

Drawings of Scandinavian Plants 91–93

Chenopodium L.

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91. *Chenopodium ficifolium* SMITH 1800

Annual, erect to ascending, mostly much-branched, up to 1.5 m high. Stem angular, striated. Foliage greenish. Leaves alternate, farinose to glabrous above, conspicuously farinose beneath. Lower leaves distinctly petiolated, 3-lobed, with a cuneate base, lateral lobes shorter than the middle lobe, upward- to outward-pointing, acute, middle lobe long, often narrow and with parallel margins, sinuate to serrate, rarely entire, acute. Lamina length 1—7 cm, breadth 0.5—3 cm, length at least twice the breadth. Upper leaves usually petiolate, 3-lobed to lanceolate, entire to dentate, acute. Inflorescences rather loose, leafy except in the most terminal parts, usually branched, composed of many rather small, rounded to oblong cymes, each consisting of 5—20 clustered flowers. Flowers 5-merous, perfect, conspicuously farinose, yellowish to brownish. Perianth lobes united to one half, ovate, membranous in the outer parts, obtuse to acute, rounded to slightly keeled on the back, the keel being most pronounced in terminal flowers. The perianth covers the seed entirely. Stamens usually 5. Pistil with two stigmas, papillated to the base. Seeds horizontal, orbicular, black, 0.8—1.0 mm in diameter, rounded to keeled in transection. Pericarp thin, usually colourless, sometimes yellowish, firmly adherent to the seed.

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

Testa lustrous, distinctly pitted, each pit 4- to many-angled, with or without radial ridges. Radicula rather short, attached to the seed. Embryo annular.

Flowering time: July to September.

Chromosome number: $2n=18$.

Variation: *C. ficifolium* varies in most vegetative characters, such as height, leaf size and dentation of the leaf margins. However, two taxa are distinguishable, *C. ficifolium* ssp. *ficifolium* and ssp. *blomianum* (ÆLLEN) ÆLLEN. Ssp. *ficifolium* has rather large, broad, outward- to forward-pointing lateral lobes, and the testa has regular, often six-angled pits similar to honeycombs, lacks radial ridges. By contrast, ssp. *blomianum* has small, outward-pointing lateral lobes and the testa has more irregular, somewhat oblong pits, as well as radial ridges. Most Scandinavian records refer to ssp. *ficifolium*.

Habitat and distribution: *C. ficifolium* occurs as a more or less occasional weed on cultivated and waste ground. The two taxa have somewhat different distribution areas. *C. ficifolium* ssp. *ficifolium* occurs in most of Europe and in Asia eastwards to Persia, Pamir and the southernmost part of Siberia. On the other hand, ssp. *blomianum* is native to India and the eastern parts of Asia, from China to the eastern part of Siberia and Japan. In addition ssp. *blomianum* occurs as a weed in Europe. In Scandinavia *C. ficifolium* is most common in the southern parts, according to HANSEN & PEDERSEN (1968)

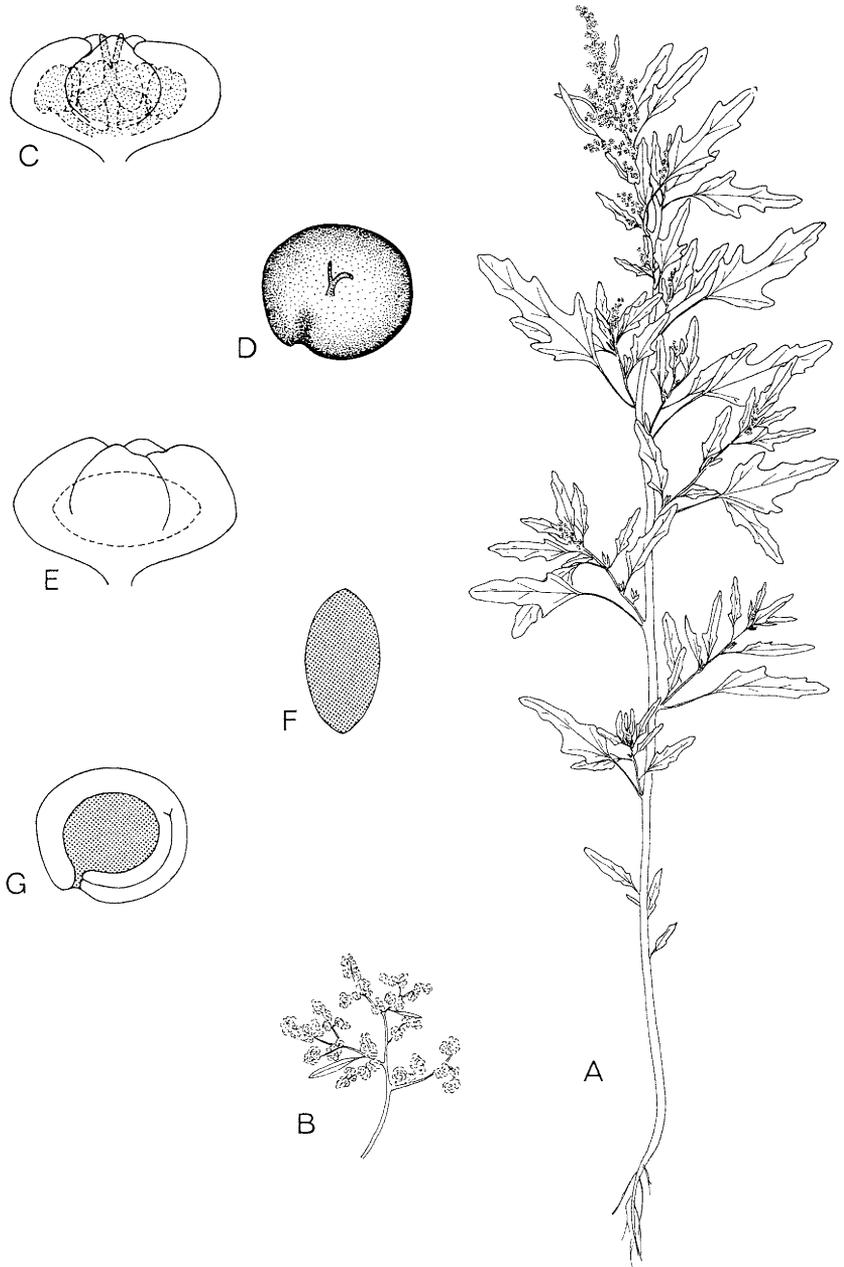


Fig. 91. *Chenopodium ficifolium* SMITH. — A: Habit. — B: Detail of an inflorescence. — C: Hermaphrodite flower. — D: Fruit. — E: Horizontal fruit, enclosed in the perianth. — F: Seed in transection. — G: Section through a seed showing the embryo. — A—B: $\times 0.5$. — C—G: $\times 20$.

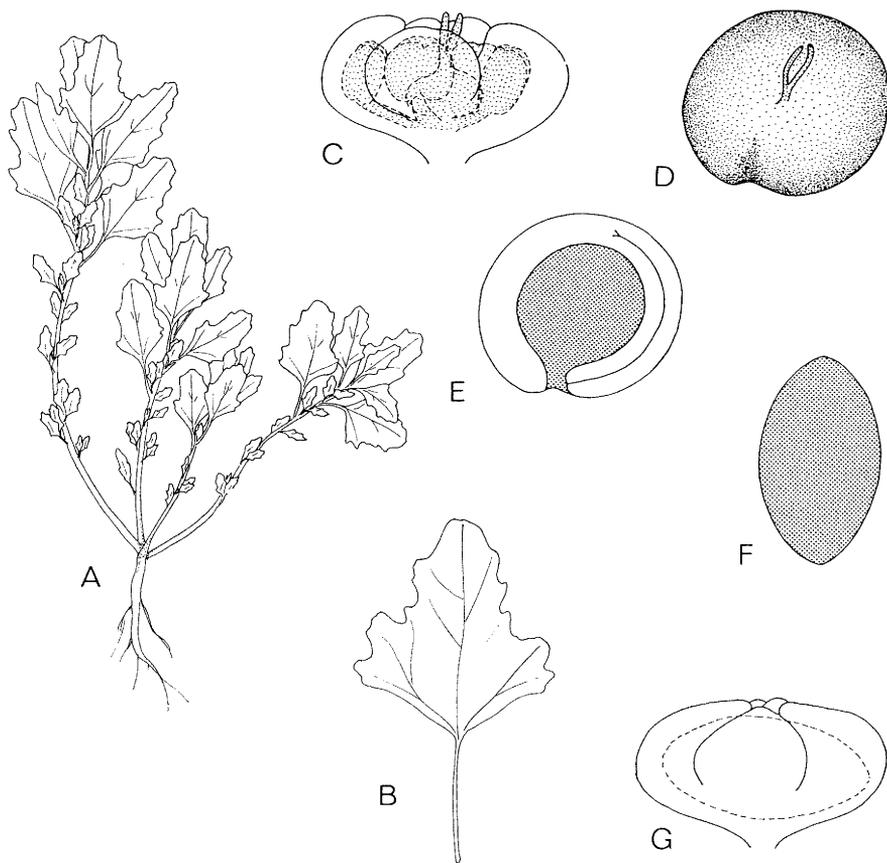


Fig. 92. *Chenopodium hircinum* SCHRAD. — A: Habit. — B: Shape of a large, lower leaf. — C: Hermaphrodite flower. — D: Fruit. — E: Section through a seed showing the embryo. — F: Seed in transection. — G: Horizontal fruit, enclosed in the perianth. — A—B: $\times 0.5$. — C—G: $\times 20$.

even well-established in the surroundings of Copenhagen, but scattered localities are found northwards to the Swedish provinces of Gästrikland—Bohuslän, and in Norway along the coast from Oslo to Sör-Trøndelag. One or two records are known from Finland.

92. ***Chenopodium hircinum* SCHRAD. 1833**

Annual, erect to ascending, usually much-branched, up to 1.2 m high and with an unpleasant smell. Stem angular, striated. Leaves alternate, green and gla-

brous above, green to grey and farinose beneath. Lower leaves distinctly petiolate, 3-lobed, with a cuneate base. Lateral lobes broad, forward-pointing, dentate, reaching to about one half of the leaf, obtuse to acute, middle lobe short, rather broad, sinuate to dentate, mostly with prominent, broad forward-pointing and acute teeth, apex obtuse to acute. Lamina length 0.5—5 cm, breadth 0.5—4 cm, about as long as broad. Upper leaves petiolate and 3-lobed. Inflorescences leafy, spike-like or paniculate. Flowers 5-merous, perfect, conspicuously farinose. Perianth

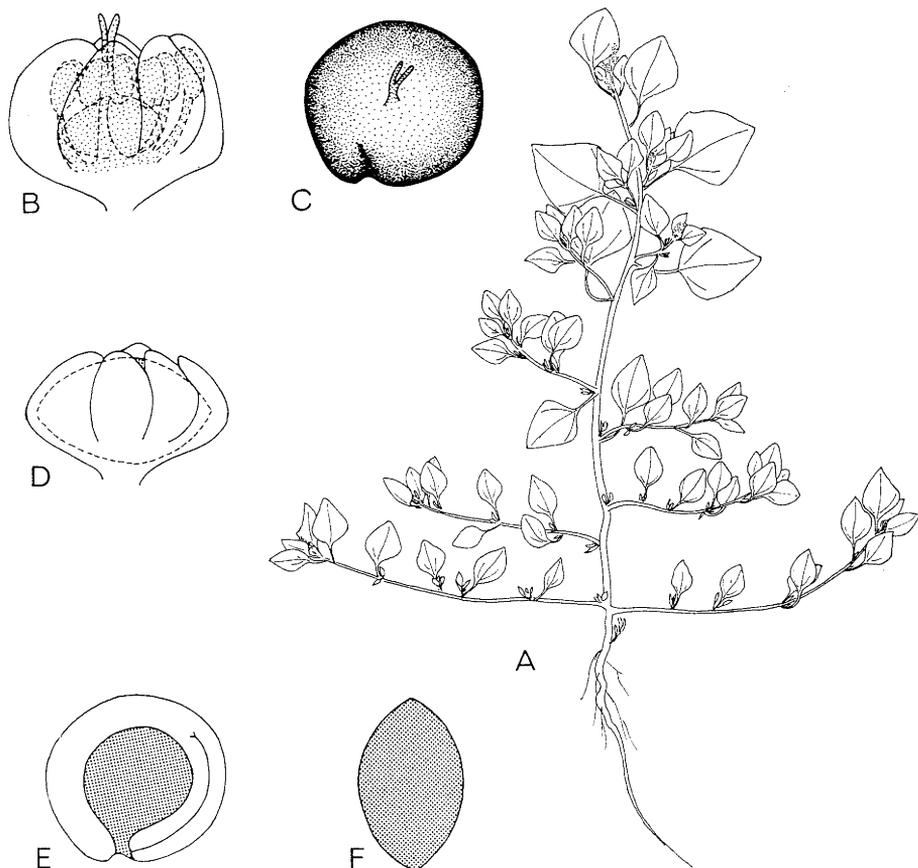


Fig. 93. *Chenopodium vulvaria* L. — A: Habit. — B: Hermaphrodite flower. — C: Fruit. — D: Horizontal fruit, enclosed in the perianth. — E: Section through a seed showing the embryo. — F: Seed in transection. — A: $\times 0.5$. — B—F: $\times 20$.

lobes ovate, united to one half, green to brownish in the centre, somewhat lighter in the outer parts, obtuse to acute, slightly keeled on the back. The perianth covers the seed entirely. Stamens usually 5. Pistil with two rather long, papillated stigmas. Seeds horizontal, orbicular, black, 1.0—1.4 mm in diameter, rounded, rarely keeled in transection. Pericarp yellowish-green, firmly adherent to the seed. Testa lustrous, with usually six-angled, somewhat oblong pits, and radial ridges. Radicula indistinct, rather short and thick, attached to the seed. Embryo annular.

Flowering time: August to October.

Chromosome number: $2n=18$.

Habitat and distribution: *C. hircinum* is an occasional weed growing on waste ground, usually close to harbours, factories or mills. It is native to South America, but introduced in Europe, South Africa and Mexico. In Scandinavia scattered localities in Denmark, from the eastern part of Jylland to Sjælland, in Sweden northwards to Uppland, Medelpad—Bohuslän, and in Norway along the coast from Oslo to Sör-Trøndelag. One or two records are known from Finland.

Note: The vegetative development is generally good in Scandinavia, but plants with well-developed seeds are rarely found. *C. hircinum* is similar to *C. ficifolium*, but the leaves have a shorter and broader midlobe, and the lamina length is about equal to breadth.

93. *Chenopodium vulvaria* L. 1753

Annual, 3—40 cm high, prostrate to erect, much-branched and with an unpleasant smell due to trimethylamine. Lower branches long, decumbent to ascending. Stem more or less angular, slightly striated. Leaves alternate, the lowermost ones sometimes opposite, greenish and glabrous to farinose above, greyish and conspicuously farinose beneath. Lower leaves long-petiolate, about as long as broad, length 1—4 cm, breadth 1—3 cm, ovate to deltoid, cuneate to rounded at base, mostly entire, rarely with a small, broad lobe on each margin at the broadest part, apex obtuse to acute. Upper leaves petiolate, deltoid to lanceolate, entire. Inflorescences short, almost leafless, mainly situated in the terminal parts of the branches, spike-like to paniculate. Flowers 5-merous, perfect, conspicuously farinose. Perianth united at the most to one half, the lobes broadly ovate, green to brownish, acute to obtuse, somewhat keeled on the back. The perianth only partly covers the seed. Stamens 5. Pistil

with rather long stigmas, papillated to one half. Seeds horizontal, orbicular, black, 1.0—1.3 mm in diameter, slightly keeled in transection. Pericarp yellowish, farinose or smooth, rather thin, and easily detached from the seed. Testa lustrous, faintly sculptured by radial furrows. Radicula insignificant, rather short and broad, attached to the seed. Embryo annular.

Flowering time: July to September.

Chromosome number: $2n=18$.

Habitat and distribution: *C. vulvaria* occurs as a weed on waste ground usually close to human settlement, such as farmyards, road-sides, mills, but also on seashores. Frequently distributed in the Mediterranean parts of Europe, less common in other parts of Europe, in the southern parts of Asia eastwards to Pamir. In addition introduced to North America and Australia. In Scandinavia it seems to have been more common previously. Scattered localities in Denmark, from the eastern part of Jylland to Sjælland, in Sweden mainly along the coasts northwards to Västerbotten and Bohuslän, in Norway mainly along the south coast from Oslo to Vest-Agder. In Finland some records from Åland to Nyland.

LITERATURE CITED

- HANSEN, A. & PEDERSEN, A. 1968. Chenopodiaceernes og Amaranthaceernes udbredelse i Danmark. — Bot. Tidsskr. 63: 205—288.

Evolutionary Trends in the *Atriplex triangularis* Group of Scandinavia

II. Spontaneous Hybridization in Relation to Reproductive Isolation

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ABSTRACT

GUSTAFSSON, M. 1973. Evolutionary trends in the *Atriplex triangularis* group of Scandinavia. II. Spontaneous hybridization in relation to reproductive isolation. — Bot. Notiser 126: 398—416.

In Scandinavia the *Atriplex triangularis* group is composed of five closely related, partly sympatric taxa. Spontaneous hybridization is fairly common within the group. The degree of reproductive isolation between the taxa varies in different regions of Scandinavia. The relation between the frequency of spontaneous hybrids and the degree of reproductive isolation is discussed. Some taxa remain distinct, although external isolating mechanisms are lacking or very weak. Cultivated hybrid offspring, derived from hybrid seeds collected in nature, show great morphological variation, decreased germination and to a certain extent reduced fertility. Morphological segregation towards the parent species is not combined with a restoration of fertility. The origin of *A. longipes* DREJ. ssp. *kattegatense* TURESS. is discussed.

INTRODUCTION

Hybridization may be of importance from an evolutionary point of view owing to the ability to produce new types by recombination. However, the effects of hybridization on the evolutionary process are to a great extent dependent upon the species complex within which it acts, upon the breeding system and lack of or existence of isolation barriers. The F_1 hybrids may have high fertility values and display regular meiosis, if the crossing barriers are mainly external. But hybrid sterility and/or reduced viability are generally present to some extent at least, either in the first or second generation. There are numerous examples of the effects and strength of such internal

barriers in different species complexes representing many plant families (for references see STEBBINS 1950, GRANT 1971 and DOBZHANSKY 1970). But even via partially sterile hybrids there may be a gene flow from one species to another, especially through repeated backcrossing combined with selection and introgressive hybridization (ANDERSON 1949).

As already pointed out by TURESSON (1925) spontaneous hybridization is fairly common in the *A. triangularis* complex, which comprises five diploid ($2n=18$) taxa, viz. *A. calotheca* (RAFN) RAFN & FRIES, *A. glabriuscula* EDMONDST., *A. longipes* DREJ. ssp. *longipes* and ssp. *praecox* (HÜLPH.) TURESS. and *A. triangularis* WILLD. The present investigation is con-

cerned with reproductive isolation between the taxa, morphological features and the distribution of spontaneous hybrids, and cultivation experiments of progenies derived from seeds produced by natural hybrids. It has only been possible to determine the origin of these hybrids to a limited extent and they may therefore represent backcrosses towards the parent species, as well as various derivatives of self-fertilized hybrids.

REPRODUCTIVE ISOLATION

According to DOBZHANSKY (1970) the isolating mechanisms may be divided into two main groups, prezygotic and zygotic mechanisms. The prezygotic mechanisms prevent or reduce the formation of hybrid zygotes, while the zygotic isolating mechanisms or internal barriers reduce the viability and/or fertility within already-formed hybrid zygotes. The question of internal barriers has been discussed in a previous paper (GUSTAFSSON 1973). All taxa cross easily and produce viable and fertile hybrids. Only in crosses with *A. longipes* ssp. *praecox* is reduced fertility common, due to the frequent occurrence of paracentric inversions in that taxon. However, reduced germination is shown in all hybrid combinations.

PREZYGOTIC ISOLATING MECHANISMS IN THE *A. TRIANGULARIS* GROUP

The prezygotic isolating mechanisms within the *A. triangularis* group are shown in Fig. 1.

SPATIAL ISOLATION: All taxa in the *A. triangularis* group are at least partly sympatric, i.e. they have overlapping areas of distribution in some parts of Scandinavia. No real spatial or geographical isolation exists, although the degree of overlapping between populations of *A. longipes* ssp. *praecox* versus *A. calotheca* and *A. glabriuscula* is small. In the Baltic

area, where *A. longipes* ssp. *praecox* is common, both *A. calotheca* and *A. glabriuscula* are relatively rare. Although intensive field-work has been carried out the author has never seen them growing together so that the opportunity for gene exchange seems to be rather small at present.

ECOLOGICAL ISOLATION: Local and ecological differentiation have been observed within most taxa of the *A. triangularis* group (cf. TURESSON 1922). But ecological isolation between taxa is only obvious between some taxa in the Baltic region, viz. *A. longipes* ssp. *praecox* versus *A. longipes* ssp. *longipes* and *A. calotheca*. *A. longipes* ssp. *praecox* grows in open, more or less ephemeral habitats in the lower parts of sea-shore meadows, dominated by a low type of vegetation. By contrast, *A. calotheca* and *A. longipes* ssp. *longipes* inhabit marshes with tall vegetation, such as communities dominated by *Scirpus maritimus* and/or *Phragmites communis*. *A. triangularis* seems to be unspecific in this respect, as it occurs in most kinds of littoral biotopes.

All four taxa in the western part of Scandinavia may occur together in marshes, i.e. *A. calotheca*, *A. glabriuscula*, *A. longipes* ssp. *longipes* and *A. triangularis*. Possibly they have preferences for different parts of the marsh, but in some micro-niches at least they are all mixed.

In the northernmost part of Norway *A. longipes* ssp. *praecox* and *A. triangularis* are found in the same habitats, i.e. exposed marshes.

SEASONAL ISOLATION: In the *A. triangularis* group seasonal isolation prevents or obstructs hybridization between *A. longipes* and the other species, while *A. calotheca*, *A. glabriuscula* and *A. triangularis* flower simultaneously in areas where they occur sympatrically. However, the degree of seasonal isolation varies in different regions of Scandinavia, due to the flowering period of *A. longipes*. In the

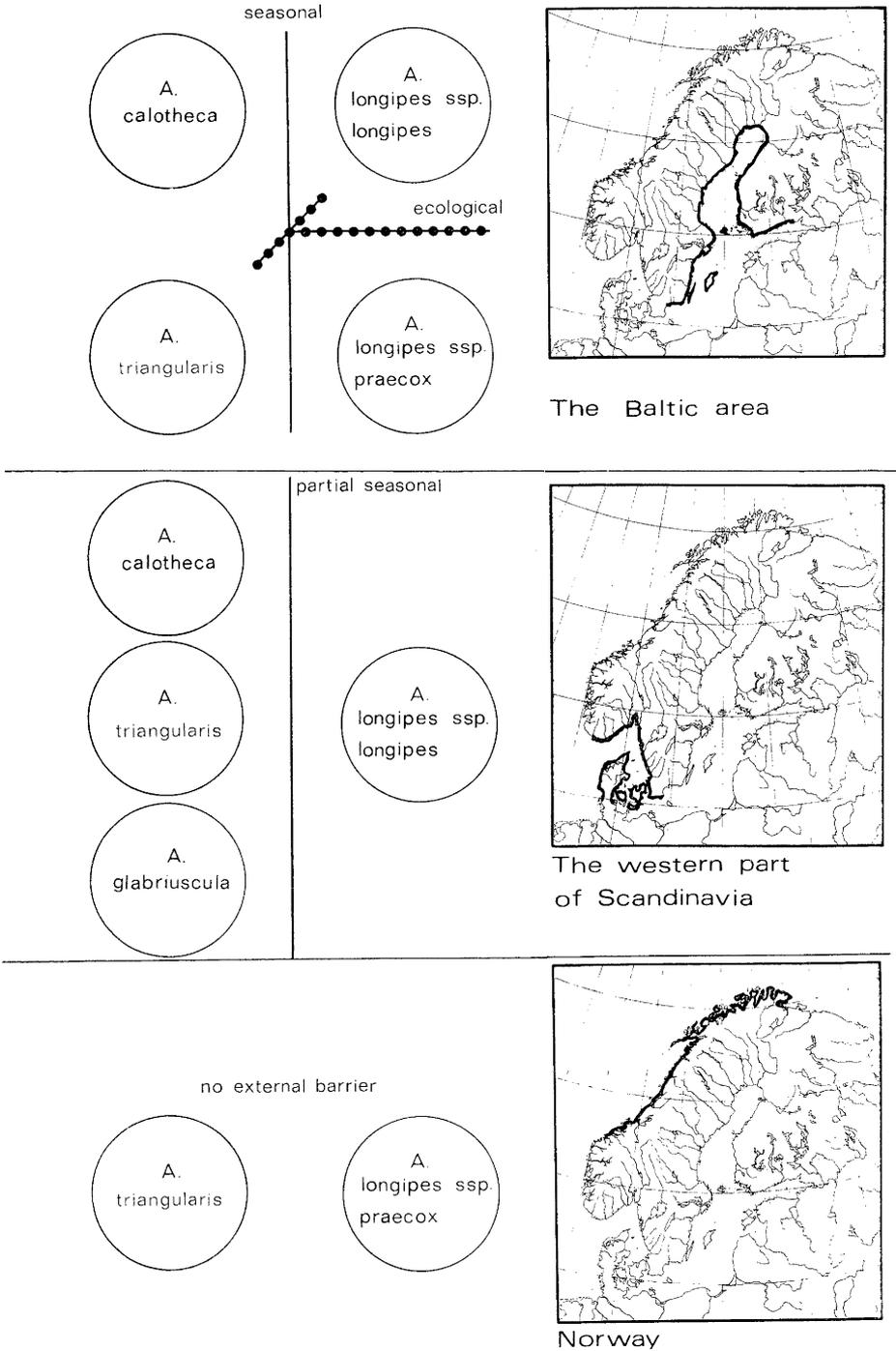


Fig. 1. Prezygotic isolating mechanisms between taxa in the *A. triangularis* group in different regions of Scandinavia.

