.8	2.6	1.2	1.1	1.2
	nigrescens	.612±.087	78	9	10	11	12	13	13	15	16	7.2	5.3	3.5	2.4	2.2	1.1	1.1	1.1
	creticus	.738±.082	76	10	11	12	12	13	12	14	15	7.1	4.9	4.2	3.2	2.7	1.2	1.1	1.1
	asiaticus	.855±.028	84	10	10	11	12	12	13	15	16	8.6	4.9	3.8	2.9	2.5	1.2	1.1	1.1
	millefoliatus	.839±.040	89	10	11	11	12	12	13	14	16	7.8	4.6	3.2	3.0	2.4	1.2	1.1	1.0
	cortusifolius	1.049±.027	108	10	11	12	12	13	12	14	16	9.9	4.4	4.2	3.4	3.0	1.2	1.1	1.1
Section *Physophyllum* (x=8): Haploid sets of type 5-0-3																			
2n	*bullatus*		70	10	11	11	11	12	12	15	16	8.0	6.0	4.2	3.9	2.7	1.1	1.1	1.1
Section *Ficaria* (x=8): Haploid sets of type 5-1-2																			
2n	**ficaria*		114	10	10	9	13	9	15	15	18	9.9	9.8	5.6	4.0	2.1	1.5	1.2	1.1
4n	*ficaria*	1.994±.307	124	10	10	11	12	11	13	16	17	9.9	5.6	4.0	3.1	2.3	1.6	1.1	1.2
			102	10	10	11	11	12	12	15	18	9.6	5.8	4.4	3.7	2.6	1.7	1.2	1.1

Ploidy/Species		DNA	CL	RCL in % of CL	Centromere Position
Section *Ranuncella* (x=8): Haploid sets of type 4-0-4					
2n	*gramineus*	.579±.020	70	8 10 10 12 13 14 16 17	6.2 4.9 4.0 2.9 1.2 1.2 1.2 1.1
	bupleuroides	.673	66	9 9 10 11 13 14 16 17	7.1 5.3 4.7 3.3 1.2 1.1 1.1 1.1
	calandrinioides	.693±.023	68	9 8 9 12 12 14 17 18	6.6 5.2 4.1 3.3 1.1 1.0 1.0 1.1
4n	*parnassifolius*	.812±.016	54	7 8 10 14 13 14 16 16	4.3 3.7 2.7 2.5 1.2 1.1 1.0 1.2
			42	8 10 12 11 10 14 15 19	4.2 3.6 3.3 2.6 2.1 1.1 1.1 1.0
Section *Thora* (x=8): Haploid sets of type 4-0-4					
2n	*thora*	.397	58	8 8 11 12 12 14 16 18	5.7 4.7 3.3 2.9 1.2 1.1 1.1 1.0
	hybridus		56	8 8 9 12 13 13 16 19	5.6 5.3 4.4 2.2 1.1 1.2 1.0 1.1
Section *Aconitifolii* (x=8): Haploid sets of type 4-0-4					
2n	*aconitifolius*		58	9 10 11 12 12 13 15 16	7.4 4.7 3.7 2.6 1.2 1.2 1.2 1.1
Section *Leucoranunculus* (x=8): Haploid sets of type 4-0-4					
2n	*alpestris*	.330	63	7 10 11 11 12 14 16 18	5.8 3.7 2.9 2.6 1.2 1.0 1.1 1.1
	traunfellneri		52	8 9 11 12 12 13 16 18	5.2 4.9 4.7 2.7 1.1 1.1 1.1 1.1
	crenatus	.370±.037	58	8 9 10 12 12 13 16 18	5.0 4.3 3.6 2.9 1.1 1.1 1.1 1.1
Section *Crymodes* (x=8): Haploid sets of type 4-0-4					
2n	*glacialis*	.373±.016	48	8 9 9 12 12 15 16 19	4.4 3.9 3.7 2.6 1.1 1.2 1.0 1.0
Section *Coptidium* (x=8): Haploid sets of type 4-0-4					
2n	*lapponicus*	.956±.046	102	7 9 10 12 12 13 17 18	6.5 5.9 2.9 2.3 1.2 1.2 1.1 1.0
Section *Halodes* (x=8): Haploid sets of type 4-0-4					
2n	*cymbalaria*	.407±.022	51	8 10 10 12 13 14 15 17	7.8 5.7 3.8 2.4 1.1 1.1 1.1 1.0
6n	*plantaginifolius*	1.353±.103	62	11 11 10 12 13 14 14 15	8.8 4.8 3.9 2.5 1.1 1.1 1.0 1.1
			56	11 12 11 12 13 13 14 14	9.9 5.9 3.5 2.3 1.2 1.1 1.0 1.1
			48	12 12 12 14 11 13 13 13	7.4 5.0 4.6 2.4 1.2 1.1 1.1 1.0
Section *Pseudaphanostemma* (x=8): Haploid sets of type 4-0-4					
2n	*hystriculus*		88	9 10 10 11 13 14 15 16	4.6 3.6 3.3 2.0 1.1 1.2 1.1 1.0
Section *Auricomus* (x=8): Haploid sets of types 3-1-4, 3-2-3, 4-0-4					
2n	*abortivus*	.273±.012	44	8 12 9 11 12 15 15 16	2.9 2.9 2.3 1.6 1.2 1.1 1.0 1.1
	rhomboideus	.275±.010	51	9 8 12 11 13 14 15 17	3.6 2.7 2.3 1.9 1.2 1.3 1.1 1.1
4n	*affinis*	.423±.033	44	11 10 9 11 11 14 15 16	2.9 2.3 1.4 1.2 1.8 1.4 1.2 1.0
			32	9 10 10 12 13 14 14 17	4.3 2.9 1.7 1.2 1.8 1.2 1.1 1.4
	auricomus	.300	46	7 9 12 13 13 13 16 16	4.9 4.2 2.4 1.5 1.3 1.2 1.1 1.0
			37	8 10 9 13 13 13 15 19	6.7 3.8 2.6 2.1 1.5 1.1 1.2 1.2
	cassubicus		66	9 11 11 11 14 14 15 15	4.2 2.7 2.6 1.5 1.3 1.2 1.1 1.1
			50	10 11 11 9 13 14 16 16	3.2 3.0 2.4 1.9 1.2 1.1 1.1 1.2
	allenii	.460±.022	—	— — — — — — — —	— — — — — — — —
6n	*nivalis*	.666±.015	—	— — — — — — — —	— — — — — — — —
	eschscholtzii	.726±.015	56	11 9 12 10 13 13 15 16	3.8 2.8 2.6 1.4 1.2 1.1 1.2 1.1
			44	8 10 11 10 13 15 16 16	5.4 3.0 2.5 2.0 1.4 1.1 1.1 1.2
			40	9 10 11 11 14 15 15 16	4.9 2.6 2.5 2.0 1.2 1.1 1.1 1.0
8n	*cardiophyllus*	.660±.032	50	8 11 11 13 13 14 14 15	3.7 2.8 2.4 1.4 1.2 1.5 1.1 1.1
			46	8 10 11 14 13 13 14 15	3.8 2.8 2.3 2.0 1.2 1.1 1.1 1.0
			37	9 8 12 12 14 14 15 15	3.4 2.8 2.0 1.0 1.0 1.8 1.2 1.1
			33	8 9 11 12 14 14 15 17	4.1 3.1 3.0 1.2 1.5 1.3 1.0 1.1

Ploidy/Species	DNA	CL	RCL in % of CL								Centromere Position							
6n *insignis*	.892±.090	78	10	11	11	13	11	13	15	16	5.8	5.4	3.1	2.8	1.1	1.5	1.2	1.1
		66	12	12	12	13	12	12	12	14	7.3	4.5	3.3	3.1	1.1	1.1	1.1	1.6
		48	10	11	14	12	11	13	14	15	5.2	5.1	4.6	2.8	2.5	1.4	1.0	1.1
**lyallii*		63	14	9	11	11	10	13	15	18	9.9	4.4	4.1	3.0	1.4	1.4	1.0	1.2
		50	13	9	11	9	11	13	14	18	4.7	4.5	4.3	4.0	1.4	1.1	1.2	1.2
		38	12	10	7	7	13	13	15	23	4.7	4.5	4.1	3.0	1.3	1.8	1.1	1.2
Section *Flammula* (x=8): Haploid sets of types 4-1-3 and 5-1-2																		
4n *flammula*	.689±.025	49	10	14	11	13	8	11	16	16	4.8	3.8	2.8	2.7	2.6	1.2	1.1	1.0
		37	13	9	11	14	6	11	15	19	5.0	4.0	3.4	2.7	1.8	1.2	1.1	1.0
var. *ovalis*		51	10	13	10	12	9	14	15	18	5.0	3.6	3.6	3.1	1.5	1.2	1.0	1.1
		41	11	13	12	10	8	13	15	20	8.0	5.6	3.6	2.5	1.3	1.0	1.3	1.1
var. *filiformis*	.675±.032	43	10	11	10	12	10	12	16	18	3.7	3.0	2.9	2.6	1.3	1.3	1.1	1.0
		34	11	10	13	12	8	10	16	18	4.0	3.1	2.9	2.2	1.3	1.7	1.1	1.2
6n var. *filiformis*	.822±.022	61	10	10	11	12	10	13	16	17	4.5	3.9	2.9	2.6	1.3	1.1	1.2	1.0
		53	10	11	12	13	9	11	14	19	4.3	4.0	3.0	2.6	1.5	1.2	1.1	1.0
		46	11	9	12	15	9	10	13	19	4.2	4.0	3.0	2.8	1.6	1.2	1.1	1.1
16n *lingua*	2.374±.970	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
2n *ophioglossifolius*	.634±.020	82	10	10	11	13	8	14	16	18	8.5	6.1	4.8	3.3	2.4	1.4	1.1	1.1
Section *Micranthus* (x=8): Haploid sets of type 5-1-2																		
2n *lateriflorus*	.257±.010	49	10	10	11	12	8	13	17	19	8.6	4.9	4.2	3.6	2.8	1.3	1.0	1.1
Section *Echinella* (x=8): Haploid sets undetermined (below: 4-2-2 and 5-1-2)																		
4n *arvensis*	.718±.023	52	11	11	9	12	12	14	15	16	9.9	6.7	5.6	3.8	1.8	1.6	1.1	1.1
		37	8	13	8	11	12	14	17	17	6.3	5.9	4.0	3.8	2.4	1.1	1.4	1.1
Section *Echinella* (x=7): Haploid sets of types 5-0-2 and 5-1-1																		
2n *chius*	.400±.020	49	—	10	11	12	14	13	18	21	—	5.9	5.6	3.1	2.8	2.6	1.1	1.1
4n *parviflorus*	.699±.027	56	—	10	12	11	13	12	19	22	—	4.9	4.1	2.7	2.5	2.4	1.2	1.1
		47	—	12	12	11	11	12	20	22	—	5.8	4.6	3.4	2.8	2.0	1.1	1.1
2n *pentandrus*	.277±.001	26	—	11	11	14	13	14	17	19	—	4.6	4.2	3.9	3.2	2.4	1.7	1.1
Section *Hecatonia* (x=8): Haploid sets of types 3-2-3 and 4-1-3																		
4n *sceleratus*	.397±.014	48	7	12	11	12	13	13	14	16	3.5	2.7	2.6	1.3	1.6	1.5	1.0	1.1
		35	7	12	11	9	13	14	16	18	4.0	3.0	2.5	1.7	1.3	1.0	1.8	1.2
8n var. *multifidus*	.858	58	12	10	12	12	12	13	13	15	3.0	2.6	2.5	1.3	1.0	1.3	1.5	1.2
		50	10	9	13	13	13	13	14	15	3.0	2.5	2.5	2.3	1.4	1.1	1.1	1.2
		41	10	9	13	10	13	13	15	15	3.5	2.8	2.4	1.4	1.1	1.4	1.3	1.1
		32	11	11	14	9	12	14	14	16	4.0	2.6	2.5	2.1	1.4	1.3	1.1	1.2
gmelinii	.873±.030	47	10	10	9	12	13	13	15	17	7.3	4.2	2.5	1.6	1.1	1.2	1.3	1.1
		38	10	8	11	12	13	13	16	17	4.8	4.0	4.0	1.1	1.7	1.1	1.1	1.4
		33	10	8	11	12	13	14	16	16	4.2	3.8	3.0	1.1	1.8	1.1	1.1	1.3
		28	10	9	10	11	12	15	16	17	4.1	4.0	3.7	3.0	1.1	1.0	1.3	1.4
6n *inundatus*	.523±.018	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Subgenus *Batrachium* (x=8): Haploid sets of types 4-3-1, 5-3-0, 4-2-2																		
2n *peltatus*		44	6	9	15	11	14	12	14	19	3.5	3.3	2.4	2.3	2.3	1.5	1.4	1.4
sphaerospermus	.295±.028	47	7	11	11	12	13	14	15	17	4.3	2.9	2.3	2.2	1.6	1.8	1.4	1.1
4n *baudotii*	.469±.018	52	7	13	9	11	12	14	14	17	2.9	2.8	2.3	2.0	1.6	1.4	1.3	1.3
		38	8	14	12	13	9	13	14	15	3.3	2.6	2.3	2.3	1.1	1.4	1.8	1.4
6n *tripartitus*	.506±.025	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
longirostris		57	8	9	11	11	13	14	16	18	7.6	3.3	2.4	2.3	1.5	1.0	1.1	1.2
		47	9	10	9	12	13	15	16	16	3.7	3.2	2.4	1.9	1.8	1.5	1.1	1.1
		41	9	10	8	12	13	15	16	18	3.2	3.0	3.0	2.3	1.4	1.5	1.0	1.1

Ploidy/Species	DNA	CL	RCL in % of CL								Centromere Position							
Ceratocephalus (x=7): Haploid sets of type 2-0-5																		
2n *testiculatus*		30	—	9	11	15	15	16	17	17	—	2.9	2.6	1.2	1.3	1.0	1.1	1.1
6n *falcatus*	.591 ± .036	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Trautvetteria (x=8): Haploid sets of type 4-0-4																		
2n *carolinensis*		130	8	9	11	12	12	13	16	18	5.2	4.9	4.7	2.7	1.1	1.1	1.1	1.1

rican species (e.g., *R. uncinatus* .698) are in the "small" size range if notice is taken of their ploidy levels.

Except for *R. constantinopolitanus,* a hexaploid member of the *R. velutinus* group, all the European or Oriental species studied have chromosome numbers at the diploid or tetraploid level, as previously reported by other authors (see BOLKHOVSKIKH et al. 1969). The three western North American species studied are tetraploids, as previously reported by TAYLOR and MULLIGAN (1968) for *R. uncinatus* and *R. occidentalis* from Queen Charlotte Is, and by COONEN (1939), SNOW (1959), and GREGSON (1965) for *R. californicus.*

Polyploidy in *R. acris* ssp. *granatensis* and ssp. *strigulosus* — taxa here reported to be tetraploid — was conjectured on morphological grounds by COLES (1971), who accepts both of them as distinct species on the basis of their distribution and ecology. HARA and KUROSAWA (1956) report three ploidy levels, 2n, 4n, and 6n, in the *R. acris* group in Japan. They confine *R. acris* to diploid races, treating the E. Asian polyploids (which are described as distinct from diploids in their ability to form subterranean stolons) as *R. grandis* HONDA.

R. acris ssp. *granatensis* has twice the number of chromosomes as ssp. *acris* while appearing to have less than twice the amount of nuclear DNA. This suggests that it has smaller chromosomes than the latter. However, detailed karyotype analysis indicates that its complement cannot be uniformly smaller than that of ssp. *acris,* rather, it seems to consist of two diploid chromosome sets differing in size. While subdivision of polyploid complements into diploid subsets is arbitrary, it can be seen in Table 1 that subsets isolated in ssp. *granatensis* on the basis of chromosome size are virtually identical in terms of relative chromosome lengths in percent of diploid complement length, as well as centromere position. Only their CL values differ, the larger set (73 μ) exceeding the smaller one (56 μ in the same cell) by approximately 30 % of its length. *Note:* These size differentials — assuming that they are not artifacts — suggest that polyploids such as *R. acris* ssp. *granatensis* are amphiploids, and reflect differences in DNA content among phylogenetic progenitors at lower ploidy levels. Similar size differentials have been found in a number of polyploid *Ranunculi.* The observed differences are real in the event that their values appreciably exceed those expected from introduced variation of one sort or another. Karyotype studies in composite polyploid hybrids of species differing in DNA content (unpubl.) suggest that in the case of tetraploid complements, the introduced variation can range from approximately 5 to 15 % in terms of CL values of the respectively smaller diploid subsets. Critical values for various levels of ploidy are at present unknown, but size differentials as great as in ssp. *granatensis* (30 %) are in all probability real. It is also clear, from DNA comparisons, that the observed variation must involve whole chromosome sets, and inspection of Table 1 will tend to confirm this in terms of their chromosomal parameters.

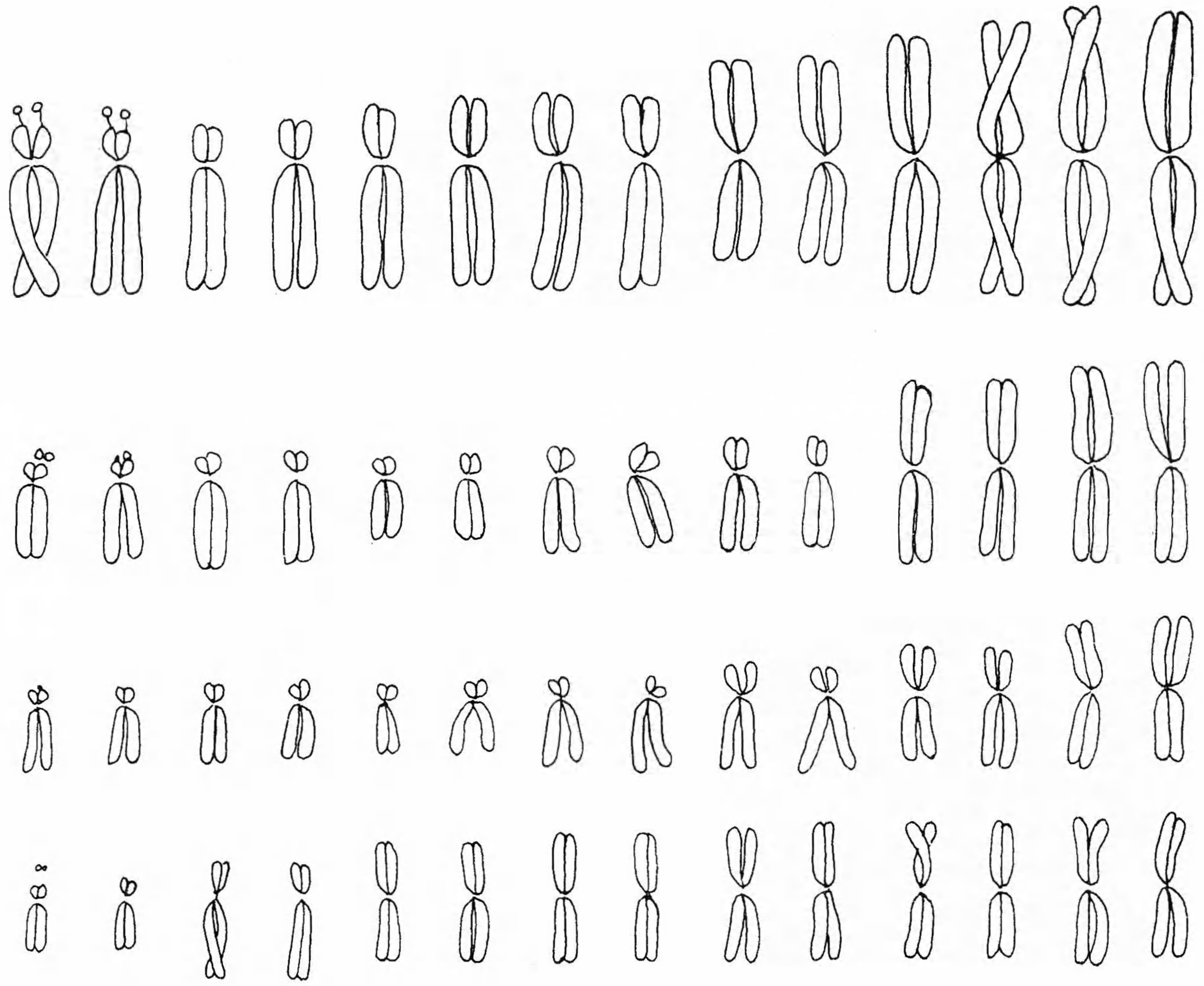

Fig. 1. Karyotypes of diploid species based on x=7, genera *Ranunculus* and *Ceratocephalus*. — Top row: *Ranunculus acris* (sect. *Ranunculus*); second row: *R. chius* (sect. *Echinella*); third row: *R. pentandrus* (sect. *Echinella*); bottom row: *Ceratocephalus testiculatus*. The *Ceratocephalus* karyotype is distinct in the predominance of metacentric or near-metacentric chromosomes. — ×4,200.

Species based on x=7 in section *Ranunculus* have common morphological attributes, as follows: terete pedicels (rather than grooved); glabrous tori; and, except in *R. velutinus* and *R. constantinopolitanus,* patent-spreading rather than reflexed sepals (terminology of DAVIS 1960; TUTIN 1964). Western North American species, distinct though they are in floral structure, vaguely resemble *R. acris*. BENSON (1948 p. 72) discusses suspected sterile hybrids between *R. acris* and *R. uncinatus* collected in Alaska by J. P. ANDERSON (Dutch Harbour; Gull Isl.; Juneau), and VAN SCHAACK (Aleutian Is.).

DAVIS (1960) classifies species of section *Ranunculus* in two morphological series, (i) *Rhizomatosi,* species with elongate, oblique or horizontal rhizomes; (ii) *Praemorsi,* species with short, erect, rhizomes or corms. Yet as far as concerns the present species, no clear division of this sort seems to obtain. *R. lanuginosus* for instance might be described as intermediate between *R. velutinus* (praemorse) and *R. sericeus* (creeping rhizome), though in its general morphology it combines attributes of the former and *R. acris*. However this may be, DAVIS stresses that the division in rootstock types is not as clear "in Europe" as it is among Oriental species of section *Ranunculus*. He writes (p. 105): "Plants with praemorse or elongate rhizomes are often referred to *R. acris* L. s.l. — a species that, on the sum of its characters and general affinities, certainly belongs to the *Praemorsi.*" It would be a helpful coincidence if the problematic species were all based on x = 7.

SECTION RANUNCULUS SPECIES BASED ON x = 8

In contrast to species based on x = 7, those with the chromosome number based on x = 8 seem clearly referable either to the "*Praemorsi*" or "*Rhizomatosi*". Moreover, DAVIS's subdivision is reflected in karyotypes. It is therefore adopted below.

A. *Rhizomatosi*: *R. cappadocicus* WILLD., 2n = 16; Royal BG Kew (accession from Turkey); Leningrad BG; *R. montanus* WILLD., 2n = 32; Wroclaw BG; Munich BG; TH. EGLI, Wädenswil (cult.); Switzerland: Kt. Graubünden, Davos-Laret, E. LANDOLT, 12 Aug. 1971; *R. gouanii* WILLD., 2n = 16; Munich BG; Station Nat. d'Essais, Versailles (accession from the Eastern Pyrenées); *R. grenierianus* JORD., 2n = 16; Switzerland: Kt. Graubünden, Davos, E. LANDOLT, 28 July 1971; *R. oreophilus* BIEB., 2n = 16; Switzerland: Kt. Schwyz, Saasberg ob Richisau, E. LANDOLT, 14 Sep. 1971; *R. recurvatus* POIR., 2n = 32; Ontario: St. George, C. & M. HEIMBURGER 2372, 20 May 1967; Rice L., C&MH 2385, 17 June 1967; Turkey Pt., C&MH 2371, 20 May 1967; Bloomsburg, C&MH 2377, 20 May 1967; St. Williams forestry station, C&MH, 28 May 1970.

The species studied have chromosome complements of five acrocentric and three metacentric pairs per diploid set (Table 1). It seems worth noting their resemblance to the x = 7 series, species with *four* acrocentric and three metacentric pairs.

R. cappadocicus is an unusually distinct Oriental species which DAVIS (1960) has characterized as "relict". It has a DNA value of .759 placing its chromosomes nearly in the size category "large". The remaining species studied are in the medium size range. All are diploids or tetraploids, as previously shown by other authors, e.g., for *R. cappadocicus* by ALEXANDROVA (1967, *R. ampelophyllus* SOM. & LEV.); *R. montanus* group, LANDOLT (1954, 1956); *R. recurvatus,* COONEN (1939). LANDOLT (1954) shows that *R. montanus* is an amphitetraploid combining genomes of *R. carinthiacus* HOPPE and probably *R. grenierianus.*

Rhizomatosi based on x = 8 are like certain members of the x = 7 series in having terete pedicels; patent-spreading sepals; tripartite, incompletely segmented leaves; and similar rootstock characteristics. They differ from the x = 7 series in possessing pubescent tori. This attribute may indicate a differentiating feature correlated with chromosome base number in section *Ranunculus,* since species of the *Praemorsi* series based on x = 8 (see below) likewise have pubescent tori.

R. recurvatus is an isolated North American member of the *Rhizomatosi* series based on x = 8, in terms of the above attributes as well as karyotype. According to BENSON (1940, 1948), it is unique in attributes of the nectary scale. BENSON nevertheless groups it together with a species of the x = 7 series — *R. uncinatus* — which it resembles in floral structure and achene morphology. HULTÉN (1968) has pointed out that reports of *R. recurvatus* from the USSR (Commander Is, OVCZINNIKOV 1937) are based on *R. occidentalis* ssp. *nelsonii* — a taxon presumably of the x = 7 series.

B. *Praemorsi* (Northern Range): *R. macrophyllus* DESF., 2n = 16, 1 pop.; *R. bulbosus* L. s.l., 2n = 16, 6 pops.; — ssp. *gallecicus* (FREYN ex WILLK.) P. W. Ball & Heywood, 2n = 16, Coimbra BG; *R. pratensis* C. PRESL., 2n = 16, 2 pops.; *R. nemorosus* DC., 2n = 16, 2 pops.; *R. polyanthemos* L., 2n = 16, 5 pops.; *R. repens* L., 2n = 32, 6 pops. (European BG); Quebec: Valcartier, C. HEIMBURGER, Aug. 1970; Ontario: Toronto (cult.); *R. quelpaertensis* (LEV.) NAKAI, 2n = 16, Tokyo BG; *R. chinensis* L., 2n = 16, Copenhagen BG; *R. pensylvanicus* L. FIL., 2n = 16; Alberta: Pinehurst L., P. J. SCOTT 60, 5 June 1971 (as *R. macounii*); Aguasabon Gorge, C. & M. HEIMBURGER 2400, 7 Aug. 1967; Wisconsin: U of Wisc. Arboretum; Wilderness Res. Center, Basswood L., W. J. JOHNSON, 26 Aug. 1970; Ontario: Chippewa, D. M. ROBB, 1966; Deep River, M. MOORE, 1967; Roslin, C&MH 6070, 29 Aug. 1970; Speyside, C&MH 6234, 3 Nov. 1970; Lindsay, C&MH 6515, 12 Aug. 1971; Trent, C&MH 6022, 19 July 1970; *R. macounii* BRITT., 2n=48; Mackenzie Dist.: Le Grand Detour, Slave R., W. J. CODY 13892, 24 July 1965; Alberta: Ranfurly, C&MH 2416, 29 Aug. 1967; Edson, C&MH 2392, 29 Aug. 1967.

Praemorsi differ from the *Rhizomatosi* series based on x=8 in having one, rather than three, metacentric chromosome pairs per diploid set. Chromosome complements of the type described in Table 1 have been illustrated for species of the *R. bulbosus* group in Portugal, NEVES (1944 a); for *R. nemorosus* and allied species, HESS (1954); *R. repens, R. bulbosus* group, GREGSON (1965); *R. quelpaertensis* (*R. ternatus* var. *glaber*), *R. hakkodensis* NAKAI, KURITA (1957 a, 1961 a). DNA values are in the "medium" range, but North American species have appreciably lower values than Eurasian ones. One of them, *R. pensylvanicus,* is predominantly annual. It is here reported to be diploid in Ontario, Wisconsin, and Alberta. *R. macounii* is a partly sympatric hexaploid with a tendency to be annual but more often biennial or perennial. (Unlike *R. pensylvanicus*, it is perennial or at least biennial when cultivated under greenhouse conditions.) Its chromosome number was first reported by KAPOOR and LÖVE (1970), who also confirm that earlier reports for the same species by LÖVE and RITCHIE (1966), followed by LÖVE and KAPOOR (1967), were probably erroneous and need no longer be taken into account. *R. chinensis* is an E. Asian diploid fairly closely resembling *R. pensylvanicus,* though, peculiarly, classified by OVCZINNIKOV (1937) in subgenus *Hecatonia* (LOUR.) DC.

R. repens, a species capable of large-scale vegetative reproduction, is generally reported as tetraploid, but TOMASZEWSKI (1959) found several populations in Poland to be diploid, and other authors report diploids from Japan (MATSUURO and SUTÔ 1935) as well as Bulgaria (KUZMANOV and KOZUHAROV 1969). The present accessions are tetraploid. *R. repens* is noteworthy in a number of respects: its chromosomes are markedly smaller than those of Eurasian diploids studied here; in DNA content, it resembles North American species, e.g. *R. macounii*; there are no significant size differences within its tetraploid complement.

C. *Praemorsi* (Southern Range): New Zealand: *R. hirtus* BKS. & SOL., 2n=16, Copenhagen BG; Australia: *R. lappaceus* SM., 2n=16; NSW: Ulmarra, P. COVENY 2175, 30 Sep. 1969, NSW 118562 (Royal BG Sydney, B. BRIGGS); *R. graniticola* MELV., 2n=16, Royal BG, Sydney; Mexico: *R. geoides* H.B. & K., 2n=64, U of California BG, Berkeley; Ontario: *R. septentrionalis* POIR., 2n=64; Amberley, N. STRAUS, 10 June 1967; St. Williams forestry station, C. & M. HEIMBURGER 2373, 20 May 1967; Red Bay, K. H. ROTHFELS, 20 May 1967; Speyside, C&MH, 3 June 1967; Stoney Creek, C&MH, 10 Sep. 1970; *R. hispidus* MICHX., 2n=32; Turkey Pt., C&MH 2378, 20 May 1967; St. George, C&MH, 20 May 1967; Turkey Pt., C&MH 3672, 28 May 1970; Mississauga, Credit R., 12 June 1972; *R. fascicularis* MUHL., 2n=32; Morrison L., K. H. ROTHFELS and E. SEXSMITH, 14 May 1967; Dalrymple L., KHR, 14 May 1967, 25 May 1967; Brechin, KHR, 31 May 1970; Turkey Pt., C&MH, 28 May 1970.

These species are distinct from "Northern" *Praemorsi* in their increased number of acrocentric chromosomes per diploid set (Table 1), but karyotypes in both are otherwise alike. DNA values are in the lower medium range. Australian species are unusual in possessing prominent secondarily constricted chromosomes. BRIGGS (1960, 1962) has illustrated details of this feature for various species of the *R. lappaceus* group.

The inclusion of North American species under the heading "Southern" requires justification. The species involved are from the pan-American taxonomic complex designated the *R. septentrionalis* group by BENSON after its well-known Eastern North American member. The center of distribution is in Mexico, and its origin probably Southern. The North American component includes a single species, *R. orthorhynchus,* in the West, and a group of species (essentially those studied here except for *R. geoides*) in the East. A common attribute of these species is the elongate, straight, persistent style, as pointed out by BENSON.

Species of the *R. septentrionalis* group are even-polyploid at the tetraploid or octoploid levels. There are no "Northern" *Praemorsi* involving such high ploidy levels. COONEN (1939) previously studied *R. fascicularis* and *R. septentrionalis,* reporting both to be tetraploid. (The present counts suggest that the latter is, in fact, octoploid.) *R. geoides* (octoploid) and *R. hispidus* (tetraploid) have not been previously counted. RAHN (1960) studied *R. praemorsus* H.B.K., reporting octoploids from Argentina, tetraploids from alpine Ecuador. TAYLOR and MULLIGAN (1968) report tetraploid counts for *R. orthorhynchus* on Queen Charlotte Is. Thus no diploids are known in the group. (A reported count of 2n=14 in *R. sibbaldioides* H.B.K. in Mexico, STOUTAMIRE and BEAMAN 1960, is clearly aberrant, the possibility of a firmly established deviating chromosome base number in this group being remote.)

In contrast to the high ploidy levels of these American *Praemorsi* are diploid chromosome numbers reported for species of the *R. lappaceus* group in Australia (BRIGGS 1960).

SECTION RANUNCULUS
EURASIAN ANNUAL SPECIES

R. sardous CRANTZ, 2n=16, 4 pops.; *R. trilobus* DESF., 2n=48, 4 pops.; *R. marginatus* D'URV. (ssp. *trachycarpus*), 2n=32, 3 pops.; *R. muricatus* L., 2n=48, 5 pops.

The above species are annuals with distinctly sculptured pericarps of the *R. sardous*—*R. cornutus* complexes in Europe and the Orient. Hybridization and cytogenetic studies by GREGSON (1965) demonstrate genomic relationships among species at four ploidy levels (2n, 4n, 6n, 8n). *R. muricatus* includes hexaploids as well as octoploids (NEVES 1944 a, GREGSON 1965). Illustrations by GREGSON and NEVES show that karyotypes of these species resemble those of perennials, such as *R. bulbosus,* of section *Ranunculus.* The present results confirm this in terms of karyotype patterns (Table 1) but not for chromosome size — annual species having markedly lower DNA contents than perennials (e.g. *R. sardous* .429, *R. bulbosus* .6).

BENSON treats those annuals introduced in North America in section *Echinella* DC. OVCZINNIKOV treats *R. sardous* and *R. bulbosus* in Cycle *Bulbosi* of section *Ranunculus,* but classifies the remaining species in a separate subgenus *Pachyloma* (SPACH) OVCZ. DAVIS (1960) shows that their elaborate pericarps provide valuable diagnostic characters but lead to no natural basis of classification.

SECTION RANUNCULASTRUM DC.

R. oxyspermus BIEB., 2n=16, 2 pops.; *R. psilostachys* GRIS., 2n=16, 2 pops.; *R. monspeliacus* L., 2n=32, 3 pops.; *R. illyricus* L., 2n=32, 5 pops.; *R. pedatus* WALDST. & KIT., 2n=16, 5 pops. (ssp. *pedatus*); *R. millefoliatus* VAHL, 2n=16, 4 pops.; *R. creticus* L., 2n=16, 2 pops.; *R. asiaticus* L., 2n=16, 6 pops.; *R. severtsovii* RGL., 2n=16, Leningrad BG; *R. gregarius* BROT., 2n=16, Coimbra BG; *R. nigrescens* FREYN, 2n=16, Coimbra BG; *R. cortusifolius* WILLD., 2n=16, 6 pops.