Baltic region the seasonal isolation is absolute. *A. longipes* ssp. *praecox* starts flowering in the middle of May, ssp. *longipes* at the end of May and the flowering period lasts till the end of June in both taxa. The fruits of *A. longipes* ssp. *praecox* have already ripened when the other taxa start flowering at the end of July or beginning of August.

In western Scandinavia seasonal isolation is only partial. Most individuals of *A. longipes* ssp. *longipes* flower in June or at the beginning of July and the fruits ripen at the end of August. But, particularly in populations from the Swedish west coast, there are a few individuals still flowering at the beginning of August when the other taxa begin to flower. The degree of overlapping is about one week in culture experiments and probably about the same in nature.

In the northern part of Norway there is at the most an insignificant isolation barrier of this kind. *A. longipes* ssp. *praecox* and *A. triangularis* flower at the same time, from the middle of July to the beginning of August. However, in cultivation experiments populations of *A. longipes* ssp. *praecox* originating from Norway flower at the same time as those from the Baltic region. Obviously, genes causing a rapid rate of vegetative development and early flowering exist in both Norwegian and Baltic populations. However, in Norway the long hard winter does not admit of germination until April—May and despite a rapid rate of development *A. longipes* ssp. *praecox* has not the opportunity to flower before the middle of July. In this region the vegetative development of *A. triangularis* is as fast as that of *A. longipes* ssp. *praecox*. A special ecotype characterized by a rapid rate of development has probably evolved, as the vegetative development of *A. triangularis* from the southern parts of Scandinavia demands a relatively long period of time.

MORPHOLOGY AND DISTRIBUTION OF SPONTANEOUS HYBRIDS

The following data are based on natural hybrids observed by the author, as well as on specimens of hybrid origin from the following Herbaria: C, H, LD, O, S, UPS (the abbreviations according to Index Herbariorum). All the hybrids investigated were vegetatively well-developed and seed-setting was good.

A. longipes ssp. *longipes* × ssp. *praecox*

Two transitional form series have been observed. In most characters, such as height, leaf size, length and shape of bracteoles, there are successive transitions from one subspecies to another.

Fruits ripen in July.

Distribution: One record from the island of Gotland and one from the province of Södermanland.

Habitat: Both hybrid swarms are observed in sea-shore meadows.

A. calotheca × *A. longipes* ssp. *longipes*

Most hybrids have rhomboid, rarely triangular lower leaves with a cuneate base, entire to lacinate margins and often prominent basal lobes. Upper leaves often lanceolate to rhomboid, with entire or irregularly dentate margins. Bracteoles rhomboid to hastate, with lacinate or dentate margins. Bracteoles situated in the leaf axils stalked, the others sessile or shortly stalked.

Fruits ripen in September.

Distribution: In Denmark some records are known from the neighbourhood of Copenhagen, one from the southwestern part of Sjælland and one from Fyn. In Sweden there are some localities around Malmö, one in Halland, one in Blekinge and one on Öland.

Habitat: Mainly occurring in *Scirpus maritimus* communities.

A. calotheca × *A. triangularis*

Most of the expected recombination types have been observed. Specimens with

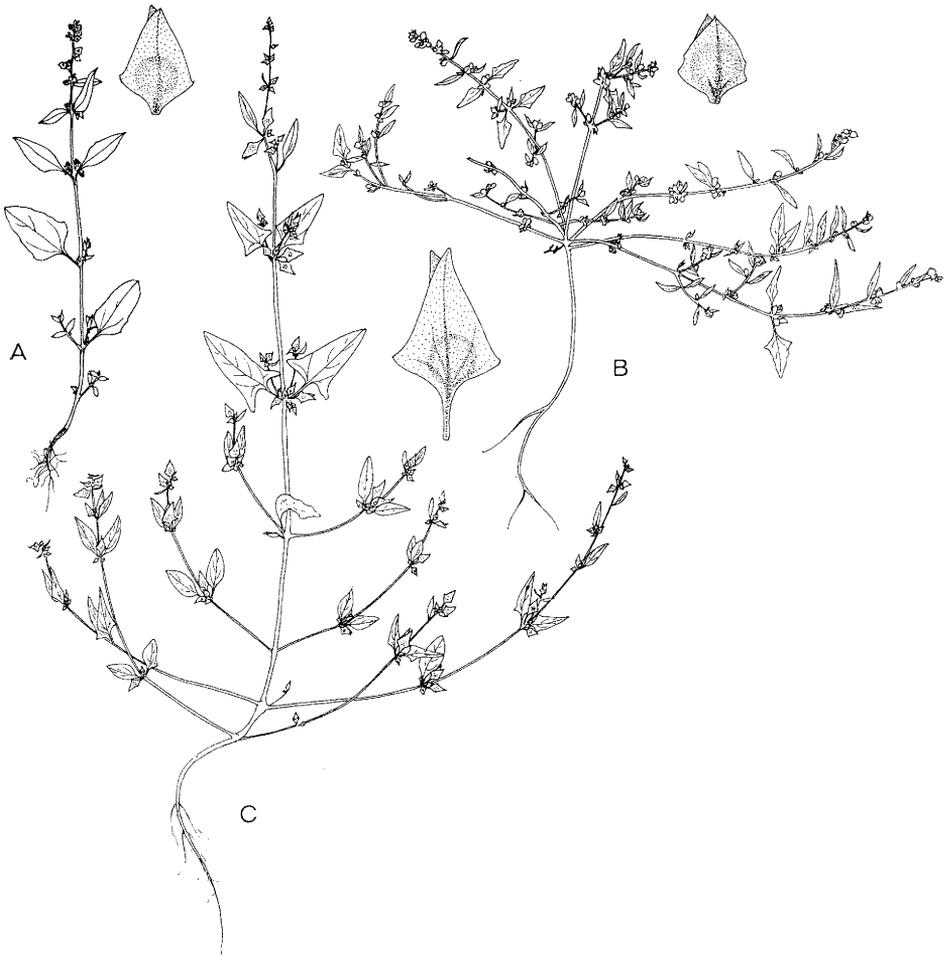


Fig. 2. Morphological appearance of three hybrid derivatives, as a result of spontaneous hybridization between *A. longipes* ssp. *longipes* and *A. triangularis*. Type B is similar to *A. longipes* ssp. *kattegattense* TURESS.

both intermediate appearance of leaves and bracteoles occur, as well as those with leaves similar to *A. triangularis* but with bracteoles similar to those of *A. calotheca* and vice versa.

Fruits ripen in August to September.

Distribution: Hybrid swarms are common on both sides of Öresund and on the island of Öland, in addition one locality has been found in Halland.

Habitat: Almost solely confined to marshes dominated by *Scirpus maritimus*.

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A. glabriuscula × *A. longipes* ssp. *longipes*

Lower leaves rhomboid to triangular, usually somewhat cuneate at base. Bracteoles thick and fleshy, black to brown at base, herbaceous and green in the upper parts, united up to the middle or only at the base. Bracteoles situated in leaf axils stalked, terminal ones mostly sessile.

Fruits ripen in August to September.

Distribution: In Denmark five records are known from Sjælland, two from Fyn,

and one from the island of Samsö. In Sweden observed in three localities around Göteborg.

Habitat: Different kinds of marshes.

A. glabriuscula × *A. triangularis*

Leaves similar to the parent species. Bracteoles intermediate, i.e. usually rhomboid, length about equal to breadth, often fleshy and thick at the base, herbaceous in the upper parts, mostly black to brown at base, green in the upper parts, only united at base. The surface of the bracteoles smooth or few-veined.

Fruits ripen in September to October.

Distribution: Three records are known from Jylland in Denmark and five from the Swedish west coast.

Habitat: More or less exposed marshes.

A. longipes ssp. *longipes* × *A. triangularis*

Three morphologically different hybrid derivatives may be distinguished, mainly distributed in different habitats, although transitional form series have been observed. The morphological features of these hybrid segregates are illustrated in Fig. 2.

Type A: Erect to ascending, usually small, lower leaves rhomboid to triangular, with a cuneate base, upper ones triangular to rhomboid. Bracteoles triangular to rhomboid, often with dentate margins, sessile including the axillary ones.

Type B: This type has been described as *A. longipes* ssp. *kattgatense* by TURESSON (1925). Prostrate or decumbent, rarely erect, rather short main stem, long basal branches, lower leaves rhomboid to triangular, with a cuneate base, rather long, forward- to outward-pointing basal lobes, upper leaves rhomboid to lanceolate. Bracteoles ovate to rhomboid, margins usually entire, those situated in leaf axils shortly stalked to sessile, the terminal bracteoles sessile.

Type C: Erect to ascending, usually tall, lower leaves triangular, upper ones rhomboid to triangular, mostly with dentate

Table 1. Distribution in different habitats of hybrid derivatives originating from spontaneous hybridization between *A. longipes* ssp. *longipes* and *A. triangularis*. n indicates the number of populations investigated. The characteristics of the different types is illustrated in Fig. 2.

Habitat	Morphological type		
	A + B %	C %	n
<i>Scirpus maritimus</i> and <i>Phragmites communis</i>	25	75	10
Exposed marshes, cliff crevices	97	3	15

margins. Bracteoles situated in leaf axils stalked, the terminal ones sessile.

Fruits ripen in August to September.

Distribution: The three hybrid forms have similar areas of distribution. Some records are known from Denmark, particularly common along the Swedish west coast, northwards to the southern parts of Norway. In fact, most populations along the Swedish west coast investigated by the author include individuals of hybrid origin.

Habitat: The ecological preferences of the three types are summarized in Table 1. The frequencies of the types in different habitats represent only a rough estimation of 25 populations along the Swedish west coast in 1970. But probably the figures show the general trend. Type C is almost restricted to marshes dominated by *Scirpus maritimus* and/or *Phragmites communis*. By contrast types A and B are most frequent in habitats exposed to the sea, such as cliff crevices and exposed, stony marshes with sparse or low vegetation.

A. longipes ssp. *praecox* × *A. triangularis*

Transitions are common in the northern part of Norway. The hybrids are usually distinguishable from *A. longipes* ssp. *praecox* by being taller, by having larger and broader lower leaves and sessile bracteoles,

Table 2. Germination of seeds derived from different spontaneous hybrids in nature. n indicates the number of hybrid offspring tested. For comparison germination of seed samples originating from natural populations of "pure" taxa is shown.

Hybrid combination	Germination %										n	
	0	10	20	30	40	50	60	70	80	90		100
<i>A. calotheca</i> × <i>A. longipes</i> ssp. <i>longipes</i> ..	—	1	—	2	—	—	—	—	—	—	—	3
<i>A. calotheca</i> × <i>A. triangularis</i>	—	—	—	3	2	1	1	—	—	—	—	7
<i>A. glabriuscula</i> × <i>A. triangularis</i>	—	—	1	1	—	—	—	—	—	—	—	2
<i>A. longipes</i> ssp. <i>longipes</i> × <i>A. triangularis</i>	1	1	8	4	1	—	—	2	—	1	—	18
Total	1	2	9	10	3	1	1	2	—	1	—	30
%	3.3	6.7	30.0	33.3	10.0	3.3	3.3	6.7	—	3.3	—	
"Pure" taxa	—	—	—	—	4.2	4.2	18.8	31.3	33.3	8.3	—	48

from *A. triangularis* by the somewhat cuneate base of the lower leaves.

Fruits ripen in August.

Distribution: Frequently distributed in the northern part of Norway, from Trondheim to the peninsula of Varanger. No hybrid has been observed in the Baltic area.

Habitat: Occurs sympatrically with the parent species in marshes.

CULTIVATION EXPERIMENTS ON NATURAL HYBRIDS

The cultivation experiments on hybrids occurring in nature include investigation of germination, male fertility and morphological features. Seeds of natural hybrids, collected in 1971, were kept in separate bags and later sown in pots which were placed in the Botanical Gardens, Lund.

All the hybrid plants investigated originated from the seeds produced by spontaneous hybrids after free pollination. The hybrid offspring probably represent backcrosses towards the parent species, as well as various derivatives of self-fertilized hybrids. Thus, the whole material represents hybrid combinations of unknown origin. The number and origin of the hybrid progenies are listed at the end of this paper.

Germination

In most cases 50 seeds of each hybrid plant were selected at random and altogether the germination of 30 hybrid seed samples was investigated. The number of seed samples of each hybrid combination and their germination are summarized in Table 2. The germination of seed samples originating from "pure" populations of the taxa is shown for comparison.

The hybrid seeds usually germinate poorly, only 17 % of the seed samples having a germination value higher than 50 %. Seeds originating from hybrids between *A. calotheca* and *A. triangularis* seem to germinate more successfully than other hybrid combinations. Despite a certain degree of overlapping, the germination of hybrid seeds is reduced compared with that of seed samples of "pure" populations. The proportion of seed samples with a germination higher than 50 % is 17 % and 96 % respectively.

Vegetative Development

The vegetative development was quite normal in all hybrid offspring except for G 233X-12 (*A. longipes* ssp. *longipes* × *A. triangularis*), where all the plants had deformed leaves.

Table 3. Morphological segregation in offspring of natural hybrids. In the combinations *A. calotheca* × *A. triangularis* and *A. longipes* ssp. *longipes* × *A. triangularis* only some progenies are represented in detail. n indicates the number of individuals investigated.

Progeny code	Hybrid segregates similar to			n
	First-mentioned parent	± intermediate	Second-mentioned parent	
<i>A. calotheca</i> × <i>A. longipes</i> ssp. <i>longipes</i>				
G 233X-1	5	19	0	24
G 233X-2	2	6	1	9
G 233X-3	5	3	1	9
Total: 3 progenies	12	28	2	42
<i>A. calotheca</i> × <i>A. triangularis</i>				
GBCK-7	1	7	12	20
GHHX-7	3	10	8	21
GHHX-8	20	7	1	28
G 233X-4	7	14	1	22
4 other progenies	56	36	3	95
Total: 8 progenies	87	74	25	186
<i>A. glabriuscula</i> × <i>A. triangularis</i>				
G 236X-8	4	13	3	20
G 236X-9	2	7	4	13
Total: 2 progenies	6	20	7	33
<i>A. longipes</i> ssp. <i>longipes</i> × <i>A. triangularis</i>				
Progenies of the <i>kattegatense</i> type				
G 169-Ka	—	15	—	15
G 233X-8	3	7	10	20
G 236Y-1	1	8	7	16
8 other progenies	3	21	7	31
Total: 11 progenies	7	51	24	82
Progenies of other hybrid types				
G 233X-7	1	22	2	25
G 234X-7	5	7	2	14
G 236X-3	2	5	19	26
9 other progenies	10	30	27	67
Total: 12 progenies	18	64	50	132

Morphological Variation and Fertility

The morphological variation within hybrid progenies is summarized in Table 3 and shown in Fig. 3. The distribution of fertility values of different hybrid offspring is summarized in Table 4.

A. calotheca × *A. longipes* ssp. *longipes*

Morphological appearance of 42 individuals representing three hybrid off-

spring has been investigated. About one third of the material segregates towards the parent species, mainly towards *A. calotheca*. Most recombination types have been observed, but individuals with lacinate leaves combined with long-stalked bracteoles have not been observed. The pattern of morphological variation within offspring is similar and the differences between offspring small.

Fertility: 31 plants have a fertility

Table 4. Male fertility values in offspring of natural hybrids. n indicates the number of individuals investigated and N the number of offspring.

Progeny code	Fertility %									n	N
	30	40	50	60	70	80	90	100			
A. calotheca × A. longipes ssp. longipes											
G 233X: 1—3	—	—	1	—	—	9	31	41	3		
%	—	—	2.4	—	—	22.0	75.6				
A. calotheca × A. triangularis											
GBCK	—	—	—	—	—	1	34	35	2		
GHPX	—	—	—	—	—	1	12	13	1		
GHHX	—	—	—	—	1	7	46	54	3		
G 233X	—	—	1	—	1	8	28	38	2		
Total	—	—	1	—	2	17	120	140	8		
%	—	—	0.7	—	1.4	12.1	85.7				
A. glabriuscula × A. triangularis											
G 236X: 8—9	—	—	—	1	5	4	16	26	2		
%	—	—	—	3.8	19.2	15.4	61.5				
A. longipes ssp. longipes × A. triangularis											
The <i>kattegatense</i> type											
G 231: 1	—	—	—	—	1	3	11	15	1		
G 233X: 8	—	1	4	2	4	7	6	24	1		
G 236Y: 1—9	1	—	1	2	5	14	27	50	9		
Total	1	1	5	4	10	24	44	89	11		
%	1.1	1.1	5.6	4.5	11.2	27.0	49.4				
Other types											
G 233X: 7, 9, 11—12	—	1	—	1	4	13	57	76	4		
G 236X: 3, 5, 7	—	—	—	—	1	12	26	39	3		
G 234X: 6, 7, 10—12	—	—	—	2	—	6	23	31	5		
Total	—	1	—	3	5	31	106	146	12		
%	—	0.7	—	2.1	3.4	21.2	72.6				

higher than 90 %, 9 plants between 80 and 90 % and finally one plant has a fertility value as low as 59 %.

A. calotheca × *A. triangularis*

The variation within eight progenies from four localities has been studied. About 60 % of the individuals segregate towards the parent species, primarily towards *A. calotheca*. Most of the expected recombination types have been observed. All the offspring are composed of both plants that are more or less intermediate and ones similar to one of the parents. However, the frequencies of the morphological

segregates are quite different in different offspring. In GHHX-7 and G 233X-4 intermediate types are most frequent, while in GBCK-7 the majority of the plants segregate towards *A. triangularis* and in GHHX-8 towards *A. calotheca*.

Fertility: Most hybrid plants have high fertility values, about 86 % of the material has higher than 90 % stainable pollen and only 2 % below 80 % stainable pollen.

A. glabriuscula × *A. triangularis*

The morphological appearance of 33 plants representing two offspring has been

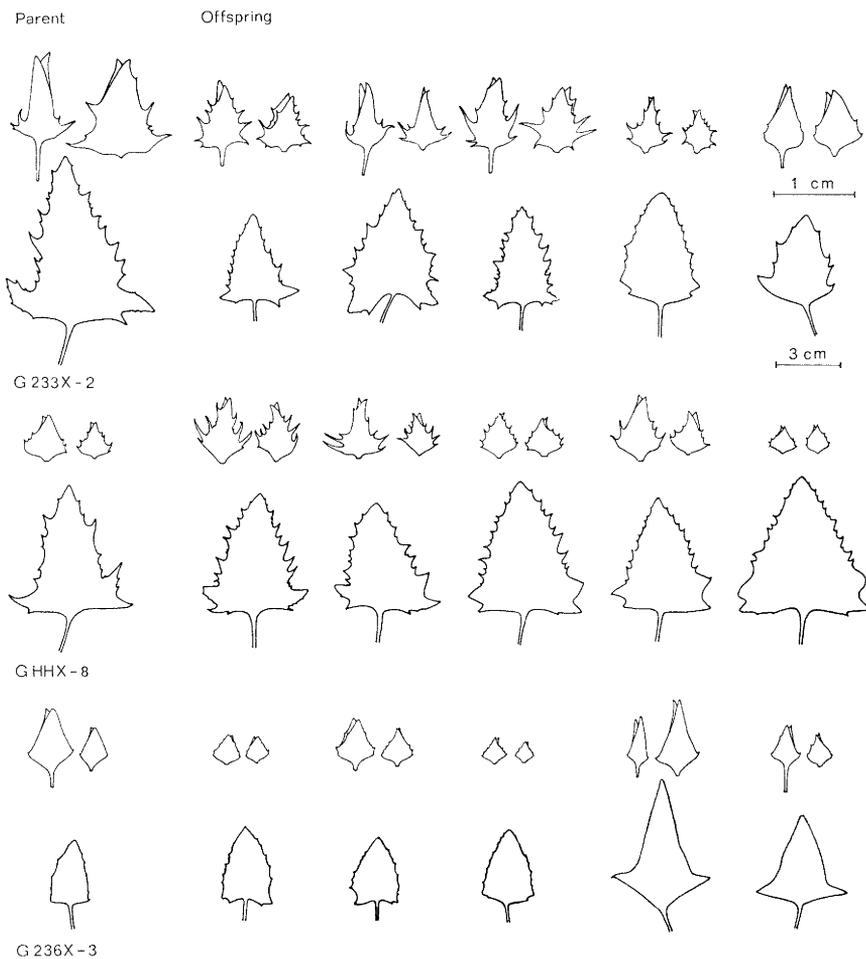


Fig. 3. Morphological variation within three hybrid offspring, raised from seeds produced by spontaneous hybrids. Offspring G 233X-2 represents *A. calotheca* × *A. longipes* ssp. *longipes*, GHHX-8 *A. calotheca* × *A. triangularis* and G 236X-3 *A. longipes* ssp. *longipes* × *A. triangularis*.

investigated. Intermediate types seem to be most frequent in both the progenies.

Fertility: Sixteen of 26 plants have a fertility higher than 90 %, 4 between 80 and 90 % and 6 less than 80 %.

A. longipes ssp. *longipes* × *A. triangularis*

The morphological appearance of 216 plants representing 23 hybrid offspring

has been examined. On the whole the majority of the plants segregate towards *A. triangularis* or are intermediate, only a minor proportion segregate towards *A. longipes* ssp. *longipes*. Offspring of the *kattgatense* type seem to have a somewhat higher frequency of intermediate plants than offspring of other types of spontaneous hybrids.

Table 5. Relation between morphological segregation and male fertility in offspring of natural hybrids. n indicates the number of individuals investigated.

Morphological types	Male fertility %								n
	30	40	50	60	70	80	90	100	
A. calotheca × A. longipes									
Progenies G 233X-1—3									
Similar to the parents	—	—	—	—	—	5	9	14	
± intermediate	—	—	1	—	—	4	21	26	
A. calotheca × A. triangularis									
Progenies G 233X-4—5									
Similar to the parents	—	—	—	—	1	6	10	17	
± intermediate	—	—	1	—	—	2	15	18	
A. glabriuscula × A. triangularis									
Progenies G 236X-8—9									
Similar to the parents	—	—	—	1	2	2	6	11	
± intermediate	—	—	—	—	3	2	10	15	
A. longipes ssp. longipes × A. triangularis									
Progenies G 233X-8, G 236Y-1—9									
Similar to the parents	—	1	1	—	5	8	16	31	
± intermediate	1	—	3	2	3	11	14	34	
Total									
Similar to the parents	—	1	1	1	8	21	41	73	
%	—	1.4	1.4	1.4	11.0	28.8	56.2		
± intermediate	1	—	5	2	6	19	60	93	
%	1.1	—	5.4	2.2	6.5	20.4	64.5		

Offspring of the *kattegatense* type: A certain variation is present in both the offspring G 233X-8 and G 236Y-1, while offspring G 169-Ka is exclusively composed of plants similar to the *kattegatense* type. This small variation has also been observed in two other offspring (G 174 and G 220) cultivated from 1968 to 1971.

Offspring of other types: All the three offspring show a certain variation. In offspring G 233X-7 intermediate plants dominate, while in G 236X-3 segregation towards *A. triangularis* and in G 234X-7 intermediates and plants similar to *A. longipes ssp. longipes* are most frequent.

Fertility: Male fertility of 235 plants representing 11 offspring of the *kattegatense* type and 12 of other kinds of hybrids has been investigated. The frequency of plants with reduced fertility is

high in both groups, only about 50 % and 73 % respectively of the plants have fertility values higher than 90 %.

Relation between Male Fertility and Morphological Segregation in Hybrid Offspring

In most hybrid offspring there is a certain variation in morphology and male fertility. In Table 5 the male fertility values of plants morphologically similar to one of the parent species are compared with those of intermediate ones. In this case it seemed practical to combine all the more or less intermediate hybrids into one group, although they actually represent morphologically rather dissimilar

hybrid segregates. Only some of the most variable offspring of each hybrid combination have been checked. They all show that there is little or no correlation between morphological constitution and male fertility. Hybrids that are most similar to the parents have about the same degree of reduced fertility as intermediate ones. The results indicate that morphological characters of the taxa and male fertility are controlled by different genetic factors.

Seed-setting

The seed-setting was generally rather poor, but this may be due to experimental error. Within the *A. triangularis* group wind pollination probably occurs (see GUSTAFSSON 1973). All the hybrid offspring were kept in greenhouses where dispersal of pollen-grains is not very effective.

CROSSING EXPERIMENTS INVOLVING *A. LONGIPES* SSP. *KATTEGATENSE* TURESS.

In order to investigate the possible origin of the *kattegatense* type, it has been crossed with populations of *A. longipes* and *A. triangularis*. TURESSON (1925) presumed that this type was closely related to *A. longipes* ssp. *longipes* and described it as *A. longipes* ssp. *kattegatense*. The plants used in these crossing experiments are similar to the material determined by TURESSON, i.e. they have a prostrate or decumbent habit, long slender basal branches, leaves with a somewhat cuneate base and shortly stalked, rhomboid to ovate bracteoles, usually with entire margins. The aims of the crossing experiments were twofold: to test if the *kattegatense* type shows a closer chromosomal affinity to one of the species and to analyze morphological variation within both F_1 and F_2 progenies.

Vegetative Development, Meiosis and Male Fertility

The vegetative development was quite normal in all the hybrids. Data of meiosis and male fertility are summarized in Table 6. Meiosis has been investigated in three crosses, one between *A. triangularis* and *kattegatense* (Gk 44), and two between *A. longipes* ssp. *praecox* and *kattegatense* (Gk 11 and Gk 42). Metaphase I is quite normal with the formation of nine bivalents, while bridges and laggards are formed at anaphase I. The meiotic behaviour is similar to that observed in other crosses within the *A. triangularis* group and bridge formation is probably due to heterozygosity for paracentric inversions (GUSTAFSSON 1972, 1973). The variation pattern in male fertility observed in cross Gk 49 also supports the assumption that reduced fertility is due to heterozygosity for structural rearrangements, rather than to fertility decreasing genes.

Male fertility of 51 and 74 F_1 hybrids of *A. triangularis* × *kattegatense* and *A. longipes* × *kattegatense* respectively has been investigated. Hybrids with reduced fertility are common in both combinations, only about one third has a fertility higher than 90 %. However, crosses with *A. triangularis* seem to have a higher frequency of hybrids with a fertility of less than 80 % than those with *A. longipes*, particularly if crosses with *A. longipes* ssp. *longipes* only are considered. This difference is also obvious in the F_2 progenies, individuals with high fertility values are most frequent in F_2 families of *A. longipes* ssp. *longipes* × *kattegatense*.

Morphological Variation within F_1 Progenies

Morphological variation within F_1 families is on the whole larger than that of other crosses between taxa. The morphological segregation is not presented in detail as a free recombination of morpho-

Table 6. A survey of meiosis and male fertility in the crossing combinations *A. longipes* × *kattegatense* and *A. triangularis* × *kattegatense*. n indicates the number of hybrid plants investigated, M the mean fertility and N the number of F₂ offspring investigated.

Meiosis

Cross no.	°/o good pollen	Metaphase I	Anaphase—Telophase I			Anaphase—Telophase II		
			Normal	Bridges	Laggards	Normal	Bridges	Laggards
11	89	9 bivalents	102	1	5	—	—	—
42—2	82	9 bivalents	—	—	—	95	1	1
42—3	73	9 bivalents	168	17	2	—	—	—
44	58	9 bivalents	51	6	1	—	—	—

Male fertility in F₁

Cross number	Fertility %								n	M
	30	40	50	60	70	80	90	100		

A. longipes × *kattegatense*

Ssp. longipes participating

Gk 14	—	1	2	—	—	—	—	3	51.3
Gk 24	—	—	—	—	6	9	4	19	84.2
Gk 43	—	—	—	—	—	2	12	14	93.2
Gk 46	—	—	—	—	—	2	9	11	94.0
Gk 47	—	1	3	—	—	—	—	4	50.4

Ssp. praecox participating

Gk 11	—	—	—	—	—	5	—	5	85.7
Gk 23	—	—	—	—	—	1	—	1	88.2
Gk 42	—	—	—	—	4	2	—	6	76.6
Gk 48	—	7	3	1	—	—	—	11	49.0
Total	—	9	8	1	10	21	25	74	74.7
%	—	12.2	10.8	1.4	13.5	28.4	33.8		

A. triangularis × *kattegatense*

Gk 44	—	1	3	2	—	—	—	6	56.8
Gk 45	—	—	—	2	1	2	5	10	84.6
Gk 49	—	5	6	1	—	—	7	19	67.6
Gk 50	—	—	—	6	5	1	4	16	78.1
Total	—	6	9	11	6	3	16	51	71.8
%	—	11.8	17.6	21.6	11.8	5.9	31.4		

Male fertility in F₂

Crosses	Fertility %								n	N
	30	40	50	60	70	80	90	100		

<i>A. longipes ssp. longipes</i> × <i>kattegatense</i> ..	—	1	—	—	1	7	13	22	3
<i>A. longipes ssp. praecox</i> × <i>kattegatense</i> ...	—	1	4	6	7	10	5	33	8
<i>A. triangularis</i> × <i>kattegatense</i>	1	1	2	2	3	—	4	13	2

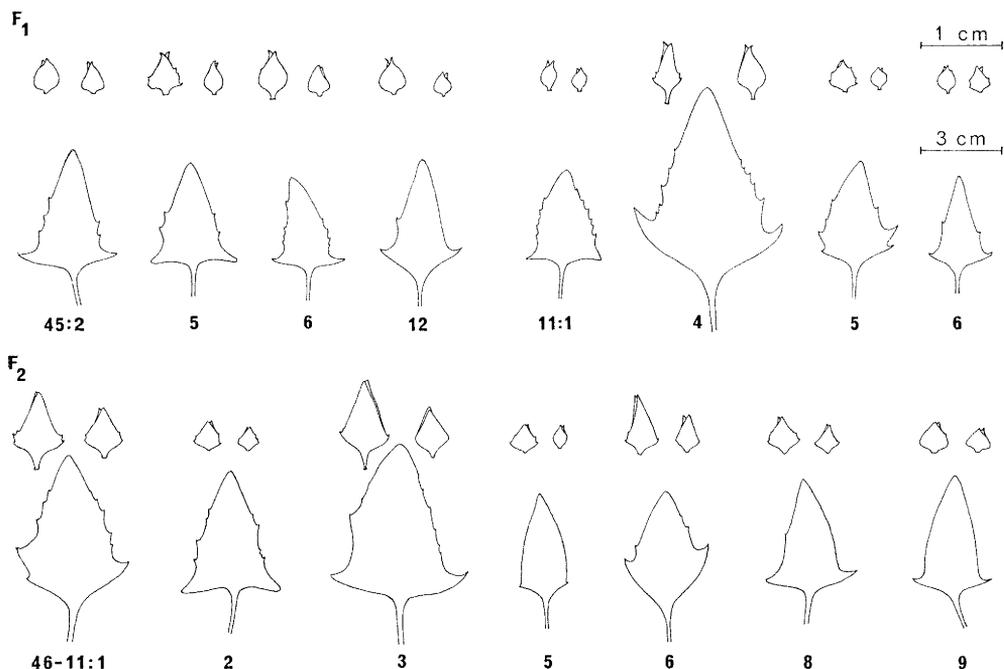


Fig. 4. Morphological variation within F_1 and F_2 progenies in crosses with the *kattegatense* type. Cross number Gk 45 represents *A. triangularis* \times *kattegatense*, Gk 11 *A. longipes* ssp. *praecox* \times *kattegatense* and Gk 46-11 *A. longipes* ssp. *longipes* \times *kattegatense*.

logical characters occurs, which complicates a classification of the plants into morphological types. But, the variation in leaves and bracteoles of two F_1 progenies is shown in Fig. 4.

In crosses between *A. longipes* and *kattegatense* the shape of the lower leaves varies within most progenies, from ones similar to *A. longipes* to those typical for *kattegatense*. The bracteoles are mostly shortly stalked or sessile, but long-stalked, axillary ones occur as well in some progenies. A certain amount of variation is also present in crosses with *A. triangularis*. Within all progenies the base angle of the lower leaves varies from somewhat cuneate to truncate. The bracteoles are shortly stalked or sessile.

In most of the crosses vegetative characters such as height, colour, leaf size and size of bracteoles are very variable.

Morphological Variation in F_2

The morphological variation in the F_2 generation is considerable (Fig. 4, Gk 46-11). In crosses with *A. longipes* most of the F_2 individuals resemble *A. longipes* or *kattegatense*, but other recombination types occur as well. In almost all progenies there are some plants that resemble *A. triangularis*, having triangular leaves with a truncate base and sessile bracteoles. The F_2 individuals, in crosses with *A. triangularis* mainly segregate towards *A. triangularis* and *kattegatense*, but occasionally also towards *A. longipes*.

THE ORIGIN OF THE KATTEGATENSE TYPE

The differences in degree of hybrid sterility give the impression that *kattegatense* shows a closer chromosomal affinity

to *A. longipes* ssp. *longipes* than to *A. triangularis*. But in fact, the differences are rather small and of subordinate importance. Investigation of meiosis indicates that reduced fertility is to a great extent due to heterozygosity for structural rearrangements. In the combination *A. triangularis* × *kattegatense*, cross Gk 44 is composed exclusively of hybrid plants with highly reduced fertility, which indicates genome differences in the parents. One parent is probably homozygous for one or more structural rearrangement, the other "normal" or homozygous for another rearrangement. Conversely, the pattern of variation in Gk 45, Gk 49 and Gk 50 indicates heterozygosity for structural rearrangements in one of the parents, the other being "normal" or heterozygous for another rearrangement. Thus, in the crossing combination *A. triangularis* × *kattegatense* homozygous structural differences in the parents may occur in one cross, heterozygous differences in three crosses. The figures for *A. longipes* ssp. *longipes* × *kattegatense* indicate homozygous differences in two crosses and heterozygous ones in one to three crosses. Thus, the differences in hybrid sterility are probably only due to a higher frequency of structural heterozygosity in the parents in the combination *A. triangularis* × *kattegatense*. Further, the fertility values may not be directly comparable, as the *kattegatense* parents in the two crossing combinations originate from different populations.

The cultivated offspring of *kattegatense* raised from seeds collected in nature show considerable morphological variation. In most offspring hybrid segregates similar to *A. longipes* ssp. *longipes* and *A. triangularis* respectively as well as intermediate ones have been observed. However, a few offspring show little or no morphological variation. Variation in most characters has also been observed in the artificial crosses between *A. longipes* and *kattegatense* as well as between *A. triangularis* and *kattegatense*. The variation in F_1 of

these crosses is on the whole greater than in crosses between populations of "pure" taxa, which indicate gene heterozygosity in the parents of the *kattegatense* type. In F_2 , crosses between *A. longipes* ssp. *longipes* and *kattegatense* give rise to plants resembling *A. triangularis*. In addition, some hybrid plants, derived from artificial crossing between *A. longipes* ssp. *longipes* and prostrate forms of *A. triangularis*, are rather similar to plants of the *kattegatense* type. All these facts indicate that the *kattegatense* type is a more or less well-established product of hybrid origin, rather than an ecotype of *A. longipes* as proposed by TURESSON (1925).

DISCUSSION

Most of the hybrid offspring investigated within the *A. triangularis* complex are variable, both as regards male fertility and morphological features. Evidently hybridization leading to introgression and backcrossing are processes that are going on continuously especially in populations from the Swedish west coast. Different variation patterns, particularly between hybrid progenies of *A. calotheca* × *A. triangularis*, may indicate that intermediate hybrids as well as those representing backcrosses towards the parent species occur in nature. But occasionally established hybrid populations of the *kattegatense* type occur.

The number of hybrids formed within the *A. triangularis* group varies in different regions of Scandinavia. The number of hybrids and hybrid combinations is rather small in the Baltic region, where reproductive isolation is most pronounced. No hybrid between *A. calotheca* and *A. longipes* ssp. *praecox* has been observed. Gene exchange between these taxa is prevented by the joint action of ecological and seasonal isolation. Admittedly *A. calotheca* is rare in the Baltic region, but hybridization may occur at least on the island of Öland, where both taxa occur. A combination of these two barriers is

obviously very strong and effectively prevents any hybridization. Ecological isolation on its own is not quite sufficient, as indicated by the formation of hybrid swarms between *A. longipes* ssp. *longipes* and ssp. *praecox*. But the number of such hybrids is virtually small, bearing in mind how common both taxa are in this region. In spite of ecological isolation gene exchange has occasionally been observed in many other species complexes, e.g. between *Phlox maculata* and *Phlox glaberrima* (LEVIN 1963), in the *Potentilla anserina* aggregate (ROUSI 1965) and between *Tripleurospermum inodorum* and *T. maritimum* in the British Isles (KAY 1972).

In the Baltic area, the seasonal isolation is strong between *A. calotheca* and *A. longipes* ssp. *longipes*, and between *A. longipes* ssp. *longipes* and *A. triangularis*, although one or two hybrids are found. Hybridization may occur under exceptionally unsuitable natural conditions. A factor such as grazing may influence the flowering time. If the flowering shoots are eaten off, new shoots will generally develop and this delays the flowering time considerably. Re-flowering has been observed a few times in marshes used for grazing. This displacement may be sufficient to cause hybridization between taxa which are normally isolated.

Hybrid derivatives are common in populations along the western parts of Scandinavia. The only known external barrier, partial seasonal isolation, obstructs only to some extent the frequent exchange of genes between *A. longipes* ssp. *longipes* and *A. triangularis*. Hybrids of this kind are rather rare in Denmark, more common along the Swedish west coast. About one half of the populations investigated in the provinces of Halland and Bohuslän have some kind of hybrid derivatives of these species. Partial seasonal isolation also exists between *A. longipes* ssp. *longipes* versus *A. calotheca* and *A. glabriuscula*. However, the number of these

hybrids is less than between *A. longipes* ssp. *longipes* and *A. triangularis*.

The absence of external barriers results in the formation of fairly extensive hybrid swarms particularly between *A. calotheca* and *A. triangularis* in the western part of Scandinavia, and between *A. longipes* ssp. *praecox* and *A. triangularis* in the northernmost part of Norway.

Hybridization in the *A. triangularis* group is prevented by or at least highly reduced by seasonal and/or ecological isolation, while weaker barriers such as partial seasonal isolation are of relatively small importance.

The effects of the external barriers are more or less reinforced by internal isolation mechanisms. The germination of seeds produced by spontaneous hybrids is less than that of seed samples of "pure" taxa. Usually less than 50 % of the hybrid seeds are viable. Seeds derived from artificial crosses also germinate poorly (GUSTAFSSON 1973). Germinative seeds give rise to hybrid plants which seem to be just as vigorous and vegetatively well-developed as normal plants. In most hybrid combinations about 25 to 50 % of the hybrids show reduced male fertility, i.e. they have less than 90 % stainable pollen. The fertility values of hybrid offspring correspond rather well with those obtained in artificial crosses (see GUSTAFSSON 1973). In all hybrid combinations tested morphological segregation towards the parent species is not combined with restoration of male fertility. The seed-setting of hybrids occurring in nature seems to be as high as that in normal plants.

The effects of hybridization and introgression are highly dependent upon the establishment of the hybrid derivatives. According to ANDERSON (1949) a successful establishment is influenced by two main factors, the ability of adaptation of the hybrid progenies and suitable habitats. ANDERSON has pointed out that physiological properties will segregate in the same way as morphological ones do. Thus,

a great number of more or less different morphological and physiological recombination types may evolve through hybridization, more or less adapted to certain habitats. The establishment of the hybrids will be counteracted by natural selection and competition with other species. In changing or heterogeneous habitats hybrid derivatives may have selective advantages and be able to inhabit biotopes beyond those of the parent species, but only on the assumption that they are at least partially fertile and possess some favourable gene combinations. According to ANDERSON, hybrid segregates survive to a great extent in "hybridized" habitats only, that is highly changed ones which have been subject to human activity or catastrophic natural forces. The most drastic changes are probably those caused by man, but new, suitable habitats or micro-niches may also arise through natural climatic, geological or edaphic changes. The relation between the establishment of hybrid derivatives in disturbed habitats has been observed in many species aggregates, e.g. in *Iris* (RILEY 1938), in *Cistus* (DANSEREAU 1941) and in *Vaccinium* (CAMP 1942).

In the *A. triangularis* group most natural hybrids and hybrid swarms occur in the same habitats as the parent species. The only exceptions constitute recombination types of *A. longipes* ssp. *longipes* × *A. triangularis*, which show adaptation and ecological preference to different habitats. It has already been pointed out that one recombination type mainly occurs in *Scirpus maritimus* communities and others in exposed biotopes. The *kattogatense* type in particular shows ecological preference that differs from those of the parent species. It usually inhabits the lowest parts of exposed marshes where the vegetation is sparse and open places common. These areas are extremely exposed to the sea and especially during the autumn violent storms may remove the vegetation in these parts. Open places suitable for establishment are probably created now and then. Prostrate forms of *A. longipes*

ssp. *longipes* and *A. triangularis* may inhabit exposed marshes as well, but they usually grow in higher parts.

Sympatric speciation or maintenance of closely related, sympatric species usually demands some kind of isolating mechanism. But within the *A. triangularis* group the sympatric taxa *A. calotheca*, *A. glaberrimula* and *A. triangularis* remain distinct, even though external barriers to gene exchange are lacking or very weak. This is also true for *A. longipes* ssp. *praecox* and *A. triangularis* in the northernmost part of Norway. However, gene exchange between these taxa is restricted by the reduced reproductional capacity of the hybrids, i.e. a high frequency of non-germinative seeds more or less combined with reduced fertility. Further, some kind of selection occurs probably at the seedling stage, and seedlings of hybrid origin have to compete with a large number of others derived from well-established, normal plants. In addition, the recombination of genes determining the parental physiological properties may result in hybrids not so well adapted to certain habitats. It is possible that normal plants of the parent species have a certain selective advantage, as they are usually well adapted to their habitats and have a high percentage of germinative seeds combined with a high frequency of functional gametes.

Diversities between sympatric morphological types or closely related species may also be promoted by the effects of disruptive selection (MATHER 1955). In a heterogeneous habitat one morphological type can be favoured in one part of the environment and another type, with a dissimilar genetic constitution, in a different ecological niche. The results of disruptive selection are entirely regulated by the strength of the selection pressure. The greater it is the more pronounced will the effects be.

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APPENDIX I

Cultivated Progenies of Spontaneous Hybrids

Population code	Origin
A. calotheca × A. longipes ssp. longipes	
G 233X: 1—3	Sw. Hld. Falkenberg, Skreanäs
A. calotheca × A. triangularis	
G 233X: 4—5	Sw. Hld. Falkenberg, Skreanäs
GBCK: 1, 7	Sw. Sk. N Barsebäckshamn
GHFx	Sw. Hld. Falkenberg, Glommen
GHHX: 7, 8	Sw. Sk. Gässie
A. glabriuscula × A. triangularis	
G 236X: 8—9	Sw. Hld. Varberg, Getterön
A. longipes ssp. longipes × A. triangularis	
G 233X: 7, 9,	
11—12	Sw. Hld. Falkenberg, Skreanäs
G 234X: 6—7,	
10—12	Sw. Hld. Tvååker, Björkäng
G 236X: 3,	
5, 7	Sw. Hld. Varberg, Getterön
The kattegatense type	
G 168	Sw. Sk. V Bjäre, Skaudd
G 169 ka	Sw. Sk. Torekov
G 173	Sw. Hld. Åsa, Stenudden
G 174	Sw. Boh. Tjörn, Rönnäng
G 193	No. Vestfold. Tönsberg, Mostrand
G 220	Sw. Boh. Tjörn, 5 km NE Rönnäng
G 222	Sw. Boh. Instön, Färjeläget
G 231	Sw. Hld. Gullbrandstorp, Viken
G 233X: 8	Sw. Hld. Falkenberg, Skreanäs
G 235	Sw. Hld. Varberg, Äpelviken
G 236Y: 1—9	Sw. Hld. Varberg, Getterön
G 247	Sw. Sk. Vejbystrand

APPENDIX II

Crossing experiments

Cross number	Population number and origin	
	A. triangularis	× kattegatense
Gk 44	G 170: Sw. Hld. Trönninge	G 173: Sw. Hld. Åsa
Gk 45	GAA: Sw. Sk. Torekov	G 231: Sw. Hld. Gullbrandstorp
Gk 49	G 236: Sw. Hld. Varberg	G 168: Sw. Sk. Skaudd
Gk 50	G 221: Sw. Boh. Tjuvkiel	G 173: Sw. Hld. Åsa

Cross number	Population number and origin		
	A. longipes ssp. longipes	×	kattegatense
Gk 14	G 234: Sw. Hld. Björkäng		G 231: Sw. Hld. Gullbrandstorp
Gk 24	G 119: Sw. Uppl. Roslagskulla		G 174: Sw. Boh. Tjörn. Rönnäng
Gk 43	G 145: Dk. Jylland. Kolding		G 174: „ —
Gk 46	G 145: „ —		G 231: Sw. Hld. Gullbrandstorp
Gk 47	G 107: Sw. Bl. Kristianopel		G 193: No. Vestfold. Tönsberg
	A. longipes ssp. praecox	×	kattegatense
Gk 11	G 108: Sw. Öl. Köpingsvik		G 168: Sw. Sk. Skaudd
Gk 23	G 117: Sw. Gotl. Fårösund		G 174: Sw. Boh. Tjörn. Rönnäng
Gk 42	G 126: Sw. Sm. Loftahammar		G 231: Sw. Hld. Gullbrandstorp
Gk 48	G 116: Sw. Gotl. N. Själso		G 193: No. Vestfold. Tönsberg

Sertulum Papuanum 18

Two Superfluous Genera in the New Guinean Flora

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ABSTRACT

VAN ROYEN, P. 1973. Two superfluous genera in the New Guinean flora. — Bot. Notiser 126: 417—425.

The genera *Raoulia* (Asteraceae) and *Dolianthus* (Rubiaceae) are removed from the New Guinean flora and their species transferred to *Gnaphalium* and *Amaracarpus*. New descriptions of the two species involved are presented.

In the course of a study of the Asterales and Rubiaceae for the Alpine Flora of New Guinea the genus *Raoulia* HOOK. & ARN. in the former and *Dolianthus* C. H. WRIGHT in the latter family attracted my attention for various reasons. *Raoulia* seemed to be a bit out of place as its main distribution is the New Zealand area, while the genus *Dolianthus*, after being described in the Loganiaceae was later transferred to the Rubiaceae though its position was not satisfactorily solved. In particular the species of *Raoulia* posed a problem as the type material was lost and no duplicates could be traced. The situation in *Dolianthus* was only slightly better as a type specimen was available but the material turned out to be rather insufficient. Of both genera now new material turned up that could finally settle their status.

Raoulia

When describing the New Guinean *R. chiliastra*, MATTFELD (1940 p. 473) stated that "*Raoulia* and *Gnaphalium* are any-

way not separable by clear consistent details and one could describe *R. chiliastra* just as well as a *Gnaphalium*." That MATTFELD placed his species in *Raoulia* is due to the close resemblance to *R. cinerea* PETRIE from New Zealand. This may be so but ALLAN (1961 p. 701) describes *Raoulia* as having the pappus hairs in one or several series with 15—25 hairs in a single series or 50—150 when in several series. The rather few hairs of the pappus in *Gnaphalium* species in New Guinea brings them according to ALLAN's definition outside *Raoulia*, and as will be seen below this applies also to *R. chiliastra*. ALLAN incidentally mentions also that several species of *Raoulia* have been described from New Guinea but this is not so, at least the transfer of *Gnaphalium* species that could account for his submission has never been carried out though perhaps intended by ALLAN.

Unfortunately no material was available of *R. chiliastra* since whatever there was of it was lost in the 1943 burning of the Berlin Herbarium. Inquiries in other herbaria never revealed any material, a result

confirmed by Dr J. TH. KOSTER, well known author of many papers on New Guinean Asteraceae.

It was therefore that when I had two opportunities in February and November 1963 to make a fieldtrip to the Sarawaket Range in New Guinea — the type locality of *R. chiliastra* — I had a good look around for this species. MATTFELD described it as "graceful small rosettes in large numbers together and by the adventitious roots and the filiform stolones knotted together in board-hard mats". Some mat-forming species were found but these all turned out to be known *Gnaphalium* species. During the studies of some material in the Lae Herbarium in New Guinea it turned out that in January 1963 T. G. HARTLEY had been collecting also on Mount Sarawaket and among his material a *Gnaphalium* species (No. 11125) was found that could not be matched with any of the known species. It was not until 1972 when I once again took up this problem of *Raoulia* that the name *R. chiliastra* had to be applied to this material.

KOSTER in the meantime published her notes on *Gnaphalium* (KOSTER 1972), but she apparently has not seen HARTLEY's material. She only refers to *R. chiliastra* in a note to *G. brassii* MATTFELD (op. cit. p. 209) and mentions also the fact that she had not seen any material after the destruction of the type material.

From HARTLEY's material it is clear that it represents *R. chiliastra* and that it represents rather a *Gnaphalium* than a *Raoulia* in view of the few pappus hairs. Most of the *Gnaphalium* species known from New Guinea are found on Mount Sarawaket as well and *R. chiliastra* is particularly close to *G. breviscapum* MATTFELD, and to some extent to *G. clemensiae* MATTFELD. Both *R. chiliastra* and *G. clemensiae* have 5-lobed disk florets while *G. breviscapum* and *G. brassii* have 4-lobed disk florets.

HARTLEY's material was growing in dense mats and with the flowers usually hidden between the leaves this material

matches very well MATTFELD's original description. However this part of the description compares well also with *G. clemensiae* but some specimens of that species have longer stalked heads and then resemble *G. breviscapum*. MATTFELD compared *R. chiliastra* with *G. breviscapum* and *G. brassii* when taking the stalked or sessile inflorescences into account, as in *G. clemensiae* repeatedly non-stalked heads are found. Contrary to MATTFELD's opinion in comparing *R. chiliastra* with the two species mentioned it should have been compared initially with *G. clemensiae* due to the 5-lobed disk florets and to some extent later with the other two species with their 4-lobed disk florets.

Transferring *Raoulia chiliastra* to *Gnaphalium* and appending the original description by MATTFELD results in the following combination:

***Gnaphalium chiliastrum* (MATTFELD)**

VAN ROYEN, comb. nov. (Fig. 1)

Basionym: *Raoulia chiliastra* MATTFELD, Bot. Jahrb. 70 (1940) p. 473.