These tuberous-rooted, summer-dormant mostly Mediterranean species have karyotypes like those found in species of sect. *Ranunculus* with oblique or horizontal rhizomes (*Rhizomatosi*). Fig. 2 illustrates

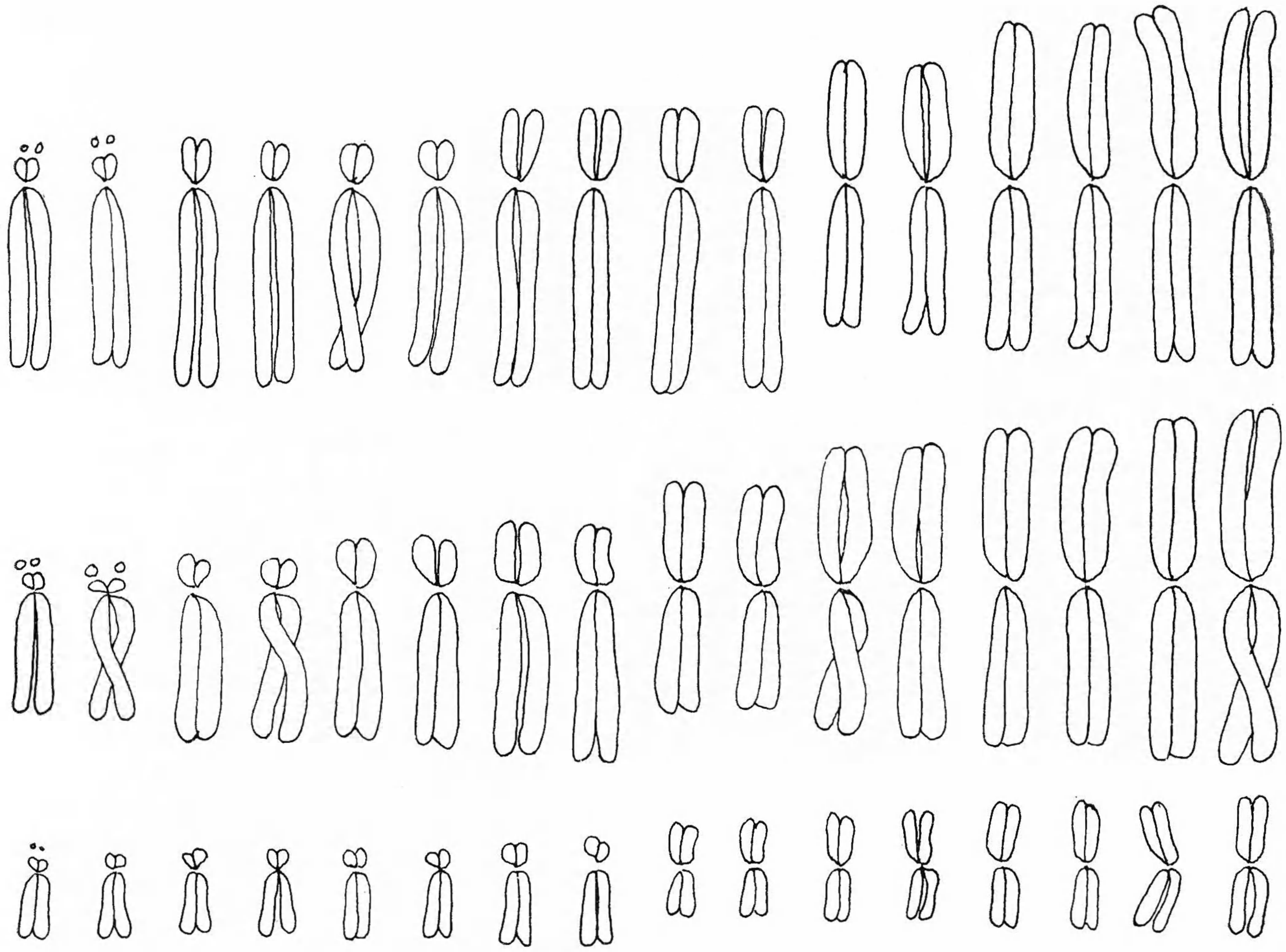

Fig. 2. Karyotypes of diploid species of *Ranunculus* sections *Ranunculastrum, Coptidium,* and *Halodes.* — Top row: *R. cortusifolius*; middle row: *R. lapponicus*; bottom: *R. cymbalaria.* Karyotype proportions of *R. lapponicus* and *R. cymbalaria* are very similar, but *R. cymbalaria* has smaller chromosomes. — ×4,200.

one of them. NEVES (1944 a) has illustrated very similar karyotypes in Iberian species, viz., *R. nigrescens, R. hollianus, R. escurialensis, R. henriquesii,* and also *R. flabellatus* DESF. Chromosome numbers reported here for *R. creticus* and *R. severtsovii* appear to be first counts. They are diploid, and diploidy is common in section *Ranunculastrum,* e.g. *R. pedatus,* TARNAVSCHI 1948; *R. nigrescens,* NEVES 1944 a; *R. gregarius,* KÜPFER 1969; *R. oxyspermus,* LARTER 1932, POPOVA 1972. The present counts in *R. psilostachys* are diploid, but POPOVA (1972) and previously LARTER (1932) report it as tetraploid. A species resembling *R. psilostachys* is *R. rumelicus* GRIS., for which POPOVA (1972) reports an interesting single count of 2n=24.

OVCZINNIKOV admits *Ranunculastrum* as a subgenus of *Ranunculus* and recognizes two sections, *Pterocarpa* and *Xiphocoma,* based mainly on a feature from the morphology of the achene. DAVIS (1965) as well as TUTIN (1964) subdivide sect. *Ranunculastrum* into series or groups which correspond to a remarkable extent to OVCZINNIKOV's, even though each author invokes unrelated distinguishing features: features from the morphology of the rootstock (DAVIS) and sepal stance (TUTIN). Of particular interest is the ability of species in one group (*Xiphocoma*) to form subterranean stolons.

Table 1 gives a breakdown of the species studied here using the subdivision of OVCZINNIKOV. It can be seen that the two groups are alike in terms of karyotype pattern. There are, however, other dissimilarities which may be significant. DNA values indicate a narrow size range in *Xiphocoma* (medium), a wide range in *Pterocarpa* (medium to large). There are polyploids in *Xiphocoma,* but none in *Pterocarpa.* Species in *Pterocarpa* are more numerous than in *Xiphocoma* and are morphologically in some respects much more diverse. Some of them have interestingly isolated distributions.

R. cortusifolius, which represents *Ranunculastrum* (i.e. *Pterocarpa*) on the Atlantic islands, has one of the largest chromosome complements in the genus (DNA= 1.049).

SECTION PHYSOPHYLLUM FREYN

R. bullatus L., 2n=16, Coimbra BG. This species is karyotypically like *Ranunculastrum,* as previously shown by NEVES (1944 a) in illustrations for both. DNA content was not determined, but CL values (Table 1) indicate medium-sized chromosomes.

SECTION FICARIA (SCHAEFFER) BOISS.

R. ficaria L., 2n=32, 3 pops. (cult. from tubers).

COOK (1963), NEVES (1944 a), GREGSON (1965), and MARCHANT and BRIGHTON (1971), have illustrated chromosomes of diploid and tetraploid populations of this species showing five acrocentric, one submetacentric, and two metacentric pairs per diploid set. The same pattern characterizes the tetraploids studied here. Chromosomes are large (DNA content as in *R. cortusifolius* of section *Ranunculastrum*). *R. ficaria* resembles species of *Ranunculastrum* chromosomally, but very little morphologically, though it is of interest that both have the same root-system of dimorphic, tuberous and fibrous roots, as DAVIS (1960) has pointed out.

SECTION THORA DC.

R. thora L., 2n=16, TH. EGLI, Wädenswil (cult.); Munich BG; *R. hybridus* BIRIA, 2n=16, TH. EGLI.

SECTION RANUNCELLA (SPACH) FREYN

R. gramineus L., 2n=16, 5 pops.; *R. bupleuroides* BROT., 2n=16, Coimbra BG; *R. calandrinioides* OLIVER, 2n=16, Munich BG; St. Andrews BG; *R. parnassifolius* L., 2n=32, TH. EGLI.

SECTION ACONITIFOLII TUTIN

R. aconitifolius L., 2n=16, Munich BG (2 pops.).

SECTION LEUCORANUNCULUS BOISS.

R. alpestris L., 2n=16, 4 pops.; *R. traunfellneri* HOPPE, 2n=16, TH. EGLI; *R. crenatus* WALDST. & KIT., 2n=16, TH. EGLI.

SECTION CRYMODES (A. GRAY) TUTIN

R. glacialis L., 2n=16, TH. EGLI.

SECTION COPTIDIUM (PRANTL) TUTIN

R. lapponicus L., 2n=16; Ontario: Raith, M. HEIMBURGER 2715, 16 June 1969; Alberta: W of Edmonton, M. HEIMBURGER, 25 June 1971.

SECTION HALODES (A. GRAY) L. BENSON

R. cymbalaria PURSH, 2n=16; Copenhagen BG; Montreal BG; Alberta: Hay Camp, W. J. CODY 14638, 11 Aug. 1965; Hanna, C&MH 14 Aug. 1967; British Columbia: Kamloops, C&MH, 25 June 1971; *R. plantaginifolius* MURR., 2n=48, Copenhagen BG.

SECTION PSEUDAPHANOSTEMMA (A. GRAY) L. BENSON

R. hystriculus A. GRAY, 2n=16, D. EMERY, Santa Barbara BG.

Table 1 shows that the above species are karyotypically rather similar. There are four acrocentric and four metacentric or near-metacentric chromosome pairs per diploid set, and — differing from sections *Ranunculus, Ranunculastrum,* and others — some of the acrocentrics are markedly smaller than the metacentrics (Fig. 2).

Similar karyotype patterns have been illustrated by BAUER (1954) in *R. alpestris, R. plantanifolius* (*R. acronitifolius* ssp. *platanifolius*), *R. glacialis*; and by KURITA (1957 a), in *R. gramineus* and *R. kawakamii* MAK. (*Halerpestes k.* (MAK.) TAMURA). KURITA reports the latter to be tetraploid. *R. plantaginifolius* (*Halerpestes ruthenica* (JACQ.) OVZ.) is hexaploid as previously reported by SOKOLOVSKAYA and STRELKOVA (1948, ex BOLKHOVSKIKH et al. 1969).

DNA values in the above sections range from small (*Leucoranunculus, Halodes, Crymodes, Thora*) to medium (*Ranuncella*) and large (*Coptidium*), but a number of species are yet to be measured. *R. hystriculus* (sect. *Pseudaphanostemma*) has large chromosomes to judge from CL values (e.g., Table 1).

FLOVIK (1936) reported *R. lapponicus* (sect. *Coptidium*) to have unusually large chromosomes in comparison with *R. hyperboreus, R. pygmaeus, R. nivalis,* and *R. sulphureus,* i.e., species of sections *Hecatonia* and *Auricomus.* In addition, FLOVIK showed it to have larger chromosomes than *R. pallasii* (sect. *Pallasiantha* (L. BENSON) TUTIN), since he reports eight large chromosomes of the *R. lapponicus* type, and 16 small or fragment-like ones attributable to *R. pallasii,* in the suspected triploid hybrid between them in Spitzbergen (=*R.*×*spitzbergensis* HADAČ, cf. TUTIN 1964).

SECTION AURICOMUS SPACH

R. abortivus L., 2n=16, Montreal BG; Ontario: Deep River, M. MOORE, 1967; St. Williams, C. & M. HEIMBURGER 2371, 20 May 1967; Alberta: Cold L., P. J. SCOTT 43, M. G. DUMAIS 5483, 7 June 1971; Mackenzie Dist.: Flat R., W. J. CODY 17686 & K. W. SPICER, 7 Aug. 1967; *R. rhomboideus* GOLDIE, 2n=16; Ontario: Midhurst, C&MH 2277, 14 May 1967; Minnesota: Princeton, A. G. JOHNSON, 8 June 1970; U of Minn. Arboretum; *R. pygmaeus* WAHL., 2n=16; Alberta: Cardinal Div., P. J. SCOTT 1641, 25 July 1971; *R. nivalis* L., 2n=48, Leningrad BG; *R. eschscholtzii* SCHLECHT.; Mackenzie Dist. (2n=32): W. J. CODY 16731; Alberta (2n=48): Bow Summit, C&MH 2414, 23 Aug. 1967; Banff Nat. Park, Hilda Creek, C&MH 2423, Aug. 1967; Whistler Mt., C&MH 2421, 26 Aug. 1967; 2n=40: Plateau Mt., 17 Aug. 1967; British Columbia (2n=48): Hamilton L., C&MH 2415, 22 Aug. 1967; U of BC botanic garden; Yukon (2n=48): C. H. D. CLARKE, 1968 (no voucher); *R. sulphureus* SOL., 2n=96, NWT: Char L., Resolute Bay, J. SCHOLZ, 1969 (no voucher); *R. allenii* ROB., 2n=32, NWT: Belcher Is., P. F. MAYCOCK 11046; *R. pedatifidus* J. E. SM., 2n=48, NWT: Belcher Is., P. F. MAYCOCK 11047; *R. affinis* R. BR., 2n=32, Leningrad BG (cultivated accessions originating in northern Siberia, Taimyr Pen.); *R. cardiophyllus* HOOK., 2n=64; Copenhagen BG; *R. auricomus* L., 2n=32, St. Andrews BG; *R. cassubicus* L., 2n=32, 2 pops.; New Zealand: *R. insignis* HOOK., 2n=48; North I.: Mt. Ruapehu, Mrs. B. ROY, CAGS 1971.

The species studied are karyotypically diverse, though not dissimilar with three to four acrocentric, and four to five submetacentric or metacentric chromosomes per haploid set (3-1-4, 3-2-3, 4-0-4 patterns, Table 1). Similar patterns have been illustrated by KAPOOR and LÖVE (1970) in *R. abortivus* and *R. adonaeus,* which they report to be diploid in Colorado, and in *R. inamoenus,* reported to be hexaploid. KURITA (1957 a) illustrated four acrocentric and four metacentric chromosomes in *R. abortivus* from a Canadian accession.

KURITA (1957 a) notes that *R. abortivus* has small chromosomes in comparison with certain other species of *Ranunculus*. Its low DNA value of .273 confirms this. Indeed, as seen in Table 1, all the species of section *Auricomus* — as far as studied here — are in the "small" chromosome size range.

Variation in chromosome number within section *Auricomus* is a subject requiring detailed study. For example, TAYLOR and MULLIGAN (1968) report *R. eschscholtzii* as tetraploid on Queen Charlotte Is. Several different numbers were determined for it here. An accession made available by W. J. CODY from the Mackenzie region was tetraploid, but material from Alberta and BC, hexaploid. Pentaploid plants in a collection by M. HEIMBURGER on Plateau Mt, Alberta, must represent some kind of hybrid, though no direct evidence for hybridization is available. A similarly uneven-polyploid count, 2n=c. 56, was reported for the same species from Colorado, by LÖVE and KAPOOR (1967). There is a series of reported counts in *R. nivalis* which repeats that of *R. eschscholtzii* (e.g., LANGLET 1932, NYGREN in LÖVE and LÖVE 1961 a).

R. affinis (*R. pedatifidus* var. *leiocarpus* (TRAUTV.) FERN., det. B. BOIVIN) is here reported as tetraploid, confirming SCHUKOVA (1967) and HOLMEN (1952, ex BOLKHOVSKIKH et al. 1969), while the present count for *R. pedatifidus* is hexaploid, like that reported by HEDBERG (1967). A hexaploid count reported in *R. affinis* by BÖCHER and LARSEN (1950) does not clarify the situation.

Another problem is the relationship of southern hemisphere species such as *R. insignis* to sect. *Auricomus* proper. FISHER (1965) includes them in *Auricomus,* though he acknowledges that LOURTEIG (1956) has treated a series of rather similar S. American alpines in a separate section, *Trollianthoideae* LOURT. HAIR (in FISHER 1965) reports the New Zealand species to be hexaploid. The karyotype of *R. insignis* (Table 1), which is much like one illustrated for *R. lyallii* HOOK. by GREGSON (1965), is unusual in combining medium-sized and small chromosome sets. There are internal size differentials of the order of 30 and 60 %, and in conjunction with the high DNA value of *R. insignis* (.892), this would suggest that among the phylogenetic progenitors of *R. insignis* at least one must have had chromosomes considerably larger than are known from "northern" members of sect. *Auricomus.*

SECTION MICRANTHUS (OVCZ.) NYÁRÁDY

R. lateriflorus DC., 2n=16, 2 pops.

SECTION FLAMMULA WEBB

R. ophioglossifolius VILL., 2n=16, 5 pops.; *R. flammula* L., 2n=32, 7 pops. (Eur. BG); — var. *ovalis* (BIGEL.) L. BENSON, 2n=32; British Columbia: Cowichan L., C. HEIMBURGER, 8 Sep. 1971; NWT: Tau L., W. J. CODY 14211; — var. *filiformis* (MICHX.) HOOK.; Ontario (2n=32): Halls L., C. & M. HEIMBURGER 6512, 12 Aug. 1971; Lindsay, C&MH 6513, 12 Aug. 1971; Uppsala, C&MH 6670, July 1972; Hearst, C&MH 2394, 2 Sep. 1969; Dorset, J. E. CRUISE, Sep. 1971; 2n=48: Grand L., Achray, M. MOORE, 21 July 1967; Barron R., Achray, M. MOORE, June 1971; Finland (*R. reptans* L., 2n=32): Helsinki BG (2 local accessions); *R. lingua* L., 2n=c. 125—128, 3 pops.

Karyotypes in sections *Flammula* and *Micranthus* (Fig. 3) are distinct in possessing an unusually short "marker" chromosome of acrocentric to submetacentric proportions. NEVES (1944 a) previously illustrated this feature in *R. flammula,* as well as *R. dichotomiflorus* FREYN and *R. nodiflorus* L., though he has apparently not seen it in *R. ophioglossifolius*; it is also evident in illustrations for *R. flammula* by GREGSON (1965); for *R. reptans* var. *flagellifolius* (NAK.) OHWI, by KURITA; and *R. lateriflorus,* by HINDAKOVA (1969).

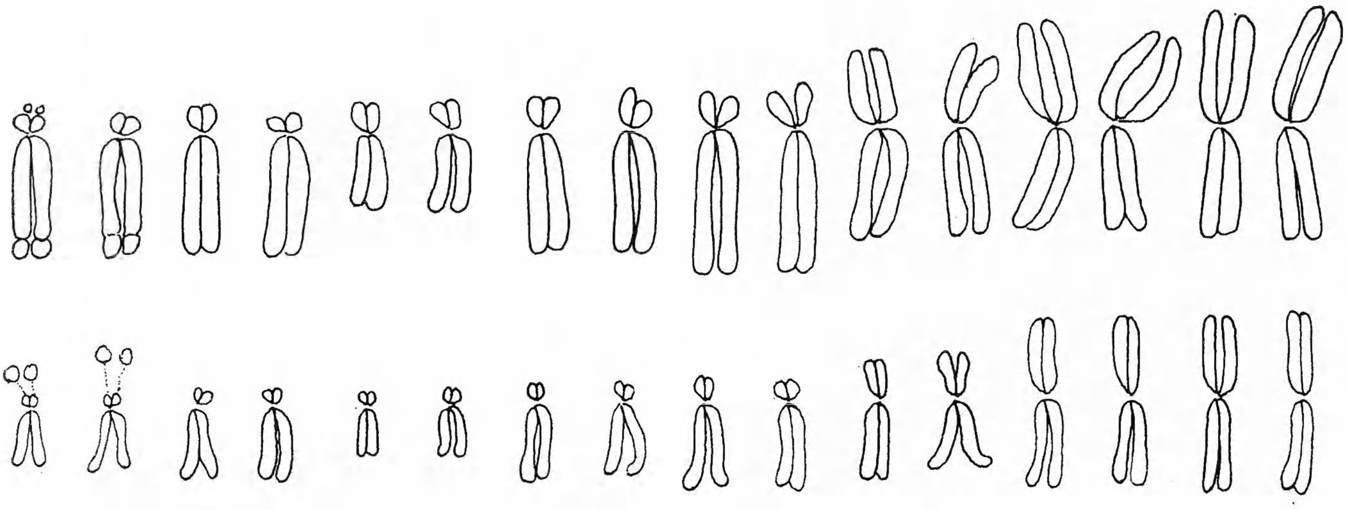

Fig. 3. Karyotypes of diploid species of *Ranunculus* sections *Flammula* and *Micranthus*: *R. ophioglossifolius* (top) and *R. lateriflorus*. — Karyotype proportions are similar, but *R. ophioglossifolius* has larger chromosomes and one of its acrocentric pairs bears prominent secondary constrictions. — ×4,200.

R. lateriflorus and *R. ophioglossifolius* are diploid annuals with similar karyotypes except for a greater than two-fold difference in chromosome size (DNA .257, .634). The perennials, *R. flammula* and *R. lingua*, have polyploid complements some of whose constituent diploid subsets differ in size (Table 1). GREGSON (1965) succeeded in hybridizing the highly polyploid *R. lingua* with *R. flammula* and reports genomic affinity between them.

SECTION ECHINELLA DC. SPECIES BASED ON x=8

R. arvensis L., 2n=32 (vars. *spinosus*, *tuberculatus*), 6 pops.

DAVIS (1960) recommends on morphological grounds that sect. *Echinella* be reinterpreted and confined to a single species, *R. arvensis*, pointing out a number of unusual features, such as pollen size, in which it is distinct. DAVIS's treatment is superficially supported by the fact that *R. arvensis* is based on x=8, the remaining species based on x=7. However, *R. hebecarpus* HOOK. & ARN in California, and an unusually distinct species, *R. pinardii* (STEV.) BOISS. in Turkey (cf. DAVIS 1960), have not been studied cytologically.

R. arvensis is karyotypically unique; unfortunately, its tetraploid complement is so heterogenous as to preclude diploid-level comparisons with other species. It is probably an allotetraploid of rather unique derivation, although NEVES (1944 a) interprets it as an "ancient autotetraploid" having undergone extensive karyotype modification. Whatever its origin, there are considerable size differences among its chromosomes. If the 16 pairs are arbitrarily grouped into sets of 8 by size (Table 1), then the overall size differential is of the order of 45 % in terms of the smaller set.

SECTION ECHINELLA SPECIES BASED ON x=7

R. chius DC., 2n=14, 4 pops.; *R. parviflorus* L., 2n=28, 4 pops.; *R. pentandrus* J. M. BLACK, 2n=14, NSW: Forbes, P. COVENY 2541, 28 Nov. 1969, NSW 118559 (Royal BG Sydney, B. BRIGGS).

R. chius and *R. pentandrus* are karyotypically distinct, though not dissimilar, from the species based on x=7 of sect. *Ranunculus*. Their karyotypes are shown in Fig. 1. *R. parviflorus* is like *R. chius* at the tetraploid level. All have small chromosomes, in fact, *R. pentandrus* (DNA .277) is one of the smallest diploid *Ranunculi* yet measured.

SECTION HECATONIA (LOUR.) DC.

R. sceleratus L., 2n=32, 8 pops. (Eur. BG); Ontario: Alliston, C. & M. HEIMBURGER 6214, 24 Oct. 1970; Vineland Station, V. Rundaus & T. R. DAVIDSON, 2 July 1968; Barrie, C&MH 6074, 6 Sep. 1970; Wisconsin: U of Wisc. Arboretum; — var. *multifidus* NUTT., 2n=64; Saskatchewan: Nokomis, C&MH 2403, 10 Aug. 1967; Alberta: Hanna, C&MH 2405, 14 Aug. 1967; Mackenzie Dist.: Slave R., W. J. CODY 13944, 25 July 1965; Brackett L., W. J. CODY 20093, 20 July 1971; *R. gmelinii* DC, 2n=64; Ontario (var. *hookeri*): Westhawk, C&MH 2419, 1 Sep. 1967; Lindsay, C&MH 6064, 29 Aug. 1970; Roslin, C&MH 6067, 29 Aug. 1970; Manitoba: Sandilands Forest Res., C&MH 2417, 1 Sep. 1967; Alberta (var. *hookeri*): 2 mi S of Sarah Creek, 10—15 mi S of Swan Hills, M. G. DUMAIS 4145 and K. ANDERSON, 10 Aug. 1968; Touchwood L., NW tip, 1 mi off lake, MDG 3737 & KA, 24 July 1968; 4 mi E of Buck L., MGD 2786 a & KA, 28 June 1968; var. *gmelinii* (det. MGD): Wabasca L., c. 85 mi N of Lesser Slave L., MGD 4154 & KA, 10 Aug. 1968; Australia: *R. inundatus* R. BR. ex DC., 2n=48; NSW: 18 mi E of Ulmarra, P. COVENY 2175, 30 Sep. 1969, NSW 118561 (Royal BG Sydney, B. BRIGGS).

R. inundatus is an odd member of section *Hecatonia* belonging to the Australasian *R. rivularis* group. It is distinct in having subterranean stolons as well as tubers. The accession studied is hexaploid and its DNA value in the category "very small".

NEVES (1944 a), KURITA (1961 a), as well as COOK (1963) have illustrated chromosomes of *R. sceleratus* and each author notes that they are small in comparison to those of other *Ranunculi*. DNA values in the present material confirm this, placing *R. sceleratus* in the small-chromosome size range. *R. gmelinii* is in the same range. Moreover, there are size differentials, of the order of 30 %, between 2n sets in both species, so parts of their complements are in a still lower size range. Low-DNA polyploids matching *R. sceleratus* or *R. gmelinii* have been found only in section *Auricomus,* although some at least as small occur in *Ranunculus* subgenus *Batrachium* (see below). Karyotypes of *R. sceleratus* and *R. gmelinii* are similar with three acrocentric, two submetacentric, and three metacentric chromosome pairs per diploid set (Table 1).

MULLIGAN and PORSILD (1969) studied *R. sceleratus* var. *multifidus* and *R. gmelinii* var. *hookeri* (*R. purshii* RICH.) in the Yukon and report both to be octoploid. The present counts confirm octoploidy for other significant parts of their ranges. HEDBERG (1967), LÖVE and RITCHIE (1966), and P. J. SCOTT (pers. commun.), found *R. gmelinii* to be diploid. This may or may not indicate unresolved taxonomic problems involving the species, but the matter is in any case complicated further by the existence of two other counts, one diploid, one tetraploid, from the USSR (SOKOLOVSKAYA 1958, 1963).

Ranunculus subgenus **Batrachium** (DC.) A. GRAY

(Voucher determinations by C. D. K. COOK except where otherwise noted.)

R. peltatus SCHRANK, 2n=16, Coimbra BG; *R. tripartitus* DC., 2n=48, Coimbra BG; *R. baudotii* GODR., 2n=32; Germany: Rügen I (Halle BG); *R. sphaerospermus* BOISS. & BLANCHE; Saskatchewan: Nokomis (2n=16), C&MH 2402, 10 Aug. 1967; Young, C&MH 2401, 10 Aug. 1967; Kindersley, C&MH 2407, 14 Aug. 1967; Environ (2n=16; no voucher), C&MH 6566, 10 July 1971; *R. trichophyllus* CHAIX, 2n=32; Belcher Is: Flaherty I., Freakly Pt., P. F. MAYCOCK and J. OP DE BEECK, 29 Aug. 1967 (det. PFM); *R. longirostris* GODR., 2n=48; Ontario: Speyside, C&MH, 1967.

Karyotypes in the above materials are uniform (Table 1), and similar uniformity is evident for the subgenus as a whole in the work of COOK (1962, 1963, 1966 a, 1966 b) and other authors, e.g. TURALA (1969, 1970, 1972), TURALA and WOLEK (1971). However, contrary to a suggestion by COOK (1966 b), *Batrachium* seems to be karyotypically fairly distinct, e.g. in the number of submetacentrics per diploid set; in their relative lengths; in the size of some of the acrocentric pairs in each set; and, to judge from the present results, in overall chromosome size. CL values (Table 1) suggest relatively small chromosomes throughout, and available DNA values place one species, *R. tripartitus,* in the "very small" size range, and two other species in the category "small".

R. longirostris is a previously uncounted North American species here reported to be hexaploid in S. Ontario. Chromosome counts in the remaining materials match those reported by COOK (1966 b) or authors quoted by him.

Based on the interpretation of COOK, at least six species of *Batrachium* are aggregates involving multiple chromosome numbers. Thus *R. peltatus* includes diploids in Portugal, tetraploids in Germany, and hexaploids in England (COOK 1962, 1966 b). LARSEN (in COOK 1966 b) and TURALA (1969) studied tetraploids in Denmark and Poland.

Ceratocephalus PERS.

C. testiculatus (CRANTZ) ROTH, 2n=14, Leningrad BG; *C. falcatus* (L.) PERS., 2n= c. 40, 1 pop.

DAVIS (1960) has reported that *Ceratocephalus* lacks an adventitious root-system of the type characterizing *Ranunculus* and argues that this is only one of several features in which *Ceratocephalus* is distinct from the latter as a genus. To these might be added karyotype pattern.

In Fig. 1, the karyotype of *Ceratocephalus testiculatus* is contrasted with three karyotypes of species of *Ranunculus* with the same chromosome base number (x=7). The former has five metacentric and two acrocentric chromosome pairs, while acrocentrics outnumber metacentrics in *Ranunculus.* A metaphase plate of *C. falcatus* with 40 or 41 chromosomes (the only plate studied) is like *C. testiculatus* in that at least 26 of the chromosomes are metacentric, however, further study of this species is necessary.

The unusual chromosome number of *C. falcatus,* 2n=40, was previously reported by LANGLET (1932) who conjectured that it might be based on x=4. FLOVIK (1936) discounted x=4 as a base number in *Ranunculus* or allied genera, realizing that numbers such as LANGLET's could result from hybridization among plants variously polyploid on x=8 — the predominant base in subfamily *Ranunculoideae* of the *Ranunculaceae.* However, the chromosome number of *C. testiculatus,* previously reported by TITOVA (1935, *C. orthoceros*), can only be interpreted as diploid on x=7, so *C. falcatus* is probably not pentaploid on x=8 but a modified hexaploid based on x=7.

As a hexaploid species, *C. falcatus* has a low DNA value (.591) placing its chromosomes in the size category "very small". CL values in *C. testiculatus* (Table 1) also suggest rather small chromosomes.

Trautvetteria FISCHER & MEYER

LONAY (1901, 1907) shows that *Trautvetteria* resembles *Ranunculus* (e.g. *Crymodes*) in achene structure. Following TAMURA (1967), it is a genus composed of three species: *T. japonica*; *T. grandis* (W. North America); and *T. carolinensis* (E. North America). The present accession of the latter has a diploid chromosome complement of four acrocentric and four metacentric pairs (Table 1), a pattern also characterizing certain species of *Ranunculus* (e.g. *Crymodes,* Table 1). Its chromosomes are quite large but DNA content remains to be determined. KURITA (1961 a) previously studied *T. japonica*; he describes its chromosomes as large and his karyotype illustration shows a pattern like the above.

DISCUSSION

The purpose of these comments is to bring out facts of interest from the point of view of phylogeny. Classification, although touched upon in some parts of this paper (e.g., sect. *Ranunculus*), is a subject for further study.

Phyletic Status of Ranunculus

Phylogenetic reviews of the ranunculaceous genera by LANGLET (1932), GREGORY (1941), and TAMURA (e.g., 1962 a, 1962 b, 1966, 1967, 1968) seek to establish a fundamental phyletic dichotomy on cytological grounds, with one branch evolving into subphyla of the "*Thalictrum*" type (small-chromosome), the other, of the "*Ranunculus*" type (large-chromosome). *Ranunculus* is regarded as one of the more derived members of subfamily *Ranunculoideae* of the large-chromosome branch. Consequently, TAMURA (1967), noting that chromosomes of some species of *Ranunculus* seem actually quite small, proposes hypothetically that perhaps in the Ranunculoideae "short chromosomes may be regarded as an advanced character".

The Interpretation of Löve and Löve

While there exists no detailed review of *Ranunculus* phylogeny and karyotypes, LÖVE and LÖVE (1961 b), in their discussion of the treatment of *Ranunculus* by BENSON (1940), have given a brief cytotaxonomic outline of the genus. LÖVE and LÖVE argue that ". . . cytological features known from the collective genus indicate very clearly that at least most of (the) subgenera are evolutionarily distinct units, some of which hardly are closely related". They propose to re-interpret most of them — *Ceratocephalus, Cyrtorhyncha, Oxygraphis, Crymodes, Batrachium, Ficaria, Coptidium* (inclusive of *Pallasiantha*) — as separate genera, and they intimate that there are yet other taxa in *Ranunculus* which may require similar treatment.

The Bauer Karyotype

LÖVE and LÖVE's interpretation is, of course, perfectly valid, provided that:

(i) Karyotypes of *Oxygraphis, Crymodes,* etc., really are different, and

(ii) that they are distinct not merely in terms of size. The latter point is obvious at least in a general way, there being many examples of closely related taxa differing in respect to chromosome size (e.g., species of *Chrysanthemum,* TANAKA and SHIMOTOMAI 1961, TANAKA 1966).

Be this as it may — it is clear that, in order to conform to an interpretation such as LÖVE and LÖVE's, chromosomal variation among the taxa in question would have to be both extensive and of a type affecting the external appearance of the karyotype. Thus one would expect variation of more than one kind — including, first, changes in chromosome base number, since base number varies within the Ranunculoideae and indeed in *Ranunculus,* secondly, changes in karyotype composition and, thirdly, perhaps size.

In the evidence available here (Table 1), the first and obvious fact is that superficially identical karyotypes, distinguishable *only* by size and only so in some of the cases, occur in a whole series of subdivisions. At least eight distinct taxa are involved: three holarctic subdivisions, viz., sections *Coptidium, Halodes, Crymodes*; the North American section *Pseudaphanostemma*; and four of the Old World sections studied, viz., *Ranuncella, Thora, Aconitifolii,* and *Leucoranunculus.* The common karyotype, basically a pattern of four acrocentric and four metacentric or near-metacentric chromosome pairs (Fig. 2, rows 2—3), may be designated the "Bauer" karyotype, having been previously described by her (BAUER 1954) in three of the above sections. Being as widespread as it is, it may yet be found elsewhere in the genus. Indeed the karyotype recently illustrated by KAPOOR and LÖVE (1970) for *Ranunculus ranunculinus* NUTT. of section *Cyrtorhyncha* has, as far as can be judged, a pattern quite resembling the Bauer pattern.

The occurrence of superficially identical karyotypes in these taxa can, of course, be interpreted in different ways, but not without taking into account three additional facts. First of all, the species involved are rather dissimilar, sharing key attributes in a comparatively small number of features. In the second place, DNA values in the "Bauer" taxa were shown to vary over an approximately three-fold range, so that there is, in fact, some "cytological" evidence of phyletic differentiation between them. It may be objected that variation of the same kind, and nearly as extensive, exists also *within* certain sections of *Ranunculus* where it seems to involve closely related species (e.g., sect. *Ranunculastrum*). But this lack of taxonomic correlation does not greatly interfere with the argument since in both cases the variation can only signify relatively high, not relatively low, degrees of phyletic isolation.

Thirdly, the Bauer pattern has been shown to characterize not only species of the genus *Ranunculus,* but also species of *Trautvetteria.* The relationship of the latter to *Ranunculus* seems fairly close (Fig. 4), but its small size, and the disjunct distribution of its species suggest that it is phyletically not very recent. I am therefore convinced that chromosome complements of the Bauer type represent, at least in *Ranunculus,* a less derived, ancestral pattern. This hypothesis is one to be followed up in ranunculoid genera such as *Callianthemum, Adonis* (Fig. 4), and perhaps in such taxa as *Paroxygraphis* W. W. SMITH in the eastern Himalayas, *Laccopetalum* ULBRICH in the high mountains of Peru, and others.

To regard the Bauer pattern as ancient is free from assumptions about phyletic age of species in which it is seen. Also, taxa exhibiting the common pattern may or may not be "evolutionarily distinct" in the sense of LÖVE and LÖVE (1961 b). But even so, one thing is clear: as far as is known, the Bauer pattern occurs exclusively in smaller taxa, including some — such as *Pseudaphanostemma, Coptidium* — which appear to be monotypic. In view of this, it would not, in fact, be surprising if their species were for the most part rather ancient.

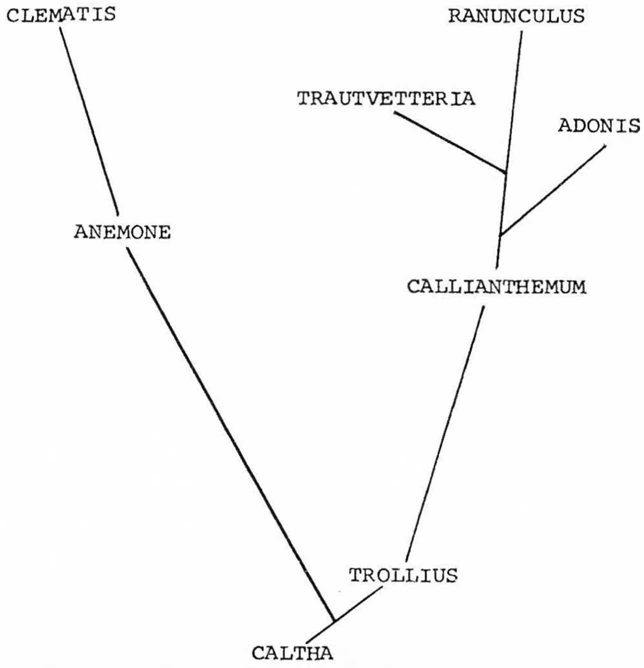

Fig. 4. Phyletic relationships among genera of the Ranunculaceae subfamily Ranunculoideae, after TAMURA (1962 a).

It is of interest in this connection that BENSON (1942) should characterize the following North American *Ranunculi* as "relics of ancient floras", basing his argument on their isolated or scattered distributions: species of sections *Cyrtorhyncha, Arcteranthis, Pseudaphanostemma, Oxygraphis, Crymodes, Pallasiantha, Coptidium,* as well as — less convincingly — *Echinella* (*R. hebecarpus*) and *Batrachium* (*R. lobbii*). BENSON notes other details supporting his view, for instance that "*R. hystriculus* (sect. *Pseudaphanostemma*) has a range in California almost coinciding with that of . . . *Sequoia* . . . in the Sierra Nevada".