Small, perennial, up to 10 mm high herb, stoloniferous, growing in dense mats. *Stems* upright, 2—5 mm long, or stemless, glabrous. *Leaves* densely rosulate, linear or linear-lanceolate, 2.5—10 by 0.4—1 mm, acutish at tip, at base sheath-like, 3-nerved, midrib grooved above, prominent below; margin entire, thin, flat; herbaceous, spreading, scattered white arachnoid woolly on either side but rather soon entirely glabrous or with a few remaining hairs on underside of midrib; sheath straw-like, narrowly ovate, 1.5—3 mm long, 3-nerved, with the same type of pubescence as limb but very soon glabrous. *Heads* sessile, enclosed by the leaves, 2—5 mm long, 1.5—2.5 mm across. *Phyllaries* c. 15, in 3 or 4 series, outer ones linear-lanceolate, 2.5—3.5 by c. 1 mm, median ones oblong-lanceolate or elliptic, 2.5—3 by c. 1 mm, acutish, 1-nerved, glabrous, margin scarious in upper

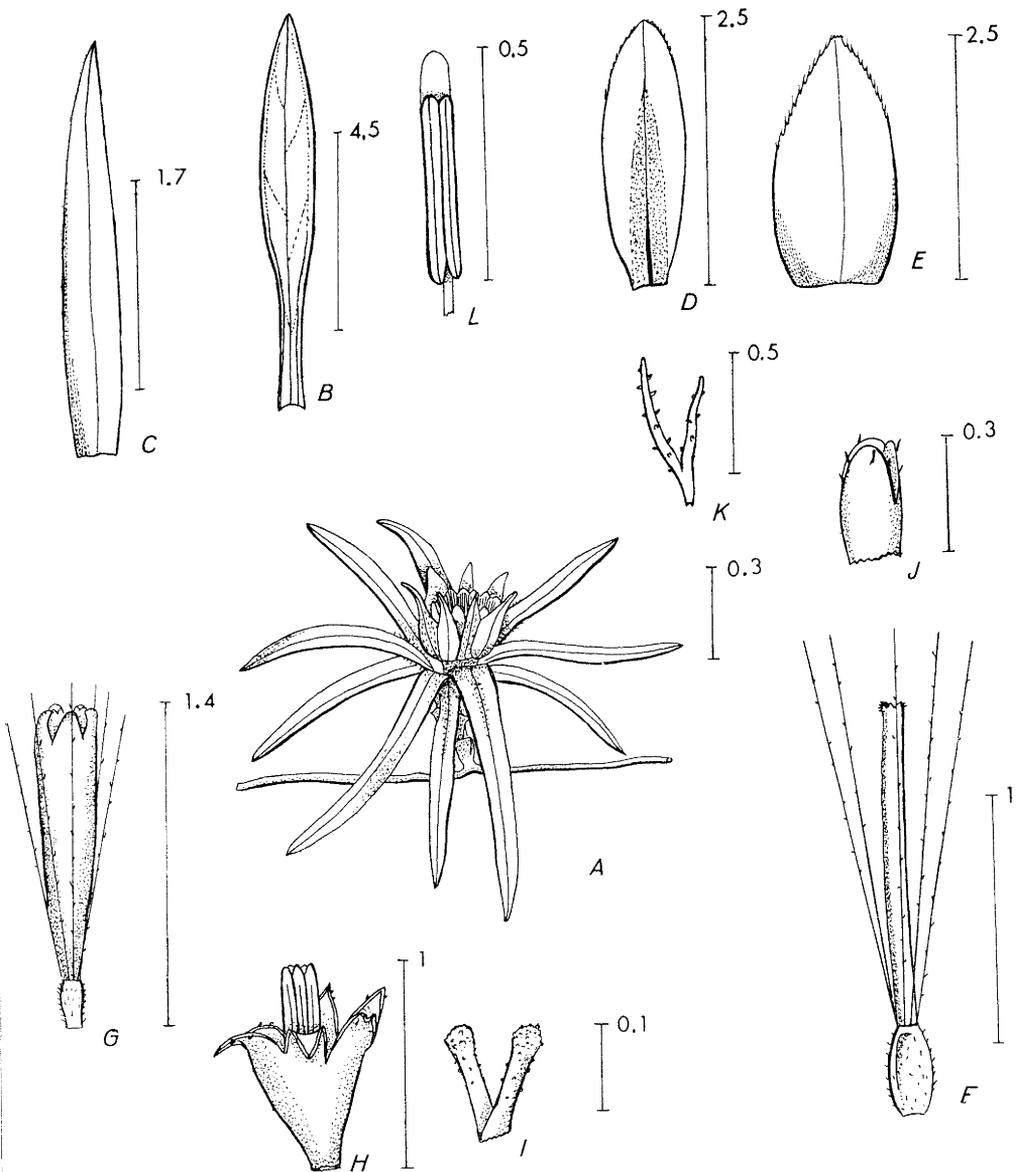


Fig. 1. *Gnaphalium chiliastrum* (MATTFELD) VAN ROYEN. — A: Habit. — B: Leaf, underside. — C: Outer phyllary, hairs left out. — D, E: Median phyllaries. — F: Marginal floret. — G: Disk floret. — H: Tip of disk floret. — I: Stigma of disk floret. — J: Tip of corolla of marginal floret. — K: Stigmas of marginal floret. — L: Stamen of disk floret. — Drawn after HARTLEY 11125.

parts. Receptacle flat, glabrous. *Marginal florets* ♀, 30—45. Corolla narrowly tubular, 2—2.5 mm long, slightly widened at either end, 3-lobed, lobes ovate, c. 0.1 mm long, rounded, with a few papillae at tip. Style 1.5—2 mm long, glabrous, stigmatic branches subulate, c. 0.2 mm long, scattered papillate. Pappus hairs 0—10, in one series, 1.5—2.1 mm long, free or at base adhering to each other, without papillae at base, scattered barbellate, narrowed at tip. Achene oblong-ellipsoid, c. 1 by 0.2 mm, narrowed at either end, slightly 3-sided, with scattered patent, claviform papillae. *Disk florets* ♂, 7—10. Corolla tubular in lower part, funnel-shaped widened in upper half, 2.8—3 mm long, glabrous, 5-lobed at tip, lobes triangular or ovate, c. 0.2 mm long, acutish, margins thickened, on outside scattered papillate, erect when young but later curving outwards. Stamens c. 2.5 mm

long, anthers linear, 0.5—1 mm long, with a long rounded appendage at tip, base caudate. Style 2.5—2.8 mm long, glabrous, stigmatic branches strapshaped, c. 0.5 mm long, subclaviform widened at tip, with scattered papillae. Pappus and achenes similar to those of the marginal florets.

TYPE SPECIMEN: CLEMENS 5898, in B, destroyed.

NEOTYPE SPECIMEN: HARTLEY 11125, in BISH.

DISTRIBUTION. Territory of New Guinea, Sarawaket Range, on the highest summit (=Mt Sarawaket!), c. 4000 m (CLEMENS 5898, April), 3750 m (CLEMENS 5910, April), 3000 m (HARTLEY 11125, Jan.).

ECOLOGY. In alpine regions growing among boulders and on bare soil, 3000—4000 m. Fl. & fr. Jan., April.

NOTE. *G. chiliastrum* can be distinguished from the other three known alpine species as follows:

Leaves when young subdensely to densely white woolly, but very soon glabrous. Pappus hairs 0—10, not papillate at base. Corolla of disk florets 5-lobed *G. chiliastrum*
 Leaves even when older at least on underside densely white woolly. Pappus hairs well over 10, papillate at base. Corolla of disk florets 4-lobed, rarely 5-lobed
 *G. brassii*, *G. breviscapum*, *G. clemensiae*

Dolianthus

The genus *Dolianthus* was described by C. H. WRIGHT in 1899, but was placed by its author in the Loganiaceae. The material was collected by A. GIULIANETTI on Mount Scratchley and consists of a few small branches with leaves, one fully developed flower and one bud. WRIGHT must have suspected that the genus could be Rubiaceae as he compares it with the Madagascarian genus *Hymenocnemis* HOOKER in that family. The ovary was said to be superior and this is probably the reason that WRIGHT placed the genus after all in the Loganiaceae.

BREMEKAMP (1937) on the request of VAN STEENIS studied the material again and came soon to the conclusion that the genus was Rubiaceae. At the same time he points out that *Dolianthus* differs from the other genera in the Loganiaceae by

the shape and size of its rather large, interpetiolar stipules and in its uni-ovular ovary cells. This aroused BREMEKAMP's suspicion about the proper place of the genus but as only one flower was present, apart from the one dissected and later mounted by WRIGHT, he did not dare to open this one and "unable to get to the bottom of this question" he suggests that what WRIGHT describes as ovary was in fact the thick disk on top of it and that the ovary itself is inferior. Also the shape of the calyx and the insertion of the corolla led him to believe that *Dolianthus* should be placed in the Rubiaceae. He further points out that the flowers are terminal and not axillary, that the two flowers in GIULIANETTI's material are respectively 4- and 5-lobed, the stamens are inserted somewhat above the middle of the tube, the anthers are dorsifix and obtusely bilobate at the base, not sagittate,

and all these details induced him to believe that the genus should be placed in the Psychotriacae. The uni-ovular ovary cells, the erect ovules, the valvate aestivation of the corolla-lobes, and the short stigma-lobes point to that group.

In discussing various genera that are related to *Dolianthus* BREMEKAMP also considers *Amaracarpus*. It resembles that genus in its terminal inflorescence, the smallness of its leaves, and the presence of the same kind of rather thick, rufous hairs on the young shoots. However its flowers are much smaller and there is moreover a considerable difference in habit from *Amaracarpus* as in the latter the main branches resemble bipinnate leaves with the branchlets and leaves all arranged in the same more or less horizontal plane, while in *Dolianthus* the ramification is a kind of pseudo-dichotomy, and the leaves point in all directions.

All this may have been true in the time that BREMEKAMP wrote his note but since then a number of species in *Amaracarpus* have been described that deviate considerably in habit from the picture given by BREMEKAMP. MERRILL and PERRY (1946) already pointed out the differences they found compared with the original description by BLUME (1826). In that description and in most later papers the calyx and corolla are said to be 4-merous. However VALETON (1927), followed by MERRILL and PERRY in 1946 mention in several species that the calyx is sometimes 5-merous. During my studies of the abundant material of *Amaracarpus* now available I have found this to happen over and over again and that even a 6-lobed corolla is found in one of the so far undescribed species. As to the number of stamens this was found in one of MERRILL and PERRY's species to be 7, so quite a variation can be noticed. They furthermore point to the difficulty of some of their new species to be fitted in *Amaracarpus* due to the fact that these plants are glabrous (*A. bicolor*, *A. coeruleus*, *A. buxifolius*, *A. clemensiae*

and *A. archboldiana*), that the stipules are rounded and not 2-tipped as in the original species of BLUME, that they are oblong or ovate, and that in this group of species the flowers are much larger than in two other groups of species distinguished by them. They would have preferred to place that group in *Dolianthus* but hesitate to do so on the grounds that in that genus no bracteoles are reported, a detail clearly specified by BREMEKAMP. In material recently collected by COODE and STEVENS on Mount Scratchley the inflorescences still do not show any bracteoles. However in MERRILL and PERRY's *Amaracarpus clemensiae* and in several new species recently found but not yet described the inflorescences are found without bracteoles either while very closely related species are found with bracteoles. Apparently this detail of absence or presence of bracteoles is not enough to separate *Amaracarpus* from *Dolianthus*.

BREMEKAMP mentions that the flowers of *Dolianthus* are smaller than in *Amaracarpus*. However with VALETON's and MERRILL and PERRY's species at hand together with new species found by me it is the reverse: *Dolianthus* has rather large flowers compared to the bulk of the *Amaracarpus* species. For instance *Amaracarpus brassii* MERRILL & PERRY has flowers about 1/3 the size of those of *Dolianthus vaccinioides* but all other details warrant including the first species in *Amaracarpus*.

Also according to BREMEKAMP the habit of the original *Amaracarpus* and many later described ones is quite different from *Dolianthus*. BLUME's *Amaracarpus* has branchlets resembling bipinnate leaves with lateral branchlets and leaves arranged in the same more or less horizontal plane. However already VALETON, and later MERRILL and PERRY, made it clear that the given growth form is not a constant one and can not serve entirely as a characterising detail to keep genera apart. The branching in *Dolianthus*, and for that

Table 1. A grouping of *Amaracarpus* species showing much overlap in details. The initial division is based on the shape of the stipules and the arrangement of the leaves. The numbers in the first column refer to flower arrangement as follows: 1: in fascicles; 2: solitary; 3: in dichotomous inflorescences. The ranges of leaf size in the third column are: small: 2—20 mm; medium: 20—30 mm; large: 30—150 mm long. Regarding the pubescence of the branchlets given in the fourth column, it has to be taken into account that initially this pubescence may be there but that in some species it will soon disappear and the branches appear to be glabrous.

Species	Flower arrangement	Bracts	Leaf size	Pubescence of branchlets
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Group 1. Stipules with 2 setae. Leaves in one plane with branchlets.

<i>A. belensis</i>	2	none	small	rufous pubescent
<i>A. idenburgensis</i>	1	present	small	rufous pubescent
<i>A. ledermannii</i>	2	present	medium	glabrous
<i>A. nymanii</i>	?	?	small	hirtellous
<i>A. rhombifolius</i>	2	present	small	rufous pubescent
<i>A. schlechteri</i>	1	present	medium	rufous pubescent
<i>A. simulans</i>	2	none	small	hirtellous
<i>A. xanthocarpus</i>	1	present	small	rufous pubescent

Group 2. Stipules with 2 setae. Leaves not in one plane with branchlets.

<i>A. atrocarpus</i>	2	none	sm—med	pilose
<i>A. calcicola</i>	2	none	sm—med	rufous pubescent
<i>A. brassii</i>	2	none	small	rufous pubescent
<i>A. subcaudatus</i>	1	present	large	glabrous
<i>A. trichocalyx</i>	1	present	large	rufous pubescent
<i>A. urophyllus</i>	1	present	large	pubescent

Group 3. Stipules rounded or obtuse, sometimes acute. Leaves not in plane with branchlets.

<i>A. archboldianus</i>	1	none	sm—med	glabrous
<i>A. attenuatus</i>	3	present	large	glabrous
<i>A. bicolor</i>	2	none	medium	glabrous
<i>A. brachypus</i>	2, 3	present	large	glabrous
<i>A. braunianus</i>	3	none ?	medium	glabrous
<i>A. buxifolius</i>	2	present	small	glabrous
<i>A. caeruleus</i>	2	present	small	glabrous
<i>A. clemensiae</i>	2	present	small	pubescent
<i>A. compactus</i>	2	none	small	pubescent
<i>A. confertifolius</i>	2	present	small	glabrous
<i>A. epiphyticus</i>	3	present	small	rufous pubescent
<i>A. grandicalyx</i>	?	present	med—l	hirtellous
<i>A. grandifolius</i>	1	present	large	hirtellous
<i>A. humilis</i>	2	none	sm—l	hirsute
<i>A. lauterbachii</i>	?	?	sm—med	glabrous
<i>A. leucocarpus</i>	2	none	sm—l	rufous subtomentose
<i>A. montanus</i>	?	?	small	rufous villose
<i>A. novoguineensis</i>	2	none	small	hirtellous
<i>A. trichanthus</i>	2	present	small	pilose
<i>A. trichocarpus</i>	?	?	sm—l	subvillose
<i>A. torricellensis</i>	2	none	sm—l	villose
<i>Dolianthus vaccinioides</i>	2	none	small	rufous pilose

matter in many *Amaracarpus* species described by VALETON and MERRILL and PERRY, is a kind of pseudo-dichotomy and the branchlets and leaves point in all

directions. This scheme is sometimes complicated by the formation of brachyblasts with dense foliage, for instance in *A. brassii* MERRILL & PERRY. An analysis

of these shoots shows that basically the same branching is present as along the main branches. Taking the two extreme forms one would be inclined to distinguish two genera, *Amaracarpus* and *Dolianthus*, were it not that intermediate forms between the two different types of branchings are found. Often branches that start out in a bipinnate way will continue with branchings in all directions like in *Dolianthus*.

According to BREMEKAMP the flower of *Dolianthus vaccinioides* is terminal and as such this genus differs from *Amaracarpus* BL. (in its original sense), *Hymenocnemis* HOOKER, *Saprosma* BL., *Saldinia* A. RICHARD, and *Margaritopsis* SAUVAGE, as these genera have axillary flowers. However in several species both terminal and axillary flowers and inflorescences can be found and this detail too can not be used to distinguish *Dolianthus* from *Amaracarpus*. VALETON in 1927 already pointed out that both types of insertion of the flower can be found on the same branch.

Taking all that is said into account there seems to be little or no reason to maintain *Dolianthus*. However merging it into *Amaracarpus* creates quite a variation of species in the latter. MERRILL and PERRY distinguished already three groups, remarking at the same time that no sharp distinction is present, which is confirmed in my studies of the genus. They roughly divide *Amaracarpus* as follows:

(1) Species with large leaves and for the most part with almost filiform pedunculate axillary inflorescences. Stipules more or less connate, each terminated by two setae.

(2) Species generally pubescent with rather thick hairs on young shoots and with a very distinctive habit marked by horizontally placed small leaves and branches. Flowers solitary and sessile or very shortly pedicellate, usually subtended by reduced leaves and stipules or stipule-bracts. Stipules terminated by two setae.

(3) Glabrous species with more irregular branching, often crowded leaves, with rounded-oblong or ovate stipules. Flowers larger than in either of the other groups, mostly with a granular-puberulent throat and relatively long filaments.

The second group agrees somewhat with the original description by BLUME, and so does the first group but less so. The third group is different by the rounded stipules and this would be a reason to keep it separate from *Amaracarpus*. Since this group includes *Dolianthus vaccinioides* it would mean that the name *Dolianthus* has to be used. However in view of all the intermediate stages as pointed out already by VALETON, MERRILL and PERRY, and confirmed by my studies this course can not be followed. How much the details overlap in the different groups as pointed out by MERRILL and PERRY is shown by the grouping in Table 1.

In transferring *Dolianthus* to *Amaracarpus* it becomes necessary to create a new combination which is given below including an extended description of the species.

Amaracarpus vaccinioides (C. H. WRIGHT)
VAN ROYEN, comb. nov. (Fig. 2)

Basionym: *Dolianthus vaccinioides* C. H. WRIGHT, Kew Bull. (1899) p. 106; BREMEKAMP, Kew Bull. (1936) p. 105.

Bushy, pseudo-dichotomously branched shrub up to 4.5 m high. *Branchlets* 4-ribbed to -winged, scattered antrorsely rusty brown pilose, relatively soon glabrous. *Stipules* broadly ovate or ovate-triangular, 3.5—4.5 by 3—4 mm, rounded or obtuse, scattered appressed brownish or blackish hirsute on outside and along margins, glabrescent, inside glabrous, except at base with a row of long brown hairs and some claviform glands. *Leaves* dark glossy green above, paler below, 12—18 mm long, limb elliptic, lanceolate, or elliptic-ovate, 8—12 by 3—5 mm, obtuse or obtusish at tip, sometimes in-

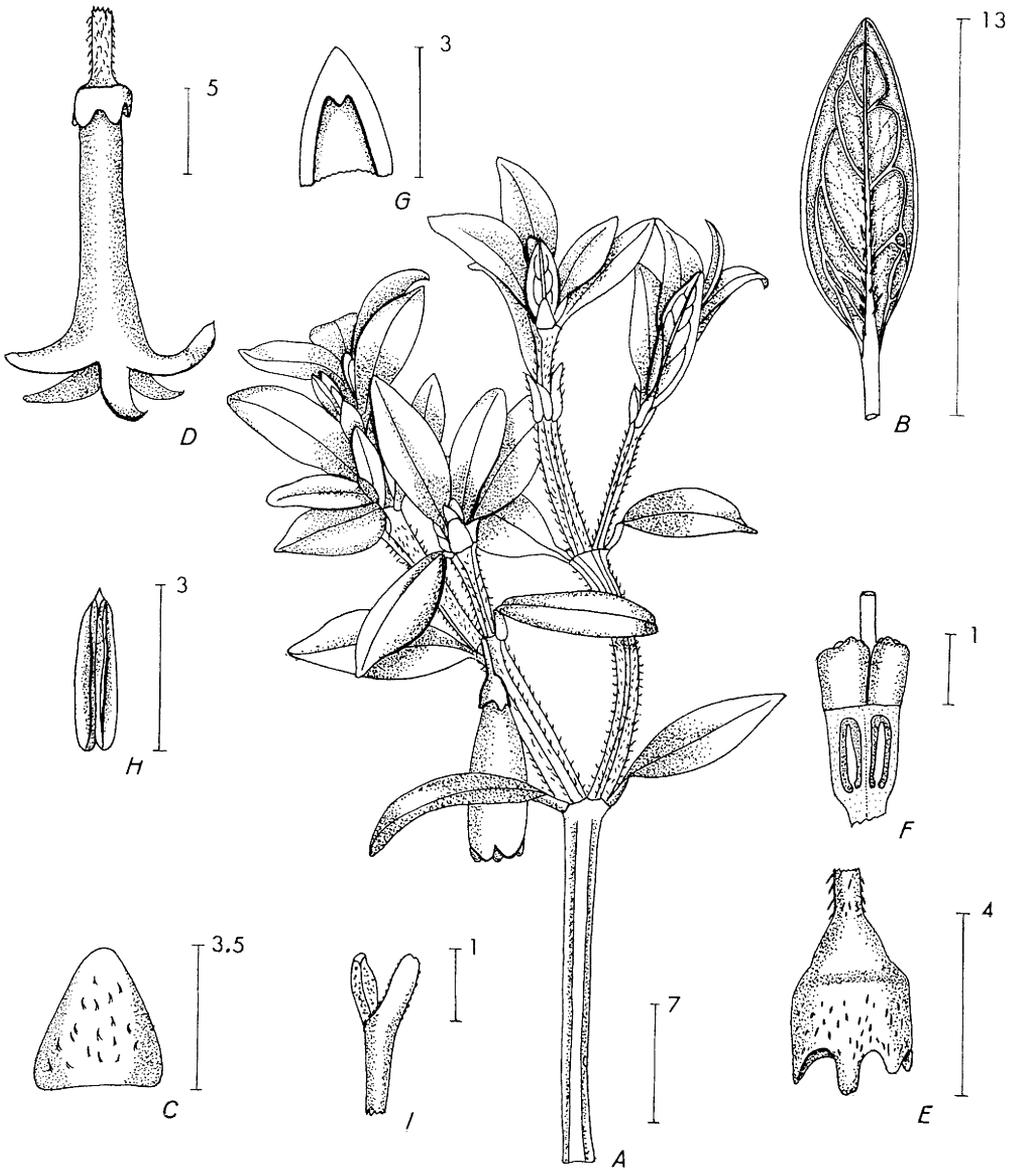


Fig. 2. *Amaracarpus vaccinioides* (C. H. WRIGHT) VAN ROYEN. — A: Habit. — B: Leaf, underside. — C: Stipule. — D: Flower. — E: Receptacle. — F: Disk and longitudinal section of ovary. — G: Tip of corolla-lobe, inside. — H: Anther. — I: Stigmas. — Drawn after COODE & STEVENS NGF 46309, except D and H drawn after GIULIANETTI s.n.

distinctly obtusely acuminate, base broadly to narrowly cuneate, midrib grooved or impressed above, stoutly prominent below, lateral nerves 3—5 on either side of mid-

rib, ascending at c. 45° , straight or curved, archingly joined near margin, not visible above, stoutly prominent below, venation widely reticulate, parallel to lateral nerves,

not or hardly visible above, prominulous below; margin slightly revolute; coriaceous, patent or spreading, often convex curved, glabrous above, on underside with coarse brown hairs along lower half of midrib only. Petioles 3—6 mm long, flat above, rounded below, glabrous. *Flowers* solitary, terminal or seemingly axillary on brachyblasts. Pedicels stoutish, 6—8 mm long, subdensely antrorse brown hairy. Bracts and bracteoles none. Receptacle 4—5 mm long, glabrous, widely campanulate in lower third, cylindrical in upper part, the 4 or 5 lobes unequal, oblong-ovate or oblong, c. 1 by 1 mm, rounded, with slightly thickened margin and scattered cystoliths. Ovary 2-celled with 1 ovule in each cell. Corolla whitish in bud, blue at tip, when mature either entirely white or with blue tips, narrowly funnelshaped, c. 18 mm long, gradually widening towards throat, glabrous, with relatively numerous cystoliths, lobes 4 or 5, oblong or oblong-ovate, 3.5—5 by 2—2.5 mm, acute at tip and hooked on inside, in open flower slightly flaring outwards, glabrous. Stamens 4 or 5, inserted in the throat, 3.5—4.5 mm long, filaments subulate, 1.5—2 mm long, glabrous, connective at tip with several cystoliths, anthers linear, c. 3 mm long, acuminate or rounded at tip, cells round at base. Disk ringshaped, irregularly humped, c. 1.5 mm across, c. 1 mm high, glabrous. Style 15—20 mm long, glabrous, stigmas oblong, c. 1 mm long, thin, papillate on inside. Berry not seen.

TYPE SPECIMEN: GIULIANETTI s.n., in K.

DISTRIBUTION. New Guinea, Papua, Mount

Scratchley, 3050—3965 m (GIULIANETTI s.n., COODE & STEVENS NGF 46309, May).

NOTE. Recently COODE & STEVENS (1972) identified their material as *Amarcarpus caeruleus* MERRILL & PERRY. However in *A. caeruleus* bracteoles are present which are not found in *A. vaccinioides*. Also the leaves of *A. caeruleus* are quite larger and flat whereas those of *A. vaccinioides* are more coriaceous with revolute margins and rather glossy above. The corolla of *A. caeruleus* is pubescent on inside while that of *A. vaccinioides* is glabrous.

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Some Adaptive Genetic-evolutionary Processes Accompanying Polyploidy in the Indian *Alliums*¹

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ABSTRACT

GOHIL, R. N. & KOUL, A. K. 1973. Some adaptive genetic-evolutionary processes accompanying polyploidy in the Indian *Alliums*. — Bot. Notiser 126: 426—432.

The 300 species of the genus *Allium* which have so far been worked out cytogenetically, exist in over 411 cytotypes. Of these about 34 % are polyploids. The occurrence of so many polyploids in *Allium* suggests that they have adopted mechanisms which help them to escape the bottleneck of sterility. The present paper puts on record four such methods adopted by the polyploid *Alliums* of India, namely, centric chiasma localization, imposition of genetic balance, bulbifery and vegetative reproduction. The paper is based on our investigation on 22 cytotypes belonging to 17 species.

INTRODUCTION

The significance of polyploidy as a means of major evolutionary advance within a group depends largely on the reproductive potential of the polyploid taxa. Compared with diploids, the polyploids are characterized by higher sterility on account of disturbed meiosis and/or physiological unbalance. Thus chromosome doubling is a hindrance rather than a help. In the genus *Allium*, however, of about 300 species with known chromosome numbers, 34 % are polyploids. Polyploidy ranges from triploidy to octoploidy; tetraploids being most frequent followed in order by triploids, hexaploids, pentaploids, etc. (Fig. 1). In addition to

these, two species, namely *A. angulosum* and *A. nutans*, represent two big polyploid complexes with the chromosome numbers ranging from 60 to 100 and from 64 to 108 respectively (DARLINGTON & WYLIE 1955; FEDOROV 1969; ORNDUFF 1967, 1968, 1969 and MOORE 1970, 1971). The existence of such a high degree of natural polyploidy suggests that polyploidy in the genus has been accompanied by some genetic-evolutionary processes which have compensated for the initial adaptive disadvantages attendant on raw polyploids. The present communication attempts to put on record some of these adaptive mechanisms.

MATERIAL AND METHODS

The work is based on a study of 22 cytotypes belonging to 17 species (Table 1). The voucher specimens have been deposited at the Kashmir University Herbarium. Root tip mitoses, male meiosis and pollen mitoses

¹ The paper was read at the First All India Congress of Cytology and Genetics, held at Chandigarh in 1971.

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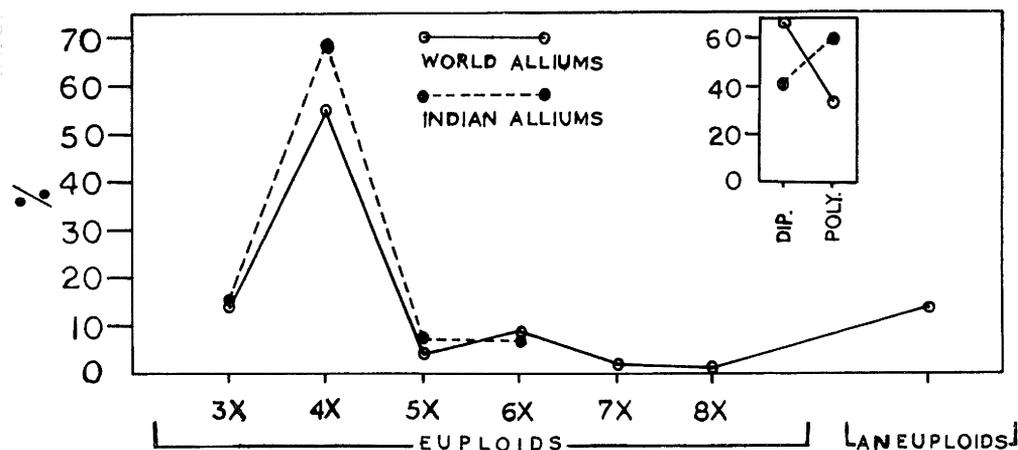


Fig. 1. Graphic representation of the range, type and frequency of polyploidy in the genus *Allium*.

were studied following the schedule used by KOUL & GOHIL 1970 a, b and KOUL, SHARMA & GOHIL 1971.

OBSERVATIONS AND DISCUSSION

The polyploids screened are either autopolyploids or segmental allopolyploids. In both these types of polyploids chromosomes pair but crossing-over and chromosomal segregation at meiosis produce gametes with disharmonious gene combinations resulting in sterility. The methods employed by these taxa to stabilize and increase their reproductive potential are as below.

Centric Chiasma Localization

Earlier studies by KOUL & GOHIL (1970 a) revealed that *Allium ampeloprasum* is a segmental allotetraploid ($2n=4x=32$) with sufficient genetic compatibility between the associated genomes (AAA'A"). The progenitors of this numerical hybrid are so closely related as to permit chromosome pairing and multivalent formation. Surprisingly, however, male meiosis of this taxon is free of multivalents; chromosomes pair into 16 bivalents (Fig. 2 A) and only 4 of the 640 chromosomes ana-

lysed were involved in quadrivalent association. The total suppression of multivalents is caused by the localization of chiasmata in the centromeric region due probably to the availability of only very short segments for effective pairing.

While localized chiasmata in diploids have a limited role in preserving certain linkage groups by considerably reducing crossing-over, in polyploid species such as *A. ampeloprasum* and the autotetraploid *A. porrum* (LEVAN 1940) centric chiasmata boost the fertility by eliminating all segregational abnormalities attendant on multivalent formation.

In species of *Allium* in general, the chiasma frequencies are lower and localization greater in pollen mother cells than in embryo sac mother cells (VED BRAT 1966). Development of large quantities of seed, all with a full complement of 32 chromosomes, by the tetraploid *A. ampeloprasum*, however, indicates little difference in chromosome behaviour between the two sexes.

Imposition of Genetic Balance

In sexually reproducing plants genetic balance is imposed either before or after

Table 1. Species of *Allium* studied. * indicates local names.

Name of the species	2n	Place of collection	Voucher number
<i>Allium cepa</i> L.			
var. <i>cepa</i>	16	Cultivated	RN 4
var. <i>viviparum</i> (Pran)*	24	Cultivated	RN 6
<i>A. ascalonicum</i> L.	16	Cultivated	RN 52
<i>A. sativum</i> L.	16	Cultivated	RN 8
<i>A. ampeloprasum</i> L.			
Leek	32	Cultivated	RN 2
Peer*	32	Pampore	RN 38
Great-headed garlic	48	Bhadarwah	RN 3
<i>A. chinense</i> G. DON.	32	Cultivated	RN 7
<i>A. rubellum</i> BIEB.	16	Poonch	RN 39
	24	Kathua	RN 40
	32	Pampore	RN 41
<i>A. stracheyi</i> BAKER	16	Simthou Pass	RN 42
<i>A. consanguineum</i> KUNTH	16	Bhadarwah	RN 43
	16	Gurez	RN 53
	16	Harwan	RN 54
<i>A. platyspathum</i> SCHRENK			
var. <i>falcatum</i>	32	Bodh Kharbu	RN 44
<i>A. blandum</i> WALL.	32	Meena Marg	RN 45
<i>A. thomsoni</i> BAKER	32	Meena Marg	RN 36
<i>A. tuberosum</i> ROTT. ex SPRENG.	32	Agra	RN 9
<i>A. bakeri</i> REGEL	32	Sikkim	RN 47
<i>A. govanianum</i> WALL.	16	El Pathar	RN 46
<i>A. oreoprasum</i> SCHRENK	16	Bodh Kharbu	RN 48
<i>A. atropurpureum</i> WALDST. & KIT.	16	Srinagar	RN 49
<i>A. neapolitanum</i> CYR.	35	Amritsar	RN 51

fertilization (at gametic or at embryonal stage) by the elimination of unbalanced forms during or before differentiation. The pollen grains of autotetraploid *A. tuberosum* ($2n=4x=32$), which is also a weak desynaptic, are subjected to the test of this principle (GOHIL & KOUL 1972). High quadrivalent frequency (5.9 per cell) in pollen mother cells coupled with precocious dissociation of chromosomes in 5 % desynaptic cells lead to segregational irregularities (Table 2).

It is evident that chromosome distribution is normal in only 25.3 % of the cells and the remainder show segregational errors. Basing our expectation on these data, pollen grains varying in chromosome number from 12—18 should be formed, besides a small percentage of micropollen grains with only 1—3 chromosomes.

Pollen grain mitoses was studied from anthers of several different flower buds and chromosome counts were made from 131 intact pollen grains (Table 3 and Fig. 3) at first nuclear division.

Taking 16 as the haploid number, about 43.3 % grains are subhaploid; a rather uncommon feature. The unusually high percentage of subhaploid grains entering mitosis in *A. tuberosum* is accounted for by their polyploid nature. Since 8 is the basic number, only grains with chromosomes less than this number are in reality submonoploid. Although segregation errors such as lagging, etc., are expected to lead to the formation of submonoploid and genetically weaker pollen grains it seems that such grains either do not enter mitosis or divide later than the balanced ones as is the case in *A. paniculatum* (VED BRAT 1967).

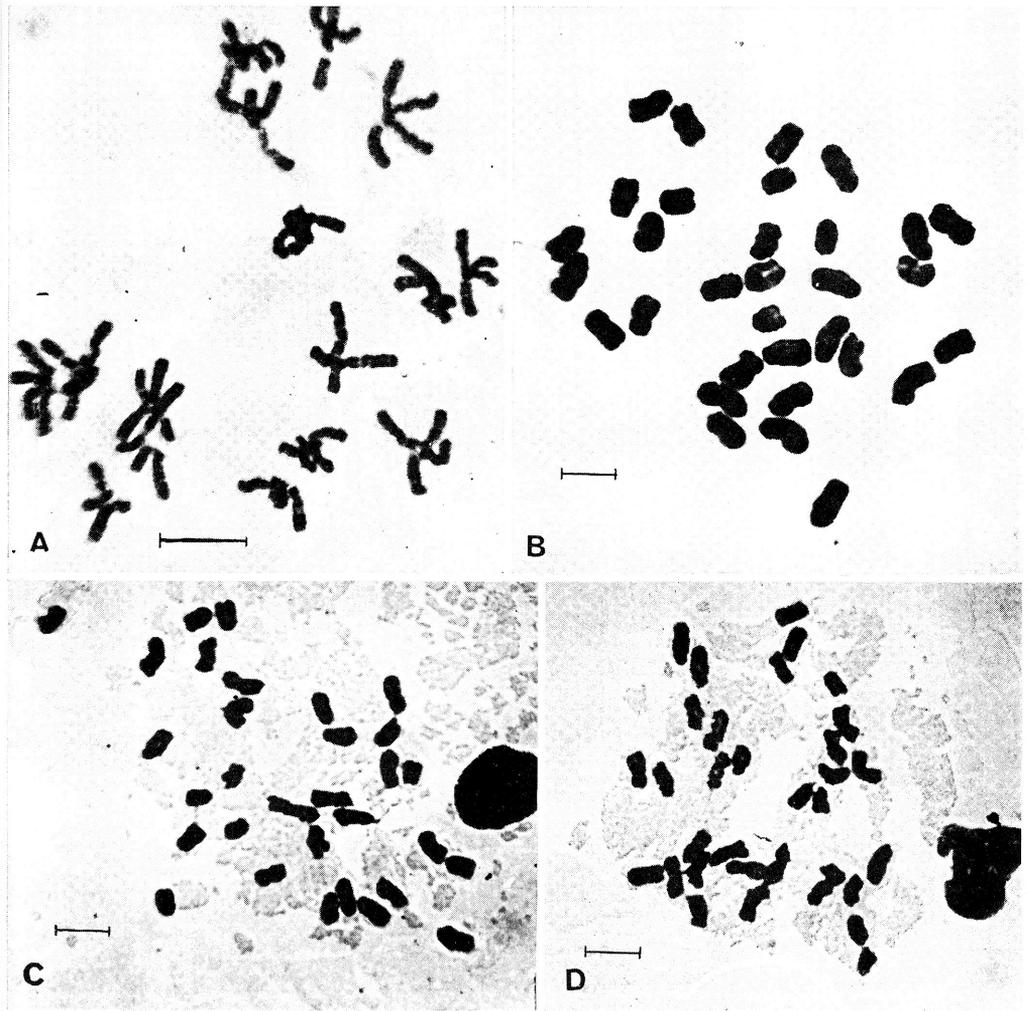


Fig. 2. A: A PMC of *Allium ampeloprasum* showing 16 bivalents all with centric chiasmata. — B—D: Pollen mother cells of tetraploid, monosomic and trisomic of *A. tuberosum*. All the three cells show complete desynapsis and contain 32, 31 and 33 chromosomes respectively. — Scale 10 μ .

Table 2. Anaphase distribution in *Allium tuberosum* ($2n=32$).

Distribution	16	16	16	16	17	17	17	18	18	18
	16	1	2	3	1	2	2	1	1	2
	16	15	14	13	15	14	13	14	13	12

No. of cells 19 13 9 6 6 5 4 5 5 3

% 25.3 17.3 12.0 8.0 8.0 6.6 5.3 6.6 6.6 4.0

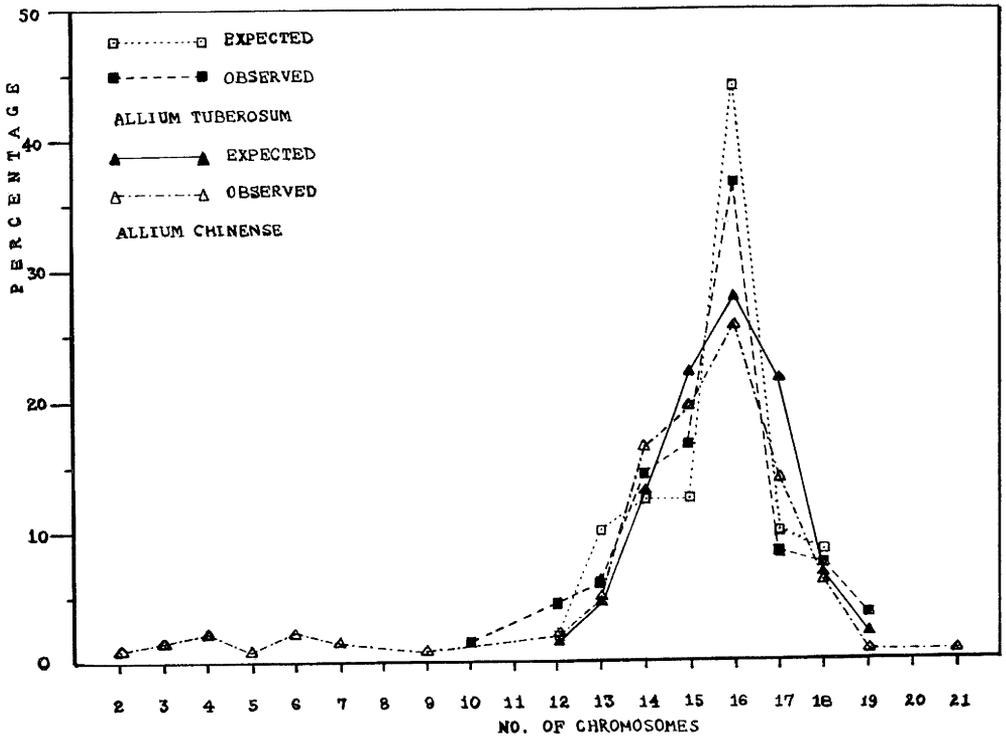


Fig. 3. Graph showing observed and expected chromosome numbers in the pollen grains of *Allium tuberosum* and *A. chinense*. (Expected on the basis of anaphase I segregation).

The chromosome numbers in the pollen grains vary around the mean 15. 36.6 % of the grains have a full complement (16 chromosomes) but the bulk of the pollen grains (47.1 %) have the chromosome numbers 14, 15, 17 and 18. The frequency of hypohaploid pollen grains, however, is double that of the hyperhaploid grains (43.3:19.7) as is also true in triploid *A. carinatum* and *A. rubellum* (VED BRAT 1967). In the subhaploid pollen grains chromosome deficiencies vary from 6.25—37.5 %. Such a high chromosome loss may be explained by the polyploid nature of the species.

Seed progeny was raised through sibbing. Of the 50 plants scored 46 had a full complement ($2n=32$), two (4 %) plants were monosomic ($2n=4x-1=31$; Fig.

2 C) and two others (4 %) were trisomic ($2n=4x+1=33$; Fig. 2 D). Viewed from the extent of variation in chromosome numbers of pollen grains, the range of variation seems to have been considerably narrowed, either before or after fertilization. With the elimination of unbalanced types, the reproductive potential of this autotetraploid species is increased.

Vegetative Apomixis

True vegetative apomixis is that where propagules replace some or all of the flowers in the inflorescence. Speaking in strict terms this is known as pseudovivipary or bulbifery. In some species such as *A. ampeloprasum* (4x) and *A. tuberosum* (4x) vivipary is partial and re-

Table 3. Chromosome numbers at first pollen mitosis in *Allium tuberosum* ($2n=4x=32$).

Chromosome number	10	12	13	14	15	16	17	18	19
No. of pollen grains . . .	2	6	8	19	22	48	11	10	5
%/o	1.5	4.5	6.1	14.5	16.7	36.6	8.3	7.6	3.8

presents an accessory means of reproduction. In triploid *A. cepa* var. *viviparum* and tetraploid *A. chinense*, however, bulbifery is the only method of reproduction to the exclusion of sexuality. Sexual sterility in the triploid *A. cepa* var. *viviparum* is caused by the awkward segregation of trivalents and univalents resulting in abortive first division of meiosis and the formation of genetically unbalanced gametes (KOUL & GOHIL 1971). In one stroke, therefore, triploidy removes the possibility of orderly reduction and fertilization imposing conditions required for the institution of apomixis.

Male meiosis in tetraploid *A. chinense* is highly irregular on account of anomalies in chromosome pairing. Of the 832 chromosomes studied, 456 were involved in multivalent associations and 116 were unpaired (Fig. 4 A). The result of recombination during meiosis is reflected in the chromosomal constitution of pollen grains. The numbers found in the pollen grains are $n=2-7, 9, 12-19$ and 21 (Fig. 3). Though 25.7 % of the grains are numerically balanced, these are, however, unbalanced structurally, for, they bear chromosomes which do not correspond in structure to the basic karyotype. Development of such gametes leads to total sexual sterility.

Total suppression of sexuality and the loss of reproductive capacity is compensated in these species by the development of bulbils in the inflorescences. The bulbils in *A. cepa* var. *viviparum* arise at the foot of the flower stalks (KOUL & GOHIL 1971), but in *A. chinense* they arise from within the flowers (Fig. 4 B). The growth of bulbils is very fast and they produce

leaves while still attached to the mother plant. When they were removed and put in soil they produced new plants.

Vegetative Reproduction

Vegetative propagation through the development of underground bulblets is a rule in species of the genus *Allium* (although the capacity varies from group

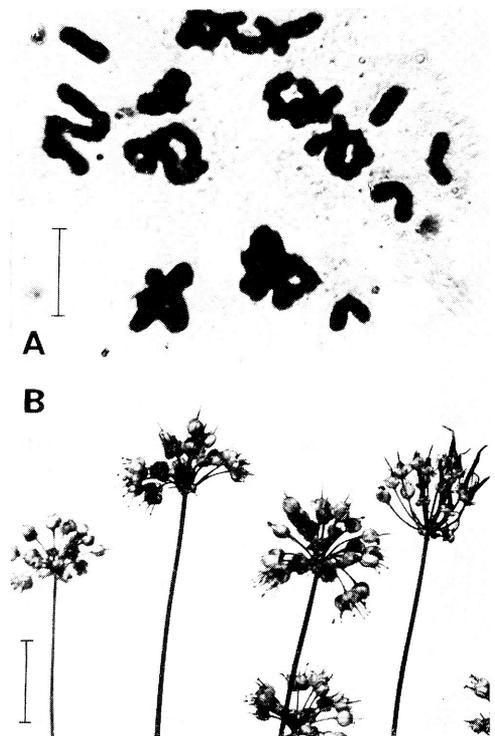


Fig. 4. *Allium chinense*. — A: A PMC at Metaphase I, showing $4IV+3III+1II+5I$. Scale 10μ . — B: Normal and bulbil-bearing inflorescences. Scale 2 cm.

to group). In the sexually fertile polyploids such as *A. tuberosum*, *A. ampeloprasum* and *A. rubellum* (all tetraploids), it provides an accessory means of reproduction to increase the number of those products of meiosis and fertilization which are particularly favoured. For sexually sterile species, however, this provides the only means of propagation and is, therefore, all important. In being a conservative system, vegetative reproduction is able to conserve all genotypes. The hexaploid ($2n = 6x = 48$) race of *A. ampeloprasum* (great-headed garlic) and triploid *A. rubellum* are able to survive and propagate in nature only through vegetative multiplication.

ACKNOWLEDGEMENTS

The authors are grateful to Prof. P. KACHROO for providing them with the necessary facilities and to the authorities of Central National Herbarium, Calcutta, and Forest Research Institute, Dehradun for the help rendered in the identification of the various species of *Allium*. The senior author is grateful to the University Grants Commission and Council of Scientific and Industrial Research, New Delhi, for financial assistance.

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Cytological Observations on Some West Himalayan Mosses IV

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ABSTRACT

KUMAR, S. S. 1973. Cytological observations on some West Himalayan mosses IV. — Bot. Notiser 126: 433—436.

Cytological observations are made on the somatic chromosomes of seven moss taxa belonging to the families Leucodontaceae, Meteoriaceae, Thuidiaceae (3 species), Brachytheciaceae and Entodontaceae.

The chromosome number $n=10$ for *Papillaria fuscescens* is given for the first time. The number $n=11$ in *Levierella fabroniacea* is different from the number reported previously ($n=21$).

The cytological studies of the mosses of the Western Himalayas is one of the research projects of our department. The present paper, part of this project, deals with seven moss taxa.

The material investigated was regenerated in Knop's solution. The apical part of each regenerant, pretreated with 0.1 % colchicine for 3—4 hours, was fixed in acetic-alcohol (1:3) for 8—12 hours and then squashed in aceto-lacmoid by the usual technique. Camera lucida drawings were made at a uniform magnification.

Voucher specimens are deposited at the herbarium of the Department of Botany, Panjab University, Chandigarh.

Leucodontaceae

Leucodon secundus (HARV.) MITT. — $n=9$ (Fig. 1 A)

Mussoorie (Camel Back Road) on *Quercus dilatata*.

The present count $n=9$ confirms two earlier reports (KHANNA 1960; CHOPRA & KUMAR 1967) based on meiotic studies. One of the chromosomes in the complement is conspicuously longer than other members of the set. 6 chromosomes have

a median or submedian constriction and 3 a subterminal constriction. The length of the chromosomes is 6.3, 3.3, 2.2, 1.9, 1.6, 1.5, 1.5, 1.4 and 1.2 μ .

Chromosome numbers known in two other species of this genus are $n=10$ in *L. julaceus* (HEDW.) SULL. (ANDERSON & BRYAN 1958), and $n=11$ in *L. sciuroides* (HEDW.) SCHWAEGR. (HO 1956).

Meteoriaceae

Papillaria fuscescens (HOOK.) JAEG. — $n=10$ (Fig. 1 B)

Simla (Glen) on shrubs.

The number $n=10$ appears to be the first count for this taxon. Of the 10 chromosomes, 8 have a median or submedian constriction and 2 a subterminal constriction. The longest and shortest members of the complement are heterochromatic. The length of the chromosomes is 3.7, 2.6, 2.3, 2.1, 2.0, 1.9, 1.8, 1.5, 1.4 and 1.3 μ .

RAMSAY (1967) reported $n=11$ (*P. amblyacis*, *P. flavo-limbata*, *P. flexicaulis*) and $n=22$ (*P. amblyacis*) in some Australian



Fig. 1. Gametophytic mitoses. — A: *Leucodon secundus*, $n=9$. — B: *Papillaria fuscescens*, $n=10$. — C: *Claopodium nervosum*, $n=11$. — D, E: *Herpetineuron toccoeae*, $n=11$. — F: *Thuidium tamariscellum*, $n=11$. — G: *Brachythecium buchananii*, $n=11$. — H: *Levierella fabroniacea*, $n=11$. — \times ca 2,450.

species of this genus. Two other genera of the family, viz. *Meteorium* and *Barbella*, have $n=10$ (INOUE 1965 a).

Thuidiaceae

Claopodium nervosum (HARV.) FLEISCH.
— $n=11$ (Fig. 1 C)

Simla (Glen) on soil.

The present count agrees with INOUE's report (1965 b) on the Japanese population of this species. Of the 11 chromo-

somes observed at somatic metaphase, 8 have a median or submedian constriction and 3 have a subterminal constriction. The length of the chromosomes is 4.1, 3.3, 2.9, 2.5, 2.4, 1.8, 1.6, 1.5, 1.1, 1.0 and 0.7 μ .

On the basis of the available data $n=11$ may be regarded as the basic number for this genus.

Herpetineuron toccoeae (SULL. & LESQ.)
CARD. — $n=11$ (Figs. 1 D—E)

Mussoorie (Himalaya Club) on *Quercus dilatata*.

Of the 11 chromosomes observed at somatic metaphase 7 show a median or submedian constriction and 3 a subterminal constriction. In one small chromosome (h) the position of the centromere could not be ascertained. The average length of the chromosomes is 1.9, 1.5, 1.4, 1.3, 1.2, 1.2, 1.1, 0.9, 0.9, 0.8 and 0.6 μ .