Table 2. Ploidy, relative nuclear DNA content per diploid set in terms of *Anemone virginiana* L. (=1.0), typical complement length in μ per diploid set, and frequency of acrocentric, submetacentric, and metacentric chromosomes in the haploid karyotype, in taxa containing annual species or apomicts (genera *Ranunculus* and *Ceratocephalus*). (Data of Table 1.)

Classification	Species	Ploidy	2n-DNA	2n-CL	Karyotype
Ceratocephalus (x=7)	*testiculatus*	2n	—	30	2-0-5
	falcatus	6n	.197	—	—
Echinella (x=8)	*arvensis*	4n	.359	44	mixed
Echinella (x=7)	*chius*	2n	.400	49	5-0-2
	parviflorus	4n	.349	51	5-0-2
	pentandrus	2n	.277	26	5-1-1
Micranthus (x=8)	*lateriflorus*	2n	.257	49	5-1-2
	nodiflorus	4n	—	—	—
Flammula (x=8)	*ophioglossifolius*	2n	.634	82	5-1-2
	flammula	4n	.344	43	4-1-3
	var. *filiformis*	4n	.337	46	4-1-3
	lingua	16n	.296	—	—
Ranunculus (x=8)	*sardous*	2n	.429	65	5-1-2
	trilobus	6n	.325	54	5-1-2
	marginatus	4n	.378	54	6-1-1
	muricatus	6n	.345	64	6-1-1
Ranunculus (x=7)	*uncinatus*	4n	.349	49	4-0-3
Auricomus (x=8)	*abortivus*	2n	.273	44	3-1-4
	rhomboideus	2n	.275	51	3-1-4
	affinis	4n	.211	38	2-3-3
	auricomus	4n	—	41	3-1-4
	cassubicus	4n	—	58	3-1-4
	allenii	4n	.230	—	—
	pedatifidus	6n	—	—	—
	nivalis	6n	.222	—	—
	eschscholtzii	6n	.242	47	3-1-4
	cardiophyllus	8n	.165	41	3-1-4
	sulphureus	12n	—	—	—
Hecatonia (x=8)	*sceleratus*	4n	.198	41	3-2-3
	var. *multifidus*	8n	.221	45	3-2-3
	gmelinii	8n	.218	36	3-2-3
	inundatus	6n	.174	—	—
Batrachium (x=8)	*peltatus*	2n	—	44	5-3-0
	sphaerospermus	2n	.295	47	4-3-1
	baudotii	4n	.234	45	4-3-1
	tripartitus	6n	.169	—	—
	longirostris	6n	—	48	mixed

Primitive and Advanced Chromosomal Features in Ranunculus

If one were granted that taxa characterized by the Bauer karyotype may indeed be less derived, so that they can be excluded at least from the recent phylogeny of *Ranunculus,* then one is left with more derived *Ranunculi* of basically two kinds: those which on criteria other than karyotype can only be described as "advanced", and those which (on the same criteria) are less so.

Of interest then would be any primitive and, above all, any "advanced" chromosomal features in these species (e.g., sensu TAMURA 1967), and at least the advanced features, if they really exist, should emerge simply from a tabulation of all relevant karyotypic attributes.

Table 2 lists karyotype attributes of species from presumably advanced taxa, namely those consisting entirely of annuals (*Ceratocephalus, Echinella, Micranthus*); those consisting partially of annuals but which accept unstable or extremely transitional habitats (*Flammula, Hecatonia, Batrachium*); and those with a tendency to reproduce pseudogamously (*Auricomus*: e.g., HÄFLIGER 1943, ROUSI 1956, RUTISHAUSER 1965, JANKUN and IZMAILOV 1964, IZMAILOV 1970). Also included in Table 2 are *R. sardous* and other annuals of section *Ranunculus,* although the latter could not be categorically described as advanced.

Common chromosomal attributes in these taxa are:

(i) Perhaps not surprisingly, a high incidence of polyploidy; some 40 % of the species studied are at the hexaploid or higher levels, 31 % are tetraploid, some 28 % diploid.

(ii) A relatively narrow chromosome size range in each taxon; at the diploid level, DNA values in section *Echinella* range from .27 to .4; sect. *Ranunculus* annuals, .32—.43; sect. *Hecatonia,* .17—.22; subgenus *Batrachium* .17—.29; sect. *Auricomus* .16—.27; sections *Flammula* and *Micranthus* .26—.34 — except for a single species, *R. ophioglossifolius,* whose DNA value extends the range to approximately .63. Some of these size ranges are so narrow that, were it not for the independent evidence available from karyotype analysis in polyploids, one would doubt that real size variation exists in the taxa involved.

It is also apparent that the size ranges observed in the various taxa are actually quite similar: with the interesting exception of *R. ophioglossifolius,* the species studied — as if to confirm the hypothesis of TAMURA — have "small" or "very small" chromosomes (DNA less than .4 or less than .2; *R. sardous* slightly exceeds this range with a value of .427). What seems relevant in the evidence of Table 2 is, however, not this coincidence, nor its preliminary explanation in terms of polyploid species relationships, but rather the fact that there seems to be very little else which these eight taxa have chromosomally in common. One may suspect, on the basis of their taxonomy, that their phylogenetic affinities are diverse, and the observed changes in karyotype composition from taxon to taxon (e.g., Table 2) leave one in no doubt about this point.

Nevertheless, not all of them are equally distinct. Thus, karyotypes suggest that *Micranthus* and *Flammula* are similarly derived taxa and may represent a single phylon. This conjecture is further supported by observations of NEVES (1944 b) according to which *R. dichotomiflorus* combines genomes of species from both of the taxa. Likewise, annual species classified in sect. *Ranunculus* by TUTIN appear to be closely related to perennials in that section (DAVIS 1960), although experimental evidence of this would be desirable. There is also some indication that the two "aquatic" taxa, *Hecatonia* and *Batrachium,* are in fact of similar derivation. COOK (1963) found *R. sceleratus* to be like *Batrachium* in its peculiar, transversely ridged pericarps (var. *sceleratus*) which in both cases involve presence of elongated, ranked sclereids in the periderm. Basing his opinion on the work of LONAY (1901, 1907), COOK believes that achenes of this type probably do not occur elsewhere in the genus. As for their karyotypes, it appears that *Hecatonia* and *Batrachium* are, by and large, the only taxa in *Ranunculus* with chromosome size ranges extending into the category "very small" (DNA less than .2) — the question is only whether a common size range has much to do with common derivation.

The Phyletic Position of Sect. Ranunculastrum

Having evidence that chromosome size variation exists, but is not very extensive, in a whole series of advanced taxa, it is tempting to conclude that the condition is typical for cases like these. Where, therefore, chromosome size varies greatly, among taxa of one kind or another, one will be inclined to regard them almost categorically as relatively ancient. That at least some of the taxa characterized by the BAUER karyotype are in this category has already been shown. It remains to be determined whether the same applies to other taxa involving extensive size variation, primarily here the species of the large section *Ranunculastrum.*

DAVIS (1960) groups all the species of *Ranunculastrum* in a preliminary taxon designated *Grumosi,* that is, perennials with dimorphic, tuberous and fibrous roots, in which he includes also the section *Physophyllum.* He regards *Grumosi* as a major adaptive group in the genus and traces its origin as follows: "It is evidently an advanced and specialized group, and it seems very likely that it evolved (at least as far as sect. *Ranunculastrum* is concerned) from ancestral *Praemorsi* (sect. *Ranunculus*) by the development of dimorphic roots. Fleshy roots are already well-established in some southern representatives of the *Praemorsi* . . .". However this may be, DAVIS concedes that the group is probably *not* of recent derivation, since he adds: ". . . the large size of sect. *Ranunculastrum,* its morphological diversity and wide distribution suggest that the group, despite its specialized nature, is of very considerable age."

While the present study is too small for a discussion of the many questions raised by this, it is clear that to characterize *Ranunculastrum* as ancient is tantamount to admitting it as the only *major* ancient taxon extant in the genus. Thus its phyletic position is a matter of some interest.

The following observations seem significant in this respect. Firstly, it appears that there is a whole class of karyotypes which has, so far, not been observed in *Ranunculastrum,* common as it is in other parts of the genus, i.e., karyotypes with "small" chromosome complements (DNA less than .4). Unfortunately, this is evidence of a kind subject to conflicting phylogenetic interpretations, so that it seems best to ignore it for the moment, concentrating instead on the other fact: that the size range observed — whatever its lower limit — is wide. Secondly, karyotype proportions in sect. *Ranunculastrum* were shown to be constant among the species studied, and also for species studied by NEVES (1944 a), so the common pattern of five acrocentric and three metacentric pairs (Fig. 2, row 1) is presumably an ancestral one. Thirdly, the same pattern occurs also in species of (a) sect. *Physophyllum,* and (b) sect. *Ranunculus,* where it apparently characterizes the whole *Rhizomatosi* series. Yet it has not been found among species of the *Praemorsi* series — a puzzling coincidence in terms of the phylogenetic role assigned by DAVIS to "ancestral *Praemorsi*".

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Taraxacum leporinum spec. nov.

Sten Nordenstam and J. L. van Soest

Nordenstam, S. & van Soest, J. L. 1974 12 30. Taraxacum leporinum spec. nov. — Bot. Notiser 127: 490—492. Lund. ISSN 0006-8195.

Taraxacum leporinum is described as a new species. It belongs to the *T. langeanum* group which comprises four species.

Whether this group belongs to sect. *Erythrosperma* Dahlst., as has been thought up to now, or to sect. *Palustria* Dahlst., is discussed.

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Taraxacum leporinum S. Nord. & van Soest spec. nov. (Fig. 1)

Planta 0.5—1 dm alta, basi araneosa. Folia sat obscure subprasino-viridia, petiolus rubroviolaceis, angustis (parte inferiore sat alatis), nervo mediano rufopurpureo. Folia usque ad 10 cm longa, lobata, subglabra; lobi laterales utrique usque ad 7, lineares, integri vel dorse denticulato, acuti vel acutissimi, patentes vel interdum paulo recurvi; interlobia sat longa, angusta, subintegra; lobus terminalis in foliis exteriores anguste sagittatus, usque ad 20 mm longus, acutus vel subobtusus, in foliis intermediis et interiores sublineare, usque ad 10 mm longum, acutum, lobulis basalibus linearibus vel anguste triangularibus, usque ad 3 mm longis. Scapi numerosi, rubroviolacei, saepe curvati, parce (sub involucre subdense) araneosi. Involucrum c. 14 mm longum, basi crassiusculum, fuscoviride. Squamae exteriores adpressae vel subadpressae, ovatae usque ad 3.5 mm latae, 7 mm longae, in apicem rufoviolaceum attenuatae, margine late ± albo vel purpureo instructae, interiores apice atroviolaceae, omnes laeves. Calathium paulo radians, saturate luteum. Ligulae marginales angustae, planae, extus stria atropurpurea ornatae. Antherae vacuae. Stylus et stigmata sat obscure fuscescentia. Achenium rubrobadium, pyramide inclusa c. 4.5 mm longum, superne spinolosum, ceterum laeve, in pyramidem anguste cylindricum, c. 1 mm longum abrupte abiens. Rostrum 10 mm longum. Pappus subsordide albus, 5.5 mm longus.

Holotypus: Öland: Ventlinge, c. 300 m E of the church. Together with *T. vestrogothicum, T. balticum, T. limnanthes, T. suecicum, T. intercedens, T. langeanum,* 24.5.1973, leg. Sten Nordenstam (S). — Isotypus in herb. v. Soest 54944.

The name *T. leporinum* is chosen because the leaves (thicker and more rigid in *intercedens* and seldom damaged by animals) seem to be eaten by hares.

Among the species accompanying *T. leporinum, T. vestrogothicum* is unexpected. This species has earlier only been reported on Öland from Alböke, Föra and Böda in the northern part of the island (Saarsoo & Haglund 1963), but had been seen by one of us (Nordenstam) about 800 m E of the church in Ventlinge in May 1962.

T. leporinum is allied to *T. intercedens* Markl., but differs from the latter in having bluish and not greyish leaves with ± linear and not distinctly triangular side lobes, these being longer than in *T. intercedens,* often recurved and distinctly acute; the terminal lobe is longer. The pyramid of the darker red-brown achene is thinner and longer.

From *T. vestrogothicum* Dahlst., which is similar in leaf shape, it differs in the reddish achenes and the lack of pollen. Further, the rostrum is somewhat shorter and the pyramid narrower. The outer ligulas have darker stripes and the inner involucral bracts are distinctly dark violet.

T. leporinum belongs to a small group of *Taraxacum* with reddish achenes, pointing to sect. *Erythrosperma* Dahlst., and with a series of morphological features

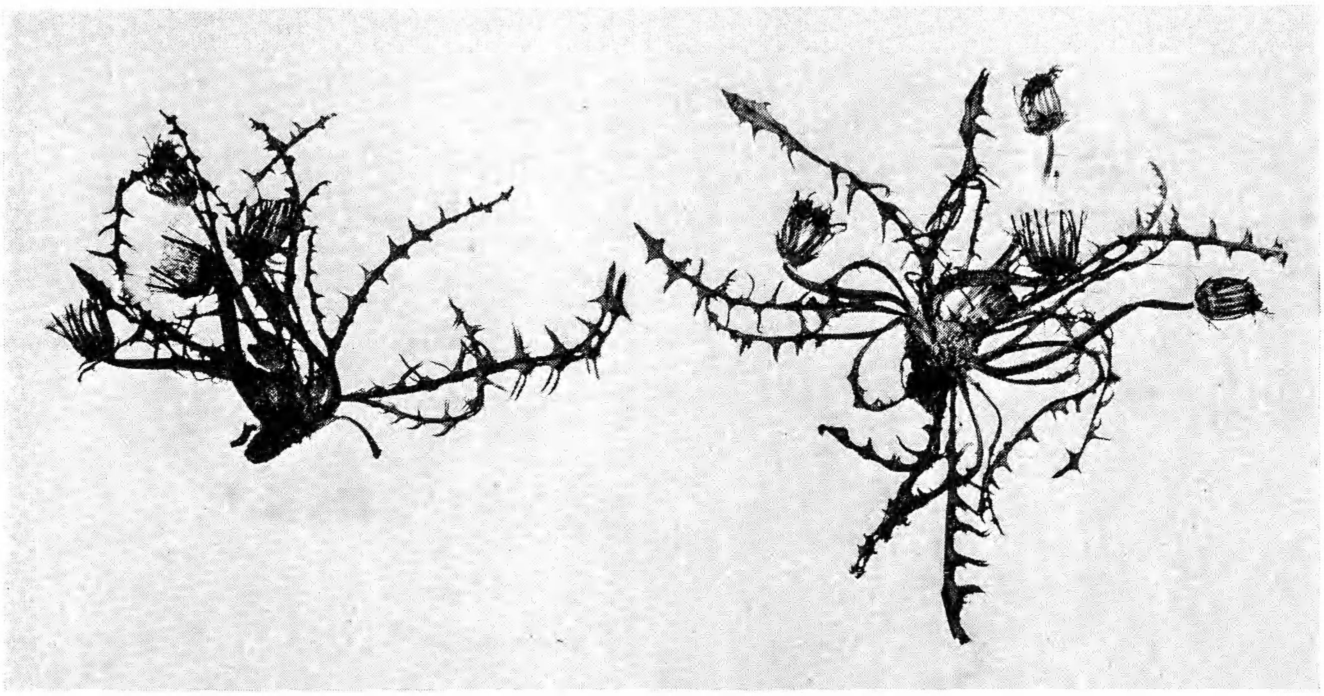

Fig. 1. *Taraxacum leporinum* S. NORD. & VAN SOEST, holotypus (S). — ×0.4. — Photo A. SUNDVALL.

pointing to sect. *Palustria* DAHLST. Four species belong to this group named *Taraxacum langeanum*-Gruppe by DOLL (1973 pp. 5, 30), viz. *T. intercedens* MARKL., *T. langeanum* DAHLST., *T. westhoffii* HAGD., V. SOEST & ZB., and *T. leporinum* S. NORD. & V. SOEST. Up to now this group has been considered a part of sect. *Erythrosperma* because of the red achenes, partly also because here and there gibbosities have been observed on the involucral bracts, though only vaguely.

The red colour of the achene is a feature not only of sect. *Erythrosperma* but of 13 out of the 39 sections of *Taraxacum*. In these 13 sections the achene is exclusively red (sect. *Rhodocarpa* V. SOEST: *T. schroeterianum* HAND.-MAZZ.) or the colour may be more or less dominant (sect. *Erythrosperma* DAHLST. em. LINDB. FIL., sect. *Erythrocarpa* HAND.-MAZZ. em. DAHLST. em. V. SOEST). However it may also be present to some degree, in other sections sometimes only exceptionally. For instance in sect. *Obovata* V. SOEST only *T. obovatum* (WILLD.) DC. ssp. *obovatum* has red achenes; in sect. *Tibetana* V. SOEST only two species have red achenes, viz. *T. eriopodon* DON (s. str.) and *T. sikkimense* HAND.-MAZZ. In other cases red-fruited forms of normally grey-fruited species are known such as in sect. *Spuria* DC.: *T. montanum* (CAM.) DC. f. *rubrofructum* V. SOEST. All this means that too much stress must not be laid on the colour of the achene, in particular not when characterizing sections.

Therefore the question may be raised as to whether the group under consideration really belongs to sect. *Erythrosperma* or to sect. *Palustria*, or, possibly, whether it could be considered an "intermediate" section.

It must be said that gibbosities on the bracts are not known in sect. *Palustria*, a feature in favour of sect. *Erythrosperma*. On the other hand, the characteristics of the leaves and involucres, and the ecological features, strongly favour sect. *Palustria*. As far as we can see the shape of the achenes is not conclusive.

If one prefers to consider the group as an intermediate section the possibility of a hybrid origin must be taken into account.

In the case of *T. westhoffii* it would then probably be a hybrid between a species of sect. *Erythrosperma* and one of sect. *Palustria* (in casu *T. palustre* (LYONS) SYMONS or *T. maritimum* HAGD., V. SOEST & ZB.). As regards the three Baltic species the habitats of species of both sections are always close together.

Further study seems to be necessary. For the present we only wish to raise the question of the taxonomic position and affinities of this interesting group of *Taraxacum*.

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Studies in African Cyperaceae XI

New Taxa and Combinations in Abildgaardia Vahl

Kåre Arnstein Lye

LYE, K. A. 1974 12 30. Studies in African Cyperaceae XI. New taxa and combinations in Abildgaardia Vahl. — Bot. Notiser 127: 493—497. Lund. ISSN 0006-8195.

One new species and one new variety are described from Uganda, viz. *Abildgaardia ugandensis* K. LYE sp. nov. and *A. hispidula* (VAHL) K. LYE var. *pyriformis* K. LYE var. nov. *A. ugandensis* K. LYE has previously been confused with *Bulbostylis schimperiana* (HOCHST.) C. B. CL.

The modern circumscription of this genus involving the sinking of *Bulbostylis* KUNTH ex C. B. CL. in *Abildgaardia,* necessitates the coining of 30 new combinations for East African species and varieties of *Abildgaardia*.

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Abildgaardia ugandensis K. LYE sp. nov.

Herbae perennes. *Culmi* dense caespitosi, 10—25(5—50) cm alti, 0.3—0.5 mm lati. *Folia* culmo breviora, 5—20 cm longa et 0.3—0.7 mm lata. *Bracteae* ad 12 mm longae. *Spiculae* numerosae, 4—8 mm longae et 2—3 mm latae. *Squamae* numerosae, ferrugineae plurinervosae. *Nux* 0.8 mm longa.

TYPUS SPECIEI: LYE 184, 6.XI.1968. Uganda, West Mengo district, Entebbe, along Lake Victoria, VR 4006, 1,140 m (MHU holotype, EA, K, UPS isotypes).

Abildgaardia ugandensis (Figs. 1, 2) is a rather densely tufted perennial without swollen stem-bases. Culms usually 10—25 (rarely 5—50) cm long and 0.3—0.5 mm thick, usually glabrous except for a few scattered short spine-like hairs below the inflorescence. Leaves 5—20 cm long and 0.3—0.7 mm broad, flat or canaliculate (or with margins completely inrolled), with short spine-like hairs on the ridges. Leaf-sheath very pale brown to almost white, transparent, glabrous or slightly hairy, with up to 10 mm long flexuose hairs in the throat.

Inflorescence of 3—10 sessile spikelets forming a compact head. Main inflorescence-bract 3—12 mm long with long flexuose hairs between leaf-blade and the subula. Spikelets obtuse, up to 8 mm long and 3 mm broad, but usually 4—5 mm long and 2 mm broad. Glumes numerous, glabrous or pubescent, reddish-brown with 3-nerved, usually green midrib ending below the apex; margin ciliate; apex obtuse or emarginate (the midrib often breaks in the middle as the achene matures). Achene about 0.8 mm long with very distinct longitudinal ribs and narrower transverse ribs between the main ribs.

On poor sandy soil and shallow soil on rocks, also in seasonally wet grassland, 1,100—1,300 m. Common along the shores of Lake Victoria, and known from the following Ugandan districts: Busoga, East Mengo, Masaka, Teso, West Mengo.

Abildgaardia ugandensis has previously been confused with *Bulbostylis schimperiana* (HOCHST. ex A. RICH.) C. B. CL. The holotype of *Fimbristylis schimperiana* HOCHST. ex A. RICH. in Paris is, however, the same as *Fimbristylis humilis* A. PETER, i.e. an annual species with darker glumes and deciduous style-base (cf. Fig. 3).

Specimens seen: CHANDLER 1362 (KAW, K), 2502 (K); DAWE 32 (KAW), 259 (KAW, K);

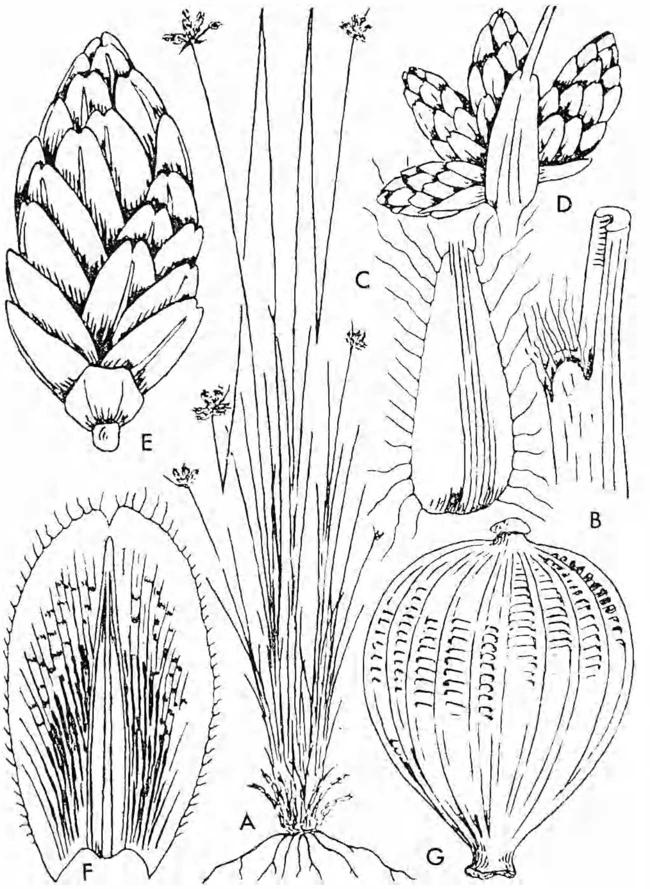

Fig. 1. *Abildgaardia ugandensis* K. Lye. — A: Habit, slightly reduced. — B. Throat of leaf-sheath. — C: Base of main inflorescence-bract. — D: Inflorescence. — E: Spikelet. — F: Glume. — G: Achene. — Drawn from Haines 4027 (Kazi, West Mengo, Uganda). Original by Richard Wheeler Haines.

Dümmer 4460 (K); Haines 4027 (MHU, K); Kertland 490 (MHU); Langdale-Brown 2314 (KAW), 2358 (KAW, EA); Lind 137 (MHU, EA), Lock 67/14 (MHU, EA), 68/189 (MHU); Liebenberg 467 (KAW); Lye 94 (MHU), 184 (MHU, EA, K), 1830 (MHU), 2978 (MHU, K), 5022 (MHU), 5097 (MHU), 5365 (MHU, EA, K); Maitland 1188 (KAW, K); Mukiibi 250 (MHU), Norman 44 (K); Rose 603 (MHU); Wood 23 (K), 198 (K), 340 (EA, K), 355 (EA), 603 (ENT, K), 772 (ENT, EA, K).

Abildgaardia hispidula (Vahl) K. Lye var. **pyriformis** K. Lye var. nov.

Herbae annuae, pubescentes. *Culmi* caespitosi, 5—30 cm alti et 0.2—0.6 mm lati, gracillimi. *Folia* 5—15 cm longa et 0.2 mm lata. *Bracteae* ad 15 mm longae. *Spiculae* 1—6, 4—8 mm longae et 2—3 mm latae. *Squamae* ovatae, 3 mm longae, rufae. *Nux* 1.3 mm longa et 1.0 mm lata.

TYPUS: Haines 4208, Moroto, Karamoja, Uganda (MHU holotype).

Abildgaardia hispidula var. *pyriformis* is a slender tufted annual with numerous culms and slender roots (Fig. 4). Culms 5—30 cm high and 0.2—0.6 mm thick, deeply ridged and densely set with short hairs; base of culms covered by very pale translucent old leaf-sheaths. Leaves 5—15 cm long and about 0.2 mm wide, canaliculate and densely set with short hairs (0.1—0.2 mm long), but throat and leaf-sheath with 2—3 mm long slender hairs; leaf-sheath very pale, transparent.

Spikelets in a simple umbel-like anthela or solitary. Main bracts leafy, 5—15 mm long, densely hairy. Spikelets 4—8 mm long and 2—3 mm broad. Glumes about 3 mm long, reddish-brown with a very distinct green midrib (distinctly protruding in the lower glumes, slightly or not protruding in the upper ones); short hairs present on margin, surface and midrib. Style with 3 style-branches. Achene about 1.3 mm long and 1.0 mm broad, with a very distinctly cuneate base (sometimes even more distinct from the upper part of the nutlet than shown in the figure), white or pale brown; surface transversely wavy except for the 3 protruding tuberculate ribs; swollen base of the style either deciduous or persistent as a distinct brown knob (thus showing an intermediate position between the two genera *Bulbostylis* and *Abildgaardia*).

On sandy roadside ditches and in eroded parts of shrubland, 1,150—1,200 m. Probably locally common in Karamoja, Uganda.

Specimens seen: Haines 4208 (MHU); Wilson 180 (EA), 1028 (EA). Another collection, viz. Wood 748 (EA, K) from Bugisu district, is somewhat intermediate in character to var. *hispidula*.

This variety differs from var. *hispidula* in the more slender root system and the narrower basal part of the nutlet.

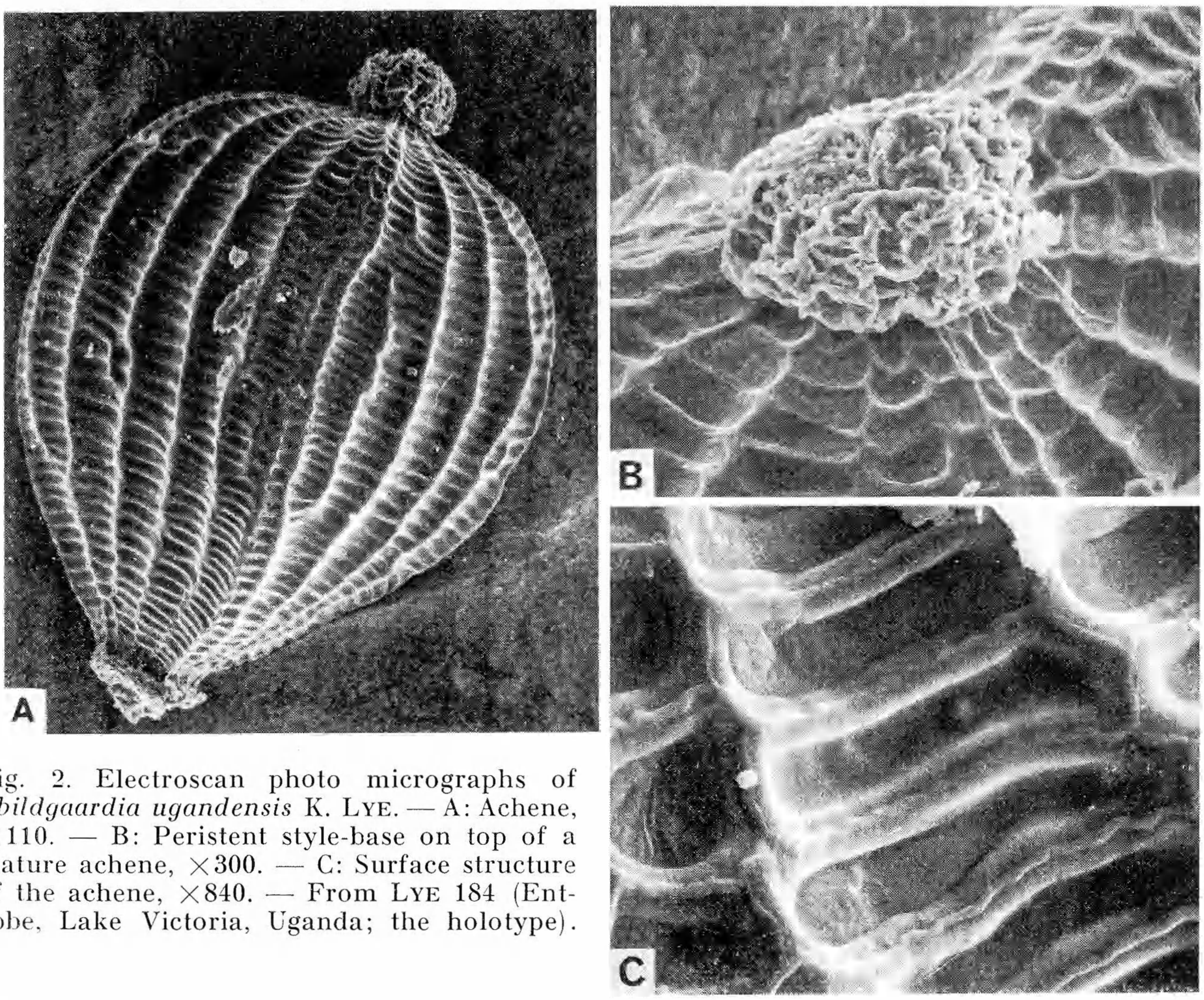

Fig. 2. Electroscan photo micrographs of *Abildgaardia ugandensis* K. LYE. — A: Achene, ×110. — B: Persistent style-base on top of a mature achene, ×300. — C: Surface structure of the achene, ×840. — From LYE 184 (Entebbe, Lake Victoria, Uganda; the holotype).

NEW COMBINATIONS

Recently the generic concept of *Abildgaardia, Fimbristylis* and *Bulbostylis* has been considerably altered, cf. KRAL (1971), GORDON-GRAY (1971), and LYE (1971, 1973). BODARD (1963) and HOOPER & NAPPER (1972) have, however, followed the old treatment of CLARKE (1902), a system which the present author believes should be completely abandoned.

The following new combinations of *Abildgaardia* are needed for "The Sedges of Uganda and Kenya":

Abildgaardia abortiva (STEUD.) K. LYE comb. nov. — *Fimbristylis abortiva* STEUD. in Syn. Pl. Glum. 2: 111 (1855).

Abildgaardia argentobrunnea (C. B. CL.) K. LYE comb. nov. — *Bulbostylis argentobrunnea* C. B. CL. in Flora Trop. Afr. 8: 440 (1902).

Abildgaardia buchananii (C. B. CL.) K. LYE comb. nov. — *Bulbostylis buchananii* C. B. CL. in Flora Trop. Afr. 8: 437 (1902).

Abildgaardia burchellii (FIC. & HIERN) K. LYE comb. nov. — *Fimbristylis burchellii* FIC. & HIERN in Trans. Linn. Soc. ser. 2, Bot. 2: 28, t. 6 B, Fig. 7—15 (1881).

Abildgaardia capillaris (L.) K. LYE comb. nov. — *Scirpus capillaris* L. in Spec. Plant. I: 49 (1753).

Abildgaardia cardiocarpoides (CHERM.) K. LYE comb. nov. — *Bulbostylis cardiocarpoides* CHERM. in Rev. Zool. Bot. Afr. 24: 298 (1934).

Abildgaardia clarkeana (BODARD) K. LYE comb. nov. — *Bulbostylis clarkeana* BODARD in Bull. Soc. Bot. Fr. 108: 308 (1961).

Abildgaardia coleotricha (A. RICH.) K. LYE comb. nov. — *Fimbristylis coleotricha* HOCHST. ex A. RICH. in Tent. Fl. Abyss. 2: 506 (1851).

Abildgaardia congolensis (DE WILD.) K. LYE comb. nov. — *Bulbostylis congolensis* DE WILD. in Pl. Bequaert. 4: 194 (1927).

Abildgaardia contexta (NEES) K. LYE comb. nov. — *Trichelostylis contexta* NEES in Linnaea 10: 146 (1836).

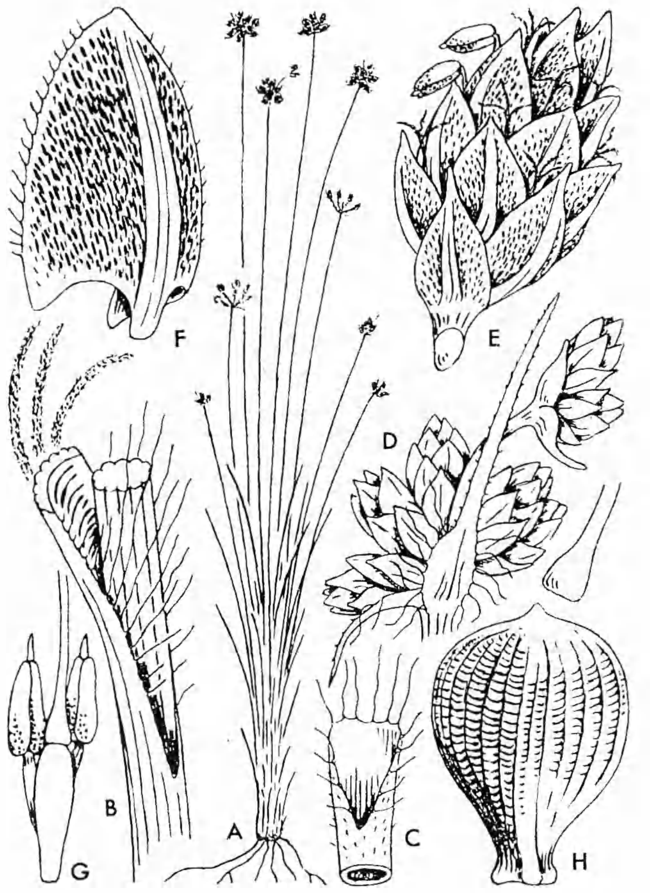

Fig. 3. *Abildgaardia schimperiana* (A. RICH.) K. LYE, syn. *Fimbristylis humilis* A. PETER. — A: Habit, slightly reduced. — B: Throat of leaf-sheath with culm and leaf-base. — C: Sheath. — D: Inflorescence. — E: Spikelet. — F: Glume. — G: Flower with ovary and two stamens. — H: Achene. — Drawn from HAINES 4037 (Bukwa-Kapchorwa, Sebei, Uganda). — Original by RICHARD WHEELER HAINES.

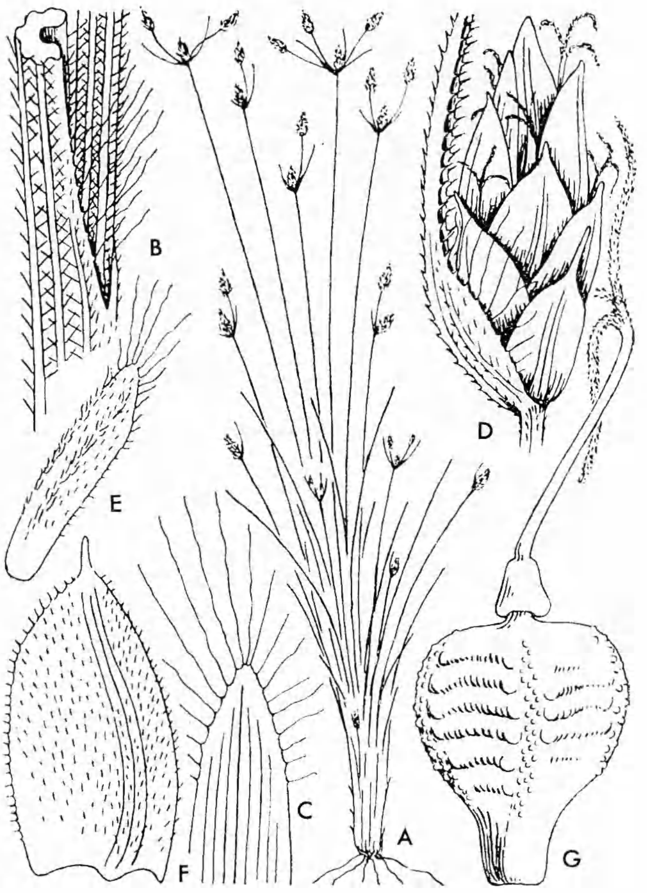

Fig. 4. *Abildgaardia hispidula* (VAHL) K. LYE var. *pyriformis* K. LYE. — A: Habit, slightly reduced. — B: Throat of leaf-sheath. — C: Leaf-sheath. — D: Spikelet. — E: Prophyll. — F: Glume. — G: Achene. — Drawn from HAINES 4208 (Moroto, Karamoja, Uganda; the holotype). — Original by RICHARD WHEELER HAINES.