INOUE (1965 b) reported the same chromosome number for the Japanese populations of this species.

Thuidium tamariscellum (C. MUELL.)
BOSCH & LAC. — $n=11$ (Fig. 1 F)

Mussoorie (Convent Lane) on rocks.

The present report, $n=11$, confirms an earlier count (CHOPRA & KUMAR 1967) for this species. Of the 11 chromosomes observed at somatic metaphase, 7 have a median or submedian constriction and 3 have a subterminal constriction. In one small (h) chromosome the position of the centromere could not be made out clearly. The length of the chromosomes is 4.5, 4.1, 4.0, 3.8, 3.1, 3.0, 2.6, 2.3, 2.2, 2.1 and 1.6 μ .

The chromosome numbers known in other species of this genus are $n=10$ in *T. bipinnatulum* (as *T. micropteris*, YANO 1957), *T. glaucinum* (SANNOMIYA 1955), *T. kanedae* (SHIMOTOMAI & KOYAMA 1932), *T. uliginosum* and *T. viridiforme* (YANO 1957); $n=11$ in *T. cymbifolium* (INOUE 1965 b; CHOPRA & KUMAR 1967), *T. delicatulum* (ANDERSON & BRYAN 1958), *T. furfurosom* (also $n=22$, RAMSAY 1967),

T. glaucinum (GANGULEE & CHATTERJEE 1960; INOUE 1965 b), *T. minutulum* (AL-AISH & ANDERSON 1960), *T. recognitum* (STEERE 1954), *T. scitum* (ANDERSON & BRYAN 1958), *T. sparsifolium* (CHOPRA & KUMAR 1967), *T. tamariscinum* (SMITH & NEWTON 1968; RAMSAY 1969; WIGH & STRANDHEDE 1971).

It would be desirable to carry out meiotic studies on taxa which show both the chromosome numbers i.e. $n=10$, 11. It is not unlikely that the tiny chromosome may have escaped observation.

Brachytheciaceae

Brachythecium buchananii (HOOK.) JAEG. — $n=11$ (Fig. 1 G)

Mussoorie (Convent Lane) on rocks.

The present count, $n=11$, substantiates our earlier report (CHOPRA & KUMAR 1967) based on meiotic study. Of the 7 chromosomes with a median or submedian constriction, one chromosome is heterochromatic and also possesses a secondary constriction towards the distal end. Three chromosomes have a subterminal constriction. In one chromosome the position of the centromere could not be ascertained. The average length of the chromosomes is 2.4, 2.2, 1.9, 1.6, 1.4, 1.3, 1.2, 1.2, 1.1, 1.0 and 0.7 μ .

This polymorphic species comprises three cytological races with $n=11$, 22 (CHOPRA & KUMAR 1967) and $n=10$ (SANNOMIYA 1955; INOUE 1967). The first two races do not show any significant morphological differences. It would be desirable to compare plants with $n=11$, 22 and $n=10$ in order to know whether or not there is any difference between the Indian and the Japanese material.

Entodontaceae

Levierella fabroniacea C. MUELL. — $n=11$ (Fig. 1 H)

Mussoorie (Himalaya Club) on *Aesculus indica*.

Of the 11 chromosomes counted at somatic metaphase, 7 have a median or submedian constriction and 3 have a subterminal constriction. In one small (h) chromosome the position of the centromere could not be located with certainty. The average length of the chromosomes is 1.7, 1.5, 1.2, 1.2, 1.1, 1.0, 1.0, 0.9, 0.8, 0.7 and 0.6 μ .

CHOPRA and KUMAR (1967) reported $n=21$ for two populations of this species. Those populations may be regarded as hypodiploids based on $n=11$.

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Developmental Anatomy and Germination of Seeds of Anchoté, *Coccinia abyssinica* (W. & A.) Cogn. (Cucurbitaceae)

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ABSTRACT

GETAHOUN, A. 1973. Developmental anatomy and germination of seeds of anchoté, *Coccinia abyssinica* (W. & A.) Cogn. (Cucurbitaceae). — Bot. Notiser 126: 437—449.

Anchoté is a tuberous perennial with annual vines, cultivated in parts of Ethiopia for its edible tubers. The aerial part is typical of many cucurbitaceous plants in having simple tendrils, unisexual flowers and small melon-like fruits.

The mature seed is composed of a seed coat, a large embryo and a pellicle enclosing the embryo. The embryo is straight and has two thick cotyledons containing reserve food, a minute epicotyl and a short hypocotyl-radicle axis. All the characteristic arrangements of the future primary vascular tissues are evident in the procambial tissue. The seed coat has (1) an epidermal layer consisting of the remains of radially elongated cells bearing rod-like lignified thickenings on the radial and tangential walls, (2) a thick-walled parenchymatous region often differentiated into two parts, (3) a distinct layer of sclerenchyma and (4) a region of thin-walled parenchyma with a single vascular bundle. The inner part of the parenchyma often disintegrates or remains with the pellicle and leaves a gap between it and the seed coat. The pellicle is interpreted as the remains of the nucellus and endosperm.

Maximum seed germination occurs in darkness and at temperatures between 20°C and 30°C. The rate of germination is affected by the structure of the seed coat, the pellicle and the maturity of seeds.

INTRODUCTION

Anchoté is a tuberous perennial with annual vines (Fig. 1). The name anchoté is derived from Gallignia, a native language spoken by the Galla tribe in Ethiopia, and refers to the edible tuber of the cultivated races of *Coccinia abyssinica* (W. & A.) COGN. The tubers of wild plants of this species are inedible while the fruits are edible. On the other hand, the fruits of the cultivated anchoté are not eaten.

The aerial portion is a vine which climbs by means of simple tendrils and dies after the fruits have matured. The underground tuber produces new shoots

with the onset of the "small rains" in March and April each year. New shoots are produced from tubers by meristems at their tops that remain green throughout the year. The aerial vine characteristically has three to five strong branches which usually bear either staminate or pistillate flowers. Staminate flowers are in racemes and pistillate flowers are borne singly at the nodes. The reddish-yellow fruits are oval to cylindrical in shape and resemble miniature water-melons averaging 3.8 cm long. They contain an average of about 150 seeds per fruit at maturity. The stem is strongly bent away from the leaf at

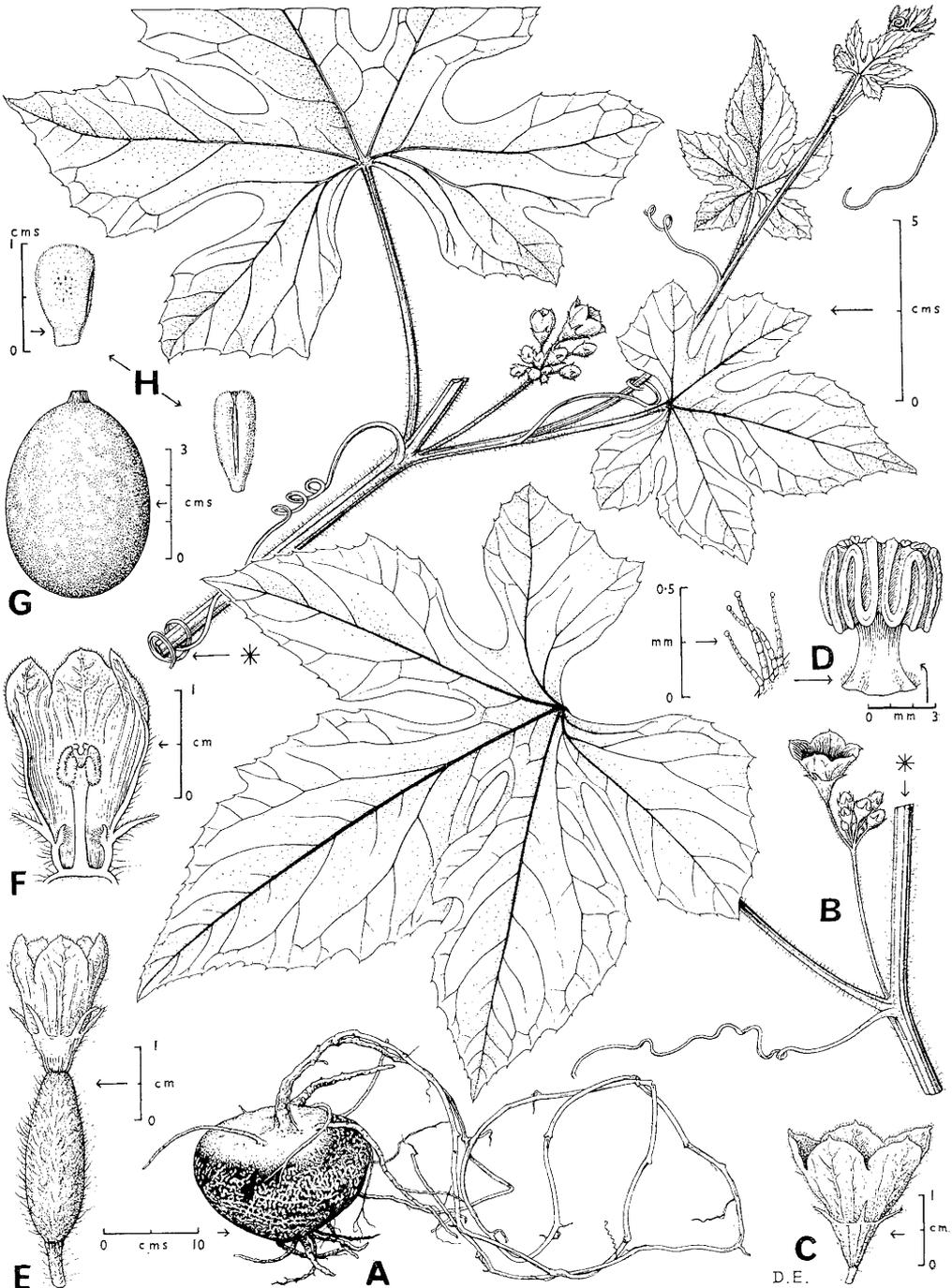


Fig. 1.

each node in a zigzagging pattern. Young stems are angular and become roundish with age. The leaves have broad cordate blades and long petioles. Many mature leaves are five-lobed while some are not.

In Ethiopia, the cultivation of anchoté is sporadic, but widespread in the western and southwestern provinces of Wollega, Kaffa, Sidamo, and Illubabor. Tuberous species of *Colocasia*, *Dioscorea*, and *Musa* are also extensively cultivated. In these provinces, anchoté is cultivated from 1,300 m to 2,800 m elevation where the annual rainfall ranges from 762 mm to 1,016 mm, but it also occurs in more arid regions in its wild state.

REVIEW OF LITERATURE

Development and Structure of Seeds

The development and structure of seeds of several species of Cucurbitaceae have been studied by FICKEL (1876), YASUDA (1901), KIRKWOOD (1905), BARBER (1909), REICHE (1921), CHAKRAVORTI (1947), JOHANSEN (1950), SINGH (1952, 1953), ESAU (1953, 1960), and SINGH (1961, 1964, 1965 a, 1965 b, 1967). Of these, only KIRKWOOD (1905) and CHAKRAVORTI (1947) worked on *Coccinia*.

KIRKWOOD (1905) made a comparative study of the family based on *Coccinia* and 12 other genera. He found that two or three transverse divisions of the zygote resulted in a proembryo formation and a rudimentary suspensor. Subsequent divisions proceeded without regularity and formed a globular pyriform mass from which the embryo broadened distally. The root-cap and dermatogen were differentiated at the same time. The cotyledons were developed during subsequent growth and the epicotyl was organized very late. The entire endosperm was consumed by the developing embryo but a considerable amount of perisperm was present in the mature seed (CHAKRAVORTI 1947).

CHAKRAVORTI (1947) studied the development of the female gametophyte and seed of *Coccinia*. He reported that three distinct zones were formed from the outer integument which gave rise to the seed coat. The innermost zone consisted of a single layer of

cells that were radially elongated with scanty cytoplasm and thin walls. The middle zone was characterized by variable numbers of cell layers in different regions of the ovule. The outermost zone was characterized by radially elongated cells with thin walls and scanty cytoplasm similar to cells of the innermost zone but the cells were much larger. He stated that the seed was enclosed by an additional covering composed of four distinct types of cells derived from the carpellary tissue. This coat was not connected with the ovule except at the funiculus. A similar structure was reported for other cucurbitaceous plants by HOHNEL (YASUDA 1901) but he considered the first of the ten layers of cells of the seed coat of cucurbitaceous plants to arise from the epidermis of the carpel. CHAKRAVORTI (1947) did not mention the presence or absence of a "pellicle", a papery tissue between the seed coat and the embryo, although this structure has been reported in other cucurbitaceous plants (FICKEL 1876, YASUDA 1901, BROWN 1940, 1941, 1942, SCHLISING 1969, ESAU 1960). They reported that a pellicle completely enveloped the embryo. ESAU (1960) considered it to be composed of the inner epidermis of the seed coat and two to three layers of nucellar tissue while the others considered it to be the remains of endosperm and nucellar tissue.

SINGH (1952, 1953) and SINGH (1961, 1964, 1965 a, 1965 b, 1967) made comparative studies on the development and structure of seeds of many cucurbitaceous plants and concluded that mature seeds differed in shape, size, colour and texture, but they had certain common anatomical features which could be designated as characteristic of the family. Individual characters of seeds in a given species remained so constant under varying environmental conditions that several workers have used external characters of seeds for the delineation of species in the family (RUSSELL 1931, SINGH & BHANDARI 1963, SINGH 1964, 1967).

Germination

No work on germination in species of *Coccinia* has been found. BROWN (1940, 1941, 1942) studied the growth and gaseous exchange of seeds of *Cucurbita pepo* and concluded the pellicle had a profound effect on the rate of germination by influencing the rate of gaseous exchange of the seed. MAYER

Fig. 1. *Coccinia abyssinica*. — A: Mature tuber with old branches. — B: Branches with leaves, tendrils and inflorescences. — C: Staminate flower. — D: Androecium of staminate flower. — E: Pistillate flower. — F: Pistillate flower longitudinally sectioned. — G: Fruit. — H: Seed, face- and side-views.

and POLJAKOFF (1963) reported that the pellicle was more permeable to carbon dioxide than to oxygen. They thought this condition ensured the extension of germination over a period of time.

HILL (1916) stated that typical germination was epigeal in cucurbitaceous plants. WHITING (1938), working on *Cucurbita*, reported that the root protruded between the halves of the seed coat and that the peg made its first appearance as a small lateral ridge at the end of 48 hours of germination. He indicated that the cotyledons were pulled from the seed coats as the hypocotyl elongated and that the curved portion of the hypocotyl with the expanding cotyledons broke through the ground in one week. Similar results were also reported by HOLROYD (1924), HUFFORD (1938), and HAYWARD (1938).

HILL (1916) and SCHLISING (1969) on *Marah* spp., SINGH (1965 b) on *Sechium edule* and YASUDA (1901) on *Trichosanthes* and *Gymnostemma* reported hypogeal germination in these species as an exception in the family. In *Sechium edule*, primordia for roots were organized in the seed, seeds germinated within the fruits, and the cotyledons remained inside the seed and fruit. In the genus *Marah*, instead of a radicle emerging first from the seed at germination, the minute radicle and epicotyl were pushed down into the soil by the elongating fused bases of the cotyledons which formed a hollow tube containing the embryonic axis at its base. The blades of the cotyledons were left in the seed and the plumule broke through the tube when the root was well developed.

MATERIAL AND METHODS

Seeds and fruits were obtained from plants grown at Debre-Zeit (Shoa) and Alemaya (Harar) Agricultural Experiment Stations, Ethiopia from seeds collected in the province of Wollega. Plants were grown in pots and flats in greenhouses at the University of Florida, Gainesville, Florida, but none could be made to set seed.

Craf II and III were employed as fixatives for leaves, cotyledons, and seedling stages. Seeds were fixed in FAA. Other fixatives were used but with less success. Samples were dehydrated by the tertiary butyl alcohol (TBA) method, infiltrated, and embedded in "Tissumat" (SASS 1951).

Sections were cut at five, eight, ten, twelve or fifteen μ , depending on the organ, its stage of development or the tissue being investigated.

Three staining techniques were employed: tannic acid, iron chloride, and safranin (FOSTER 1934); safranin and fast green (JO-

HANSEN 1940); and iron haematoxylin counterstained with safranin and fast green. Temporary sections treated with phloroglucinol, Sudan III, or IKI were used to supplement the permanent slide preparations.

Drawings were mostly made from cleared material. Kodak Panatomic-X film was used for the photomicrography.

OBSERVATIONS

Seeds

Seeds of anchoté developed from typical anatropous ovules which occurred in six placental areas that were located in the manner that is well known in several genera of the family. During the time the embryo-sac was developing, an ovule consisted of a very large nucellus which was narrowed gradually to the micropyle, an inner integument about three cells thick, and a much thicker outer integument (Fig. 2 B). Integuments were distinct for about half the length of the ovule on the side opposite the funiculus and the outer one was much thicker on this side of the micropyle.

Stages of reproduction that occurred in the nucellus were not included in this study, but it was evident that the nucellus was still massive at the time the embryo was beginning to grow and that the endosperm was not large.

Growth and differentiation during the development of the seeds was most apparent in the outer integument which produced essentially all tissues of the seed coats, and in the embryo which used up endosperm almost as fast as it destroyed nucellar tissues (Fig. 2 A). This resulted in each mature seed being composed of (1) a seed coat, (2) a large embryo, and (3) a membrane-like structure consisting of a few layers of cells closely adhering to the embryo but separated from the seed coat.

Seeds were about 9 mm long, 4 mm wide and 2 mm thick and about 26 weighed 1 gram when air dried. Their surfaces were greyish-white on their flat sides and brown on their rims. About 25

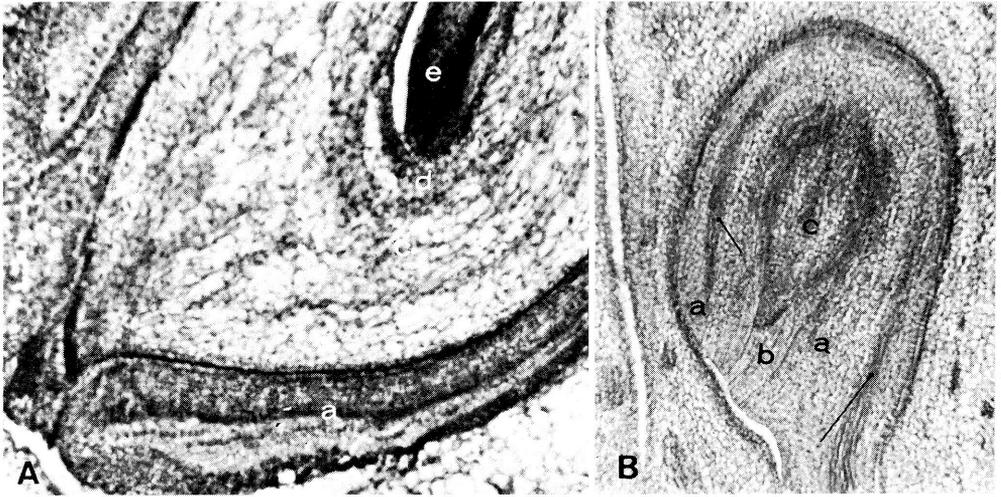


Fig. 2. A: Longitudinal section of an ovule after fertilization showing differentiation of the outer integument and disappearance of the inner integument. A proembryo and endosperm are evident. $\times 370$. — a, differentiating outer integument; c, nucellus; d, endosperm; e, proembryo. — B: Longitudinal section of an ovule before fertilization from transverse section of immature fruit showing a flask-shaped nucellus and the two integuments. $\times 370$. — a, outer integument; b, inner integument; c, nucellus. Arrows show procambial strands.

ridges and grooves were barely visible lengthwise. The seeds and the surfaces were soft to the touch. The hilum, micropyle and raphe were not easily observed.

Structure of the Mature Seed

THE SEED COAT. The seed coat was composed of the following regions: (1) epidermal layer, (2) thick-walled parenchyma, (3) sclerenchyma of macrosclereids, and (4) thin-walled parenchyma (Figs. 3, 4).

The outermost walls of the epidermal cells in the mature seed had disintegrated and only the inner walls with their lignified thickenings remained as slender rods about 500μ long. These lignified projections of radial and tangential walls remained unbranched for most of their length, but were branched once or more towards their tips. These thickenings had wall markings which appeared as deposits that tapered rapidly from broad bases. In

dry seeds, these rod-like thickenings formed the most external structure of the seed coat and served as distinct features (Fig. 4 B). Investigation of young seeds showed columnar, nucleated and thin-walled cells forming the outermost layer of the seed coat.

The second region of the seed coat was composed of thick-walled parenchymatous cells of many sizes. Cells in the centre were the largest, while outer and inner layers of cells were smaller (Fig. 4 B). Larger ridges were $230\text{--}250 \mu$ wide and 11 to 12 cell layers thick, and smaller ridges were about 80μ wide and only 6 cells thick (Fig. 4 A). Ridges were due to cells being numerous and large while grooves occurred where cells of this zone were few and smaller. The grooves were only 3 to 4 cells deep. The innermost cells of this region had thicker walls. Cells in the centre of this region had many small intercellular spaces and extensive pitting on their radial and tangential walls.

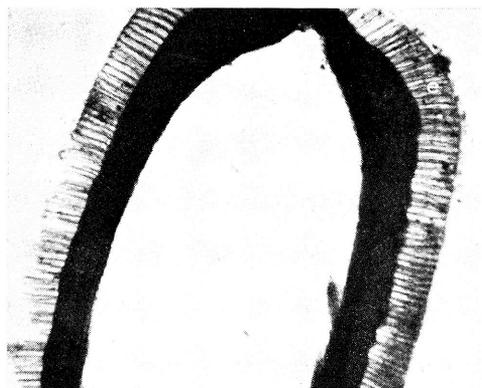


Fig. 3. Free-hand transverse section of immature seedcoat showing the columnar, nucleated outer epidermis (e) of the outer integument. $\times 270$.

The inner portion of this region stained intensely, lacked intercellular spaces, and cells were fibre-like in shape but their walls were unpitted. The characteristic ribbing of seeds was due to variability of cell layers making up this region. Those at the rim of the seed were large and ridges became progressively smaller towards the sides of the seed (Fig. 4 A). Thus the seed coat was considerably thinner on the sides of the seed.

The sclerenchyma, the third region of the seed coat, was composed of a single layer of uniform macrosclereids. The thick-walled cells were slightly elongated in transverse section and were palisade-like in shape. Cell lumina, when present, were very small. Mechanical rigidity of the seed coat was afforded by this highly lignified layer and region two. The layer of macrosclereids was absent in the micro-pylar region of the seed coat.

The innermost region of the seed coat, region four, was composed of loosely arranged parenchymatous cells of large size and of compact small cells and was on the inside of the macrosclereid layer. Cells lying next to the macrosclereid layer had thick walls and were pitted. This region comprised 15 to 20 cell layers, the innermost ones often being ruptured.

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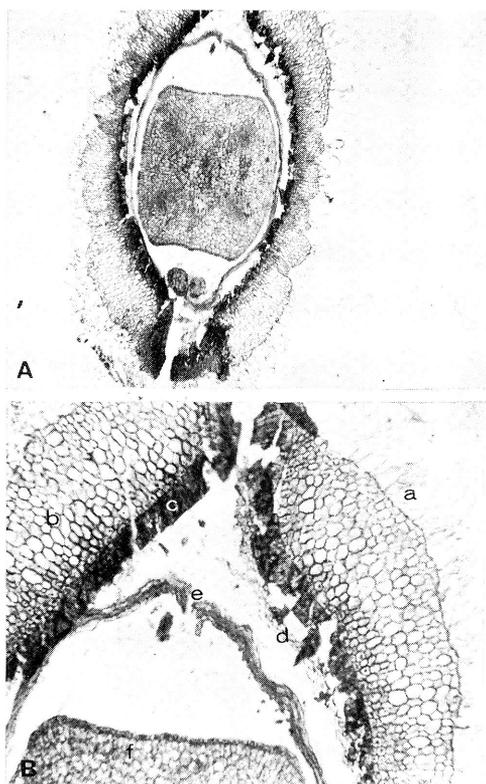


Fig. 4. Transverse section of a dormant seed through the node of the embryo. — A: Entire seed. $\times 110$. — B: Detail of part of the seed. $\times 270$. — a, epidermal thickenings; b, thickened parenchyma zone; c, sclerenchyma layer (macrosclereids); d, parenchyma zone; e, pellicle; f, embryo.

A single layer of compact parenchyma cells often appeared to remain intact and accompanied the "pellicle". In this region a single unbranched vascular strand of three or four tracheary elements in diameter extended from the hilum to the chalazal area and partway along the opposite edge of the seed.

PELLICLE. Mature embryos were enclosed by a thin, translucent membrane formed by three to five tangentially elongated, collapsed cells (Fig. 4 B). This membrane remained with the embryo and was detachable only after being softened

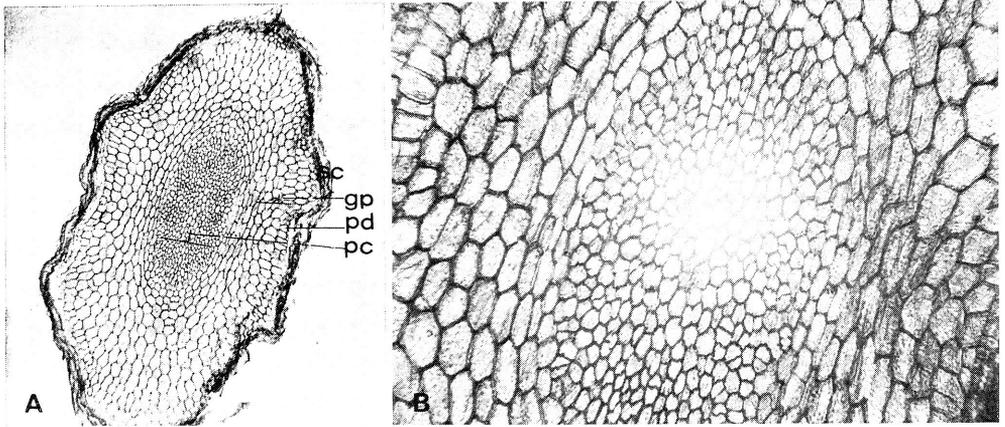


Fig. 5. Transverse section of a dormant seed at the junction of hypocotyl-embryonic root (transition) zone. — A: Entire embryo with seedcoat. $\times 130$. — B: Detail of embryo. $\times 1,200$.
 gp, ground parenchyma; pc, procambium; pd, protoderm; sc, seedcoat.

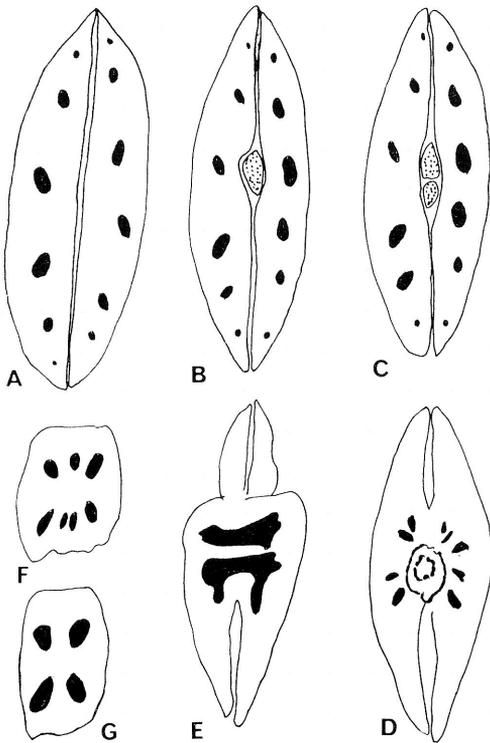


Fig. 6. Diagrams of sequence of transverse sections of a soaked embryo showing vasculature. Dark area, procambium; dotted

by imbibed water. Transverse sections of dry seeds revealed an area devoid of tissue between the seed coat and pellicle. The gap was formed largely by the collapse of much of the parenchymatous region of the seed coat. The origin and development of the pellicle was not studied in detail. It was observed that the inner integument did not contribute to its formation. It was probably composed of remains of the nucellus and endosperm and often included parenchymatous cells from the seed coat.

EMBRYO. Each embryo was straight and composed of two cotyledons that were thick and flat, a short hypocotyl-radicle axis and a minute epicotyl (Figs. 5, 6). In a few instances the remains of the suspensor were discernible in whole mounts of embryos. Embryos measured 7 mm long, 3 mm wide and 1 mm thick.

areas, epicotyl including leaf primordium. — A: Cotyledons above epicotyl. — B: At the level of primordium of leaf and epicotyl. — C: Cotyledons at the epicotyl with the primordium of the first leaf. — D: At the base of cotyledons. — E: At the cotyledonary node. — F: Upper hypocotyl. — G: Lower hypocotyl. $\times 18$.

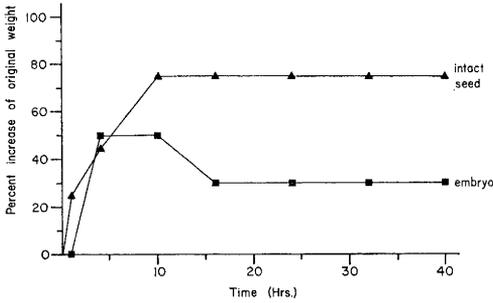


Fig. 7. Imbibition of tap water by intact seeds and excised embryos at room temperature under light.

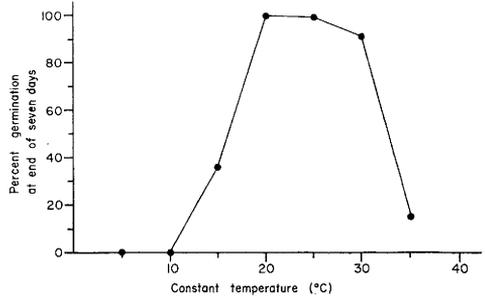


Fig. 8. Germination temperatures of anchoté under darkness.

Fifty-two embryos weighed 1 gram. The hypocotyl-radicle axis was only 1 to 1.5 mm long and the epicotyl was even smaller in size. Thus, cotyledons were 6/7 the total length and accounted for as much as 85 per cent of the embryo volume.

The radicle was a short and conical apex on a short hypocotyl, but its structure was not studied in detail. The only features showing differentiation were a procambial core, an apical meristem and a root cap (Fig. 5).

The hypocotyl of a dormant embryo was usually 0.1 mm long and characteristically oval in transverse section. This outline was not produced by large numbers of cells at the ends of the oval but rather by the large radial dimensions of cells. The ground meristem outside the procambial strands was composed of seven to eight layers of thin-walled cells. Six procambial strands arranged in two groups of three each in the upper end of the hypocotyl and four procambial strands towards the lower end of the hypocotyl were distinct (Fig. 6 F, G). Four procambial strands at the lower end of the hypocotyl were also arranged in two groups, each oriented towards ends of the oval. These four merged downward into a cylinder of procambium around a central ground meristem in the area which later developed the transition. As the diameter

of the hypocotyl decreased downwards, the central ground meristem decreased and was replaced by the procambium of the radicle.

The large thick cotyledons were ob lanceolate with prominent main veins (Fig. 6 A—C). The mesophyll was differentiated into two sharply defined palisade layers and a multilayered region of compact starchy cells. The protoderm was composed of small closely packed cells in a single layer which appeared to have a cuticle. All cells including the protoderm and procambial cells were filled with stored material, mostly starch.

The epicotyledonary meristem had a uniseriate tunica and a massive corpus. There were no leaf primordia. The vasculature of the cotyledonary node showed solid procambial areas which appeared as two plates with procambial extensions into cotyledons.

Germination

Seeds of anchoté had a very low water content and imbibed water quickly. Intact seeds increased in weight by 25, 44.5 and 75 per cent after soaking for 1, 2, and 4 hours respectively (Fig. 7). Excised embryos did not imbibe water until after soaking for 2 hours but they had increased their original weight by 50 per cent at the end of 4 hours (Fig. 7). There

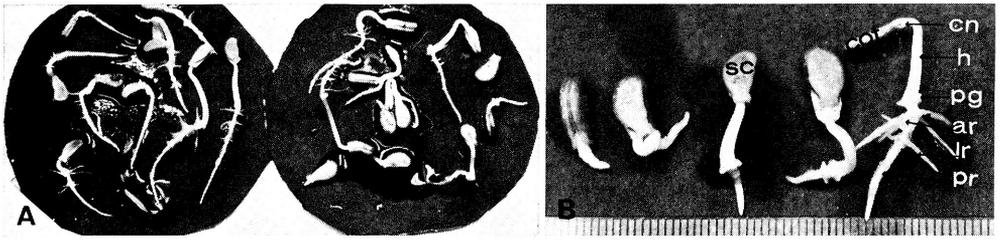


Fig. 9. A: Seven-day-old seedlings grown in darkness (left) and light (right) at room temperature. Note that some seeds under light have barely germinated while in others well-developed hypocotyls and primary roots have developed. The rate of germination in light is slower and less uniform than in darkness. $\times 0.65$. — B: Seven-day-old seedlings germinated in darkness at 20°C showing the variation in the rate of germination of seeds, and in parts of seedlings, ca. $\times 0.8$. — ar, adventitious root; cot, cotyledons; cn, cotyledonary nodes; h, hypocotyl; lr, lateral root; pg, peg; pr, primary root; sc, seedcoat.

was no further weight increase by intact seeds beyond 75 per cent. Excised embryos, on the other hand, showed a slight decrease of imbibed water with time, so that at the end of 40 hours' soaking they had retained only 30 per cent of their original weight increase (Fig. 7).

Protein bodies in cells of the embryo swelled during germination. These protein bodies gradually disintegrated into fragments and disappeared as they were digested. The degree of degradation of protein bodies and of starch grains was related to the distance from the nearest procambial strand. The embryonic root apex had a conspicuous accumulation of starch.

Seed viability remained high at the end of four years' storage at room temperature. Germination percentage was almost 100 per cent, yet older seeds showed a considerable increase in the time required for germination. Four-year-old seeds required about 16 days under greenhouse conditions while seeds less than a year old germinated in less than 4 days.

Figure 8 shows germination temperatures of anchoté in darkness. No germination occurred at temperatures between 5°C and 10°C . Percentage of germination increased between 15°C and 30°C then dropped rapidly above 30°C . Direct thermal damage to hypocotyls and pri-

mary roots occurred at 35°C , because they turned brown before young seedlings died. Hypocotyls were more sensitive to temperature than were primary roots. The optimum temperature range was from 20°C to 30°C since germination was nearly 100 per cent within this range. The rate of germination was higher near and at 30°C , where the elongation of both the primary root and the hypocotyl was the highest. The hypocotyl elongated 0.8 mm, 1.3 mm and 3.0 mm, and the primary root 3.0 mm, 3.2 mm and 3.7 mm at the end of 6 days' germination at 20°C , 25°C and 30°C , respectively, with adequate moisture and aeration. The rate of elongation of the primary root as compared to that of the hypocotyl was much higher at lower temperature.

Seeds germinated better in the dark than in the light. After 76 hours at room temperature only 65 per cent of the seeds had germinated in the light compared to 80 per cent in the dark. After 5 days the percentages were 65 and 100 respectively. Initial embryo growth was greater in the dark than in the light but this difference became less at the end of seven days (Fig. 9 A).

The radicle emerged from the seed coat in less than 48 hours at 30°C . Its emergence through the micropyle was the first external evidence of germination. It show-

Table 1. Effects of seed position in the soil on the rate of germination, hypocotyl and peg development and root system at the end of 19 days. Hypocotyl length at the end of 10 days is given in brackets.

Seed position	Hypocotyl			Peg	Root system	Rate of germination
	Length (cm)	Thickness	Shape			
Horizontal	3 (1.0)	normal	curved	large shield	main root weakly leading, profusely branched	2
Vertical with micropylar end upwards	0.5 (0.5)	thick	vertical	not apparent	much-branched	3
Vertical with micropylar end downwards	3.7 (0.8)	normal	vertical	ring	main root leading	1

ed immediate geotropism after protruding between halves of the seed coat. The primary root continued to elongate rapidly prior to the growth of other embryo parts and was 1 mm long at the end of 72 hours. The hypocotyl increased in diameter before elongating, in part due to the peg being formed at the top of the root and, concurrently, the cotyledons expanded. These changes caused the seed coat to split for half the length of the seed (Fig. 9 B). The hypocotyl soon underwent a limited amount of elongation and immediately bent sharply at the base of the cotyledons that were still lying within the halves of the seed coat (Fig. 9 B). Splitting of the seed coat did not proceed beyond this point despite the continued expansion of the cotyledons and the presence of the hypocotyl arch. Instead, this opposing pull of the rapidly elongating hypocotyl arch against the peg pulled the cotyledons out of the hard seed coat. The seed coat remained in the soil, capping the peg. The freed cotyledons and plumule emerged from the soil after six days by growth of the hypocotyl as the arch was forced upwards through the soil. When seeds were planted with the micropylar ends downward, seed coats were raised above ground capping the cotyledons causing the latter to remain pressed together, with the hypocotyl axis remaining short and stubby (Table 1).

The hypocotyls were also short when the seeds were planted shallowly.

The cotyledons which had turned green early in the germination period expanded and assumed a horizontal position after the cotyledons and plumules had emerged from the ground. Both the cotyledons and the aerial parts of the hypocotyl continued to develop chlorophyll. More than 50 per cent of the hypocotyl elongation above the peg was from the upper hypocotyl and that of the lower hypocotyl was negligible. Epicotyls had produced three leaf primordia six days after germination but the axis had not elongated.

DISCUSSION

Seeds

The early development of anchoté seeds is similar to that reported by CHAKRAVORTI (1947) for *Coccinia indica*. The formation of the embryo agrees with the description given for *Coccinia* (KIRKWOOD 1905) and *Cucumis* (SINGH 1953). The development of the seed coat is similar to reports given for other species in the family (SINGH 1952, 1953; SINGH 1961, 1964, 1965 a, 1965 b, 1967). However, it differs from that observed by CHAKRAVORTI (1947) in *Coccinia indica* in which "three concentric zones differentiate from the outermost layer of the outer integument." His

diagrammatic representation of the structure of the mature seed in longitudinal section shows three concentric zones, designated A, B, C, and an undescribed fourth layer. While a similar number of layers occurs in anchoté seeds, the description of the "zones" given by him is not true of the layers of the seed coat of anchoté. Only the middle layer, "zone C", morphologically approximates the thick-walled parenchymatous region of anchoté. CHAKRAVORTI described another covering layer derived from carpellary tissue and also characterized by four concentric zones. No such additional carpellary covering exists in anchoté seeds. Instead, the surface layer consists of the lignified remains of radially elongated cells of the epidermis of the outer integument. Carpellary tissue around the seed does not adhere to the seed surface in anchoté.

The thin papery membrane between the seed coat and the embryo was not mentioned by CHAKRAVORTI (1947). KIRKWOOD (1905) studied the embryology in the family and reported it for *Coccinia*. It has been seen in the seeds of many other genera of the family. BROWN (1940, 1941, 1942) studied the role of the membrane in the germination of seeds of *Cucurbita pepo* and used the term "pellicle". This term has been applied to the identical structure observed in the seeds of anchoté. The function of the pellicle in the germination of anchoté seeds is discussed below.

Germination

Intact seeds increase by 75 per cent of their original weight by imbibition during the initial phase of germination. Much of this increase is due to the hygroscopic nature of the epidermal thickenings of the seed coat and to absorption by the cotyledons. Most imbibed water absorbed by the embryo seems to have diffused through the micropyle and the immediate parenchymatous region of the seed coat because

the cotyledons are still dry when the hypocotyl-radicle has imbibed water. The parenchymatous nature of the micropylar region of the seed coats also probably aids the rapid protrusion of radicles during germination.

Excised embryos are enveloped by pellicles which remain intact. The delay in imbibition by as much as two hours is attributed to this membrane for, when it is punctured or removed, excised embryos readily imbibe water. The cuticle on the epidermis of the cotyledons also may affect absorption by them.

Until the pellicle and the seed coat are broken during the later stages of germination, the embryo is surrounded by an air-jacket. The presence of this air-jacket necessitates an exchange between the embryo and the air-gap through the pellicle and between the air-gap and the germinating medium through the seed coat. Structural features of the seed coat indicate that its restriction to gaseous exchange must be much greater than that of the pellicle. Thus if gaseous exchange between the germinating medium and the air-gap depended solely on diffusion, the seed coat could determine the rate of the entire process. The continuity of the seed coat is interrupted by the micropyle. The tissue of the seed coat surrounding the micropyle is parenchymatous. The pellicle completely envelops the embryo. Although the permeability of the seed coat may be less than that of the pellicle, it cannot control the gaseous exchange so long as the micropylar end remains open. Exchange between the air-gap and the atmosphere probably takes place through the micropyle. The pellicle seems to be the controlling factor in gas and water exchange between the embryo and its environment.

Different rates of germination within a given sample of seeds may be correlated with differences in stages of seed development within the same fruit. While retaining a relatively high percentage of germination, seeds are uniformly slower

in germinating after prolonged storage. This may be due to the accumulation of gases such as carbon dioxide which may increase the pressure in the air-gap. Movement of oxygen and water through the micropyle may be reduced as a result of that pressure.

The effect of temperature on germination may be a direct effect on chemical processes and on the diffusion of gases. Temperature and availability of water may influence carbohydrate digestion and rate of respiration. Temperatures of 20°C and lower retard germination. At temperatures of 25°C to 30°C, water is a limiting factor in germination.

The fact that the initial rate of germination is higher in the dark than in the light may result from the effect of light on the mobilization of stored foods.

Germination of seeds and rates of growth of anchoté seedlings are identical with those in *Cucurbita* (WHITING 1938) and *Citrullus* (HUFFORD 1938).

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Karyologische Untersuchungen in der Gattung *Echium* L.

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ABSTRACT

FRITSCH, B. 1973. Karyologische Untersuchungen in der Gattung *Echium* L. — Bot. Notiser 126: 450—458.

Chromosome numbers have been determined for 12 species of the genus *Echium* L. For 3 species idiograms are presented, and for 4 species the morphology of chromosomes is described. *E. russicum* GMEL. has $n=6$, very large chromosomes and stands isolated within the genus. *E. italicum* L. has $n=8$, including a large satellite chromosome. *E. wildpretii* PEARS. represents a third type with $n=8$ and chromosomes of normal size. Chromosome numbers and morphology give reason to establish 4 groups, which might be referred to three distinct ways of evolution. The problematic existence of diploid plants in *E. vulgare* L. is briefly discussed. A list of all hitherto known chromosome numbers within the genus is given.

EINLEITUNG

Die Gattung *Echium* ist ein umfangreicher und sehr variabler Verwandtschaftskreis. Sie umfaßt Sträucher, Stauden, Biennen und Annuellen, die in Macaronesien, im Mittelmeergebiet, in West-, Mittel- und Osteuropa sowie in Westasien vorkommen. Bis jetzt wurden etwa 200 Arten beschrieben, von denen nach den Untersuchungen von KLOTZ (1959) aber nur ca. 50 anerkannt werden können. Die nomenklatorischen Verhältnisse in der Gattung sind deshalb sehr schwierig. Die vorliegende Arbeit schließt sich aus diesem Grunde bis auf wenige Ausnahmen den Auffassungen von KLOTZ an.

Die erste infragenerische Gliederung nahm DE CANDOLLE (1846) vor. Er unterscheidet krautige und sträuchige Arten und bewertet auch die Dichte der Synfloreszenz. KOCH (1849) trennt nach der Beschaffenheit des Griffels die Sektionen *Holostigma* (mit dem Typ *E. russicum* GMEL., monotypisch) und *Schizostigma* (mit dem Typ *E. italicum* L., alle übrigen

Arten). DE COINCY (1900, 1903) stützt sich bei seiner Einteilung auf die Beschaffenheit des Anulus. Er stellt die drei Sektionen *Eleutherolepis*, *Gamolepis* und *Pachylepis* auf. Diese Einteilung wurde von fast allen späteren Autoren übernommen. Die neueste Gliederung der gesamten Gattung ist von KLOTZ (1959) vorgenommen worden. Auf der Grundlage der Gesamtähnlichkeit der Pflanzen unterscheidet er 10 Sektionen. BRAMWELL (1972) untersuchte die macaronesischen Arten und gliedert diese Gruppe in 8 Sektionen. Sowohl KLOTZ als auch BRAMWELL weisen darauf hin, daß die Gliederung DE COINCYS nicht die natürliche Verwandtschaft widerspiegelt.

Die ersten Chromosomenzahlen von *Echium* stellte STREY (1931) fest. Er untersuchte 6 Arten. LITARDIÈRE (1943) veröffentlichte die bisher umfangreichste Liste von Chromosomenzahlen in dieser Gattung. Er führte die untersuchten Arten dem System von DE COINCY entsprechend auf. Am Ende seiner Arbeit bildete er auf der Grundlage der Chromosomenzahlen

vier Gruppen, die die von ihm angenommenen Ploidiegrade repräsentieren. Eine weitere größere zytologische Arbeit legte BRITTON (1951) vor. In den letzten zwei Jahrzehnten wurden von vielen weiteren *Echium*-Sippen die Chromosomenzahlen festgestellt. Bisher hat aber nur ARARATJAN (1948) den Karyotyp einer Art (*E. russicum* GMEL.) beschrieben.

Als Grundzahl innerhalb der Gattung wird $x=8$ angenommen (STREY 1931, BRITTON 1951) bzw. $x=4$, auf welche LITARDIÈRE (1943) seine Polyploidreihen aufbaut. Dadurch kann er ohne Schwierigkeiten *E. russicum* ($2n=24$) als hexaploide Stufe einbeziehen. Da bei dieser Art aber auch $2n=12$ Chromosomen gezählt wurden, kann man sie auch nicht als triploid auf der Basis $x=8$ (KLOTZ 1960) ansehen. In der vorliegenden Arbeit soll deshalb versucht werden, den Aussagewert von Zahl und Morphologie der Chromosomen für die taxonomische Gliederung der gesamten Gattung darzulegen, und insbesondere die Chromosomenverhältnisse bei *E. russicum* zu klären.

MATERIAL UND METHODE

Im Botanischen Garten Jena standen mir 7 Arten zur Verfügung. *E. vulgare*, *E. russicum* und *E. gaditanum* waren im Freiland ausgepflanzt, *E. pininana*, *E. aculeatum*, *E. wildpretii* und *E. candicans* wurden als Topfpflanzen im Kalt haus gehalten. Im Samenaustausch mit anderen Botanischen Gärten konnten die übrigen untersuchten Arten erworben werden. Von *E. vulgare* konnte ich an verschiedenen Orten Samen von Wildmaterial sammeln.

Von allen Arten wurden ausschließlich Wurzelspitzen untersucht, die entweder den Topfballen oder an Keimlingen entnommen wurden. Eine zweistündige Vorbehandlung des Materials mit einer gesättigten wäßrigen Lösung von Paradichlorbenzol bei Zimmertemperatur erwies sich als notwendig, um die Insertionen an den Chromosomen sichtbar zu machen. Nach der ein- bis zweistündigen Fixierung in Alkohol/Eisessig 3:1 bei Zimmertemperatur wurden die Wurzelspitzen mit $n\text{-HCl}$ hydrolysiert, entweder 10 min lang bei 60°C oder 12 min lang bei Zimmertemperatur, mehrmals mit Wasser gespült und in Eisen-Karmin-Essigsäure überführt. Nach mindestens 24 Std. waren die

Chromosomen gefärbt und das Material konnte nach der Quetschmethode verarbeitet werden. Die Untersuchungen erfolgten mit einem Mikroskop Zeiss Lg OB (Objektiv Zeiss HI 90, Okulare Zeiss $12,5\times$ bzw. $15\times$). Die Längenmessung der Chromosomen wurde mit dem Zeiss Schrauben-Messokular ausgeführt, die Zeichnungen mit Hilfe eines Abbe'schen Zeichenapparates.

ERGEBNISSE

Von *E. russicum*, *E. wildpretii* und *E. italicum* lag so viel Material vor, daß ich Idiogramme aufstellen konnte (Abb. 1). Von weiteren 9 Arten ermittelte ich die Chromosomenzahlen (Abb. 2).

Echium russicum GMEL. — $2n=12$ (Abb. 1 A)

Die Chromosomen sind bei dieser Art bedeutend größer als bei allen anderen Arten. Sie lassen sich nach ihrer Form gut ansprechen und unterscheiden sich in den Schenkelverhältnissen klar voneinander. Die von ARARATJAN beschriebene Morphologie konnte ich im Prinzip bestätigen. Somit unterscheidet sich *E. russicum* sowohl durch die Grundzahl $x=6$ als auch in der Größe der Chromosomen von allen untersuchten Arten sehr eindrucksvoll. Es ähnelt in diesen Merkmalen keiner anderen, bisher untersuchten Art.

Echium wildpretii PEARS. ex HOOK. FIL. — $2n=16$ (Abb. 1 B)

Der diploide Chromosomensatz besteht aus 8 verschiedenen Paaren, die sich zum Teil deutlich in Form und Länge unterscheiden. Bei den SAT-Chromosomen befinden sich die Satelliten auffallenderweise am langen Schenkel der Chromosomen. 2 Chromosomenpaare sind isobrachial, 4 Paare heterobrachial inseriert; bei 2 Paaren war keine Insertion erkennbar.

Echium italicum L. — $2n=16$ (Abb. 1 C)

Im Chromosomensatz dieser Art fällt ein Paar besonders großer Chromosomen

Tabelle 1. Chromosomenzahlen der untersuchten Arten.

Art	2n	Herkunft des Materials
<i>E. aculeatum</i> POIR.	16	Bot. Garten Orotava
<i>E. candicans</i> L. FIL.	16	Bot. Garten Jena
<i>E. hoffmannseggii</i> LIT.	16 (32)	Bot. Garten Coimbra (Wildmaterial)
<i>E. gaditanum</i> BOISS.	32	Bot. Garten Coimbra (Wildmaterial)
<i>E. italicum</i> L.	16	Bot. Garten Budapest (Wildmaterial)
<i>E. lycopsis</i> GRUFB.	16	Bot. Garten Coimbra (Wildmaterial)
<i>E. pininana</i> WEBB & BERTH.	16	Bot. Garten Coimbra (Wildmaterial); Bot. Garten Orotava
<i>E. russicum</i> GMEL.	12	Bot. Garten Uppsala
	12 (24)	Bot. Garten Szeged
<i>E. spinescens</i> MED.	16	Bot. Garten Uppsala
<i>E. thyrsoiflorum</i> MASSON ex LINK in BUCH	16	Bot. Garten Oslo (Wildmaterial); Bot. Garten Barcelona
<i>E. vulgare</i> L.	32	Bot. Garten Uppsala; Wildmaterial Jena, Bad Langensalza, Cottbus, Gatersleben, Rumänien
<i>E. wildpretii</i> PEARS. ex HOOK. FIL.	16	Bot. Garten Orotava

auf, die auch einen Satelliten tragen. Die Länge dieser Chromosomen übertrifft die der anderen bei weitem. Auch bei *E. italicum* sind 2 Chromosomenpaare isobrachial und 4 Paare heterobrachial inseriert, während die restlichen 2 Paare keine Insertionen zeigen. Außer dem bereits beschriebenen Paar tragen auch die Chromosomen eines der kleinen heterobrachialen Paare Satelliten.