Abildgaardia densa (WALL.) K. LYE comb. nov. — *Scirpus densus* WALL. in ROXB. Fl. Ind. ed. 1, I: 231 (1820).

Abildgaardia filamentosa (VAHL) K. LYE comb. nov. — *Scirpus filamentosus* VAHL in Enum. 2: 262 (1806).

Abildgaardia filamentosa (VAHL) K. LYE var. *holubii* (C. B. CL.) K. LYE comb. nov. — *Bulbostylis cardiocarpa* (RIDL.) C. B. CL. var. *holubii* C. B. CL. in Flora Trop. Afr. 8: 434 (1902).

Abildgaardia filamentosa (VAHL) K. LYE var. *metralis* (CHERM.) K. LYE comb. nov. — *Bulbostylis metralis* CHERM. in Arch. Bot. Caen 4, Mém. 7: 34 (1931).

Abildgaardia glaberrima (KÜK.) K. LYE comb. nov. — *Bulbostylis glaberrima* KÜK. in Notiz. II. Bot. Gard. Berlin IX: 308 (1925).

Abildgaardia hispidula (VAHL) K. LYE comb. nov. — *Scirpus hispidulus* VAHL in Enum. 2: 276 (1806).

Abildgaardia hispidula (VAHL) K. LYE var. *filiformis* (C. B. CL.) K. LYE comb. nov. — *Bulbostylis filiformis* C. B. CL. in Flora Trop. Afr. 8: 441 (1902).

Abildgaardia hispidula (VAHL) K. LYE var. *oligostachys* (A. RICH.) K. LYE comb. nov. — *Fimbristylis oligostachys* HOCHST. ex A. RICH. in Tent. Fl. Abyss. 2: 505 (1851).

Abildgaardia humilis (KUNTH) K. LYE comb. nov. — *Isolepis humilis* KUNTH in Enum. Pl. 2: 207 (1837).

Abildgaardia johnstonii (C. B. CL.) K. LYE comb. nov. — *Bulbostylis johnstonii* C. B. CL. in Flora Trop. Afr. 8: 442 (1902).

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Abildgaardia miegei (BODARD) K. LYE comb. nov. — *Bulbostylis miegei* BODARD in Bull. Soc. Bot. Fr. 108: 307 (1961).

Abildgaardia oritrephes (RIDL.) K. LYE comb. nov. — *Fimbristylis oritrephes* RIDL. in Trans. Linn. Soc. ser. 2, Bot. 2: 155 (1884).

Abildgaardia pusilla (A. RICH.) K. LYE comb. nov. — *Fimbristylis pusilla* HOCHST. ex A. RICH. in Tent. Fl. Abyss. 2: 506 (1851).

Abildgaardia schimperiana (A. RICH.) K. LYE comb. nov. — *Isolepis schimperiana* HOCHST. ex A. RICH. in Tent. Fl. Abyss. 2: 501 (1851).

Abildgaardia scleropus (C. B. CL.) K. LYE comb. nov. — *Bulbostylis scleropus* C. B. CL. in Flora Capensis (ed. W. T. THISELTON-DYER) 7: 207 (1898).

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Studies in African Cyperaceae XII

New Taxa and Combinations in Fimbristylis Vahl

Kåre Arnstein Lye

LYE, K. A. 1974 12 30. Studies in African Cyperaceae XII. New taxa and combinations in Fimbristylis Vahl. — Bot. Notiser 127: 498—499. Lund. ISSN 0006-8195.

Fimbristylis robusta K. LYE is described from Masaka district in Uganda. This species resembles *F. ferruginea* (L.) VAHL, but lacks the pubescent glumes of that species, and *F. longiculmis* STEUD., but has well-developed leaves and an entirely different habitat.

The following new combinations are coined: *Fimbristylis complanata* (RETZ.) LINK var. *keniaeensis* (KÜKENTH.) K. LYE and *F. complanata* (RETZ.) LINK var. *subaphylla* (BOECK.) K. LYE.

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Fimbristylis robusta K. LYE sp. nov.

Herbae perennes robustae. *Rhizoma* horizontaliter repens lignosum percrassum. *Culmi* 35—50 cm alti. *Folia* 0.8—1.5 mm lata. *Bracteae involucrantes* 5—15 mm longae. *Anthelae* 5—6 spiculosae. *Spiculae* ovoideae vel ovoideo-ellipsoideae terestes 7—12 mm longae. *Squamae* 4—5 mm longae. *Stigmatae* 2. *Nux* 1.4—1.8 mm longa et 1.4 mm lata.

TYPUS SPECIEI: LYE 6213, 6.VI.1971. Uganda, Masaka district, 4—5 km north of Lake Nabugabo, grid ref. UQ 7767, 1,140 m (MHU holotype).

Fimbristylis robusta K. LYE (Fig. 1) is a perennial with a very robust swollen stem-base and very thick creeping rhizome, or with numerous crowded rhizomes giving robust tussocks. Rhizome up to at least 4 cm long, slightly flattened and about 7 mm wide and 5 mm thick, but appearing even thicker (to about 10 mm) with the persistent, often fibrous basal leaf-sheaths; the woody central part of the rhizome reddish. Stem 35—50 cm long and 0.5—1.0 mm thick, rounded or slightly flattened, glabrous, with rounded distinct or obscure ridges. Leaves 0.8—1.5 mm wide, flat or canaliculate, with spine-like teeth on margins especially near the tip; all leaves basal; leaf-sheaths pale brown, the throat with a very dense rim of hairs.

Inflorescence a pseudoumbel with 1 sessile and 4—5 stalked spikelets. Largest inflorescence-bract leafy, but only 5—15 mm long. Spikelets 7—12 mm long and 3.5—5.5 mm wide, lanceolate, dark brown, with numerous spirally set glumes. Glumes 4—5 mm long, glabrous, strongly concave with shortly mucronate midrib, chestnut-brown but with paler midrib; the lowest glume sterile, triangular and much narrower than the upper fertile glumes. Stamens 3, with flattened filaments. Ovary with about 2.7 mm long style, fimbriate above, and 2 rough style-branches. Achene 1.4—1.8 mm long and about 1.4 mm wide, obovate with narrow base, biconvex, yellowish with numerous longitudinal striations, but mature achene probably darker.

In seasonally wet grassland, 1,140 m (3,750 ft). Very rare. Only known from the type-locality.

Specimens seen: Lye 4345 (MHU, K), 6213 (MHU, EA, K).

This plant is easily recognized on its thick creeping or congested rhizome and few spikelets. It has some characters in common with *F. scabrida, F. pilosa,* and *F. madagascariensis,* but cannot really be confused with any of these. It is possibly most closely related to *F. ferruginea* (but lacks the pubescent glumes of that species) and *F. longiculmis* (but has well-developed leaves).

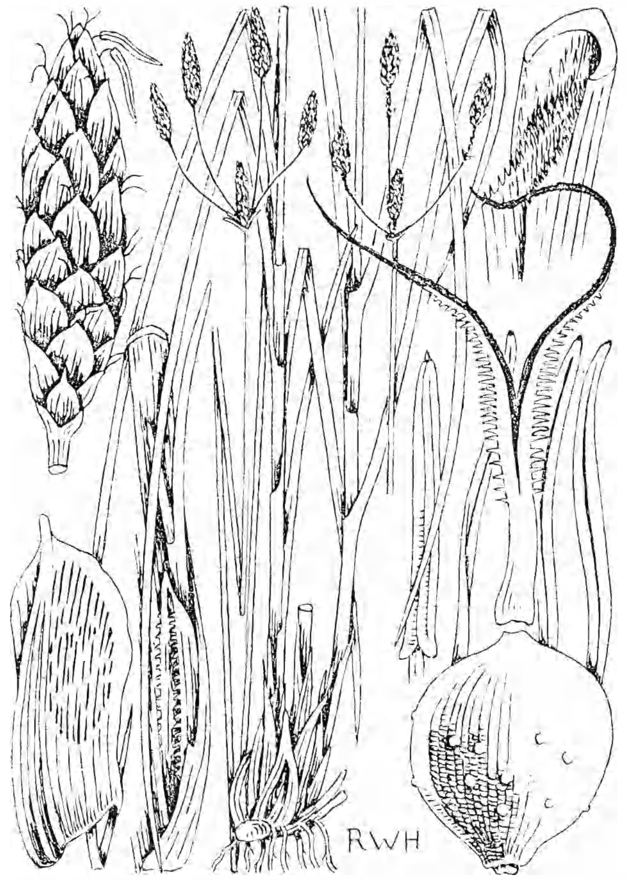

Fig. 1. *Fimbristylis robusta* K. LYE. Drawn from the type-material, LYE 6213. — Original by RICHARD WHEELER HAINES.

NEW COMBINATIONS

The following new combinations are needed for "The Sedges of Uganda and Kenya":

Fimbristylis complanata (RETZ.) LINK var. *keniaeensis* (KÜKENTH.) K. LYE comb. nov. — *Fimbristylis keniaeensis* KÜKENTH. in Notizbl. Bot. Garten Mus. Berlin-Dahlem, no. 85, bd. 9: 307 (1925).

Fimbristylis complanata (RETZ.) LINK var. *subaphylla* (BOECK.) K. LYE comb. nov. — *Fimbristylis subaphylla* BOECK. in Flora 62: 565 (1879).

Studies on the Vegetation of the Bhadarwah Hills

I. Altitudinal Zonation

V. Kaul and Y. K. Sarin

Kaul, V. & Sarin, Y. K. 1974 12 30. Studies on the vegetation of the Bhadarwah Hills. I. Altitudinal zonation. — Bot. Notiser 127: 500—507. Lund. ISSN 0006-8195.

The vertical distribution of plant communities at altitudes of between 1,600 and 3,900 m has been studied in the Bhadarwah Hills in the western Himalayas in the State of Jammu and Kashmir, India. There is a well-marked zonation of vegetation from lower to upper elevations. The lower zone between 1,600 and 1,900 m comprises forests of *Quercus incana, Q. floribunda* and *Pinus wallichiana*. The intermediate slopes extending from 1,900 to 2,600 m have almost pure stands of *Cedrus deodara* while localities situated from 2,600 m to the upper timber limit at 3,700 m are covered with *Abies pindrow* forests. In all these zones the oaks are restricted to drier situations while moist slopes bear various species of conifers. Each component species appears to have an optimum and a minimum range of temperature and moisture. Prevalence of a favourable temperature-moisture regime at elevations differing from the usual altitudinal zone of a species, leads to the growth of the latter at altitudes far above or below their normal altitudinal zones. This explains the occurrence of *Abies pindrow* and other high-altitude elements in moist and cool ravines and valleys at lower elevations, and a further ascent of species of lower altitudes on warm and dry southerly slopes.

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INTRODUCTION

The Himalayas, the massive chains of mountains situated to the north of the Indian sub-continent, form a very interesting ecological area. In their vast expanse, ranging vertically from about 1,000 m above sea level to well above 9,000 m and stretching longitudinally from the comparatively dry areas of Kashmir in the west to typically wet localities in Assam, a variety of environmental conditions are met with. Thus moving from west to east one finds a uniform gradient in the environmental pattern in terms of temperature, humidity, rainfall and snowfall, etc. Similar gradients are found from lower to higher elevations, though the temperature changes take place more quickly. These changes naturally lead to marked disparities in the structure and composition of vegetation between one place and another, and observations made in one place do not generally hold good for others near by. The information at present available pertains mostly to the areas lying east of the River Ravi. The areas situated to the west, including the whole of Jammu and Kashmir, have not yet been studied. The present investigation was, therefore, begun to study the structure, composition and distribution pattern of the vegetation in these parts. The present paper deals with the distribution of vegetation in relation to *altitude*.

Area Studied

The Bhadarwah Hills lie roughly between the longitudes of 75°11′ and 76°10′ E and the latitudes of 31°11′ and 32°N in the State of Jammu and Kashmir, India. The tract is very rugged and mountainous.

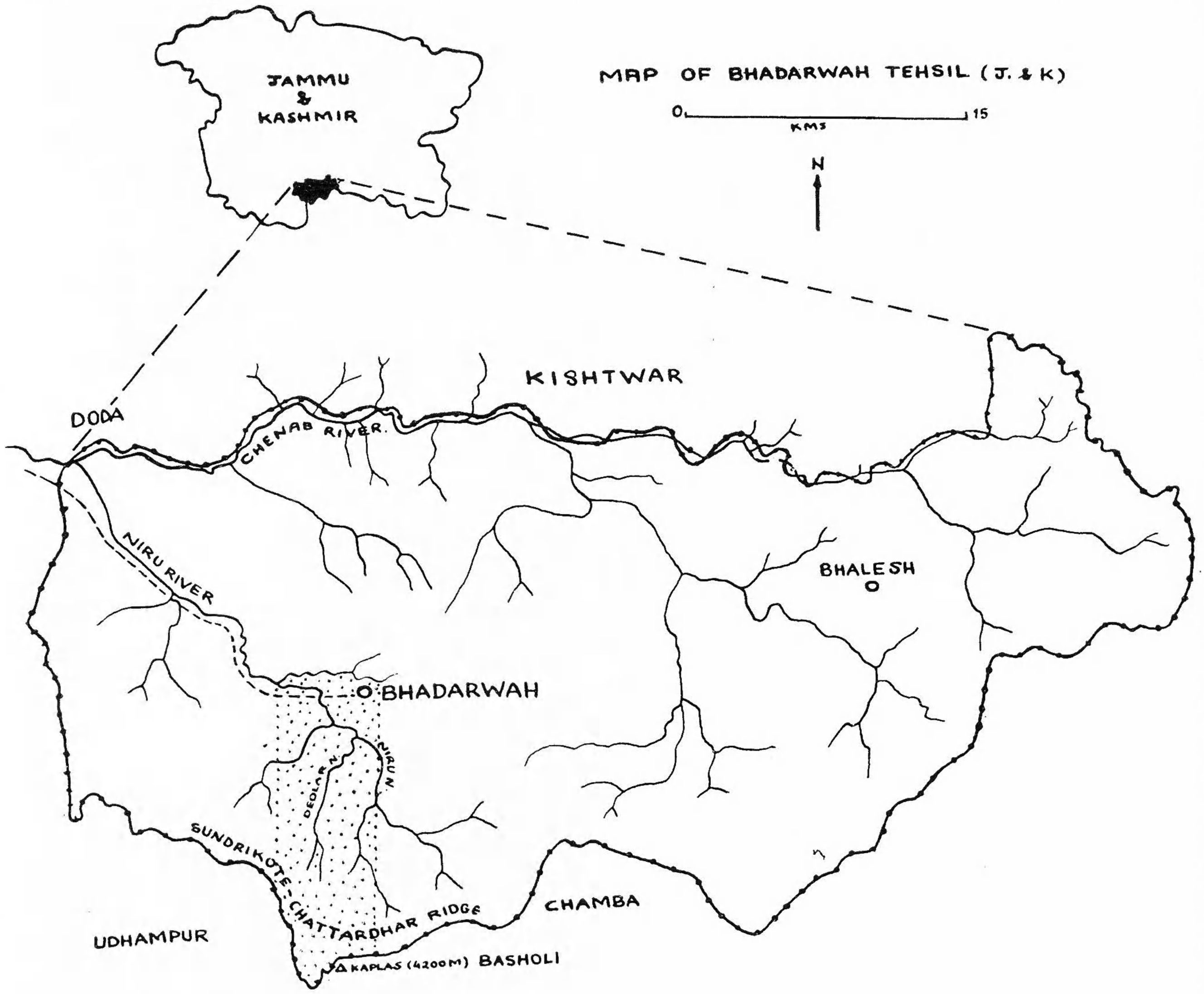

Fig. 1. Map of Bhadarwah Tehsil showing the localities sampled (shaded).

It includes a narrow valley adjacent to a perennial stream, the Niru River (Fig. 1). The valley is flanked on both its eastern and southern sides by the Sundrikote-Chattardhar Ridge which, emerging from the basal plain of the valley at more than 1,600 m above mean sea level attains its maximum elevation of 4,341 m at Kaplas. A number of spurs branching off vertically from this ridge and extending towards the Niru Valley have terraced slopes up to an elevation of 2,400 m and becoming steep to precipitous beyond this.

Climate

The temperature and precipitation data computed from meteorological records are given in Tables I and II. The average annual precipitation is around 1,117 mm. The precipitation during winter months, mostly in the form of snow, accounts for more than 50 % of the total annual precipitation. January is the coldest month of the year. The temperature rises abruptly during April and reaches 28°C during June and July. Night temperatures start falling from October onwards.

Geology and Soil

The major rock types in the area are granite, mica-schists and phyllites besides other geological formations. The typical soil produced by the decomposition of mica-schists and granite is a loose sandy

Table I. Mean, maximum and minimum temperature in °C recorded at Bhadarwah.

Month	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Maximum ..	11.7	13.5	12.9	16.2	23.2	28.7	28.2	27.2	25.9	23.4	14.3	11.6
Minimum ..	0.5	1.7	3.1	7.4	10.4	14.0	16.4	16.2	10.8	6.0	3.9	1.2
Mean	6.1	7.6	8.0	11.8	16.8	21.3	22.3	21.7	18.3	14.7	9.1	6.4

Table II. Mean monthly precipitation in mm recorded at Bhadarwah over a period of 20 years. — Average precipitation for the whole year=1,117 mm. Average precipitation for the four winter months of December to March=572.5 mm. Average precipitation for the eight months from April to November=544.5 mm.

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
170.0	196.0	132.5	80.0	70.5	45.0	125.0	130.5	40.0	27.5	22.5	77.5

loam. The occurrence of secondary deposits over extensive areas has, however, greatly changed the edaphic complex. The soil on glacial moraine, fluvioglacial fans and flood plains is deep and heavy, while that on rock outcrops, talus slopes and scree deposits is shallow and coarse in texture.

Environment and Altitude

Since the area under consideration is extremely mountainous, the altitude ranging from about 1,600 m in the Niru Valley to 3,950 m at the foot of Kaplas peak, this greatly influences both the physiological and climatic conditions as well as the general environmental complex as a whole, as is described below.

TEMPERATURE. The decrease in temperature with increasing height has been investigated in detail in different parts of the world. BLANFORD (1875) recorded a decrease of 1°F per 1,000 feet increase in elevation. According to ROBBINS (1917) and PRICE & EVANS (1937) the temperature in the Rocky Mountains decreased at 3°F per 1,000 feet increase in elevation. Recently, OZENDA (1954), after studying the phenomenon in a number of localities, calculated the average decrease in temperature at 0.55°C per 100 m rise. In the absence of any meteorological data for localities situated above 1,600 m in the area under investigation, OZENDA's coefficient for temperature decrease was used for calculating probable temperatures at various heights during each month of the year. The data obtained reveal a comparatively warmer climate at altitudes ranging from 1,700 to 2,000 m, with the mean monthly temperatures of 5°C throughout the year and temperatures oscillating between 21°C and 22°C in the summer months of June, July and August. There is no change in the next zone (2,000 to 2,300 m) except that the minimum temperature falls below 0°C in January and February. The climate, however, becomes quite cold at altitudes of between 2,300 and 2,900 m, the minimum temperature being < 0°C during December to March, the winter setting in early and the mean maximum temperature remaining below 19°C. Localities situated between 2,900 and 3,500 m have a typical cold climate with a minimum temperature below zero for almost six months of the year and the mean maximum temperature barely reaching 16°C. Extreme cold prevails in localities above 3,500 m. The minimum temperature in these localities is well below 0°C from October to May, while the maximum temperature during the hottest months seldom rises above 12°C remaining at 8°C for almost nine months. Temperature variations are further governed by locality factors and the degree of exposure to the direct rays of the sun. The southerly aspects are warmer than the northerly. Similarly, deep sheltered ravines and depressions have comparatively lower temperatures.

PRECIPITATION. The meteorological data with regard to precipitation at various altitudes in the present locality, as also in other near-by Himalayan localities, are not available. The precipitation has, however, been observed to increase with increasing altitude up to the intermediate slopes, beyond which it gradually declines (BLANFORD 1880, SHREVE 1922 and PURI 1960). A similar pattern of precipitation probably also occurs in the present area as the localities situated below 2,300 m, especially the valleys, experience frequent rains and are more humid.

Precipitation in the form of snow appears to exert greater influence on the environment at varying altitudes. During severe winters cumulative snowfall sometimes amounts to 200 cm or more in the Niru Valley (1,600 to 1,700 m elevation) and increases with increasing elevation till it reaches 600 cm at Seojgalli (3,200 m) and Shankharu Paddar (3,800 m). The period of snowfall also varies according to altitude. At 3,200 m the first snowfall sometimes occurs at the beginning of December and snow continues till the middle of March, while at lower elevations it occurs from January to the middle of February only. The same applies to the period of retention of snow on the ground. It melts after a few days below 2,300 m, while at altitudes of between 2,300 and 2,800 m it is retained on the ground for periods ranging from 20 to 60 days. Localities situated between 2,800 and 3,500 m remain covered with snow from the first week of December to the middle of May. Areas still higher up are not clear of snow until after June.

The other climatic factors influencing the environment of the area at varying altitudes are atmospheric pressure, insolation, wind velocity and humidity. A gradual decrease in the barometric pressure from about 65 cm at about 1,700 m to 50 cm at 3,800 m has been recorded. Similarly, the wind velocity is fairly low in the valley and along the slopes up to an elevation of 3,000 m, beyond which it increases appreciably.

It is, therefore, clear that along an altitudinal stratification of vegetation there is also a stratification of climatic conditions. This feature is, however, sometimes modified by the aspect, the gradient of mountain slopes, the density of the canopy and the dip of the underlying rock strata. The slopes facing northwest ravines are cooler than those facing east and southeast. Similarly, comparatively cooler conditions occur under a dense canopy than in areas where much of the forests have been removed. The Nakka-Puneju spur, comprising a major part of the tract under study, is situated on a dip slope and seepage along cleavage planes of rocks leads to fairly moist conditions in the valleys and the ravines. The localities situated above 3,000 m, as well as those on scarp slopes or the tops of spurs, show a general shift towards aridity due to loss of water through underground seepage, high wind velocity and a longer period of insolation.

MATERIAL AND METHODS

The study was carried out on a massive spur of the Sundrikote-Chattardhar Ridge, at elevations of from 1,600 to 3,800 m. Sampling of the forest stands was carried out by marking out a number of lines at right angles to contours in each of the stands selected on the basis of homogeneity of the stand within a particular altitudinal zone. Tree quadrats (15×15 m) were marked out along these lines at regular intervals of 100 m. The shrub and herb quadrats (5×5 m and 2×2 m respectively) were marked out within these larger tree quadrats. Inventories of component species were prepared by list count quadrat methods (OOSTING 1958). The quantitative characters noted in the field were (I) density, as number of individuals per unit area, (II) frequency of occurrence and (III) total basal area per unit area, in the case of trees above 20 cm d.b.h. measured at breast height, and at ground level for shrubs and transgressives. The data obtained were analysed according to CURTIS and MCINTOSH (1951), where percentage frequency, density and relative dominance were summed up and the summation value expressed as Importance Value Index (IVI). The vegetational status of a component species at different altitudes was determined on the basis of the IVI.

OBSERVATIONS

The mountain slopes, rising abruptly from the basal plain of the valley of the River Niru, show the vegetal types in the foothills giving way in rapid upward succession to other types each in turn predominating in only one particular altitudinal zone. These changes imply a practically complete change in the composition and structure of the vegetation which naturally leads to zonation into well-organized communities at various levels of elevation.

The forests dominated by *Quercus incana, Quercus floribunda* or *Pinus wallichiana* are restricted to elevations of between 1,600 and 1,900 m. *Quercus floribunda* and *Quercus incana* occupy lower slopes and rock outcrops up to 2,000 m on warm southerly slopes. *Pinus wallichiana* forms a belt of varying width at the foot of the Chattar-Sundrikote ridge from about 1,750 m giving way to *Cedrus deodara* at 1,900 m on northwesterly slopes. On southerly slopes it tends to be restricted to hollows and depressions, giving way to the oaks in warmer situations. The belt above this, between 1,900 and 2,600 m, is occupied by *Cedrus deodara.* These forests merge into *Pinus wallichiana* and *Abies pindrow* forests at their lower and upper limits respectively. The composition of *Cedrus deodara* forests, however, undergoes a gradual change from lower to higher altitudes. At elevations of between 1,900 and 2,100 m there is a fair amount of *Pinus wallichiana*; at altitudes of between 2,100 and 2,400 m, the stand is almost pure while above 2,400 m as well as in sheltered localities at lower altitudes *Cedrus deodara* is increasingly admixed with *Abies pindrow* and a number of the broad-leaved species of higher elevations. There is a narrow ecotone of mixed conifers, i.e. *Cedrus deodara, Abies pindrow* and *Pinus wallichiana* and *Picea smithiana* at altitudes of between 2,400 and 2,600 m. These forests are dominated by *Abies pindrow* on northwesterly slopes and *Cedrus deodara* on the corresponding slopes with a southerly aspect. All the forests except those of *Quercus semecarpifolia,* are dominated by *Abies pindrow* at altitudes of between 2,600 and 3,600 m, the upper limit being the timber limit in the area. The dominance of *Abies pindrow* is, however, broken on rock outcrops and the tops of ridges at about 2,900 m where *Quercus semecarpifolia* forms comparatively pure forests. The arboreal forests fade into bushland vegetation at about 3,500 m. The latter consists of large shrubs of *Rhododendron campanulatum* and *Viburnum nervosum* up to an elevation of 3,600 m and of low stunted shrubs of *Rhododendron campanulatum, Salix fruticulosa* and *Lonicera* spp. between 3,600 and 3,800 m.

The altitudinal zonation of the vegetation is more clearly depicted on the basis of the Importance Value Indices of the species dominating the various associations and subassociations (Fig. 2). *Pinus wallichiana,* the lowermost conifer, attains the highest IVI of 166.04 at 1,800 and 2,100 m. The IVI of *Cedrus deodara,* the next most dominant conifer, increases abruptly from 54.05 at 1,700 and 1,800 m to 198.53 at localities situated above 2,000 m with a corresponding decrease in the IVI of *Pinus wallichiana.* The highest IVI of *Cedrus deodara* (208.05) has been recorded at 2,200 to 2,400 m elevation, beyond which there is a gradual decline up to 2,500 m. The IVI of *Cedrus deodara* declines abrupt-

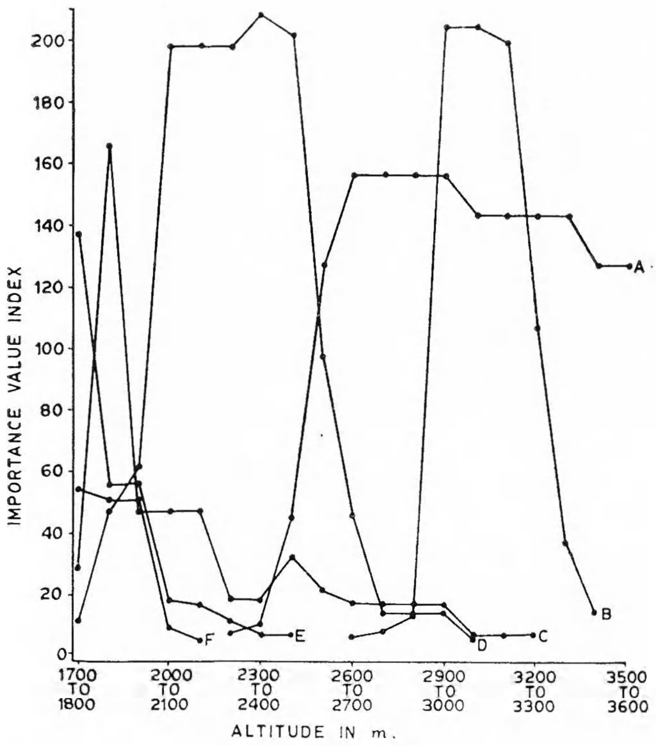

Fig. 2. Importance Value Indices of dominant trees at various elevations in the Bhaderwah Hills. — A: *Abies pindrow*. — B: *Quercus semecarpifolia*. — C: *Pinus wallichiana*. — D: *Cedrus deodara*. — E: *Quercus floribunda*. — F: *Quercus incana*.

ly at 2,550 m as the tree is replaced by *Abies pindrow* at this elevation. The latter attains its maximum Importance Value at 2,600—2,700 m zone though it maintains the IVI at a fairly high level up to 3,300 m or even beyond till the upper timber limit is reached.

The oaks and other broad-leaved species also show a similar behaviour. *Quercus incana,* the lowermost oak, attains the maximum IVI at altitudes below 2,000 m only. *Quercus floribunda* occurring next has the highest IVI at 1,700 to 1,800 m. *Quercus semecarpifolia,* the third most dominant oak, appears only at 2,700 m, attaining the maximum IVI of 206.68 at about 3,100 m, though only on granite outcrops. The other broad-leaved species generally forming the second storey in the conifer forests or constituting the broad-leaved riverine forests, also show a similar stratification. Among these *Aesculus indica* and *Acer pictum* show higher IVIs at between 2,500 and 2,900 m. *Rhus succedanea* appears at 2,200 m and fades out at 2,600 m, while *Fraxinus excelsior* and *Prunus cornuta* show a steady increase from 2,500 to 3,200 m.

The altitudinal stratification is equally apparent among the shrub element. *Berberis lycium,* occupying the lowermost altitudinal zone in the area attains the highest IVI at altitudes of between 1,700 and 2,200 m beyond which it is increasingly admixed with *Parrotiopsis jacquemontiana,* which in its turn is replaced by *Viburnum nervosum* at 2,600 m after attaining the highest Importance Value at altitudes of between 2,300 m and 2,500 m. *Viburnum nervosum,* though occurring throughout the area, shows the maximum IVI of 53.11 at altitudes above 2,600 m as is apparent from Figure 3.

Cases diverging from the above patterns are, however, not infrequent. For example, the groves formed by *Abies pindrow* in cool moist valleys and hollows at elevations far below the zone of dominance are a common sight. Similarly the IVI of *Pinus wallichiana* goes up on fairly exposed slopes even at intermediate elevations, while *Quercus floribunda* can be found occurring quite a bit higher up in warmer situations. The same is also true of the three dominant shrubs. *Parrotiopsis jacquemontiana* is gregarious in shady riverine localities even at 1,700 m while the frequency of *Berberis lycium* increases on warmer intermediate slopes. *Viburnum nervosum,* which is the dominant shrub above 2,300 m, forms dense thickets in deep shady ravines. The direction of the exposure of the slope also alters the altitudinal limits of various plant communities. *Cedrus deodara* and *Abies pindrow* attain higher Importance Values at far lower elevations in cooler northwesterly aspects than on warmer slopes facing southwest. On the other hand, *Pinus wallichiana* is encountered in fair numbers on fairly exposed and warmer slopes situated at higher elevations. Similarly the three species of oaks, though showing a well-marked alti-

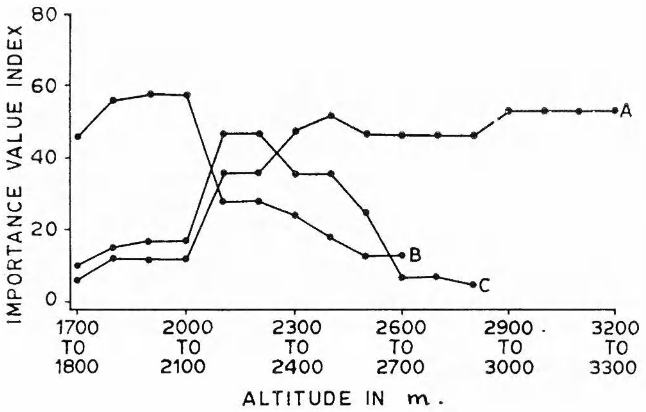

Fig. 3. Importance Value Indices of three dominant shrubs at various elevations in the Bhaderwah Hills. — A: *Viburnum nervosum.* — B: *Berberis lycium.* — C: *Parrotiopsis jacquemontiana.*

tudinal range of distribution, are more prominent in warmer situations within their respective altitudinal zones.

DISCUSSION

OSMASTON (1922) and DUDGEON and KEYNOYER (1925) recognized the temperate zone in the Garhwal Himalayas as extending from 1,650 to 3,900 m altitude above mean sea level. They further determined the altitudinal zones of various dominant trees at between 1,500 and 2,600 m for *Quercus incana*; 1,800 and 3,300 m for *Cedrus deodara*; 2,200 to 2,700 m for *Quercus floribunda* and 2,600 to 3,900 m for *Abies pindrow* and *Quercus semecarpifolia.* In the Punjab Himalayas COVENTRY (1929) described a lower temperate zone of *Pinus wallichiana, Cedrus deodara, Quercus incana* and *Quercus floribunda* between 1,600 and 2,600 m and an upper temperate zone with *Abies pindrow, Picea smithiana* and *Quercus semecarpifolia* as dominant species at 2,600—3,800 m. CHAMPION (1936) divided the temperate forests of the western Himalayas into a lower oak-coniferous zone between 1,600 and 1,900 m with *Quercus incana* and *Pinus wallichiana* as major species; a middle oak-coniferous zone comprised of *Quercus floribunda, Cedrus deodara* and *Picea smithiana* and an upper oak-coniferous zone extending from 2,600 to 3,800 m and dominated by *Abies pindrow* and *Quercus semecarpifolia.* In the area under investigation the temperate zone, extending from 1,600 to 3,700 m, is in accordance with the above observations but differs in the altitudinal distribution of various species. *Quercus incana,* extensive in the lower temperate zone in other areas, occurs only as an admixture in *Quercus floribunda* forests. The latter, on the other hand, barely extends beyond 2,000 m. The middle zone extending from 1,800 to 2,600 m is dominated by *Cedrus deodara* while *Abies pindrow* occupies the next higher belt between 2,600 and 3,700 m. *Quercus semecarpifolia,* the typical oak of the upper temperate zone in localities lying westwards of the Bhadarwah Hills, occurs only above 3,000 m being restricted to the tops of the ridges and rock outcrops.

There is a well-marked lower as well as an upper altitudinal limit for each individual species. Exceptions, however, are also not uncommon. *Abies pindrow,* maples and a few other trees of higher elevations are found forming groves in hollow and shaded ravines far below their usual altitudinal zone of occurrence. On the other hand *Pinus wallichiana* and *Quercus floribunda,* attaining maximum Importance Values in localities below 1,900 m, show an abrupt increase in IVI on the tops of the ridges and well-exposed, warmer situations up to an altitude of 2,500 m. Similarly, a given zone of vegetation usually occurs at higher elevations in moist northerly aspects than on dry southerly slopes.

The occurrence of high-altitude plants in moist shady valleys situated at lower elevations, and of the plants of lower elevations further up the dry slopes, reveal the importance of temperature and moisture in the altitudinal zonation of vegetation. SNOWDON (1933) and DAUBENMIRE (1943) consider the period of insolation, soil texture, velocity of wind, snow cover and the shade provided by the canopy to be major factors determining the distribution of plant communities in Uganda and the Rocky Mountains respectively. All these factors, however, appear to play a secondary role in controlling the moisture-evaporation balance in a locality. A longer period of insolation, high wind velocities and reduced atmospheric pressure increase the rate of evaporation. On the other hand, a snow cover of long duration, seepage through dip slopes and shade provided by a dense canopy keep the habitat cool and moist even during hot summers. The texture and the water-holding capacity of the upper layers of soil also play a major part in maintaining the moisture balance. The moisture from the soil surface evaporates more quickly from coarse-textured soils than from heavy and fine-textured soils.

Oaks and some other broad-leaved species usually grow where evaporation is quite high. Their ability to grow in such areas is probably due to their long penetrating tap-roots which are able to draw water from the deeper layers of the soil. On the other hand, the conifers, characterized by a short and much-branched root system, are restricted to habitats with sufficient moisture in the upper layers of the soil. *Quercus incana* and *Quercus floribunda* occupying rock outcrops and well-exposed slopes at the lowermost elevations seem to be better adapted to high temperatures and greater aridity, while *Quercus semecarpifolia* growing at high altitudes survives better in localities characterized by varying degrees of dryness. Of the conifers *Pinus wallichiana* and *Cedrus deodara* can withstand higher degrees of aridity, though the latter is more adapted to moderate temperatures. *Abies pindrow,* on the other hand, can be considered a typical species of low temperatures and high humidity.

Thus temperature and availability of moisture appear to be the chief factors controlling the distribution of plant communities at various altitudes in the area under investigation. Most of the other environmental factors play their part by altering these two conditions. The conclusion, however, needs to be supported by an exhaustive study of the microclimate at various levels of elevation and its effect on the germination, growth and survival of each of the component species of the vegetation.

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Cytotaxonomic Studies in Three Species of Zephyranthes

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KHALEEL, T. F. & BORAIAH, G. 1974 12 30. Cytotaxonomic studies in three species of Zephyranthes. — Bot. Notiser 127: 508—512. Lund. ISSN 0006-8195.

The cytotaxonomy of three species of *Zephyranthes*, viz. *Z. atamasco*, *Z. carinata* and *Z. texana* has been discussed. The chromosome number is $2n=12$ in *Z. atamasco* and $2n=48$ in the other two species. The genome of *Z. atamasco* is traceable in both *Z. carinata* and *Z. texana*. *Z. texana* is karyologically distinct because of the presence of satellites in one pair of chromosomes. The chromosome number in all the three species conforms to a common multiple suggesting the basic number is $x=6$.

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INTRODUCTION

Zephyranthes HERB. (=*Atamasco* GREEN) commonly known as the Zephyr-lily is a perennial herb widely cultivated for its beautiful, solitary flowers produced on long leafless, hollow scapes. This genus belonging to the subfamily Amarylloideae of Amaryllidaceae includes about 60 species (LAWRENCE 1951) both in the old world and the new world. They are mostly represented by polyploids and some aneuploids.

Although the chromosome numbers of several species of *Zephyranthes* have been reported only certain species have been thoroughly investigated cytologically (BHATTACHARYA 1972). Nevertheless, the interesting cytological behaviour of different species of this genus and the numerical variations within the same species, in addition to the modes of reproduction claim more detailed investigations. The present study on the cytotaxonomy of three species of *Zephyranthes*, viz. *Z. atamasco*, *Z. carinata* and *Z. texana* is an attempt in this line to understand the interrelationships of these species and the variations in the somatic chromosome numbers.

MATERIAL AND METHODS

Plants of each taxon were collected from Hebbal, Bangalore and from the Nandi hills, both in Mysore State, India, and grown in the greenhouse of the Botany Department of the University of Agricultural Sciences, Hebbal, Bangalore, Mysore State, India. Excised root tips were pretreated with 0.15 % colchicine for one hour and fixed in 1:3 acetic alcohol. They were stained following Feulgen's schedule. The slides were made permanent by passing them through 1:1 acetic acid and butanol, and butanol series and mounted in euparal.

Photomicrographs and camera lucida drawings were made for the karyotype analysis. The chromosomes were arranged in the order of increasing length of the short arm. The herbarium specimens of all these species bearing the numbers 1138, 30 and 1375 have been deposited in the UAS herbarium.

OBSERVATIONS

(1) *Zephyranthes atamasco* HERB. (=*Amaryllis atamasco* L.) reproduces by bulbs as well as seeds. The oval bulbs measure about 3—3.5 cm in breadth and 4—4.5 cm in length. The leaves are linear, about 45 cm long, 0.8—1.5 cm broad with blunt rounded tips. The scape is about as long as the leaf. The spathe is 2-cleft and

about 5 cm long being tubular up to 3.5 cm, partially enclosing the flower and clasping above. The flowers are white with a purplish tinge, funnel-shaped and about 9.5 cm long. The perianth consists of six lobes displayed in two whorls of three each, those of the outer whorl slightly larger than the inner ones. The stamens are six, in two whorls, the outer longer ones alternating with the inner shorter ones and bearing the 2-cm-long, versatile anther lobes. The style is longer than the stamens and bears a deeply 3 cleft stigma which spreads out. The fruit is oblong, slightly 3-notched, borne on a 9—10 cm long pedicel.

The chromosome number of this species is 2n=12. The karyotype shows the following types of chromosomes (Figs. 1 A, 2 A): Two pairs of chromosomes with subterminal constrictions (1st and 2nd pair); one pair of chromosomes with submedian constrictions (3rd pair); three pairs of chromosomes with median or near median constrictions (4th—6th pair).

(2) *Zephyranthes carinata* (SPRENG.) HERB. (=*Z. grandiflora* HERB.) reproduces only by bulbs. The bulbs are oval, about 3 cm broad and 3.5 cm long. The thick and fleshy linear leaves are about 48 cm long and 0.8 cm broad with rounded apex. The scape is about 25—30 cm long bearing a 4-cm-long, coloured spathe. The spathe is longer than the pedicel, tubular up to 2 cm and clasping above. It is not cleft. The flowers are deep pink, about 8 cm long and show a 2-whorled, 6-lobed perianth, each lobe being spathulate and about 7.5 cm long. The stamens are six, equal in length, shorter than the limb of the perianth and bear 2-cm-long versatile anthers. The style is longer than the stamens and bears a prominent stigma. The fruits are not formed.

The chromosome number of this species is 2n=48. The karyotype shows the following features (Figs. 1 B, 2 B): Nine pairs of chromosomes with subterminal constrictions (1st—6th, 9th, 12th and 16th pair); five pairs of chromosomes with submedian constrictions (7th, 8th, 10th, 11th and 19th pair); ten pairs of chromosomes with near median or median constrictions (13th—15th, 17th, 18th, 20th—24th pair).

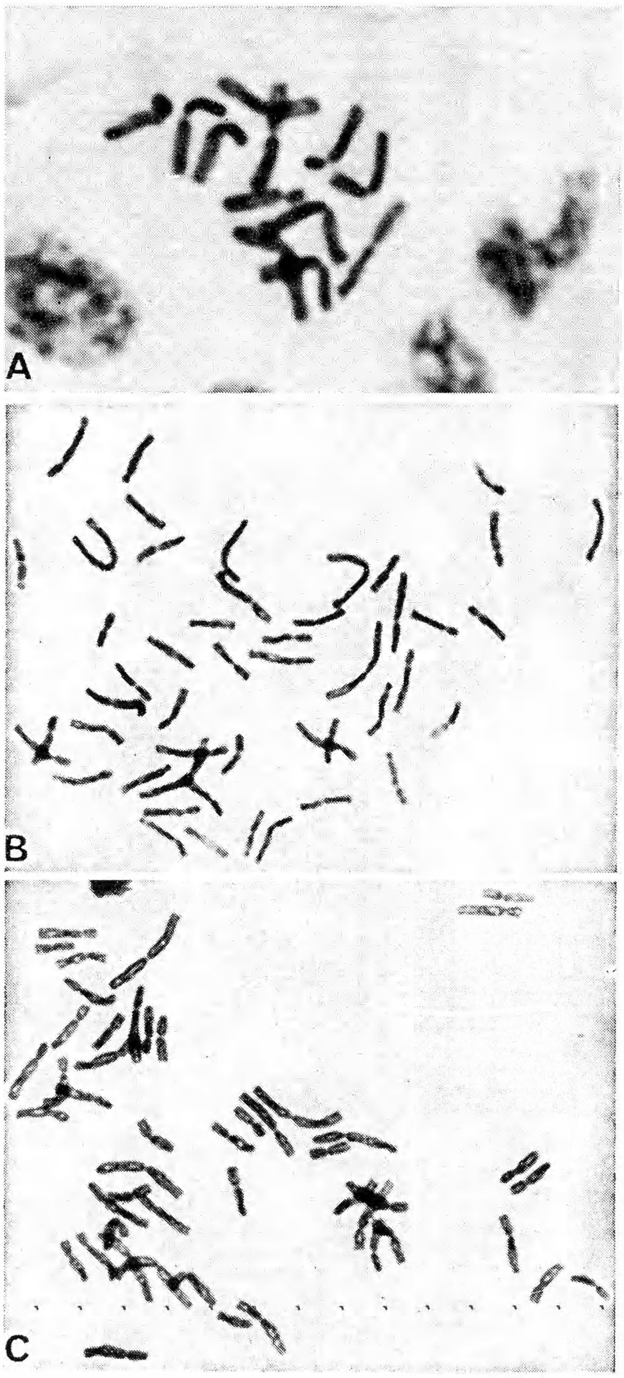

Fig. 1. Photomicrographs of somatic metaphase plates in *Zephyranthes*. — A: *Z. atamasco*. — B: *Z. carinata*. — C: *Z. texana*. — × 530.

(3) *Zephyranthes texana* HERB. reproduces both by seeds and bulbs. The bulbs are ovoid, about 2.5 cm broad and 3—5 cm long. The leaves are narrow, linear,

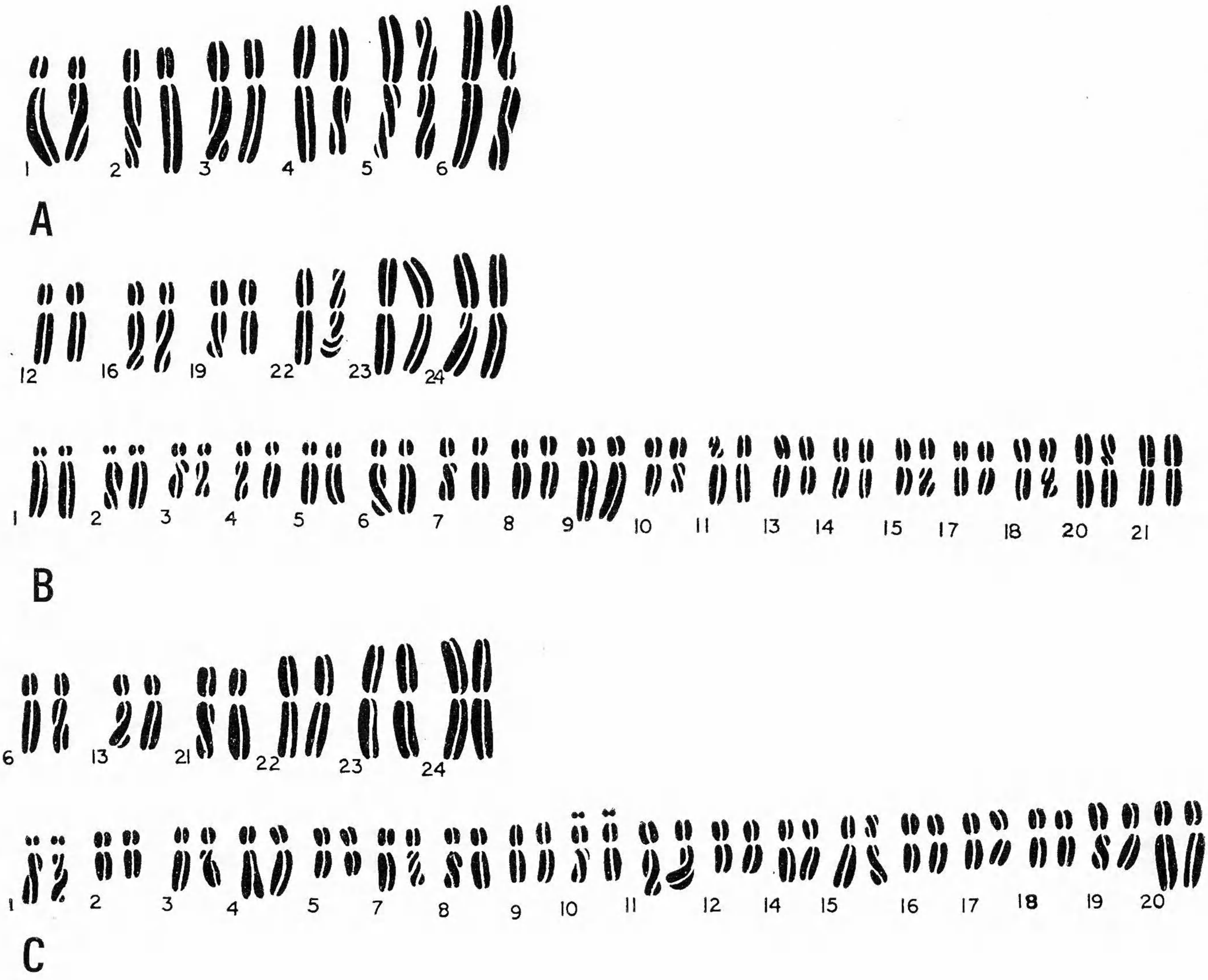

Fig. 2. Drawings of somatic metaphase chromosomes in *Zephyranthes*. — A: *Z. atamasco*. — B: *Z. carinata*. — C: *Z. texana*. — The chromosomes are arranged according to increasing length of the short arm. In B and C the genome corresponding to that of *Z. atamasco* is drawn separately. — ×840.

30—45 cm long and 0.5 cm broad, thick and fleshy with rounded tips. The scape is 25—30 cm long with a coloured 2.5 cm long spathe. The tubular spathe encloses the pedicel up to 1.5 cm and is clasping above. It is not cleft. The pedicel is longer than the spathe. The flowers are yellow, produced on 4.5-cm-long pedicels. The perianth is 6-lobed, in two whorls of three each, spathulate, about 4 cm long; the outer lobes are slightly incised and the tube shorter than the segments. The stamens are six, shorter than the limb of the perianth, all of the same length bearing 1-cm-long versatile anthers. The style is shorter than the stamens, prominent with a trifid stigma. The fruits are deeply notched.

The chromosome number is 2n=48. The karyotype analysis shows the following features (Figs. 1 C and 2 C): Seven pairs of chromosomes with subterminal constrictions (1st—4th, 6th, 8th and 13th pair); eight pairs of chromosomes with submedian constrictions (7th, 9th—11th, 14th, 15th, 20th and 21st pair); nine pairs of chromosomes with median or near median constrictions (5th, 12th, 16th—19th, 22nd —24th pair). The 10th pair of chromosomes shows satellites.

DISCUSSION

The inconstancy in the somatic chromosome numbers due to nondisjunction or endomitotic replications in asexually reproducing plants has been considered to be of importance in speciation through vegetative propagation (SHARMA 1956, SHARMA & SHARMA 1959). BHATTACHARYA (1972) on the basis of his studies on *Zephyranthes mesochloa* has concluded that the endomitotic replications may effect all or several chromosomes of a complement and are finally responsible for the numerical variations in the chromosomes.

Zephyranthes mesochloa (BHATTACHARYA 1972) shows a wide range of variation in the somatic complement with 2n ranging from 12 to 120 in addition to the hyperdiploids (between 26 and 102) and hypodiploid numbers ($2n=7+1$ fragment —23). SHARMA and GHOSH (1954) have also recorded $2n=48$ with variations such as 42, 60, 66 and 72 in this species. According to BHATTACHARYA (1972) these endomitotic replications and the nondisjunction are adopted to this species only under certain conditions of the environment affecting either a single chromosome or all the chromosomes of the complement.

In the present investigation *Z. atamasco* shows $2n=12$. FLORY (1940) has reported $2n=24$ in this species. It is likely that this variation is also a result of endomitotic replication affecting all the chromosomes of the complement. A similar variation has been observed in *Z. texana* where the present study reveals $2n=48$ as against an earlier report of $2n=24$ (SATO 1938). *Z. carinata,* however, does not show this variation. The chromosome number in this species is $2n=48$ and confirms the earlier report by YOKOUCHI (1964). It is interesting to note that all these polyploids conform to a multiple of six thus strengthening the presumption that the basic number is six.

Zephyranthes atamasco shows not only morphological but also cytological similarities to *Z. carinata*. The chromosomes in both species show the absence of satellites. The first and second pairs of chromosomes in *Z. atamasco* are similar in size and morphology to those of the 12th and 16th pairs in *Z. carinata*. The third pair is similar to the 19th pair; and the fourth, fifth and sixth pairs show similarities with the 22nd, 23rd and 24th pairs respectively. It is likely that one of the genomes of *Z. carinata* has been derived from *Z. atamasco*.

The genome of *Z. atamasco* is also traceable in *Z. texana*. The suppression of this genome is possibly responsible for the yellow colour of the flowers. However, the following chromosomes correspond to those in *Z. atamasco*:

Z. atamasco	*Z. texana*
1st and 2nd pair	6th and 13th pairs
3rd pair	21st pair
4th—6th pairs	22nd—24th pairs.

However, in spite of the common genome of *Z. atamasco* that is traceable in *Z. carinata* and *Z. texana,* the latter two species show considerable differences in their karyotype. The presence of satellites in the tenth pair of chromosomes makes *Z. texana* karyologically distinct. While seven pairs of chromosomes show subterminal constrictions in this species, nine pairs are with subterminal constrictions in *Z. carinata*. Further, the number of chromosomes with submedian constrictions is five in *Z. carinata* and eight in *Z. texana*. The number of chromosomes with median or near median constrictions is, however, nine in this species as against ten in *Z. carinata*. The morphological similarities of these two species account for the common genome.

ACKNOWLEDGEMENTS

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Karyotypes of Iris Subgenus Susiana Species in Lebanon and Syria

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WEYMOUTH, C. G. & CHAUDHARY, S. A. 1974 12 30. Karyotypes of Iris subgenus Susiana species in Lebanon and Syria. — Bot. Notiser 127: 513—521. Lund. ISSN 0006-8195.

Karyotypes of 12 taxa of *Iris* subgenus *Susiana* SPACH (=*Iris* section *Oncocyclus* (SIEMS.) BAK.) in Lebanon and Syria have been described and their inter-relationships discussed. The karyotypes were observed to constitute two major types, two intermediate types and some modified types. It has been proposed that the subgenus, as far as the species studied are concerned, be divided into two groups, the Sofaranae and Purpuro-aurantae, based on the karyotype and beard-hair characters.

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INTRODUCTION

A gap existed in the information that could clarify the inter-relations between the species in the subgenus *Susiana* SPACH (=section *Oncocyclus* (SIEMS.) BAK.) and especially between the species that are the subject of the present report. Cytological investigations of 12 available taxa (*Iris auranitica* DINSMORE, *I. barnumae* FOSTER & BAKER var. *zenobiae* MOUTERDE, *I. basaltica* DINSMORE, *I. bostrensis* MOUTERDE, *I. cedreti* DINSMORE ex CHAUDHARY, *I. kasruwana* DINSMORE, *I. kirkwoodii* CHAUDHARY, *I. kirkwoodii* ssp. *calcarea* CHAUDHARY (Inedit.), *I. sofarana* FOSTER, *I.* sp. (affin. *barnumae* FOSTER & BAKER), *I. yebrudii* DINSMORE ex CHAUDHARY ssp. *yebrudii* and ssp. *edgecombii* CHAUDHARY) was, therefore, undertaken with the aim of clarifying inter-relationships as far as possible.

MATERIAL AND METHODS

The material studied had been planted at the Agricultural Research and Education Centre of the American University of Beirut, located in the Beqaa Valley in Lebanon. The locations from which the populations were originally collected are given in Table 1.

Voucher specimens from the populations studied are in the Post Herbarium (BEI) of the American University of Beirut. The root tips were pre-treated in 0.002 mol/l solution of 8-hydroxyquinoline at about 12°C for 2(—3) hours. The usual acetic-alcohol fixation and aceto-orcein squash-staining techniques were applied. A large number of cells (in no case less than 25 cells per taxon) from a number of individuals from each taxon were studied to finalize the karyotypes.

Meiotic studies were carried out in *Iris yebrudii* ssp. *edgecombii* only. The plants of this taxon were dug up in the field and replanted at room temperature in the middle of the month of March. Individual shoots were dissected at intervals of a day or a few days to obtain flower buds. The anthers were then squashed in aceto-orcein to determine the stage of meiosis. The anthers at the right stage were obtained from only one individual. The stamens at that stage were the most developed part of the flower, the tepals being so small that they encircled the lower quarter of the anthers only.

OBSERVATIONS

The chromosome number in every taxon was observed to be 2n=20. This is consistent with all previous reports on the chromosome counts in the subgenus. Of the 12 taxa studied, the karyotype of *I. so-*

Table 1. Material studied.

Taxon	Place of collection	Collector/s
I. auranitica	Maymas, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. barnumae var. *zenobiae*	Tell Shehan, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. basaltica	Tell Kalakh & Hadidia, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. bostrensis	Shehba area, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD & C. WEYMOUTH
I. cedreti	Vicinity of Cedars of Lebanon, Lebanon	S. & Z. CHAUDHARY & C. WEYMOUTH
I. kasruwana	Laqlouq & Faraya areas, Lebanon	S. A. CHAUDHARY
I. kirkwoodii ssp. *kirkwoodii*	Bishmishly, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. kirkwoodii ssp. *calcarea*	Deir Semaan, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. sofarana	Falougha & Zehleh Pass areas, Lebanon	S. A. CHAUDHARY & Mrs G. KIRKWOOD & C. WEYMOUTH
I. sp. (affin. *barnumae*)	Sadad Road, Syria	Mrs G. KIRKWOOD
I. yebrudii ssp. *yebrudii*	Yabrud, Syria	S. A. CHAUDHARY & Mrs G. KIRKWOOD
I. yebrudii ssp. *edgecombii*	Kastel, Syria	Mrs G. KIRKWOOD

farana has been previously described by MITRA (1956). The description of the karyotype of this taxon below precedes those of the others which have been arranged in alphabetical sequence.

Iris sofarana

The chromosome complement of *I. sofarana* (Fig. 1 A) consists of 10 pairs of acrocentric (sensu RANDOLPH & MITRA 1960; telocentric 't', sensu LEVAN et al. 1965) chromosomes, as are most of the chromosomes of all the taxa studied. The chromosome pairs I, II, III and IV are relatively much longer than the rest of the chromosomes. These four pairs are of gradually decreasing length but do not differ markedly. Pair V is significantly shorter than pair IV while pairs V—X gradually decrease in length. In general pairs V—X have very much reduced short arms which appear as 'pin-heads'. The short arms on pairs I and II are somewhat larger and appear as rather globular structures. MITRA (1956) had reported satellites on chromosome pairs V, VI and VII, whereas all our plants had satellites on the chromosomes of pairs VI and VII only. Pairs VI and VII are heteromorphic in that the satellites on the two members of each pair differ in size and length of attachment threads.

Iris auranitica

The karyotype of this species (Fig. 1 B) shows a striking difference from that of the preceding taxon in that the chromosomes do not fall into well-defined length-groups, i.e. with four pairs of chromosomes markedly longer than the rest of the complement. The chromosomes in this taxon intergrade in length from I through X by only a gradual decrease in length. Another major difference is that the satellites are borne on the chromosomes pairs VI and IX instead of on VI and VII as in *I. sofarana.* (That the chromosomes in *I. aurantica* look much smaller is probably because of a more intense action of 8-hydroxyquinoline. It was observed in the

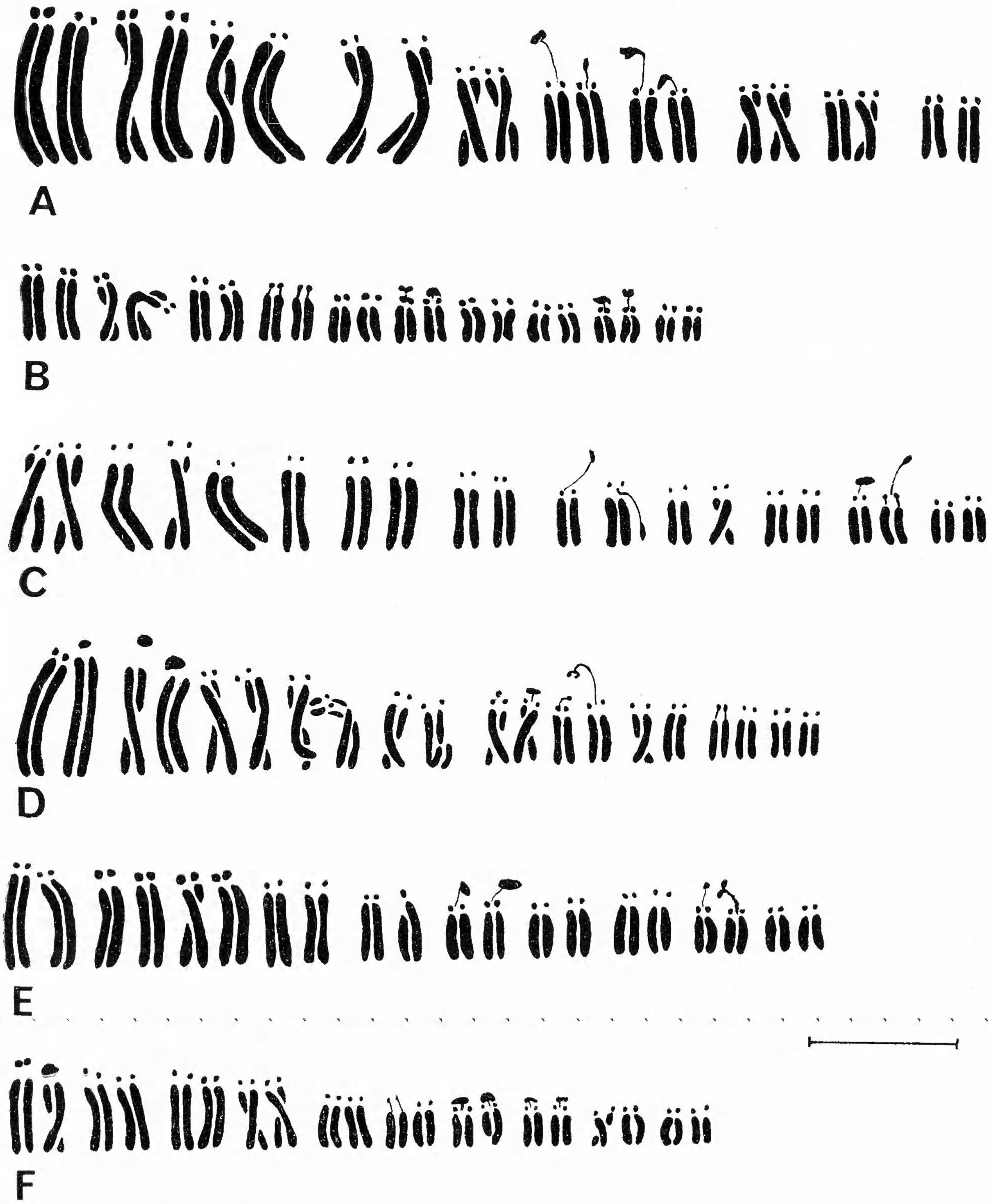


Fig. 1. Karyotypes of *Iris*. — A: *I. sofarana*. — B: *I. auranitica*. — C: *I. barnumae* var. *zenobiae*. — D: *I. basaltica*. — E: *I. bostrensis*. — F: *I. cedreti*. — Camera lucida sketches Scale = 20 μ.

present studies that the thinner the roots pre-treated, the more intense was the action of this chemical for the same length of time. In a few instances when material was put in 8-hydroxyquinoline in the field where the temperature was about 12°C and then carried in a (warm) car for about two hours, the chromosomes in all the taxa invariably showed banding or transverse irregular breaks, the latter sometimes giving an appearance of secondary constrictions. Except for these artifacts occurring under warmer conditions of temperature the degree of contraction of chromosomes within a complement and in all the taxa was observed to be consistently uniform under the influence of 8-hydroxyquinoline at the temperature and the timings used). The short arms in *I. auranitica* chromosomes are all of the 'pin-head' type. Pairs VI and IX show slight heteromorphism in the size of the satellites within each pair.

Iris barnumae var. **zenobiae**

The karyotype is essentially of the *I. auranitica* type (Fig. 1 C) with the same chromosomes, VI and IX, bearing the satellites. The short arms in all the chromosomes are of the 'pin-head' type except the chromosomes of pairs II and III where the 'pin-heads' are slightly bigger. There is a rather pronounced heteromorphism in the size of the satellites and the length of the attachment threads within each of the chromosome pairs VI and IX.

Iris basaltica

The karyotype is, basically, of the *I. sofarana* type (Fig. 1 D) with the chromosome pairs I—IV being much longer than the rest. The short arms on the chromosomes of pairs I and II are relatively bigger and not of the 'pin-head' kind. Chromosome pairs VI and VII are satellited, the satellites within each pair differing either in size (pair VI) or length of the attachment threads (pair VII).

Iris bostrensis

The karyotype is basically of the *I. aurantica* type (Fig. 1 E). However, there is a break, though not pronounced, in the intergrading of the chromosomes: the chromosome pairs I, II and III are, as a group, longer than the rest. Like *I. auranitica,* the chromosome pairs VI and IX bear satellites.

Iris cedreti

The karyotype is basically of the *I. sofarana* type (Fig. 1 F). The chromosome pairs I, II, III and IV are, as a group, much longer than the rest. Only pair I, however, has the relatively large non-pinhead kind of short arm. Also, the satellites are borne on chromosomes VII and VIII as compared with VI and VII in *I. sofarana.*

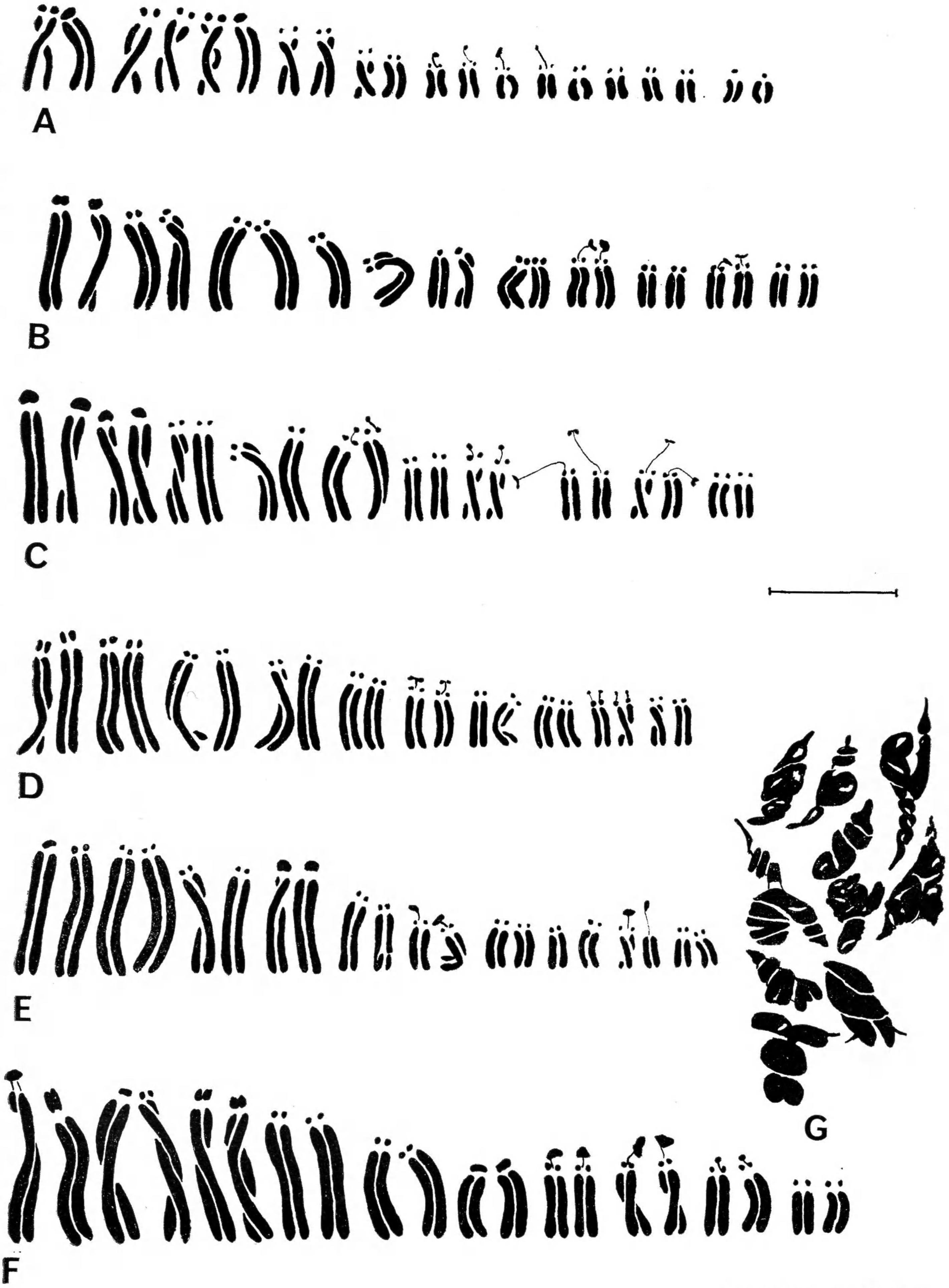
Iris kasruwana

The karyotype is basically of the *I. sofarana* type (Fig. 2 A). It differs in that the first three pairs (I, II and III) in this karyotype have the larger, non-pin-head kind of short arms instead of only the first two pairs of chromosomes as in *I. sofarana.* The satellites are borne on pairs VI and VII as in *I. sofarana.*

Iris kirkwoodii ssp. **kirkwoodii**

The karyotype, as in *I. sofarana,* consists of four (I—IV) long pairs of chromosomes the rest being shorter chromosomes (Fig. 2 B). However, pair I only has the non-

Fig. 2. A—F: Karyotpes of *Iris.* — A: *I. kasruwana.* — B: *I. kirkwoodii* ssp. *kirkwoodii.* — C: *I. kirkwoodii* ssp. *calcarea.* — D: *I.* sp. (affin. *I. barnumae*). — E: *I. yebrudii* ssp. *yebrudii.* — F: *I. yebrudii* ssp. *edgecombii.* — G: *I. yebrudii* ssp. *edgecombii,* metaphase I configuration in pollen mother cell. Chromosome pair I is in the top right hand corner of the figure. — Camera lucida sketches. Scale = 20 μ.


A
B
C
D
E
F
G

pin-head kind of short arm and the satellites are borne on the chromosome pairs VII and IX instead of on VI and VII as in *I. sofarana* or VI and IX as in *I. auranitica.*

Iris kirkwoodii ssp. **calcarea** (inedit.)

The karyotype differs from that of the preceding taxon in that pairs I and II in this taxon have the relatively large, non-pin-head kind of short arms instead of pair I only (Fig. 2 C). Also, the first five pairs (I—V) as a group are longer than the rest, and four pairs of chromosomes (V, VII, VIII and IX) bear the satellites.

Iris sp. (affin. **Iris barnumae**)

This karyotype is very interesting in that the chromosomes of pair I are distinctly of the *I. yebrudii* ssp. *edgecombii* type (below). This is shown in the shape and size of the short arms which are noticeably longer than those of any of the other members of the complement, and in that they are unequal in length (Fig. 2 D). The rest of the chromosomes are of the *I. auranitica* type including the satellited pairs. The chromosomes, however, fall into two distinct length-groups, pairs I—IV forming the long-chromosome group and pairs V—X intergrading and constituting the short-chromosome group such as the *I. sofarana* type. This species, therefore, includes in its karyotype characters of all three karyotype types.

Iris yebrudii ssp. **yebrudii**

The chromosomes of pairs I—IV are distinctly longer than the rest while pair V is of intermediate length (Fig. 2 E). Pairs VI—X constitute the short-chromosome group. Within the first four pairs, pairs I and II appear longer than pairs III and IV. Chromosome pair IV only has the relatively large, non-pin-head kind of short arms. The chromosomes of pairs VI and IX, as in *I. auranitica,* bear the satellites.

Iris yebrudii ssp. **edgecombii**

Pairs I—IV are distinctly longer than the rest while pair V is of intermediate length being distinctly smaller than the first four pairs and distinctly longer than the last five, which constitute the short-chromosome group (Fig. 2 F). Three pairs of chromosomes (VII, VIII and IX) bear the satellites. The chromosomes of pair I are heteromorphic. One member of this pair is much longer than the other, while, too, the short arm on the shorter chromosome is more than double the length of the short arm of the longer chromosome.

The metaphase configurations in PMCs were studied to determine the nature of heteromorphy in pair I (Fig. 2 G). The pairing of all the chromosomes was observed to be normal. However, the consistent presence of a side loop in the pairing configuration of pair I, suggested that the difference in the lengths of the two members was the result of a duplication of segments in one of the members, and that this was somehow being perpetuated in the population. Pair I was identified by the size and the loop which could be expected when the members were unequal. A study of pollen fertility proved inconclusive as, unfortunately, the pollen nuclei could not be stained satisfactorily.

DISCUSSION

The karyotypes of the taxa studied fall into two major groups, viz. the *I. sofarana* type (Sofarana type) and the *I. auranitica* type (Auranitica type). The typical Sofarana type of karyotype is characterized by the chromosome pairs I—IV being much longer than the rest, some of these having a larger, non-pin-head kind of short arms, and by the satellites being borne on pairs VI and VII (Fig. 3 A). *I. basaltica, I. kasruwana* and *I. sofarana* belong to this group. *I. kirkwoodii* ssp. *kirkwoodii* and *I. cedreti* are apparently modifications of this karyotype type. The taxon *I. kirkwoodii* ssp. *calcarea* is the only taxon amongst those stu-

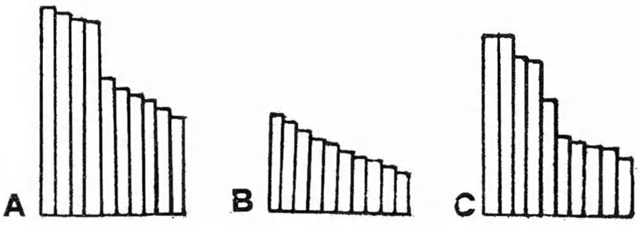


Fig. 3. Length-groups in karyotypes of *Iris*. — A: *I. sofarana*. — B: *I. auranitica*. — — C: *I. yebrudii*.

died which has satellites on four pairs of chromosomes (V, VII, VIII and IX), and five pairs of chromosomes constituting the long-chromosome group. This could be a more primitive karyotype than any other taxon within this group. The Auranitica type of karyotype is characterized by all the chromosomes intergrading gradually from the longest to the shortest (Fig. 3 B), or almost so, without a sharp break into length-groups. The chromosomes of pairs VI and IX only are satellited. All the chromosomes have the small 'pin-head' kind of short arms, although in some the short arms may be slightly larger and appear as small globular bodies. This group includes *I. auranitica, I. bostrensis* and *I. barnumae* var. *zenobiae*.

A third type of karyotype (Yebrudii type), intermediate between the Sofarana and Auranitica types, is to be seen in *I. yebrudii* ssp. *yebrudii* and *I. yebrudii* ssp. *edgecombii* (Fig. 3 C). Pairs I—IV form the long-chromosome group, pairs VI—IX the short-chromosome group, while pair V is intermediate belonging to neither of the above two length-groups. *I. yebrudii* ssp. *yebrudii*, like the Auranitica type, has the satellites on pairs VI and IX while ssp. *edgecombii* has satellites on three pairs, pair VII like the Sofarana type, pair IX like the Auranitica type and pair VIII like *I. cedreti* and *I. kirkwoodii* ssp. *calcarea*.

The taxon *Iris* sp. (affin. *barnumae*) possesses a karyotype with elements from all the above three types, viz. Auranitica, Sofarana, and Yebrudii types. This could possibly be another major type. This taxon apparently has affinities with taxa distributed in the northern Syrian desert, southwestern Turkey, adjacent Iraq, Iran and Armenia in the USSR.

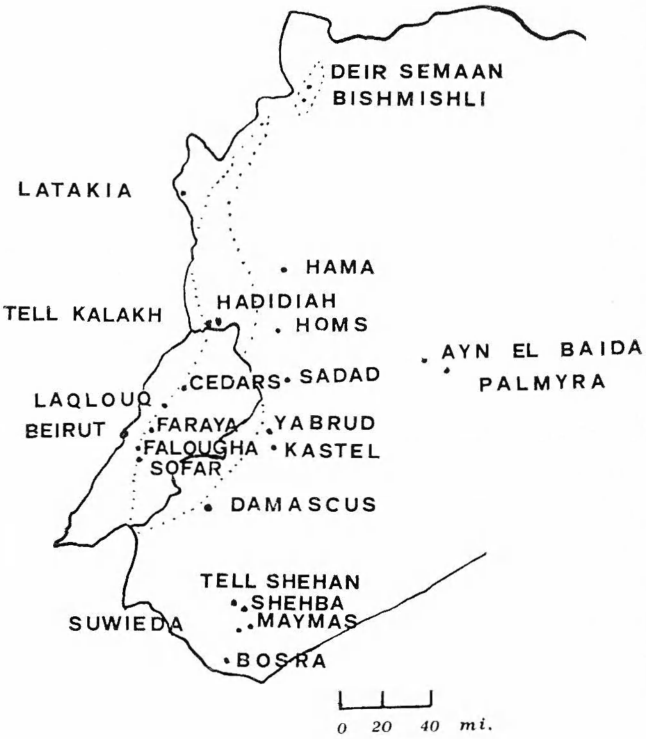


Fig. 4. Map including locations of distribution of taxa studied.

On the assumption that the more advanced the karyotype is the less symmetrical it will be and the shorter the chromosomes, we would consider the Sofarana type as the most primitive and the Auranitica type as the most advanced with the *Iris* sp. (affin. *barnumae*) karyotype and Yebrudii type as two intermediate types. Looking at the map (Fig. 4), we find that in a South—North sequence of distribution *I. sofarana, I. kasruwana, I. cedreti, I. basaltica, I. kirkwoodii* ssp. *kirkwoodii* and *I. kirkwoodii* ssp. *calcarea* constitute one group distributed in the Lebanese Mountains and extending northwards into Syria. *I. yebrudii* ssp. *yebrudii* and *I. yebrudii* ssp. *edgecombii* constitute a second group having its distribution in the north eastern Anti-Lebanon range and its foothills. *I. auranitica, I. bostrensis* and *I. barnumae* var. *zenobiae* constitute the group distributed in the southeastern Sy-

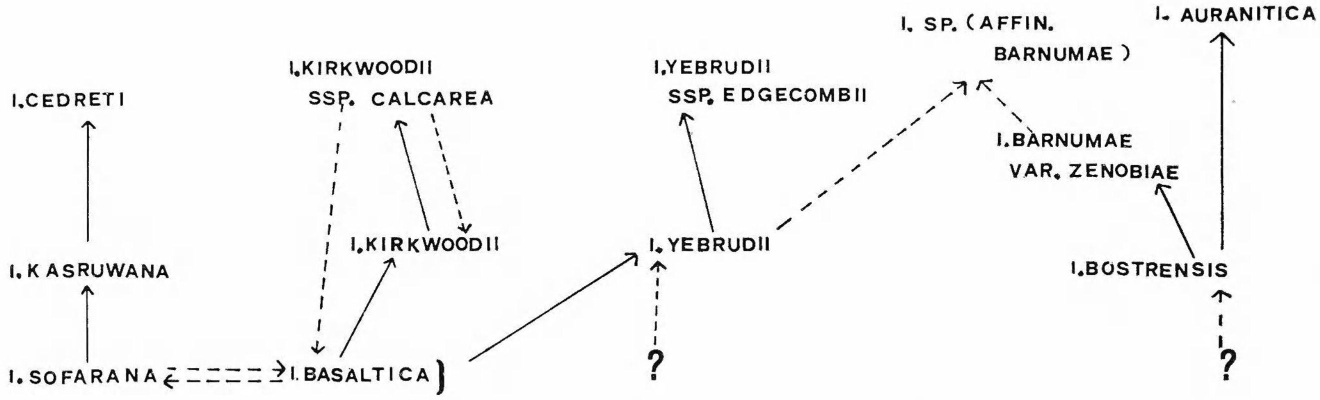


Fig. 5. Diagram showing possible inter-relationships between 12 taxa of the *Iris* subgenus *Susiana*. Dotted lines show probable paths which are less clear.

rian semi-desert region and on the volcanic peaks in the area. The probable sequence of evolution within the groups (hypothetical here, but also based on morphological evidence not presented here), based on distribution and karyotypes, is shown in Fig. 5.

The morphology of the beard hairs of these and some other taxa was also investigated as a supporting study. We found that the species of the subgenus from Lebanon, Syria and part of Palestine fall into two groups. In one group the beard hairs are microscopically papillate-echinate (Fig. 6 A) while in the other they are club-shaped and smooth (Fig. 6 B). The species belonging to the papillate-echinate groups are characterized by the Sofarana and Yebrudii types of karyotypes, while the clavate-haired species belong to the Auranitica and *Iris* sp. (affin. *barnumae*) types of karyotypes. The association of a beard-hair character with a karyotype seems to be very constant. On the basis of the information discussed above, we are strongly of the view that the subgenus *Susiana* SPACH should be divided into two groups as below, at least as far as the taxa investigated are concerned. We feel that a further division of the two groups, if considered desirable later, would be possible on the basis of morphological characters such as leaf characters, flower shape, pigmentation, etc.

Group 1. *Sofaranae*

comprising the species with papillate-echinate hair (and Sofarana/Yebrudii types of karyotypes by implication) i.e. *I. basaltica, I. cedreti, I. kasruwana, I. kirkwoodii, I. sofarana* and *I. yebrudii*. Based on beard-hair character alone, we assume that *I. hermona* DINSM., *I. lortetii* BARB., *I. samariae* DINSM. and *I. westii* DINSM. belong here.

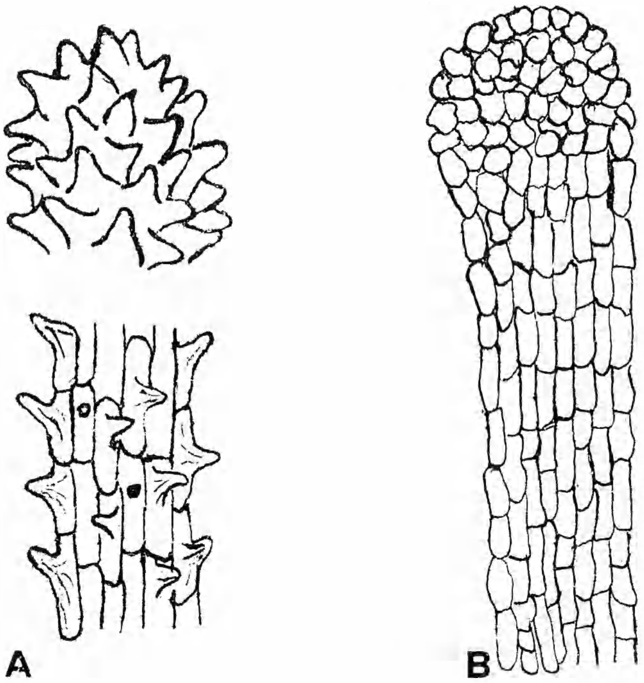


Fig. 6. Beard hairs of *Iris*. — A: Sofarana type. — B: Auranitica type.

Group 2. *Purpuro-aurantae*

comprising species with clavate, non-papillate-echinate beard hair (and Auranitica or *Iris* sp. (affin. *barnumae*) types of karyotypes by implication) i.e., *I. auranitica, I. barnumae* var. *zenobiae, I. bostrensis* and *Iris* sp. (affin. *barnumae*). Based on beard-hair character alone, we assume that *I. atrofusca* BAK., *I. heylandiana* BOISS. & REUT., *I. jordana* DINSM. and *I. nigricans* DINSM. belong here.

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Studies in African Cyperaceae XIII

New Taxa and Combinations in Isolepis R. Br.

Kåre Arnstein Lye and Richard Wheeler Haines

LYE, K. A. & HAINES, R. W. 1974 12 30. Studies in African Cyperaceae XIII. New taxa and combinations in Isolepis R. Br. — Bot. Notiser 127: 522—526. Lund. ISSN 0006-8195.

One new variety and two new species are described from East Africa, viz. *Isolepis fluitans* (L.) R. BR. var. *major* K. LYE var. nov., *I. ruwenzoriensis* R. HAINES & K. LYE sp. nov. from the Ruwenzori Mountains in Uganda and *I. kilimanjarica* R. HAINES & K. LYE sp. nov. from Mt Kilimanjaro in Tanzania. Also, one new combination is made, viz. *Isolepis graminoides* (R. HAINES & K. LYE) K. LYE comb. nov.

The distinguishing characters between the two genera *Eleogiton* LINK and *Isolepis* R. BR. have been found too slight for generic separation, and *Eleogiton* is therefore included in *Isolepis*.

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Isolepis fluitans (L.) R. BR. var. **major** K. LYE, var. nov. Fig. 1

Herbae perennes glabrescentes. *Culmus* decumbens, ad nodos radicans et longe repens. *Folia* numerosa, 2—7 cm longa et 0.7—1.5 mm lata; *vaginae* longae, brunneae. *Anthela* simplex, 1-spiculosa. *Spiculae* oblongo—lanceolatae, subacutae, 4.0—6.5 mm longae et 2.0—3.5 mm latae, 8—10-florae. *Squamae* dense imbricatae, ovatae, obtusae, fuscae; *carina* viridis. *Stamina* 3. *Stylus* longus, bifidus vel trifidus. *Nux* 1.4—1.5 mm longa et 0.9—1.0 mm lata, oblonga, conspicue apiculata, brunnea, minute muricata.

TYPUS SPECIEI: K. A. LYE n. 5754, 17.VI. 1970. Uganda, Bugisu district, near Sasa River on Mt Elgon, 1°10′N & 34°26′E, 2,850 m (Holotype MHU, isotype EA).

Differs from var. *fluitans* in having flattened peduncles, 8—10-flowered spikelets (as against 3—8 in the type variety), broader leaves, green glumes (more rarely reddish-brown) with transparent margins and a 1.5 mm long achene with a long apiculus (Fig. 1).

In alpine bogs and other wet habitats, sometimes along rivers, 2,430—3,050 m. Uncommon in Uganda (Bugisu and Kigezi), more widespread in upland Kenya and Tanzania. The specimen drawn is from Purseglove 2196 from Muhavura-Mgahinga Saddle, Kigezi, Uganda.

Isolepis kilimanjarica R. HAINES & K. LYE, sp. nov. Fig. 2

Herbae perennes glabrescentes. *Rhizoma* horizontaliter repens, flavum, ad 10 cm longum et 1.0—1.5 mm latum. *Culmus* 1—3 cm longus et 0.4—0.8 mm latus. *Folia* 2—5, 3—7 cm longa et 0.6—1.5 mm lata; *vaginae* longae, brunneae vel canescentes. *Anthela* simplex, 1-spiculosa. *Spiculae* oblongo-lanceolatae, 4—5 mm longae et 2.0—2.5 mm latae. *Squamae* 3.0—3.5 mm longae, imbricatae, lanceolatae—acutae, brunneae vel cinereae. *Stamina* 3. *Nux* 1.2—1.4 mm longa et 0.9—1.0 mm lata, elliptica, castanea, striatula.

TYPUS SPECIEI: O. HEDBERG n. 1348, 23. VI. 1948. Tanzania, Kilimanjaro, saddle between Kibo and Mawenzi, in a swamp in the

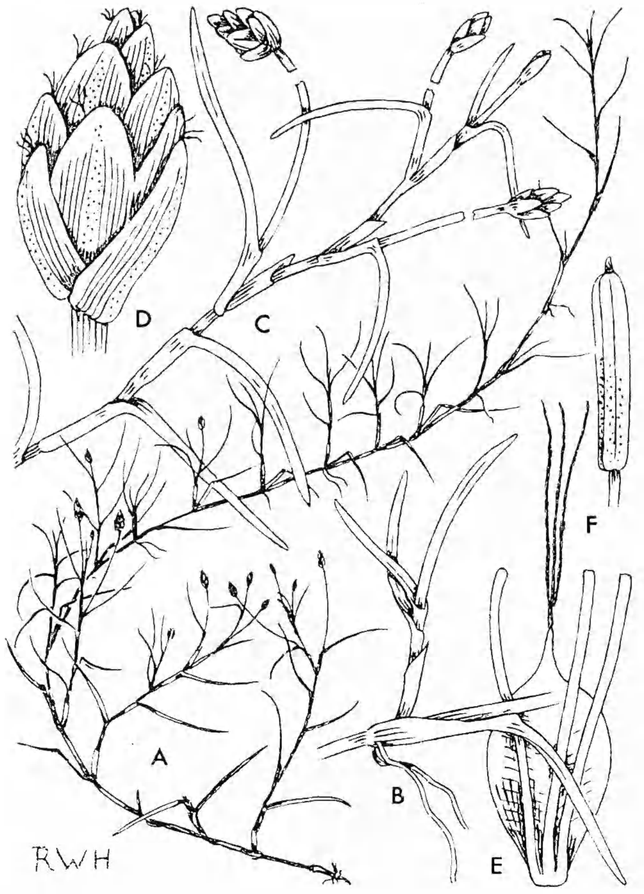

Fig. 1. *Isolepis fluitans* (L.) R. BR. var. *major* K. LYE. — A: Habit, reduced. — B: Part of stem showing lateral shoots and roots. — C: Fertile shoot with four spikelets. — D: Spikelet. — E: Achene with persistent 3-branched style and three filaments. — F: Anther. — Drawn from PURSEGLOVE 2176 (Muhavura-Mgahinga Saddle, 9,500', Kigezi, Uganda.

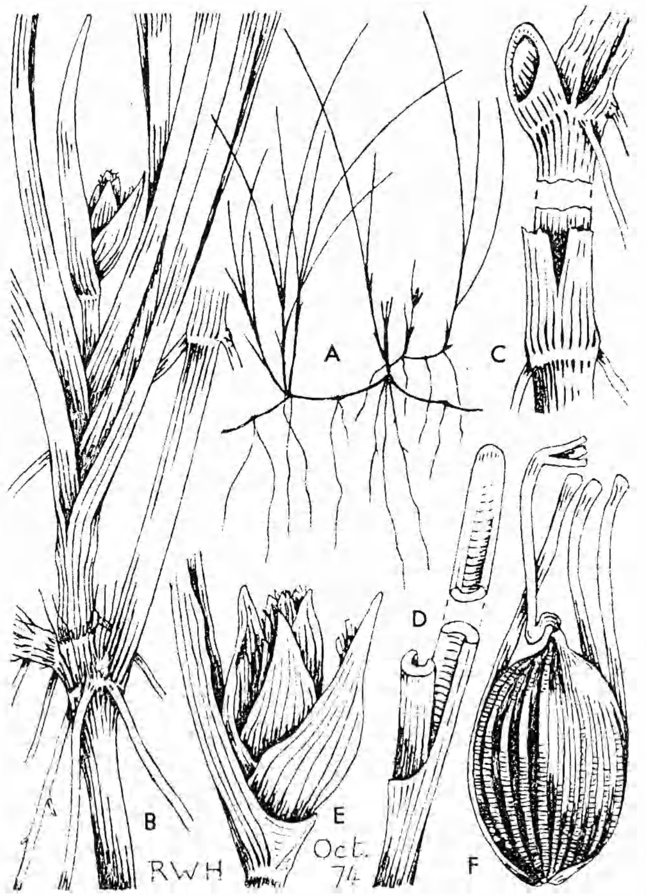

Fig. 2. *Isolepis kilimanjarica* R. HAINES & K. LYE. A: Habit, reduced. — B: Part of plant showing leafy culm with roots and inflorescence. — C: Part of plant showing extra-axillary branching — D: Leaf-sheath and leaf-tip. — E: Inflorescence. — F: Achene with persistent style and filaments. — Drawn from HEDBERG 1348 (saddle between Kibo and Mawenzi, Kilimanjaro, Tanzania, the holotype).

southern part of the saddle, 4,350 m (Holotype UPS).

Perennial sedge. Runners to 10 (or more) cm long and 1.0—1.5 mm thick, horizontal, creeping, light yellowish, golden or purplish, with leafy culms set at 0.5—2.5 cm intervals at each alternate node. Branches extra-axillary in origin, those forming the sympodial runners long-noded at the base, those of the minor branches with shorter nodes, all with a basal tubular prophyll. Culms 1—3 cm long and 0.4—0.8 mm thick, covered by grey to brown leaf-sheaths and with 2—5 leaf-blades, triangular to subterete. Leaf-blades 3—7 cm long and 0.6—1.5 mm wide, flat or somewhat inrolled, often curved, scabrid on margins and midrib, crescentic in section and veined on the convex surface, ending bluntly; leaf-sheaths grey to reddish-brown, closed when young but soon splitting, eventually rotting but the veins persisting as reddish fibres.

Inflorescence a solitary spikelet 4—5 mm long and 2.0—2.5 mm wide. Main inflorescence bract about twice as long as the spikelet, leafy with a glume-like basal part. Glumes 3.0—3.5 mm long, light yel-

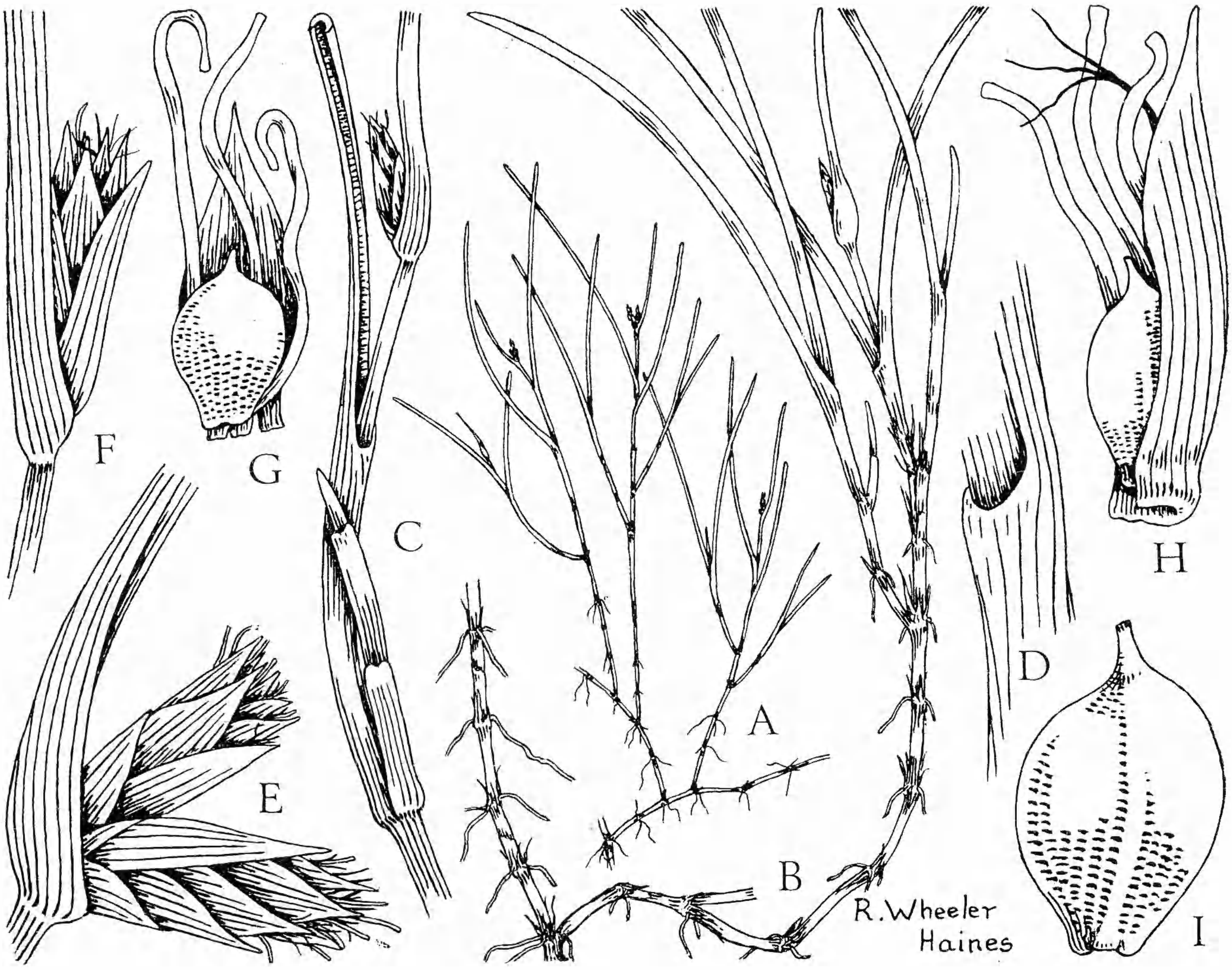

Fig. 3. *Isolepis ruwenzoriensis* R. HAINES & K. LYE. — A: Habit, reduced. — B: Fertile shoot with one spikelet. — C: Fertile shoot with spikelet magnified. — D: Detail from culm showing throat of leaf-sheath. — E: Paired spikelets. — F: Solitary spikelet. — G: Achene with glume and filaments. — H: Achene with glume, 3-branched style and filaments. — I: Achene. — Drawn from OSMASTON 3916 (Mt Ruwenzori, Uganda, 3,850 m, the holotype).

lowish-brown to purplish-brown with a distinct midrib and numerous lateral nerves, triangular-lanceolate with acute apex; the lowest glume fertile, longer than the others. Perianth absent. Stamens 3. Style trifid. Achene 1.2—1.4 mm long and 0.9—1.0 mm wide, elliptic with one flat and one rounded side, brown and shiny, strongly longitudinally ribbed, the ribs minutely transversely striate, converging towards a prominent blunt apiculum. Glumes and achenes falling separately, each achene with filaments and style attached but soon lost.

Only known from the type collection cited above.

Isolepis ruwenzoriensis R. HAINES & K. LYE, sp. nov. Fig. 3

Herbae perennes glabrescentes. *Culmus* decumbens, ad nodos radicans et longe repens. *Folia* 2—5, 2—8 cm longa et 0.5—1.5 mm lata. *Anthela* simplex, 1—2 spiculosa. *Spiculae* oblongo-lanceolatae, 4—5 mm longae et 1.0—2.5 mm latae. *Stamina* 3. *Stylus* longus, trifidus. *Nux* 1.0—1.2 mm longa et 0.8—0.9 mm lata, oblonga, conspicue apiculata, brunnea, striatula.

TYPUS SPECIEI: OSMASTON n. 3916. Uganda, Stuhlmann Pass, Ruwenzori (Holotype K).

Perennial sedge with creeping much-branched stem and numerous leaves. Stem with branches to 20 cm long and 0.5—1.0 mm thick, glabrous. Leaves 2—5 per branch, 2—8 cm long and 0.5—1.5 mm wide, flat or somewhat inrolled, glabrous. Inflorescence consisting of one solitary spike or more rarely two clustered spikes. Inflorescence bract leafy, erect, 1—2 cm long and much overtopping the inflorescence. Spikelets 4—5 mm long and 1.0—2.5 mm wide, oblong-lanceolate. Glumes 3.0—3.5 mm long, light brown with numerous distinct nerves, triangular-lanceolate with acute apex. Nutlet 1.3—1.4 mm long (including a 0.2 mm long apiculum) and 0.7—0.9 mm wide, obovate with a cuneate base and a sharp apiculum, distinctly longitudinally ribbed with minute transverse striations.

This species has previously been confused with *I. fluitans,* but it has a different inflorescence and an entirely different ornamentation of the achene. From *I. kilimanjarica* it differs in its longer leafy inflorescence bracts, different branching and its more pronounced apiculum on the nutlet.

Forming mats or dense carpets in wet places, often with running water, 3,300—3,850 m. Common on Mt Ruwenzori, Uganda, but not known outside this area.

Specimens seen: HAINES 4586 (MHU), HEDBERG 643 (EA, K), LYE 1324 (MHU), 7000 (MHU, EA, K), OSMASTON 3916 (K), 3917 (K).

NEW COMBINATION

Isolepis graminoides (R. HAINES & K. LYE) K. LYE, comb. nov. Syn. *Scirpus graminoides* R. HAINES & K. LYE in Bot. Notiser 123: 430 (1970).

ELEOGITON OR ISOLEPIS

According to some authors (cf. HESS & al. 1967) *Eleogiton* is a monotypic genus, the only species being the widespread *Eleogiton fluitans* (L.) LINK (cf. LINK 1827). However, LEVYNS (1944) mentions several South African species of *Scirpus* belonging to *Eleogiton* (i.e. her subgen. *Fluitantes*), some of which were described by NEES VON ESENBECH as early as 1836 (NEES 1836).

The genus *Eleogiton* was previously easily separated from *Isolepis* R. BR. on account of its long leafy branches and solitary terminal spikelet without a leafy inflorescence bract. However, the morphology of the three endemic East African species *Isolepis graminoides* (LYE & HAINES 1970), *I. ruwenzoriensis* and *I. kilimanjarica* is intermediate and obscures the commonly accepted generic circumscriptions. *I. ruwenzoriensis* differs from *E. fluitans* in having leafy inflorescence bracts and occasionally 2-paired spikelets, but is otherwise very similar. *I. kilimanjarica* has a solitary spikelet and a bract only twice as long as the inflorescence. In fact these East African species show a very interesting series in morphological characters from the somewhat erect-growing *I. graminoides* with an anthela of 3—4 sessile spikes (LYE & HAINES 1970) through the decumbent *I. ruwenzoriensis* with procumbent stems and 1—2 sessile or stalked spikelets to the creeping *I. fluitans* with solitary distinctly stalked spikes. *I. ruwenzoriensis* and *I. kilimanjarica* have the same ornamentation of the achene as *I. setacea* (L.) R. BR., the type-species of *Isolepis* R. BR., and it is in fact possible that *I. ruwenzoriensis* may have evolved from a hybrid between *I. setacea* or the closely related *I. costata* and *I. fluitans.*

The close relationship between the genera *Eleogiton* and *Isolepis* has become very evident through the description of the two new species *I. ruwenzoriensis* and *I. kilimanjarica.* In fact the two genera cannot be separated except on a rather arbitrary combination of characters, none of which is decisive in itself. We therefore find that we can no longer retain the genus *Eleogiton* LINK.

ACKNOWLEDGEMENTS

We would like to thank Professor O. HEDBERG for sending his unidentified specimens of *Isolepis* at Herb. UPS, and the late Miss D. N. NAPPER for valuable discussions on East African species of *Isolepis* as well as permission to study the specimens at Herb. K.

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Recurrent Ecotypic Variation in Rhinantheae and Gentianaceae in Relation to Hemiparasitism and Mycotrophy

Thomas Karlsson

KARLSSON, TH. 1974 12 30. Recurrent ecotypic variation in Rhinantheae and Gentianaceae in relation to hemiparasitism and mycotrophy. — Bot. Notiser 127: 527—539. Lund. ISSN 0006-8195.

The patterns of variation in some genera of Rhinantheae (Scrophulariaceae) and Gentianaceae, e.g. *Melampyrum, Rhinanthus, Euphrasia* and *Gentianella,* are discussed. The recurrent ecotypic variation sometimes referred to as seasonal dimorphism or pseudo-seasonal polymorphism is restricted to hapaxanthic members of these groups in temperate Europe. An analysis based on literature has shown that they are unusual compared with other NW European hapaxanths in that they exploit closed habitats and alpine vegetation. The hemiparasitism of Rhinantheae and the mycotrophy of Gentianaceae may account for this. Many of the unusual features of variation have arisen out of adaptation to a great variety of closed forestless habitats created by man in temperate Europe.

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PATTERNS OF VARIATION

Variation in some annual hemiparasitic genera of the Rhinantheae (Scrophulariaceae) is greatly complicated by what appears to be ecotypic differentiation. Originally, the pattern of variation was described as seasonal dimorphism (WETTSTEIN 1895). This concept has proved to be the result of over-simplification, WETTSTEIN's aestival and autumnal "species pairs" arising from the undue emphasis placed on the early-flowering and late-flowering variants in Central European meadows mown at midsummer.

In his *Melampyrum* monograph SOÓ (1926—27) coined the term pseudo-seasonal polymorphism for the same phenomenon. Within several species SOÓ recognized up to six types differing conspicuously in habit and flowering time in a manner that seemed to be correlated with environmental factors. The types were as follows: an autumnal race (a valley race of forests and scrublands), an aestival (or meadow) race, a montane race, a mire race, an alpine race and a segetal race. This recurrent ecotypic variation sometimes cuts across the geographical variation, which is well represented (SOÓ & WEBB 1972). Species hybridization seems to be very rare if at all present (SOÓ 1926—27).

In *Rhinanthus,* SOÓ (1970) discriminates between six recurrent variants (autumnal, aestival, vernal, montane, alpine and segetal) in several of the species. The characteristics of these variants are essentially the same as for variants of *Melampyrum.* Apart from this the variation seems to be complex and reticulate, and species hybrids have been reported.

In *Euphrasia* there are diploids and tetraploids. The reproductive barriers between species are, within each ploidy level, to a great extent ecological (YEO 1966, the author's observations). Hybridization seems to play a great part in variation within the genus, at least in W and NW Europe (YEO 1972, JØRGENSEN 1919, the author's observations). "Seasonal dimorphism" (WETTSTEIN 1896) occurs within species at both ploidy levels. In southern Sweden parallel ecologically conditioned types occur in all species (Fig. 1) and adaptations in characters other than those of habit and flowering time can be traced (the author's observations).

The similarities in the patterns of variation of *Euphrasia* and *Melampyrum-Rhinanthus* are partly disguised due to differences in taxonomic treatment. However, as the genera differ somewhat in habitat preference, there are also real differences in their patterns of variation.

To modify SOÓ's system of ecotypes to cover the variation within *Euphrasia* we would need to divide up the category "autumnal" into at least three: pastoral (pastures being one of the main habitats), ruderal (roadsides and similar habitats) and arenicole (on sandy fallows). In addition there are aestival, alpine and paludicole (fen) races, and probably also segetal and montane ones. It must be stressed, however, that the variation is essentially continuous, but as certain habitats are much commoner than others there are peaks in the range of variation within the species. The term "ecotype" is here used for these peaks.

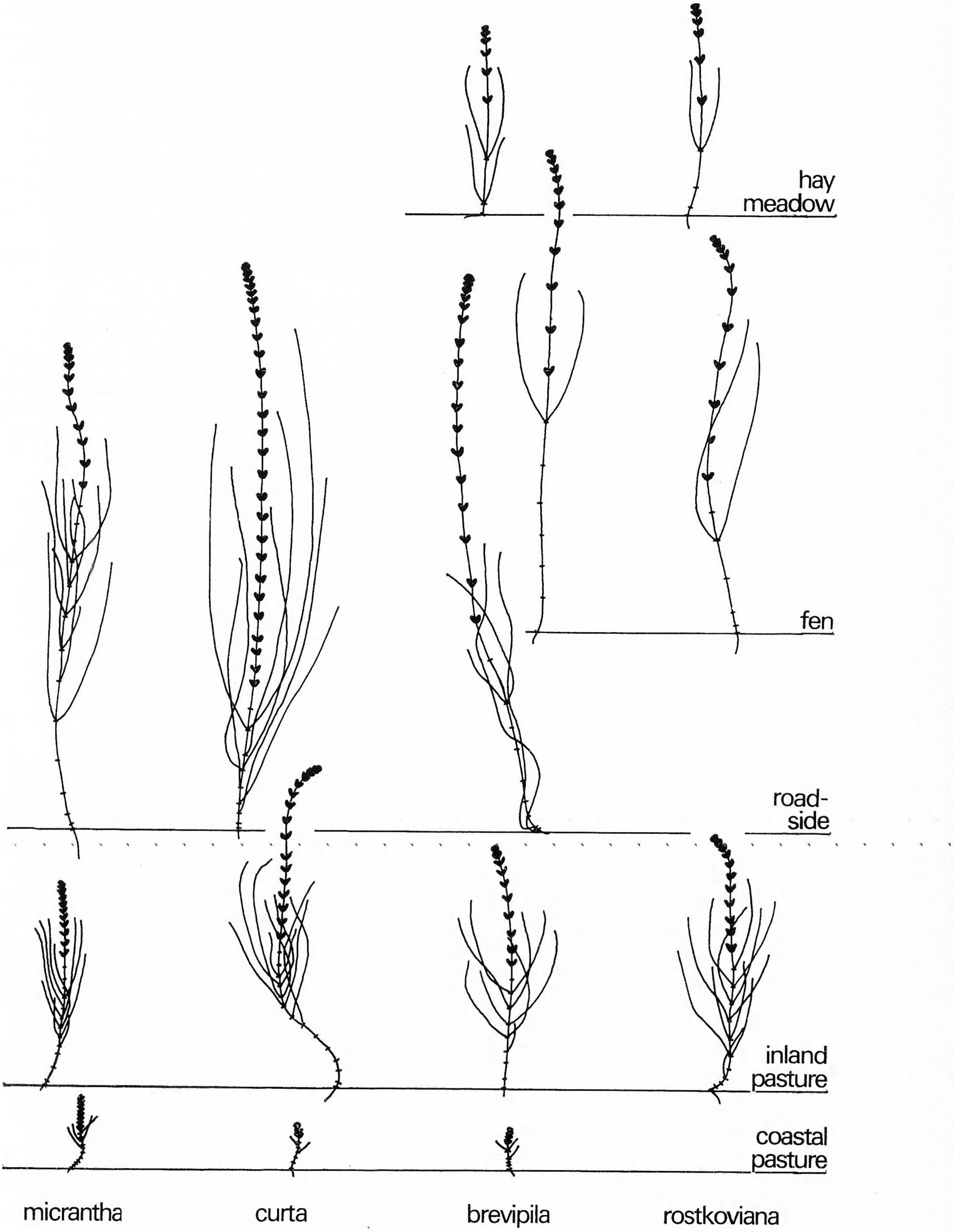
The adaptive value of the recurrent combinations of characters has been confirmed for *Rhinanthus serotinus* in TER BORG's (1972) investigation, which was built on comprehensive ecological data. However, the very fact that several species groups in a number of genera have evolved very similar types in similar habitats permits us to infer that the character combinations under consideration are of real adaptive value.

At the beginning of this century the modifiability of hemiparasitic plants was much discussed. It was even proposed that seasonal dimorphs were nothing but modifications (HEINRICHER 1903). In *Euphrasia* my own results point to a genetical background for much of but certainly not all of the habitat-correlated variation. The same is evident for *Rhinanthus serotinus* (TER BORG 1972). ROTTGARDT (1956) showed that habit characters and developmental rhythm are heritable in *Odontites,* and SMITH (1963) came to a similar conclusion for *Melampyrum pratense.*

Taxonomically the variation has been dealt with in a variety of ways. The WETTSTEIN school regarded the seasonal dimorphs in *Euphrasia, Melampyrum* and *Rhinanthus* as species. SOÓ (e.g. 1970) maintains that his pseudo-seasonal polymorphic types in *Melampyrum* and *Rhinanthus* should be regarded as subspecies, while MAYER (1972), for instance, insists on varietal rank. In *Euphrasia* WETTSTEIN's species concept is still used (now with some improvements, YEO 1972). In all three genera HARTL (1972—74) combines taxa so that there are few species, each with subspecies, varieties and subvarieties.

A wide range of ecotypic variants is also found within many species of *Gentianella*

Fig. 1. Parallel, habitat-correlated variation within four species of *Euphrasia.* Average specimens from natural localities. The variation within localities is fairly small as compared with that between localities. The characteristic habits remain to a great extent constant under cultivation. All 1/4 natural size. — All collections from the province of Skåne in southern Sweden. Author's collections (two exceptions). Parish, UTM coordinates and the author's collection number (within parantheses) given. From left to right: First row: Kungsmarken 1894, MURBECK (LD); Kungsmarken 1925, ANDER (LD). Second row: Ramsåsa, VB 2880 5820 (105); Träne, VC 3550 0420 (21). Third row: Matteröd, VC 1315 1945 (310); Finja, VC 1990 2518 (334); Visseltofta, VC 2236 5333 (593). Fourth row: N Mellby, VC 2295 1485 (557); Långaröd, VB 2700 8200 (642); V Vram, VB 3195 9330 (36); Dagstorp, UB 7920 8735 (113). Fifth row: V Karup, UC 5368 5303 (298); Grevie, UC 5828 4992 (297); V Karup, UC 5335 5460 (563).


hay meadow
fen
road-side
inland pasture
coastal pasture
micrantha
curta
brevipila
rostkoviana

MOENCH (Gentianaceae). According to PRITCHARD and TUTIN (1972) hybridization between species is common. In Scandinavian *Gentianellae* ecological differentiation seems to be important (the author's observations). Thus the pattern of variation is similar to that found in *Euphrasia* though it is further complicated by variation between the biennial and summer annual habits (MURBECK 1892; see also PRITCHARD 1972).

DISTRIBUTION OF THE PATTERNS OF VARIATION

However striking the patterns just described may be, there is no single criterion on which to judge whether the variation in a given group is of the same kind as in *Euphrasia* or *Melampyrum*. The ecotypes of SOÓ's system may be variously combined in different groups. One taxon, be it a species or a genus, may occur in a wide variety of habitats and comprise six or seven recurrent ecotypic variants, while another may be extremely specialized and comprise only one or two.

In addition, there are many cases of phenological polymorphism in plants other than Rhinantheae and Gentianaceae and the term "seasonal dimorphism" has been applied to a number of phenomena differing from the classic examples of *Euphrasia* and *Gentianella*. KRAUSE (1940) discussed all cases then known. Recently SALISBURY (1968), on the basis of occasional autumnal germination with subsequent increased development in the following year, reported "seasonal dimorphism" in species of *Anagallis* and *Lythrum*. His comparison with *Euphrasia* and *Gentianella* is, however, irrelevant since in Rhinantheae and *Gentianella* it is a question of variation in developmental rhythm in material with uniform germination behaviour. Both the early-flowering and late-flowering variants of *Euphrasia* are summer annuals.

In spite of the difficulties outlined above I have attempted to survey the literature on Rhinantheae with respect to the occurrence of the *Rhinanthus-Euphrasia* mode of variation. Apart from the genera discussed in the introduction, it is evident in the *Odontites rubra-litoralis* group (combined with some polyploidy; SCHNEIDER 1964), perhaps also in *O. lutea* (SOÓ 1966). To some extent it occurs in the *Pedicularis palustris* group (EKMAN 1909), although further study is required.

In Rhinantheae extensive ecotypic variation thus seems to be restricted to temperate European annuals, where it is almost obligate. As HARTL (1972) also noted, it is not found in perennial Rhinantheae, for example the vast majority of *Pedicularis*. The *Pedicularis palustris* group seems to be the only hapaxanth in the genus (usually biennial). Nor is it found in annuals of drier regions, such as *Bellardia, Parentucellia* and *Odontites* in the Mediterranean area. Geographical variation, and local variation that is not ecotypic, are conspicuous in the W American annuals *Cordylanthus* and *Orthocarpus*. ATSATT (1970), having exemplified the variation in *Orthocarpus* states that "the variation patterns described from many European grassland hemiparasites are remarkably similar to the kinds of patterns discussed . . . in *Orthocarpus*", and refers in particular to *Euphrasia*. He has obviously not realized that the chief complicating factor in temperate European hemiparasites is ecotypic variation. For *Euphrasia*, for instance, about 40 per cent of the diagnostic characters used by YEO (1972) are directly related to habit.

In Gentianaceae, in addition to *Gentianella, Blackstonia perfoliata* is often reported as being seasonally dimorphic. Here the variation seems to be correlated with summer annual and winter annual habits.

TOWARDS AN EXPLANATION

I consider that the intricate variation in Rhinantheae and *Gentianella* can best be regarded as being an extreme example of ecotypic differentiation, rather than a special phenomenon restricted to these two groups. Ecotypic variation will be just as wide as the properties of the colonized habitats induce, and becomes recurrent to the same extent that a particular habitat is colonized by different primary taxa. The linicolous weeds are a further example of recurrent ecotypic variation — several taxa from different angiosperm families having developed *Linum*-mimetic races in flax fields (cf. HJELMQVIST 1950).

Why, then, is ecotypic variation so extensive in the hapaxanthic Rhinantheae and *Gentianella*? It is the theory central to this paper that it results from the unusual modes of nutrition present in the two groups, making it possible for their hapaxanthic members to enter plant communities that are not available to the majority of hapaxanths.

The Rhinantheae are hemiparasitic (cf. KUIJT 1969) and are able to take up water with organic and inorganic solutes via haustorial contacts with the hosts (GOVIER et al. 1968 for *Odontites*, cf. discussion by DOBBINS and KUIJT 1973). The water pull can probably be very strong, judging from the high rate of transpiration peculiar to many Rhinantheae (SEEGER 1910). THURMAN (1965) showed that a hemiparasite (*Orthocarpus faucibarbatus*) may obtain all the water and nutrients necessary for normal growth through its host, at least in later stages of development.

The Gentianaceae have an endotrophic mycorrhiza morphologically extremely reminiscent of that in Orchidaceae (NEUMANN 1934, HARLEY 1959). Almost nothing seems to be known about the physiology of the gentianaceous mycorrhiza. In Orchidaceae, it is probable that the vascular plant takes up organic compounds from its endophyte. According to HARLEY (1959 p. 171) there is nothing to contradict the assumption that the orchidaceous mycorrhiza also plays an active part in the absorption of inorganic compounds. It is then not too bold a guess that the mycotrophy of Gentianaceae is nutritionally to some extent equivalent to the hemiparasitism of Rhinantheae. This assumption is supported by the fact that both groups have evolved entirely heterotrophic taxa that lack chlorophyll (e.g. *Voyria, Lathraea*).

The hapaxanthic hemiparasites can be assumed to be partially independent of interspecific competition as they do not compete with the vigorous root systems of the perennial plants for what nutrition or water there is available, but instead draw on the uptake and metabolic activity of the perennials. Thus they are able to grow in closed communities and in extremely low-producing or dry ecosystems. The gift of hemiparasitism can, however, only be exploited to the extent that the plants can adapt themselves to the prevailing physical environment. In a series of habitats, it is probable that factors such as grazing, mowing, shade or drought give rise to a series of conspicuous ecotypes within the plants under discussion as they are hapaxanths and thus entirely dependent on adequate seed-setting. Differential selection must act less extensively on the perennials of the same localities as they are able to resort to vegetative reproduction and reflowering. Moreover, the establishment of seedlings in closed communities is known to be a rare event in many perennials. The number of generations per time unit will be much greater for annuals than for long-lived perennials, and the differentiation is thus likely to have proceeded further in annuals, at least in comparatively new habitats.

The fact that Rhinantheae and Gentianaceae are often the only hapaxanths in their habitats appears clearly from, for instance, my field notes on several hundred *Euphrasia* localities from southern Sweden, and from TER BORG's (1972) tables on *Rhinanthus* localities in the Netherlands. The same phenomenon was noted, and attributed to the hemiparasitism, by SOÓ (1926 p. 170) with special reference to *Melampyrum*, by THURMAN (1965), PIEHL (1966) and CHUANG and HECKARD (1971) for

Orthocarpus and *Cordylanthus* in W American dry habitats, and by SMITH (1963) for *Melampyrum pratense* in nutrient-deficient and dry habitats. STAHL (1900 p. 663) realized the importance of mycotrophy for hapaxanthic Gentianaceae inhabiting closed habitats, and also made a comparison with Rhinantheae. However, as far as I know the consequences for the patterns of variation in the two groups have not been pointed out before, nor has a comprehensive review of habitat preferences been made.

HABITATS OF HAPAXANTHIC RHINANTHEAE AND GENTIANACEAE

The Basic Data

A survey of the habitat preferences of all hapaxanthic plants in NW Europe (Sweden, Norway, Denmark, Finland, Iceland and the Faeroes) has been made. The species included are those regarded by HYLANDER (1955) as being indigenous or naturalized within the region. Taxonomy and nomenclature is according to the same reference. Hybrids and infraspecific taxa are not considered as separate units here.

Data on life-forms are mainly from HYLANDER (1953, 1966), LINDMAN (1926), SYLVÉN (1906) and WEIMARCK (1963). Additional information has been obtained from HEGI (1908—1929), Flora Europaea I—III (TUTIN et al. 1964—1972) and to some extent from herbarium studies.

For each species stated to be at least sometimes hapaxanthic within the region, the notes on habitat given in the works cited above were registered. Further works consulted for this purpose include STERNER (1938), MERKER (1959) and the many contributions in the series "Danmarks Topografisk-Botaniske Undersøgelse", pub-

Table 1. Total number of obligately or facultatively hapaxanthic plant species in the habitats of NW Europe. Habitat preferences of Rhinantheae (Rh) and Gentianaceae (G) deviate from those of hapaxanthic plants in general.

General character	Habitat	Total	Found		Expected	
			Rh	G	Rh	G
Open	Roadsides, waste places	254	7	4	16.8	8.4
	Fields and gardens	125	4	—	8.3	4.1
Dry, semi-closed	Sandy grass heaths	46	1	—	3.0	1.5
	Rocky ground	25	—	—	1.7	0.8
	Calcareous gravel	24	2	—	1.6	0.8
Dry, closed	Dry meadows	19	5	1	1.3	0.6
	Dwarf shrub heaths	6	6	—	0.4	0.2
Moist to wet, closed	Moist meadows and heaths	25	12	7	1.7	0.8
	Fens	12	6	2	0.8	0.4
Shady	Scrub, forest margins	26	4	—	1.7	0.9
	Meadow forests	12	3	—	0.8	0.4
	Heath forests	1	1	—	0.1	0.0
Northern	Above timberline	11	6	2	0.7	0.4
	South-facing precipices	17	1	2	1.1	0.6
Wet to submerged, open	Seasonally flooded	64	2	3	4.2	2.1
	Mud bottoms	17	—	—	1.1	0.6
Saline	Open seashores	52	—	—	3.4	1.7
	Shore meadows	33	7	3	2.2	1.1
Total number of notations		769	67	24	—	—
Total number of hapaxanthic species		454	31	15	—	—

lished mainly in Dansk Botanisk Tidsskrift (e.g. PEDERSEN 1963).

The vegetation of the area was divided into as many kinds of habitat as seemed justifiable with regard to the nature of the basic material. A "species versus habitats" table was first set up: each species was listed for the habitats in which it seemed to be an established component. Then the sum of obligately or facultatively hapaxanthic species in each habitat was calculated. These sums are given in Table 1, as is the number of Rhinantheae and Gentianaceae in the different habitats. Their expected frequencies have been calculated as the total number of hapaxanths in each habitat multiplied by the proportion of Rhinantheae (Gentianaceae) among all hapaxanths.

In the basic data, each species is classified as annual, annual—biennial, biennial, annual—perennial, or biennial—perennial. The transitional groups are fairly large. Often, the reason for the variation is not known — it may be a case of ecotypic differentiation, haphazard genetic variation, modification or erroneous information. Occasionally, one is even in doubt as to the correctness of uniform statements on life-form. The brevity of the statements on habitat preferences in the literature adds somewhat to the uncertainties of the material.

However, as there seems to be no easily accessible more reliable basic material, one has to be content with what is available, keeping the shortcomings in mind. A test of significance of Table 1 should not be undertaken in view of the small numbers in each group.

General Trends

It is a well-known fact (e.g. WARMING 1921), and supported by Table 1 that hapaxanthic plants are largely restricted to open habitats, and to a great extent to those directly influenced by man, viz. roadsides, waste places and cultivated fields. Table 1 shows that both Gentianaceae and Rhinantheae, on the contrary, seem to be primarily adapted to closed and somewhat moist habitats such as moist meadows, fens and seashore meadows. Gentianaceae seem to be more restricted in habitat preference than Rhinantheae which are well represented also in dry closed habitats, and occur even in the driest habitats in the region: sandy steppe and calcareous gravel on limestone pavement (the *alvars* of Öland and Gotland). In the alpine habitats, the two groups together comprise most of the hapaxanthic species. Rhinantheae are also represented in scrub and forest.

The greater ecological amplitude of Rhinantheae as compared to Gentianaceae is due partly to the greater diversity of genera and of species within genera, partly to greater diversity within the species. The mean number of habitats per species (from the last two rows in Table 1) is 1.69 for all hapaxanths together (1.66 if Rhinantheae and Gentianaceae are excluded), 1.60 for Gentianaceae and 2.16 for Rhinantheae. This is so in spite of the partly narrow, ecologically founded species concept used for *Euphrasia.* Two extreme but not isolated cases may be mentioned. *Melampyrum pratense* occurs in the *Calluna* heath, in all kinds of woodland and in alpine heathland. *Euphrasia brevipila* occurs in habitats ranging from sandy steppe (*Koeleria* vegetation) to fens, and is also found in cultivated fields, along roadsides and in alpine habitats. Ecologically it is the most extensive hapaxanthic species in the NW European flora, and is morphologically differentiated accordingly.

Roadsides, Waste Places, Fields

In ruderal habitats and cultivated fields the groups under study are clearly underrepresented. This is a consequence of the fact that their general preferences diverge so strongly from those of most hapaxanths. The ruderal habitats are by no means out of reach for the two groups. The field habitat is perhaps impossible for Gentianaceae but is well exploited by Rhinantheae: *Rhinanthus serotinus* and *Melampyrum arvense* were before the turn of the century among the most aggressive weeds in rye (PEDERSEN 1963) but are now rare as field weeds.

Dry, Semi-closed Habitats

Sandy grass heaths, rocky ground, and calcareous gravel seem to be beyond the ecological range of Gentianaceae and marginal for Rhinantheae though inhabited by two *Euphrasia* taxa with *brevipila* affinities. In these habitats the perennials do not form a closed plant cover but there is plenty of room for annuals. Drought is, however, severe during the summer months and most of the annuals are early-flowering and have set seed long before mid-July. Winter annuals dominate among them and are characteristic of this type of habitat. *Euphrasia* is one of the very few annuals in this type of habitat that start flowering during or after the hottest period, and seems to be even the latest among them. There can be no doubt that it is the hemiparasitism of the plant that makes continued growth possible during the hot summer in spite of its poorly developed root system.

It is a strange sight to see a sun-burnt grass heath in September where *Euphrasia* has not only survived but is profusely flowering. It has often been stated that annuals in dry habitats fluctuate greatly in number of individuals from year to year, depending on weather conditions. I have not noted this phenomenon in Swedish *Euphrasia,* and this apparent stability in reproductive capacity may be due to the hemiparasitic mode of life.

Closed Habitats

For **dry meadows** (narrowly delimited here in relation to moister habitats) the following hapaxanths are reported to occur:

Annual:

- *Arenaria serpyllifolia*
- *Bupleurum tenuissimum*
- *Cuscuta epithymum*
- *Euphrasia,* four species
- *Melampyrum arvense*
- *Trifolium dubium*
- *T. campestre*
- *T. striatum*

Annual—biennial:

- *Linum catharticum*

Biennial:

- *Carduus acanthoides*
- *Carlina vulgaris*
- *Centaurium minus*
- *Daucus carota*

Annual—perennial:

- *Medicago lupulina*
- *Satureja acinos*

Biennial—perennial:

- *Carum carvi*

Some of the non-parasitic species in the list probably grow on open patches of ground only, or in meadow types transitional to sandy grass heaths. However, *Bupleurum tenuissimum, Trifolium dubium, Linum catharticum, Carlina vulgaris, Medicago lupulina* and *Carum carvi* should be investigated as to the reason for their occurrence in more closed habitats. *Linum catharticum* has an endotrophic mycorrhiza (STAHL 1900).

The **dwarf shrub heaths** (e.g. the *Calluna* heath) form a more extreme habitat for hapaxanths than the dry meadows: a dry closed vegetation where the supply of nutrients is even more limited (e.g. SJÖRS 1967 p. 47). The only hapaxanths present are hemiparasites, viz. five *Euphrasia* species and *Melampyrum pratense.*

The same may hold good for **moist heaths** in relation to moist meadows. Only four hapaxanths, viz. three *Euphrasia* species and *Pedicularis silvatica* are recorded from this type of habitat.

The **moist meadows** (including relatively dry types transitional to dry meadows and dwarf shrub heaths) are very rich in species in general. However, the flora includes very few hapaxanths apart from Gentianaceae and Rhinantheae. The list comprises all five lowland species of *Gentianella,* two *Centaurium* (Gentianaceae), six *Euphrasia, Pedicularis palustris* and two *Rhinanthus* species. There is only one more annual, *Bromus racemosus,* and four biennials, viz. *Cirsium palustre, Linum catharticum, Senecio aquaticus* and *S. congestus.*

The meadows and heaths (dry to moist) form a very varied group of habitats. Just as important as the edaphic factors are mechanical factors such as mowing, and grazing which can vary greatly in intensity and duration. This has particular bearing on the problem of variation in Rhinantheae and *Gentianella,* as conspicuous ecotypes are formed under the selective pressure of cultural influence.

In the **fens**, the only strictly annual plants are five *Euphrasia* species and *Gentianella uliginosa.* The other hapaxanths recorded are *Pedicularis palustris, Gentianella amarella, Cirsium palustre, Linum catharticum, Peucedanum palustre* and *Senecio congestus.* The scarcity of hapaxanths other than hemiparasites and mycotrophic plants again forms a contrast to the large number of perennials in these habitats.

The reason for the occurrence of non-parasitic and non-mycotrophic hapaxanths in fens and moist meadows is worth studying more closely. *Senecio congestus* is well known to be very erratic in occurrence, restricted to patches of open mud, and is obviously a weak competitor. But *Bromus racemosus, Cirsium palustre, Peucedanum palustre* and *Senecio aquaticus* should be investigated as to life-form, ecology and reproductive strategy.

Forests

Forests and other shady habitats are by no means inaccessible to hapaxanths. In particular the scrub forming a transition between herb-rich meadows and forest is relatively rich in hapaxanths. In deciduous forests with a dense field layer of grasses and large-leaved herbs, however, some *Melampyrum* species seem to be the only normally occurring hapaxanths. Other hapaxanths of forest and scrub tend to be restricted to open soil or stony ground in forests where the field layer is less dense.

In **heath forests**, which are poor both in species and nutrients, *Melampyrum pratense* is the only hapaxanth recorded. This species occurs even in the subarctic forests of northern Scandinavia, and in the extremely dry and nutrient-poor *Pinus silvestris* forests occurring on almost bare rocks.

Northern Habitats

As was so clearly shown by RAUNKIAER (1908) the number of hapaxanths decreases with higher latitudes and with altitude in cold-temperate climates. A plausible explanation is that the growing period is too short for these plants to reach maturity and set seed. In the seedling stage, they lose much of the early growing period, which perennials can utilize more fully (e.g. ANDERSSON & BIRGER 1912 pp. 22, 114 for Sweden, SCHROETER 1908 p. 632 for the Alps). On the Mediterranean high mountains, where insolation is greater and the growing period longer, annuals seem to be commoner (the author's observation), which may support the above hypothesis.

In NW Europe, most of the few hapaxanths that grow above the timberline are Rhinantheae (*Euphrasia, Melampyrum, Pedicularis* and *Rhinanthus*) or Gentianaceae (*Gentiana nivalis, Gentianella*). The only other hapaxanths are *Saxifraga adscendens, Sedum villosum* and *Koenigia islandica.* Just as in the lowlands, Gentianaceae and Rhinantheae tend to occur in closed vegetation whereas the other hapaxanths are restricted to open habitats such as cliffs or bare wet soil. *Saxifraga* and *Sedum* are biennials, the latter sometimes perennating by means of offshoots. *Koenigia* is an annual; its extremely small size might be adaptive in the low nutrition level of the alpine environment.

It is interesting to note that not only are there widespread hemiparasites and Gentianaceae that find entry into the alpine vegetation, but there are several alpine or northern hapaxanthic species of Rhinantheae and Gentianaceae (*Rhinanthus groenlandicus,* three *Euphrasia* species, *Gentiana nivalis,* three *Gentianella* species and *Lomatogonium rotatum*). This type of distribution is extremely rare among the other hapaxanths.

The **south-facing precipices** (with talus), where insolation is stronger, the growing period longer and the soil partly mobile, form a northern habitat better suited for hapaxanths and also well exploited by them (ANDERSSON & BIRGER 1912). There are some Gentianaceae and Rhinantheae, chiefly recruited from the alpine flora, but they do not seem to have produced any forms specifically adapted to this habitat.

Wet Open Habitats

The **seasonally flooded** habitats are among those chiefly utilized by hapaxanths in NW Europe, and are in part relatively natural. Some examples of this type of habitat are, open wet sand in dune landscapes, open mud along streams and margins of pools and the shallow, during winter water-filled depressions in the limestone pavement of Öland and Gotland. Gentianaceae and Rhinantheae are represented, in the case of *Euphrasia* and *Odontites* with specialized types.

The permanently inundated **mud bottoms** (fresh and salt water) form habitats for some hapaxanths such as the *Callitriche* species and *Salicornia strictissima.* The habitat seems to be inaccessible to Rhinantheae and Gentianaceae.

Saline Habitats

Open seashores (rocky, pebbly or sandy) constitute the habitat for many hapaxanths, but Rhinantheae and Gentianaceae are conspicuous by their absence. Perhaps the rather dry conditions in combination with scarcity of host plants (for Rhinantheae) may be the explanation.

The saline **shore meadows** are also rich in hapaxanthic species. From GILLNER's (1960) work on the shore meadow vegetation of the west coast of Sweden it seems that in this region at least, most hapaxanths are weak competitors and occur on drift material, on bare salt patches and in the temporarily submerged semi-closed communities of the lower part of the meadow. By contrast, *Odontites litoralis* and *Rhinanthus serotinus* occur chiefly in the decidedly closed Subassociation of *Odontites litoralis* within *Juncetum gerardi* where they are the only hapaxanths (GILLNER 1960 p. 49).

CONCLUSIONS AND DISCUSSION

To sum up, the patterns of variation in some Rhinantheae and Gentianaceae are made extremely complex by an exceptionally wide range of ecotypic variation in combination with standard geographical and local variation. This pattern is restricted to hapaxanthic representatives of the groups in temperate Europe.

The same hapaxanths are able to grow in habitats more or less inaccessible to other hapaxanths. The hemiparasitic habit of Rhinantheae and the mycotrophy of Gentianaceae probably decrease interspecific competition and thus bring about the unusual habitat preferences.

Descending from family and tribe level to genera and species groups, we find the correlation between type of variation and ability to colonize closed habitats to be seemingly absolute. In Rhinantheae, all hapaxanthic groups enter closed habitats, and the wide range of ecotypic variation is obligatory. For some reason, in Gentianaceae some temperate European hapaxanths (e.g. *Cicendia filiformis* and at least some *Centaurium* species) cannot stand up to the competition in closed plant communities. In these genera there is little or nothing reminiscent of the ecotypic range in *Gentianella,* which does enter the closed communities.

The species in question (except for some *Melampyrum*) seem to require plenty of light and do not grow in forests. But most of the temperate European forestless vegetation, to which the species have adapted, is man-made and thus of fairly recent origin (STRAKA 1970). This of course applies to roadsides, fields and fallows, but also to the many types of grassland that are the principal habitats for hapaxanthic Rhinantheae and *Gentianella.* Even the dry, steppe-like sandy grass heaths and the *Calluna* heath are at least in southern Sweden dependent on constant human activity. The author has observed that with the abandonment of former methods of agriculture in southern Sweden, the *Euphrasiae* and *Gentianellae* seem to disappear very rapidly. Similar statements have been made for British *Gentianella* (PRITCHARD 1972), Swedish *Melampyrum arvense* (GISLÉN 1949) and Dutch *Rhinanthus serotinus* (TER BORG 1972).

The conclusion that can be drawn is that complex variation in the hapaxanthic Rhinantheae and *Gentianella* developed side by side with the cultural evolution of man in Europe. The hemiparasitic and mycotrophic habits of the respective groups were excellent preadaptations when the newly opened habitats were colonized. This colonization resulted in adaptive radiation that developed along parallel lines in many species groups of hemiparasites and *Gentianella.* The recurrent ecotypic variation in these plants thus includes examples of recent differentiation as striking as that of the linicolous weeds (ROTHMALER 1947).

Hemiparasitic hapaxanths of the Arctic region and of hot dry regions such as W North America and the Mediterranean area, show no comparable ecotypic variation. The reason may be simply that the regions in question do not display the enormous span of forestless habitats that developed in temperate Europe through the agency of man.

The diversity of forestless habitats in prehistoric Europe must have been very much less than now, and such habitats must have been rare, like islands within the forest. With Swedish conditions in mind, I would suggest that habitats such as cliffs, serpentine outcrops, limestone pavement, alpine regions, climatic steppe, some fen types and some coastal habitats could have housed the hapaxanthic grassland species in question even before human influence was intensified.

Before the days of primaeval forest came the glacials, interglacials and early postglacial with their extensive biota migrations. During periods of migration there was probably much re-forming of plant communities and much hybridization within plant taxa such as *Euphrasia* with chiefly ecological interspecific barriers against gene exchange.

We thus can visualize cycles of expansion of and depletion of habitats that suit hapaxanthic hemiparasites and mycotrophs. The habitat expansions were probably associated with a great deal of hybridization and segregation, the habitat depletions with loss of genetic material and fixation of more or less adaptive gene complexes.

In view of this complex series of processes I do not consider it possible to point out any of the recent variants within the species as being "the undifferentiated form" left over from prehistoric or even preglacial times, as was done by early students of the genera (and even by SCHWARTZ 1935 and SCHNEIDER 1964).

As regards taxonomy, it should be taken into consideration that some of the many types recognized as ecotypic variants may be relatively old and distinct, others can be assumed to be fairly new types, while still others have perhaps originated quite recently by selection ranging over a few generations only. Moreover, even the types that are best defined may have originated separately in independent segments of the area of a species, just as parallel types have evolved in different species and genera. As a result we have both a multitude of local types adapted to local habitats perhaps with random association of some diagnostic characters, and some widespread types adapted to widespread habitats, but not necessarily older or more "primary". This complexity precludes the automatic assignment of rank to the intraspecific variants, if the taxonomical aim is a system expressing phylogenetic relationships. Taxonomic revisions based on herbarium studies only, and not including field observations from all parts of the area concerned, are likely to make the chaos that prevails within some of the groups even more pronounced than it is.

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Studies in the Aegean Flora

XXIII. Goniolimon Boiss. (Plumbaginaceae)

Hans Runemark

RUNEMARK, H. 1974 12 30. Studies in the Aegean Flora. XXIII. Goniolimon Boiss. (Plumbaginaceae). — Bot. Notiser 127: 540—545. Lund. ISSN 0006-8195.

Goniolimon collinum (GRISEB.) BOISS. and *G. sartorii* BOISS. are taxonomically discussed with descriptions, illustrations of leaf variation and distribution maps. The chromosome number $2n=34$ is recorded for both species and the karyotype (1 submetacentric, 1 subtelocentric, and 15 telocentric pairs) for *G. sartorii.* The affinities between the species and the history of the isolated maritime populations of *G. collinum* in the Aegean are discussed.

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INTRODUCTION

Four species of *Goniolimon* are known from Greece, *G. tataricum* (L.) BOISS. from Makedhonia, *G. heldreichii* BOISS. endemic to Thessalia, *G. collinum* (GRISEB.) BOISS. from Makedhonia and Thraki, and *G. sartorii* BOISS. endemic to the central and western Aegean. The two first-mentioned species have pubescent calyx tubes, the others glabrous. The genus is restricted to steppe-like habitats with the exception of the maritime *G. sartorii* and a few, newly detected maritime localities for *G. collinum* in the Aegean.

TECHNICAL NOTES

Abbreviations of collectors in locality lists: BO ROLAND VON BOTHMER, BE BENGT BENTZER, G MATS GUSTAFSSON, E LENNART ENGSTRAND, N BERTIL NORDENSTAM, R HANS RUNEMARK, S SVEN SNOGERUP, ST ARNE STRID. All the material by these collectors is preserved at LD and has been collected from 1958 to 1974.

Abbreviations of Herbaria: LD Botanical Museum, Lund, W Naturhistorisches Museum, Wien.

For cytologial studies material was raised from seeds and cultivated in the greenhouses at the Botanical Gardens, Lund. Voucher specimens are preserved at LD. Material from 2 populations (6 individuals) of *G. sartorii* and from 1 population (6 individuals) of *G. collinum,* indicated by an asterisk in the locality lists, have been studied.

Chromosome counts have been made from root tips using a modification of Navashin-Karpechenko for fixation and crystal violet with the addition of aniline for staining. Karyotype analyses have been made from root tips pretreated with 0.1 % colchicine for 3 hours, fixed in Carnoy (3 : 1), stained in feulgen and treated with 5 % pectinase for 2 hours before squashing.

KEY TO THE AEGEAN SPECIES

15—40 cm, leaves 3—7-veined, inflorescence lax, anthers yellow .... *G. collinum*
5—15 cm, leaves 1-veined, inflorescence contracted, anthers red .... *G. sartorii*

G. collinum (GRISEB.) BOISS.

15—40 cm, basally usually much-branched perennial herb. Leaves 30—120 ×8—25 mm, with 3—7 veins, linearly spathulate to broadly spathulate and abruptly contracted into a 1—5 mm broad petiole, apex acute or rarely obtuse, distinctly mucronate. Leaf shape very vari-

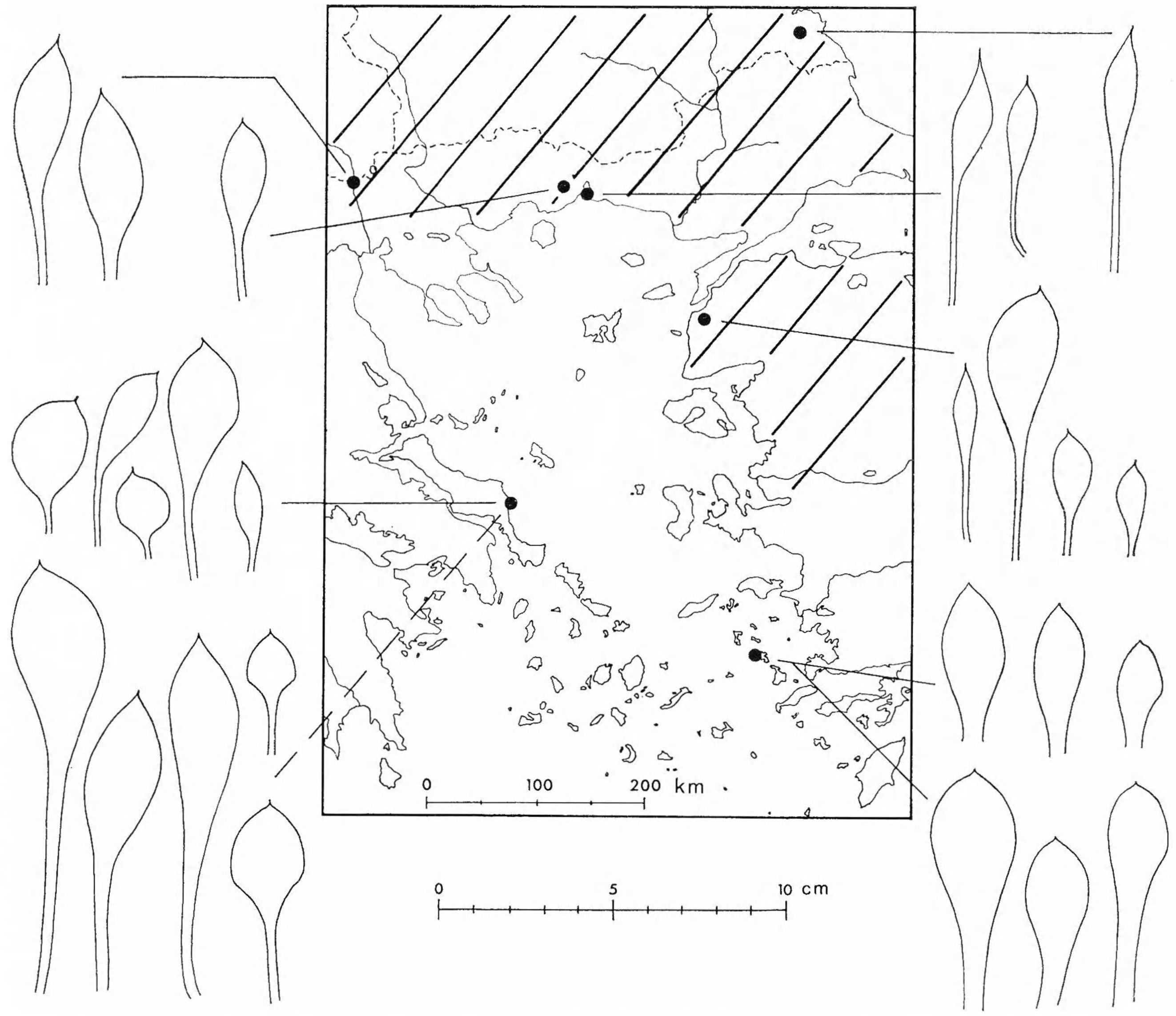

Fig. 1. Leaf variation in *Goniolimon collinum*. Solid lines represent material collected in the field, broken line cultivated material. The hatched area shows the approximate distribution of the species within the area covered by the map.

able between and within populations and within single individuals. Inflorescence scorpioid-corymbose, lax, stem 1.5—3 mm in diam., subangular or rounded and striated, main branches 40—120 mm, angular to distinctly winged, stem scales 7—11 mm, gradually tapering into a point to short, broad and acuminate, usually with a narrow hyaline margin. Spikes dense, spikelets 1(—2)-flowered. Bracts glabrous or slightly puberulous (often only on the inner faces), outer ones 3—4 mm, tapering into a point or cuspidate, auriculate, inner ones 3-fid (exceptionally 1—2-fid), auriculate, cuspices thick, usually recurved. Calyx 6—7 mm, glabrous, lobes longer than broad, in bud yellow, later white. Corolla white, anthers yellow (always?). Flowering in May and June. Chromosome number $2n=34$.

ECOLOGY. Mainly growing on steppes and dry meadows. Those collected in the Aegean in maritime sand (Thraki) and in the epilitoral zone on limestone on two islets lacking normal phrygana vegetation.

DISTRIBUTION. Widely distributed in the eastern part of the Balkan Peninsula

(Yugoslavia, N.E. Greece, Bulgaria, S.E. Roumania) and in Asia Minor. Also recorded from Lebanon.

Aegean localities: North Aegean. Thraki. Porto Lagos, maritime sand RECHINGER 10375 (LD, W). — West Aegean. Evvoia. The small islet S. of Cape Oktonia, limestone R & N 16825*. — East Aegean. Dhodecanisos. Leros. Pharios Nisia, the N. islet, limestone R & BO 46337.

VARIABILITY. The North Aegean material is "normal" *G. collinum* with narrow leaves not abruptly contracted into the petiole. The locality is closely connected with the area of distribution in N.E. Greece.

The geographically isolated material from rocky islets represents morphological extremes characterized by broad leaves more or less abruptly contracted into the petiole and by short, broad, acuminate scales with broad hyaline margins. Moreover the East Aegean population is unusually tall and vigourous (40 cm) and has extremely broad petioles and a rosette of numerous crowded (living and withered) leaves, while the West Aegean population has undivided to more or less bifid inner bracts.

G. sartorii BOISS.

5—15 cm, basally usually much-branched perennial herb. Leaves 10—40×4—12 mm, 1-veined, usually spathulate and abruptly contracted into a c. 1 mm broad petiole, apex acute or rarely obtuse, mucronate to mucronulate. Leaf shape very variable both within individuals and populations, from linear-spathulate to rounded with a cordate base. Inflorescence scorpioid-corymbose, contracted, stem 0.8—1.5 mm, subangular to rounded and striated, main branches 5—20 mm, rarely up to 40 mm, angular to indistinctly winged, stem scales 3—7 mm, acuminate to cuspidate, with broad hyaline margins. Spikes dense, spikelets 1(—2)-flowered. Bracts glabrous or slightly puberulous, outer ones 3 mm, cuspidate, auriculate, inner ones 3—5 mm, 3-fid, auriculate, cuspices thick and recurved. Calyx 5—6 mm, glabrous, lobes longer than broad, in bud yellowish, later white. Corolla white, anthers red. Flowering in April. Chromosome number 2n=34 (1 submetacentric, 1 subtelocentric, and 15 telocentric pairs).

ECOLOGY. In the epilitoral zone on large and small islands and in Attiki, on rocky ground (schists and other siliceous rock). One locality (locus classicus on Mikonos) on maritime sand dunes.

DISTRIBUTION. Several localities in the Paros and Mikonos areas in the Kikladhes, one locality in S.E. Attiki and two at the S. point of Evvoia. Usually abundant in the localities.

Localities: Attiki. Lavrion, Ergastiria 1885 HELDREICH (LD). — Evvoia. N. of Akr. Mantili R & S 11608d, RECHINGER 18900 (W). Mantili Nisos R & S 11608, RECHINGER 18853 (W). — Kikladhes. Mikonos: Ftelia 1856 SARTORI (typus, not seen), R & E 35239, Marmara R & E 36175, N. of the eastern Ag. Elias R, ST & G 39432, S. of the eastern Ag. Elias R & E 36218, the island of Tragonisi R & E 35582, R, ST & G 39397; Paros: the island of Strongilo R & BE 25440, the island of Dhespotiko, the N.E. part R & BE 28616, the islet of Tsimindiri (between Dhespotiko and Antiparos) R & BE 28559, the islet of Kavouras (N. of the Paros-Antiparos strait) R & BE 30770*, the islet E. of Kavouras (d:o) R & BE 30831, the islet of Dhiplo (d:o) R & BE 30794*.

VARIABILITY. The most conspicuous variation in leaf shape is apparently to a large extent modificative. Slight tendencies to local differentiation between the four isolated distribution areas can be traced.

Attiki. Inflorescences rather lax with branches up to 40 mm (in other populations not exceeding 20 mm). Rather conspicuous mucro.

Evvoia. Leaves with very conspicuous mucro. The only area in which leaves with cordate base have been observed.

Paros. Inflorescences very small and contracted. The only area with puberulous bracts. Glabrous, slightly puberulous and

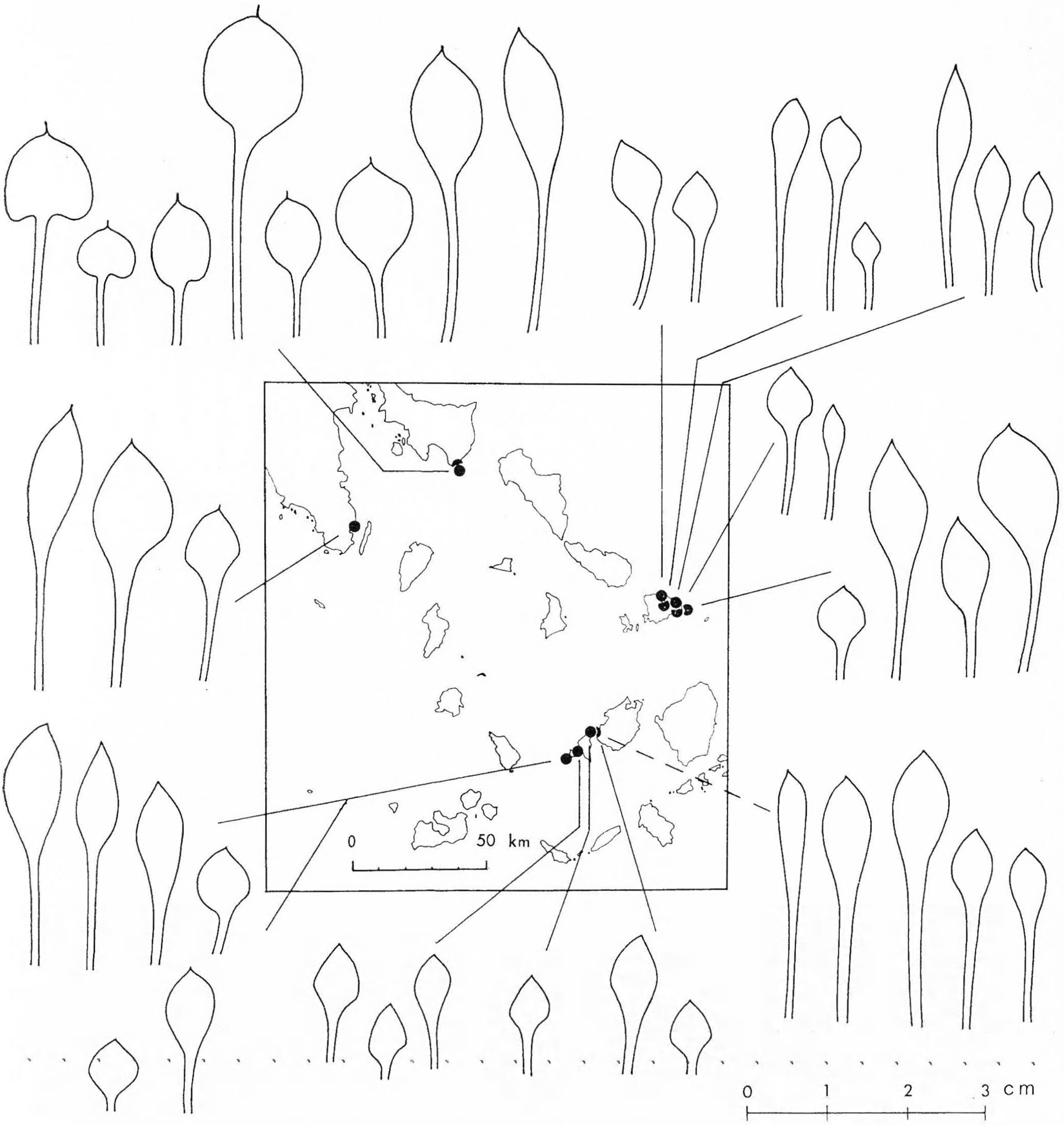

Fig. 2. Leaf variation in *Goniolimon sartorii*. Solid lines represent material collected in the field, broken line cultivated material. The map also gives the total distribution for the species.

distinctly puberulous bracts may occur in the same population.

Mikonos. Narrow leaves commoner than in other areas.

COMMENTS

G. collinum and *G. sartorii* are very similar in floral characters (flowers, calyces, bracts and spikes). In vegetative parts *G. sartorii* is mainly a miniature form of *G. collinum*. They both have the chromosome number 2n=34 not formerly recorded for the genus. Previous records are 2n=16, 32 and 36 (for references see FEDOROV 1969). They have both good pollen formation and the morphologic variation within

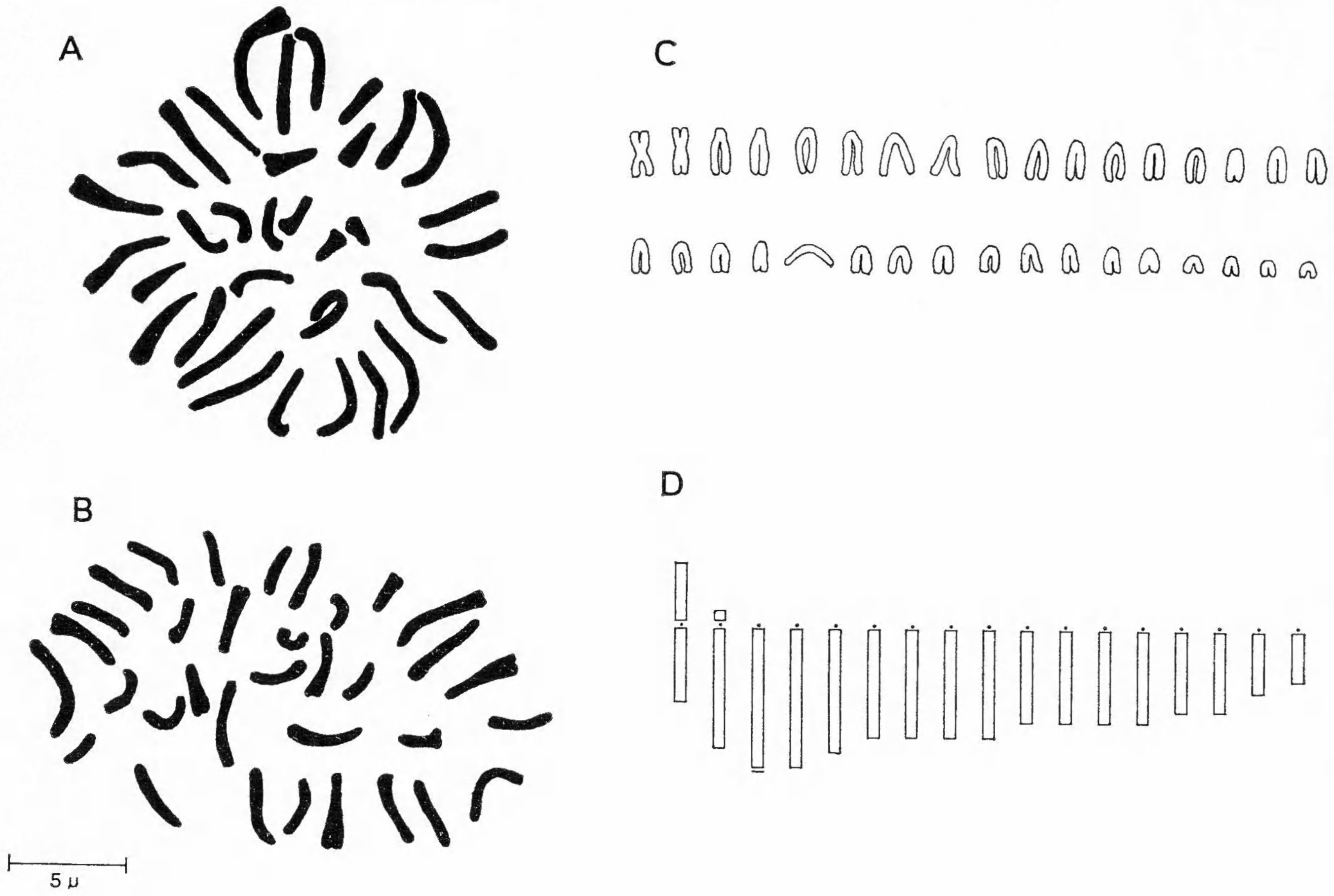

Fig. 3. Cytological observations. — A: *Goniolimon collinum,* metaphase plate (crystal violet). — B: *G. sartorii,* metaphase plate (crystal violet). — C: *G. sartorii,* late metaphase chromosomes (feulgen, pretreatment colchicine). — D: *G. sartorii,* approximative idiogram (the position of the centromere is indicated by a small dot). The satellite on one of the long telocentric chromosomes is not visible on the material illustrated.

populations indicates sexual reproduction. Apparently the species are closely related.

An analysis of the chromosomes of *G. sartorii* shows the pattern 1 submetacentric, 1 subtelocentric, and 15 telocentric pairs. Such very asymmetric karyotypes have only been reported from very few plants, e.g. in *Welwitschia, Podocarpus,* and *Tradescantia.* Karyotype analyses have not previously been published for *Goniolimon.* The very restricted information on chromosome morphology in the closely related genus *Limonium* only shows "normal" symmetric karyotypes (cf. CHOUDHURI 1942, LARSEN 1963).

During the Quaternary glaciations the steppe element penetrated far into the Mediterranean area (cf., e.g., HAMMEN et al. 1971). During such periods the two islets with *G. collinum* were probably connected with the mainland because of regression of the sea (cf. PFANNENSTIEL 1951). The two isolated localities in the Aegean probably represent two unrelated, locally evolved or selected relic populations surviving on islets with a restricted competition (both islets are poor in species and lack the normal phrygana vegetation). The importance of such islets as refugia has previously been discussed by the author (RUNEMARK 1969).

The West Aegean material of *G. collinum* and *G. sartorii* to some extent morphologically connect the species. Thus the leaf shape of *G. collinum* from Evvoia approaches that of *G. sartorii,* the material from southern Evvoia of *G. sartorii* has the very conspicuous mucro characteristic of *G. collinum* and the inflorescence of *G. sartorii* from Attiki is rather lax approaching that of *G. collinum*. It is not improbable that a contact zone has existed in the western Aegean and that a restricted gene exchange has taken place.

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Karyotype of Allium chamaespathum Boiss.

Roland von Bothmer

BOTHMER, R. VON 1974 12 30. Karyotype of Allium chamaespathum Boiss. — Bot. Notiser 127: 546—547. Lund. ISSN 0006-8195.

The chromosome morphology in *Allium chamaespathum* BOISS. is presented and is compared with that found in *A. amethystinum* TAUSCH.

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Allium chamaespathum BOISS. is an autumn-flowering species belonging to sect. *Allium* and is endemic to the Balkan Peninsula. The species is very distinct, with, for example, the leaf-sheaths covering the whole scape up to the inflorescence and with no vegetative propagation. It is rather invariable and has many characters similar to those of *A. amethystinum* TAUSCH (=*A. descendens* L. nom. ambig., see KOLLMANN 1970), as, for example, similarity of seed structure, tepal shape and tepal papillation. The morphology and distribution of *A. chamaespathum* was discussed by BOTHMER (1972) and it was considered that the species is probably related to *A. amethystinum.* The karyotype of the latter species deviates markedly from others in sect. *Allium* (BOTHMER 1970) so that a karyotype analysis of *A. chamaespathum* could give further information about possible relationship.

Material was collected in the field from three localities: B 804: Greece: Peloponnisos: Nom. Taygetos, by the road Sparta—Anavriti; steep, rocky slope facing E, 360—500 m; 24.9. 1970. Coll. J. and K. PERSSON. — B 805: Greece: Nom. Attikis: Athens, Mt Lycabettos; 1970. Coll. J. and K. PERSSON. — B 831: Greece: Peloponnisos: Old Korinthos, in a limestone cliff; 1973. Coll. M. GUSTAFSSON.

The usual Feulgen squash method was used (BOTHMER 1970). For the definition of marker chromosomes arm index (r=long arm/short arm) and satellite index (sat. i=satellite/attachment arm) were used. The figures in Table 1 are based on measurements of 10 metaphase plates from each plant.

All material studied was diploid (2n=2x=16). The karyotype is symmetrical with all chromosomes metacentric. Of the chromosome complement 3 or 4 pairs constitute marker chromosomes, all with large linear satellites (Fig. 1). Of the four plants in population B 804 three are similar and have 3 pairs of markers (Fig. 1). The fourth plant has 4 pairs of markers, two of which have very similar r- and sat-indices, but can be distinguished on differences in length. The two plants studied in population B 805 are entirely similar,

Table 1. *Allium chamaespathum.* Mean values of r- and sat-indices for marker chromosomes in three plants. The figures are based on measurements of 10 metaphase plates per plant.

Plant no.	Pair no. 5		Pair no. 6		Pair no. 7		Pair no. 8	
	r	sat. i	r	sat. i	r	sat. i	r	sat. i
B 804—03	1.05	13.47	1.29	10.55	1.21	10.44	1.15	2.38
B 805—03	—	—	1.12	12.64	1.57	8.57	1.21	2.34
B 805—04	—	—	1.27	10.63	1.58	9.25	1.20	2.31

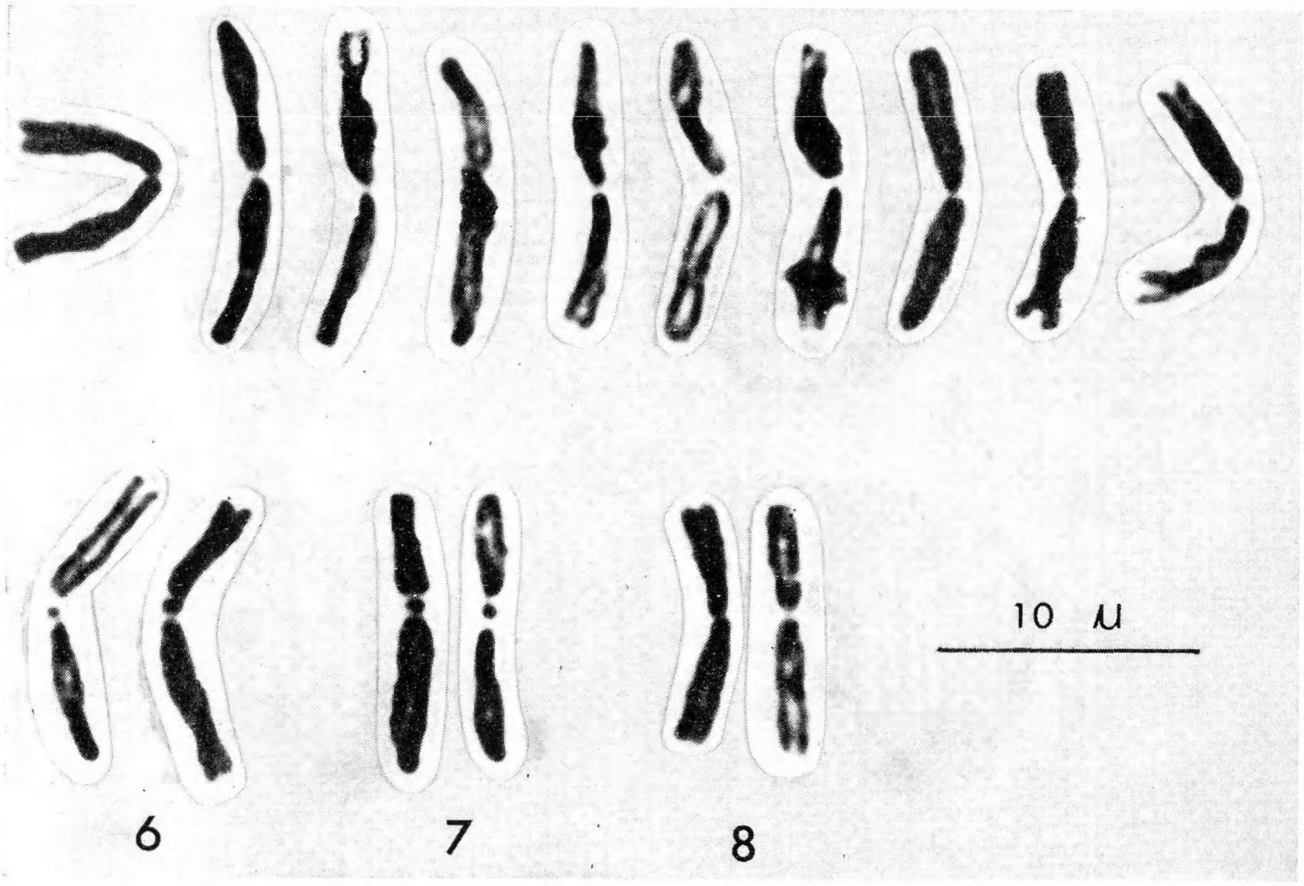

Fig. 1. *Allium chamaespathum*. Karyotype of plant no. B 804—02.

with 3 pairs of markers (Table 1). Two of the marker pairs in B 805 are fully comparable with corresponding pairs in B 804, but the third one (chromosome pair no. 7) has a higher r-index. The single plant from population B 831 has three pairs of markers similar to those shown in Fig. 1.

The karyotype of *A. chamaespathum* deviates markedly from those found in other groups of sect. *Allium* (see e.g. BOTHMER 1970) and greatly resembles that of *A. amethystinum* which has three pairs of markers, but has sat-indices between 3 and 4.5. Thus the appearance of the karyotypes does not oppose a closer relationship between these two species.

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DAHLGREN, R. (in collaboration with B. HANSEN, K. JAKOBSEN, A. KJÆR and K. LARSEN): Angiospermernes taxonomi. Bind 1. — Akademisk Forlag, Copenhagen 1974. ISBN 87-500-1395-5. — Paperback. 258 pp., about 95 text figures (drawings).

This is the first part of a textbook planned to appear in four parts. It is a typed and offset-printed compendium in Danish primarily intended for undergraduate students in Copenhagen. The parts to appear in 1975 will comprise the taxonomy of dicots and monocots and plant geography. Part one is mainly an introduction with chapters on the criteria of angiosperms, the origin of angiosperms, morphology and chemistry. A synopsis of a new system to be used in the forthcoming parts is also presented. Some chapters that seem to be somewhat peripheral to this main theme are also included. They deal with nomenclature, herbarium work and revision technique, and the history of botanical classification.

As the book is written to fill the needs of a specific course which is not introductory the different topics are covered rather unevenly, and some points may need to be supplemented on if used in other Scandinavian universities. For example, the chapter on morphology contains almost nothing on vegetative morphology or anatomy.

The aspects of floral morphology are, however, very well covered. The text is fairly concentrated, but easy to use as the illustrations are plentiful and informative. The scientific counterparts to the Danish terms are generally given. The inflorescences are quite unconventionally grouped, i.e. in closed ones (main axis terminated by a flower) comprising cymes and paniculae, versus open ones comprising racemose types as well as thyrses. This classification seems to give better a correlation with flower symmetry and current taxonomic views.

The chapter on chemical characters is perhaps too comprehensive to be learnt in detail but will be extremely useful as reference.

Some of the chapters are concentrated and will best be used as teaching texts. But the main part of the book comprises discussions on important lines of thought in modern taxonomy, and will give the student a basis for sound taxonomic thinking, and make him aware of the dangers of classification on single criteria.

As regards the origin of angiosperms, the author's opinion seems to be that they are monophyletic and that Magnoliales are similar to the original angiosperms in many respects. But the reader becomes acquainted with various conflicting hypotheses as well, e.g. MELVILLE's and MEEUSE's on the origin of the flower.

The chapter on primitive and derived characters gives a very stimulating discussion on a number of points. TAKHTAJAN's (1969) opinion on, for instance, growth habit and leaf forms of the original angiosperms is criticized. The theory is put forth that fusions like sympetaly and syncarpy may be logical consequences of the close packing of organs on the floral axis, and thus a process that is likely to have occurred several times independently.

In "morphological differentiation, reduction" principles such as divergence, convergence, false and true analogy and parallelism are illustrated with new and very convincing examples, partly from the author's own experience from the South African flora. As examples of reduction are given among others *Casuarina, Callitriche* and *Theligonum,* where close studies, partly utilizing so-called modern characters, have revealed the apparently correct systematic relationships.

In the conspectus of the angiosperm system many families are mentioned in addition to those which will be discussed in the forthcoming parts of the book. Thus a comparison with TAKHTAJAN's (e.g. 1969) system is possible. His framework is still there: for instance Magnoliidae—Ranunculidae, Hamamelidae, Caryophyllidae and Asteridae form major blocks. But DAHLGREN regards the angiosperms as a subclass — i.e. on a level with the major gymnosperm groups — and the further classification is directly into thirty superorders. Not even the mono- and dicots are given formal taxonomic rank (their relationships are critically reviewed in the concluding chapter). It seems as if the reticulate pattern of variation within the angiosperms is better accounted for in this way. In detail, there are differences in almost every comparable grouping, and many of TAKHTAJAN's orders have been entirely broken up. It is outside the scope of this review to discuss the new system thoroughly, and it will soon be presented in an international botanical journal. Then it will doubtlessly greatly stimulate the discussion on angiosperm phylogeny.

Nevertheless, however great the merits of this revised system are, it is a matter for debate whether a new system that will certainly evolve further, should have been used in a fairly elementary textbook like this one. Students who are taught this system (or TAKHTAJAN's) as the principal one will meet difficulties in handling practically every flora, handbook or herbarium, which are often arranged according to ENGLER's system.

Even if Magnoliales show many primitive characters, they have certainly not remained unchanged since the time of origin of the angiosperms. To account for this the system is illustrated not as a phylogenetic tree with Magnoliales at the root (as in TAKHTAJAN 1969 Fig. 31) but as a cross-section of a dense shrub with many major branches representing the superorders. The result is a very expressive diagram of the system as a series of irregular patches, whose areas are roughly proportionate to species content. The position of the patches, with the "primitive" superorders in the centre, reflects the relationships much better than any linear arrangement can do.

This diagram is used in mapping the distribution of twenty-five characters within the angiosperms. Superorders showing the characters are marked with black. Characters that are taxonomically relevant show a coherent pattern, while less useful ones scatter. A derived character such as zygomorphy tends to be restricted to the periphery of the figure, a presumably primary character such as woody habit is found in the centre. Such illustrations, with informative comments, are given for both time-honoured "important" characters such as sympetaly and monocotyly, and "modern" ones such as the occurrence of ellagic acid or iridoids.

Some minor negative remarks. There are some "printer's errors", and the numbering of the figures needs revising. The binding is not so strong as one could wish for in a textbook to be frequently consulted.

From the above comments it should be clear that, when the three parts to follow have appeared, a real need will have been filled: that of a textbook in angiosperm taxonomy not as comprehensive as ENGLER's "Syllabus", but less shortened than the classic "Strasburger", and, moreover, one made up according to modern principles, also taking into account the latest results from the field of research.

THOMAS KARLSSON

STAFLEU, F. (ed.): Index Herbariorum. Part I. The Herbaria of the World. 6th ed. — Regnum vegetabile 92. Utrecht 1974. 397 pp. Price for members of the International Association for Plant Taxonomy Sw.Cr. 79: 30.

Ten years have elapsed since the publication of the fifth edition of the Index Herbariorum. As it has been out-of-date for a long time the present revised and much enlarged issue is particularly welcome.

Questionnaires were sent out at the beginning of 1974 to all Herbaria known to the editors, and replies seem to have been received from the great majority of them. The Index contains all information available up to May 1, 1974. The material has been compiled by Dr PATRICIA HOLMGREN, New York, (the United States Herbaria) and Miss WIL KEUKEN, Utrecht (all other Herbaria).

Ed. 5 (1964) recorded 1,175 Herbaria whereas the present edition lists no less than 1,705 entries. These figures will give some idea of the increased activities in systematic botany during the past decade or at least of the much improved documentation of them.

As in the previous issues each Herbarium has an entry giving the full address, abbreviation according to a standard system (e.g. LD for Lund), year of foundation, number of specimens, names of director and/or curator and other staff members and research associates, including information on specialization. Important collections (collector and systematic group) are recorded, often in great detail. Periodicals issued by the institutes in question have been noted.

It is a well-known fact that the figure denoting the number of specimens often does not give a very adequate indication of the size or importance of a Herbarium. This figure should to some extent be taken cum grano salis. According to the Index the 15 largest Herbaria of the world are: Paris, Laboratoire de Phanérogamie (6,000,000 specimens), Leningrad (over 5,000,000), Genève (5,000,000), Kew (4—5,000,000), New York and Stockholm (both 4,000,000), Washington, Smithsonian Institution (3,860,000), Lyon (3,800,000), Firenze (3,500,000), Montpellier (3,300,000), Manchester and Wien, Naturhistorisches Museum (both 3,000,000), Chicago, Field Museum, Jena and Leiden (all 2,500,000).

For those institutes that have not replied to the inquiry the information given is marked "from 1964". To these can be added "Stockholm: Palynological Laboratory (SPL)", which has had the following address for the past few years: Wallenberg Laboratory, Lilla Frescati, S-104 05 Stockholm (Director: Dr J. ROWLEY). Under Leningrad: KOMAROV Botanical Institute the Cryptogamic Herbarium (Director: Dr I. I. ABRAMOV, several collaborators) has been omitted.

The Swedish reader will notice how understaffed our Herbaria are, especially compared with conditions in the other Scandinavian countries. Under Uppsala, which is one of the 20 largest Herbaria in the world (number of specimens c. 2,000,000, including a great many types), it says "Staff Members: None except the keeper". In the other Swedish Herbaria the situation is about the same. It may seem incredible, but several members of the Faculty of Science at the Uppsala University recently actually expressed the opinion that this post, now vacant, is superfluous and could be dispensed with to the advantage of other, more "progressive", subjects. This will demonstrate the disregard accorded to systematic botany in the country of LINNAEUS. In comparison it can be mentioned that the Copenhagen Herbarium (about the same size as Uppsala, i.e. with the same number of specimens) has a full-time staff of 11 botanists representing most groups of the plant system.

A useful novelty at the end of the present edition is an Index to Important Collections which is a summary, arranged after collectors' names, of the information scattered under the entries of the various Herbaria. On the other hand the chapter Geographical Arrangement of the Herbaria has been left out, where in previous editions the location of the Herbaria was listed under each country.

All taxonomic botanists will be grateful to the editors of the new "Index Herbariorum" which is an indispensable manual for their bookshelves.

OVE ALMBORN

GJÆRUM, HALVOR B.: Nordens Rustsopper. (The Rust Fungi of Scandinavia). — Fungiflora, Oslo 1974. 321 pp., 23 drawings in the text. Price N.Cr. 40:—. Can be ordered from Fungiflora, Blindernveien 46 C, Oslo 3, Norway.

ELIAS FRIES (Summa vegetabilium Scandinaviae, Vol. 2, 1849) made a compilation of the species of fungi known from the Scandinavian countries. His work was not a flora but a "check-list" including scattered taxonomic comments on species and higher groups. Since then our knowledge of Scandinavian fungi has increased considerably, but no effort has been made to summarize all the information available. Some groups (especially among the Basidiomycetes) can be considered to be fairly well known, whereas others have been much neglected since the time of ELIAS FRIES.

No doubt the rust fungi (Uredinales) belong to the best-known orders, as much work has been done on them during the past century in all four Scandinavian countries. A list (without descriptions) of the genera, species and subspecific units known from this area was published in 1953 (HYLANDER, JÖRSTAD and NANNFELDT, Enumeratio Uredinearum Scandinaviae, Opera Botanica, Vol. 1:1). This list included discussions of nomenclature and synonymy, information on type localities, host plants and a very brief summary (e.g., "D, N, F, S", no localities quoted) of the distribution of the species.

The present volume has a wider scope. Some condensed introductory chapters deal with the history of research on rust fungi in Scandinavia, biology (including different states in the life cycle and specialization on different host plants), the species concept and nomenclature, etc.

The bulk of the work comprises keys and descriptions of families, genera and species. Like HYLANDER et al., GJÆRUM has a broad species concept. Special forms adapted to different hosts are listed under the collective species with binary nomenclature, the epithets being preceded by a, b, c, etc. It is rightly emphasized, however, that these names are not in accordance with the Code of Botanical Nomenclature.

HYLANDER et al. recorded 24 genera and 264 species, whereas GJÆRUM recognizes 28 genera and 272 species.

The host plants have been listed in considerable detail for each rust species. The distribution of the rusts has been indicated by quoting numerous localities from Norway. The occurrence of a species in the three other countries has been denoted with the symbols D, N and S only.

"Nordens Rustsopper" is a comprehensive and useful guide to the Scandinavian rusts. No doubt it would have reached a much wider public had it been written in English.

OVE ALMBORN

LÖVE, Á. & LÖVE, D.: Cytotaxonomical Atlas of the Slovenian Flora. — J. Cramer, Lehre 1974. ISBN 3-7682-0932-6. xx+1241 pp. Price DM 200:—.

This Atlas deals with the vascular plants of Slovenia, which comprises the northernmost part of Yugoslavia. It might be thought that this is too small an area for a survey, and it must be admitted that the choice of area was to some extent a matter of chance. However, the area is very varied from a floristic point of view, and the book is therefore of much greater interest to botanists in general than would immediately be inferred from the regional restriction. It contains references up to 1973, which is imposing for a list of this kind, and the coverage of literature is more extensive than is usually possible. Information on geographical distribution has been added.

The information has been fed to a computer by means of punched cards, and the catalogue and bibliography have been printed direct from slightly trimmed copies of the computer printouts. The typography is rather space-consuming due to the method of listing, and some code numbers are repetitive in a way which seems unnecessary. Anyhow, information given is easy for the reader to survey, and one has reason to hope that technical errors other than punching mistakes have been kept to a minimum. The cost for manual typesetting has also been avoided for most of the volume, which has kept the price at a rather reasonable level considering the enormous amount of information given.

The Introduction is somewhat provocative. The Atlas is said to be critical in its approach, and LÖVE and LÖVE give the following declaration of their programme (p. vii): "For the compilation of this kind of atlases . . . all previously published numbers have to be critically scrutinized and the names used by their authors have to be evaluated as to exactness of definition of the category and nomenclature and possible synonymy, before they can be included." As used by the authors the word critical is extremely ambitious and even pretentious. To be meaningful in this context would imply a complete revision of all taxa included. It is difficult to see how such an immense task could be carried out.

In the Introduction the authors defend themselves against possible criticism that they have used chromosome numbers reported from outside the area under consideration. They claim that "From the evidence available it is apparent that if a species is correctly identified and exactly and evolutionarily defined, then it has the same chromosome number from whatever locality or region the material from its cytological study has originated." Maybe, but taxonomy is indeed a rather relative discipline in a state of rapid development, and "exact and professional identification", the need of which is stressed by the authors, is to some extent a matter of opinion, at least in critical and thus especially interesting groups. I prefer a system where the decision of synonymy, etc. is left to the specialist who looks up the references after having located them with the aid of a cytotaxonomical atlas. This atlas, with its rather impossible ambition to be critical, may at the worst induce optimistic readers to believe that things are better known than they are..

I looked up the genus *Heracleum* (Apiaceae), which is of special interest to me, to make a comparison with FEDOROV's atlas from 1969. LÖVE & LÖVE give considerably more references, not only from the period after FEDOROV's atlas was published. However, all references for the Central European taxon *H. sphondylium* L. ssp. *montanum* (SCHLEICHER ex GAUDIN) BRIQ. but one refer to North American and East Asian material. This is explained by the fact that *H. lanatum* MICHX. is treated as a synonym of *H. sphondylium* ssp. *montanum,* which is a highly debatable point. In cases like this where the taxonomy of a critical group is still not sufficiently known we cannot expect the treatment in a cytotaxonomical atlas to be more than provisional, and the "critical approach" may even obscure rather than clarify. I am convinced that it is not necessary to demand as much of the "critical approach" in cytotaxonomical atlases as do LÖVE and LÖVE themselves in their Introduction. An atlas of this kind is of great value as it is.

Moreover, I was unable to find one of the *Heracleum* references in the bibliography, and another reference contained an orthographic mistake. Other sample tests made did not reveal any further mistakes in the bibliography, which on the contrary seems very reliable.

The lengthy discussion above would probably have been superfluous had not the authors been ÁSKELL and DORIS LÖVE. Their enthusiastic fighting spirit sometimes forces them to defend their ideals in a rather controversial manner, but their restless activity in cytotaxonomy and their contributions to constructive debate are well-known and appreciated even by their opponents. The contributions forwarded here to the more or less philosophical discussion of the merits of chromosomes in taxonomy are, of course, not concerned with the value of the actual list of chromosome numbers and their references. The value of this is, I think, indisputable.

Áskell and Doris Löve began to put their vast knowledge of cytotaxonomical literature at the disposal of other botanists as early as in 1942 (Bot. Notiser for 1942 pp. 19—59), and another survey appeared in 1948. In 1961 they published the very useful volume "Chromosome Numbers of Central and Northwest European Plant Species" (Opera Botanica 5, 1961), and I know that they are now compiling a new cytotaxonomical atlas of Arctic plants and one of the Pteridophyta. We have every reason to be grateful to them for their activity in the service of other taxonomists. The present atlas is a great achievement, and it can be highly recommended.

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