***Echium candicans* L. FIL. — 2n=16**

(Abb. 2 H)

Die Chromosomen dieser Art unterscheiden sich auf den ersten Blick kaum von denen der folgenden Arten; sie sind klein (1,4 µm bis 2,3 µm lang) und zeigen keine krassen Größenunterschiede. Bei genauerer Untersuchung erkennt man 4 Satellitenchromosomen, von denen 2 besonders große Satelliten tragen, die oft wie die kurzen Schenkel von heterobrachialen Chromosomen wirken.

***Echium thyrsoiflorum* MASS. — 2n=16**

(Abb. 2 E)

Auch bei dieser Art sind die besonders großen Satelliten des einen Paares be-

merkenswert. Wir finden hier ebenfalls wieder 2 isobrachiale Chromosomenpaare. Die übrigen 5 Paare und das Paar SAT-Chromosomen sind heterobrachial inseriert. Die Länge der Chromosomen schwankt zwischen 1,9 µm und 2,7 µm.

***Echium lycopsis* GRUFB. — 2n=16**

(Abb. 2 A)

Durch 1 Chromosomenpaar mit Satelliten, 2 Paar isobrachiale und 5 Paar heterobrachiale Chromosomen, die allesamt zwischen 1,4 µm und 1,8 µm lang sind, wird diese Art charakterisiert.

***Echium vulgare* L. — 2n=32 (Abb. 2 D)**

Die von mir untersuchten Pflanzen sind tetraploid und enthalten im Chromosomensatz 4 Paar isobrachiale, 10 Paar heterobrachiale und 2 Paar SAT-Chromosomen. Die Satelliten sind nicht immer alle gleichzeitig sichtbar. Die Chromosomen sind ebenfalls sehr klein (1,5 µm bis 2,5 µm lang).

Echium aculeatum L. FIL. — $2n=16$
(Abb. 2 F)

E. hoffmannseggii LIT. — $2n=16(32)$
(Abb. 2 B, C)

E. pininana WEBB — $2n=16$

E. gaditanum BOISS. — $2n=32$ (Abb. 2 G)

E. spinescens MED. — $2n=16$

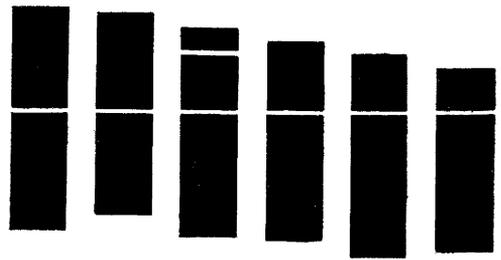
Von diesen Arten lag wenig Material vor. Deshalb konnten nur die Chromosomenzahlen bestimmt werden.

Bei *E. hoffmannseggii* fand ich in ein und derselben Wurzel neben mehreren Metaphasenplatten mit $2n=16$ (Abb. 2 B) auch eine Platte mit $2n=32$ Chromosomen (Abb. 2 C). LITARDIÈRE (1943) gibt 7 Arten an, bei denen 16 und 32 bzw. 14 und 28 Chromosomen in einer Pflanze vorkommen. Nach den Feststellungen ARARATJANS, die ich im Prinzip bestätigen kann, treten manchmal im Periblem und Dermatogen der Wurzel polyploide Zellen auf, die nur endomitotisch entstanden sein können. Solche Arten sind deshalb mit Sicherheit als diploid zu bezeichnen. Bei *E. italicum* und *E. russicum* lassen die vorliegenden Zahlen jedoch die Vermutung zu, daß diploide und tetraploide Rassen oder Individuen nebeneinander vorkommen könnten. Für *Lobostemon* sind solche Fälle von LEVYNS (1934) beschrieben worden.

Satellitenchromosomen sind im Satz jeder untersuchten Art vorhanden. Einige Autoren geben die Satelliten in ihren Zeichnungen an; andere, wie STREY (1931) und LITARDIÈRE (1943), sahen sie nur bei einem Teil der Arten. Die Zahl der Satelliten stimmt meist mit dem Ploidiegrad der Art überein (*E. russicum* und *E. wildpretii*, diploid, 2 Satelliten; *E. vulgare*, tetraploid, 4 Satelliten), doch trifft dies für *E. italicum* und *E. candicans* (diploid, 4 Satelliten) nicht zu.

DISKUSSION

Eine Einteilung, die sich nur auf die Chromosomenzahlen stützt, würde nicht



A



B



C

Abb. 1. Idiogramme von *Echium*. — A: *E. russicum*. — B: *E. wildpretii*. — C: *E. italicum*.

die wirklichen Verwandtschaftsverhältnisse widerspiegeln. Die gleichzeitige Berücksichtigung der Chromosomenmorphologie gibt uns dagegen einige Anhaltspunkte für eine natürliche Gliederung. Die 7 Arten, die zytomorphologisch genauer untersucht werden konnten, lassen sich in folgende Gruppen einteilen:

1. Arten mit $2n=16$ annähernd gleichgroßen Chromosomen, von denen 4 einen Satelliten tragen.

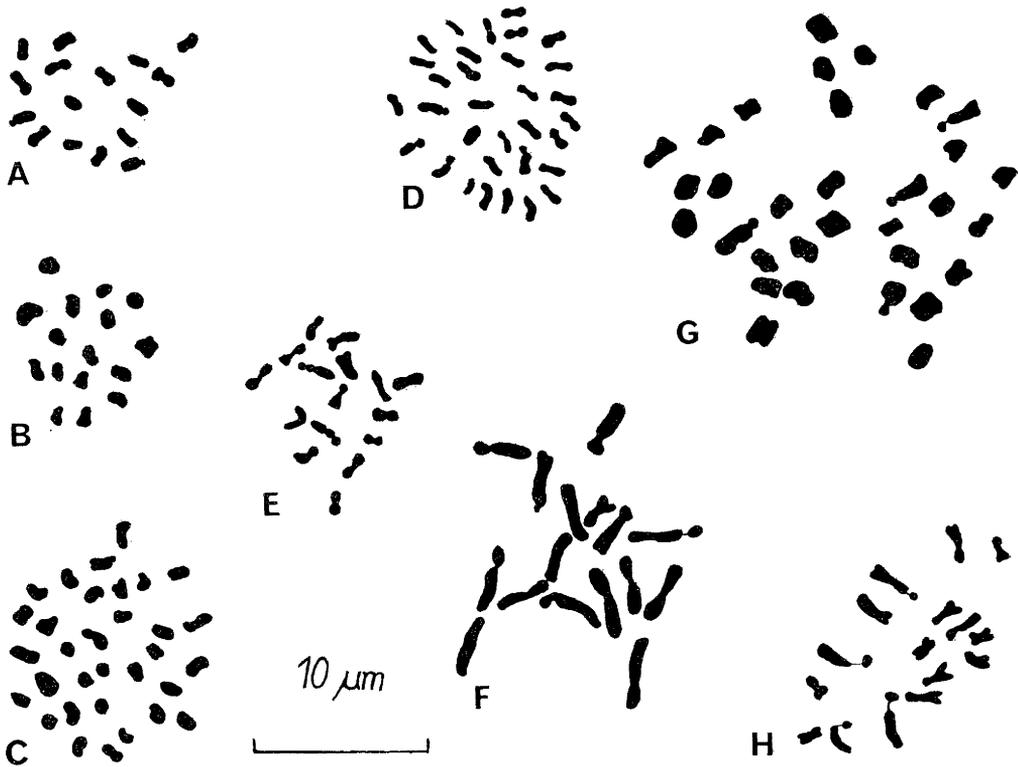


Abb. 2. Chromosomen von *Echium*. — A: *E. lycopsis*. — B, C: *E. hoffmannseggi*. — D: *E. vulgare*. — E: *E. thyrsoflorum*. — F: *E. acauleatum*. — G: *E. gaditanum*. — H: *E. candicans*.

2. Arten mit $2n=16$ Chromosomen, von denen 4 einen Satelliten tragen, 2 Chromosomen sind besonders groß.
3. Arten mit $2n=16(32)$ annähernd gleichgroßen Chromosomen, von denen 2(4) einen Satelliten tragen.
4. Arten mit $2n=12(24)$ annähernd gleichgroßen Chromosomen, von denen 2(4) einen Satelliten tragen.

Der Vertreter der Gruppe 1, *E. candicans*, ist auf den kanarischen Inseln beheimatet und wächst in der Form eines holzigen Kandelaberbäumchens. Die ausgeglichene Größe der Chromosomen gilt als ein Zeichen für Ursprünglichkeit, ebenso die holzige Sproßachse der Pflanzen.

Demgegenüber muß die andere Gruppe mit $n=8$ und 2 Satellitenchromosomen (Gruppe 2) im Prinzip als abgeleitet betrachtet werden, weil hier ein besonders großes Satellitenchromosomen vorhanden ist und der einzige bisher bekannte Vertreter (*E. italicum*) krautig ist.

Diese Entwicklungsrichtung (ein besonders großes Satellitenchromosom, krautiger Sproß) setzt *E. asperrium* fort, das ich leider nicht selber überprüfen konnte. LITARDIÈRE (1943) zeichnete eine Metaphaseplatte dieser Art. Der Gesamteindruck gleicht dem von *E. italicum*, nur fehlt im Satz ein Paar kleiner Chromosomen. Morphologisch stehen sich beide Arten nahe (KLOTZ 1960). Die Chromosomenmorphologie der restlichen drei Arten der

Sektion *Italica* ist nicht bekannt; Chromosomenzahlen liegen nur von *E. flavum* vor ($2n=16[32]$). Es ist noch zu klären, ob die oben beschriebene Chromosomenmorphologie für alle Sippen der Sektion *Italica* charakteristisch ist.

Die in der dritten Gruppe zusammengefaßten Arten besitzen im haploiden Satz nur ein Satellitenchromosom. In der Länge unterscheiden sich die Chromosomen nicht bedeutend voneinander. Dieser Typ ist weit verbreitet und schließt sowohl holzige wie auch krautige, perennierende wie annuelle Vertreter ein. Aus diesem Formenkreis könnten durch Auto- oder Allopolidie tetraploide Sippen wie *E. gaditanum* hervorgegangen sein.

Ein Gleiches trifft auch für *E. vulgare* zu, doch ist neben der aus dem subatlantischen und subkontinentalen Bereich Europas bekannten Chromosomenzahl $2n=32$ auch die Zahl $2n=16$ an Material aus dem Randgebiet des Mittelmeeres festgestellt worden. Da es im Mittelmeergebiet aber auch andere, *vulgare*-ähnliche Sippen gibt, ist eine Fehldeterminierung des von dort untersuchten Materials nicht ganz auszuschließen (BRITTON 1951). Andererseits wäre es aber auch denkbar, daß die Sippen des vermuteten Ursprungsgebietes der Art, des Mittelmeerraumes, diploid sind, während die nordwärts vorgedrungenen Sippen ihre jetzige Verbreitung durch die mit einer Polyploidisierung verbundene größere Anpassungsfähigkeit (REESE 1957, HANELT 1966) überhaupt erst erreichen konnten.

Die Gruppe 4 mit *E. russicum* läßt sich an keine der oben genannten Gruppen anschließen. Mit $n=6$ weicht diese Art erheblich von der allgemein verbreiteten Grundzahl $x=8$ ab. Bis heute sind weder zytologisch ähnliche Sippen noch Vertreter einer möglichen Übergangsgruppe bekannt. *E. asperrium* kann kein Zwischenglied sein, weil es einer ganz anderen Entwicklungsrichtung angehört. *E. russicum* hat im Vergleich zu den anderen Arten zwar ausgesprochen große Chromo-

somen, die sich aber in ihrer Morphologie im Prinzip nicht unterscheiden. Von den $n=6$ Chromosomen trägt ein heterobrachiales einen Satelliten, drei andere sind ebenfalls heterobrachial und zwei isobrachial inseriert. Die Art unterscheidet sich zytologisch und morphologisch insgesamt so gut von den übrigen Arten der Gattung, daß es durchaus gerechtfertigt erscheint, *E. russicum* in eine eigene Untergattung zu stellen.

Mit der Gattung *Echium* sehr nahe verwandt sind *Lobostemon* und *Echiostachys*. Seit Jahren ist man sich über den systematischen Rang dieser Sippen nicht einig. Während LEVYNS (1934) und BRITTON (1951) beide als selbständige Gattungen ansehen, bezieht JOHNSTON (1924, 1953) sie auf Grund der morphologischen Ähnlichkeiten als Sektion *Lobostemon* in die Gattung *Echium* mit ein. LEVYNS zählte bei beiden Sippen $n=7$ Chromosomen und Polyploide bis zur hexaploiden Stufe. Nach ihren Zeichnungen sind die Chromosomen alle etwa gleichgroß, doch treten bei einigen Arten auch größere auf. Es kommen aber niemals auch nur annähernd so große Chromosomen wie bei *E. asperrium* vor. Eine Ableitung ist über diese Art sicher nicht möglich. Von den untersuchten Arten von *Echiostachys* und *Lobostemon* wurden bisher keine Karyogramme angefertigt. Eine solche Arbeit wäre unbedingt notwendig, um auch aus zytologischer Sicht Rang und Stellung beurteilen zu können. Bis zu einer zufriedenstellenden Klärung dieses Problems ist es sicher angebracht, *Echium*, *Echiostachys* und *Lobostemon* auf gleicher Rangstufe nebeneinander zu führen.

Die vorliegende Arbeit ist die veränderte und erweiterte Fassung meiner Diplomarbeit, die ich an der Sektion Biologie der Friedrich-Schiller-Universität Jena schrieb. Besonders möchte ich Prof. Dr. G. KLOTZ für die Betreuung der Diplomarbeit, die nomenklatorische Überprüfung der Arten und die Durchsicht des Manuskripts danken. Dr. L. LEPPER bin ich für die Einführung in die Arbeitsmethodik und zahlreiche Hinweise zu Dank verpflichtet.

Tabelle 2. Liste der in der Gattung *Echium* bekannten Chromosomenzahlen.

Art	n	2n	Autor (veröffentl. als)
<i>E. aculeatum</i> POIR.		16 16; 16/32	BRITTON 1951; LARSEN 1960; vorl. Arbeit LITARDIÈRE 1943
<i>E. asperimum</i> LAM.		14 14; 14/28	LITARDIÈRE 1941 (<i>hispidissimum</i>); DELAY 1969 nach Index 1969 LITARDIÈRE 1943
<i>E. candicans</i> L. FIL.		16	vorl. Arbeit
<i>E. fastuosum</i> SALISB.	8		LEVYNS 1934
<i>E. flavum</i> DESF.		16; 16/32	LITARDIÈRE 1943
<i>E. gaditanum</i> BOISS.	16		BRITTON 1951 (<i>rosulatum</i>)
		32	STREY 1931 (<i>rosulatum</i>); LITARDIÈRE 1943 (<i>rosulatum</i>); vorl. Arbeit
<i>E. gentianoides</i> WEBB		16	BORGEN 1969
<i>E. giganteum</i> L. FIL.		16	MICHAELIS 1964; BORGEN 1970; BRAMWELL et al. 1971
<i>E. handiense</i> SVENT.		16	BORGEN 1970
<i>E. hoffmannseggii</i> LIT.		16 16 (32)	LITARDIÈRE 1943; GARDÉ & MALHEIROS-GARDÉ 1953 (<i>tuberculatum</i>); RODRIGUES 1953 (<i>tuber- culatum</i>) vorl. Arbeit
<i>E. horridum</i> BATT.		16	LITARDIÈRE 1943
<i>E. italicum</i> L.		16 16/32 32	PODLECH u. DIETERLE 1969; MAJOVSKY et al. 1970 nach Index 1970; STRID 1971; vorl. Arbeit LITARDIÈRE 1943 GADELLA et al. 1966
<i>E. leucophaeum</i> WEBB		16	BRAMWELL et al. 1971
<i>E. lusitanicum</i> L.	8	16 16	BRITTON 1951 STREY 1931; LITARDIÈRE 1943
<i>E. lycopsis</i> GRUF.	8 8	16 16	STREY 1931 (<i>plantagineum</i>); SUGIURA 1936 LITARDIÈRE 1943 (<i>plantagineum</i>); BRITTON 1951 (<i>plantagineum</i> +2 Var.)
		16	BORGEN 1970 (<i>plantagineum</i>); STRID 1971; vorl. Arbeit
<i>E. maritimum</i> WILLD.		16	LITARDIÈRE 1943
<i>E. micranthum</i> SCHOUSB. ...		16; 16/32	LITARDIÈRE 1943
<i>E. onosmaefolium</i> WEBB & BERTH.		16	BORGEN 1970
<i>E. parviflorum</i> MOENCH		16	DAHLGREN et al. 1971
<i>E. pininana</i> WEBB & BERTH.		16	LITARDIÈRE 1943; BRITTON 1951; BORGEN 1969; vorl. Arbeit
<i>E. russicum</i> GMEL.		12 12 (24) 24	ZHUKOVA 1967 nach Index 1967 ARARATJAN 1948 (<i>rubrum</i>); vorl. Arbeit LITARDIÈRE 1941; LITARDIÈRE 1943 (<i>rossicum</i>); POLYA 1950; MAJOVSKY et al. 1970 nach Index 1970
<i>E. sabulicolum</i> POMEL subsp. <i>decipiens</i> (POMEL) KLOTZ var. <i>decipiens</i>		16	LITARDIÈRE 1943 (<i>modestum</i> var. <i>decipiens</i>)
<i>E. setosum</i> VAHL	8		EL-SADEK & ASHOUR 1972
<i>E. simplex</i> DC.		16	BRAMWELL et al. 1971
<i>E. spinescens</i> MED.	8		SUGIURA 1936 (<i>creticum</i>)
		16	LITARDIÈRE 1943 (<i>australe</i> LAM.); vorl. Arbeit

Art	n	2n	Autor (veröffentl. als)
<i>E. strictum</i> L. FIL.	8	16	LINDER & LAMBERT 1965 LARSEN 1960; BORGEN 1969; BRAMWELL et al. 1971
subsp. <i>exasperatum</i> (WEBB) BRAMWELL	8		BRAMWELL et al. 1971
<i>E. sventenii</i> BRAMWELL	8		BRAMWELL et al. 1972
<i>E. thyrsoiflorum</i> MASSON ex LINK in BUCH		16	LITARDIÈRE 1943 (<i>decaisnei</i>); LARSEN 1960 (<i>decaisnei</i>); BORGEN 1969 (<i>decaisnei</i>); vorl. Arbeit
<i>E. triste</i> SVENT. subsp. <i>niva-</i> <i>riense</i> SVENT.	8		BRAMWELL et al. 1972
<i>E. thrygorrhizum</i> POMEL ...	8		REESE 1957 (<i>pycnanthum</i>)
<i>E. violaceum</i> L.	8	16	BRITTON 1951
<i>E. virescens</i> DC.		16	LITARDIÈRE 1943
		16, 24	BORGEN 1970
<i>E. vulgare</i> L.	8	16	DELAY 1969 nach Index 1969
		16	STRID 1971
		16, 32	LITARDIÈRE 1943 (+ <i>lacaitae</i>)
	16		STREY 1931
	16	32	BRITTON 1951
		32	FAHMY 1951 nach LÖVE & LÖVE 1961; LÖVE & LÖVE 1956 nach LÖVE & LÖVE 1961; MULLIGAN 1957; GADELLA et al. 1966; vorl. Arbeit
<i>E. webbii</i> COINCY	8		BRAMWELL et al. 1972
<i>E. wildpretii</i> PEARS. ex HOOK. FIL.	8	16	DI FULVIO 1965 (<i>bourgaeum</i>) STREY 1931; LITARDIÈRE 1943; BRITTON 1951; LARSEN 1960 (<i>bourgaeum</i>); vorl. Arbeit

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Supplement to Flora of Alaska and Neighboring Territories

A Study in the Flora of Alaska and the Transberingian Connection

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ABSTRACT

HULTÉN, E. 1973. Supplement to Flora of Alaska and neighboring territories. A study in the Flora of Alaska and the Transberingian connections. — *Bot. Notiser* 126: 459—512.

An attempt is made to correlate the Russian and the American concept of those species that occur or are presumed to occur on both sides of the Bering Strait, based on studies in the Leningrad Herbarium. Reference is made to recent literature on taxa dealt with in *Flora of Alaska and Neighboring Territories*. Additions, corrections and nomenclatural changes are discussed.

INTRODUCTION

With the recent discovery of immense oil and gas resources on the Arctic Slope of Alaska, and the serious ecological problems involved in the construction of the proposed heated pipeline across the state, Alaska has suddenly advanced from a relatively remote position in environmental discussion of interest mostly to Alaskans, to a central one. The uninhabited Arctic or sub-Arctic wilderness, so sensitive to human interference, will rapidly change, and one of the last large areas of undisturbed nature in the world will have disappeared.

It has been estimated that something like 15,000 to 20,000 men, working along a practically linear route, will be needed to complete the project. The effect of such an influx on the surrounding wilderness is obvious. Those concerned with the fate of the present ecological units must realize the necessity of increasing our knowledge

of the flora and fauna that provides the base for further studies. The present paper is a contribution to this knowledge.

The geographical position of Alaska makes it unusually difficult for the student of its flora to arrive at both taxonomical and nomenclatural decisions that can be accepted by students of the flora of the Old World as well as by those of the New World.

American writers only exceptionally compare their taxa with similar Asiatic ones, and real key-differences are practically lacking. Russian botanists, with problems enough to tackle within the Soviet Union's vast territory, likewise rarely concern themselves with the corresponding American taxa. The language difficulties add to the complications. Nevertheless a remarkable parallelism in the flora of the northern parts of the two continents is undeniable.

When the ranges of the Asiatic taxa and

the corresponding American taxa both reach the shores of the Bering Strait it is usually obvious that the taxa are identical, but when there is a gap in the distribution on both sides of the strait problems increase. Material from northernmost Asia is extremely scarce in Herbaria outside the Soviet Union and there are never more than single specimens available, more or less reliably determined. To get a conception of the ecological variation is practically impossible. In order to as far as possible remove these obstacles the writer spent about two months in September and October 1971, studying the Siberian flora east of the Lena River in the Leningrad Herbarium as an exchange scientist between the Swedish Academy of Science and the Russian.

There are, however, other difficulties to be overcome if one wants to establish a stable nomenclature and a stable taxonomical evaluation of the plants involved. Simple chromosome counts, which really tell us very little about the relationship between the taxa, merely seem to provoke nomenclatural changes and often create more problems than they solve.

The species concept adopted in Fl. SSSR differs from that used outside the Soviet Union and adds otherwise not-encountered complications, hard to overcome.

The subspecies concept now generally accepted by European botanists and used, for instance, in "Flora Europaea" has only recently and to a limited extent begun to be used by Americans, and is used to a still lesser extent by Soviet botanists. Furthermore this concept is interpreted in different ways. Some authors give subspecies rank to local, depauperated populations at the border of the range, deprived of part of the biotypes under environmental, mostly climatic pressure. Certainly the taxonomical analyses so far achieved are so insufficient that syntheses, so desirable, become more or less a speculation, as emphasized by MERXMÜLLER in his lecture on 'Systematic Botany — an

unachieved synthesis' (Biol. Journ. Linn. Soc. 4, 1972 pp. 311—321). However, it seems that speculation is the first step to a better understanding of the actual conditions.

The necessity of publishing a 224 page Supplement by P. A. MUNZ (1968) to the fine, then only ten-year old 'A California Flora' shows that numerous additions and nomenclatural changes must even be made in a Flora with a geographical position not as critical as the Alaskan.

Since the publication of the 'Flora of Alaska and the Neighboring Territories' in 1968 I have attempted to record corrections and nomenclatural changes as regards taxa treated there.

The establishment of a stable conception of nomenclature, circumscription and rank of the taxa can, however, only be achieved step by step. The present paper is intended as a step in this direction, based on the above-mentioned records and the work carried out in the Leningrad Herbarium.

COMMENTS

Numbers refer to the pages in Flora of Alaska and Neighboring Territories, Stanford University Press 1968.

25. The taxon described in CALDER & TAYLOR 1965 p. 1388 as *Lycopodium selago* subsp. *patens* (BEAUV.) CALDER & TAYLOR is in the writer's opinion merely an ecological form and does not merit the status of subspecies.

26. *Lycopodium* is undoubtedly an old genus which has been practical to retain, although it has been obvious that the species are not very closely related. Instead of using sections within such genera, the modern trend is to split them up into several genera, each of them comprising single species only. According to HOLUB (Preslia 36, 1964 p. 21) *Lycopodium inundatum* should be referred to the genus *Lycopodilla* HOLUB. In Fl. Europaea ROTHMAHLER referred it to the genus *Lepidotis*.

26. According to SIVILIVINSKY in Nov. Syst. Pl. Vasc. 10, 1973 p. 347, *Lycopodium inundatum* was collected at Tunca near Lake Baikal in 1834, a very unexpected locality for that plant.

28. Range extension of *Lycopodium obscurum* to Bristol Bay according to map in TAYLOR 1970 p. 58. TAYLOR considers that the typical plant and var. *dendroideum* are not "taxonomically significant". If this is so it is remarkable that only var. *dendroideum* occurs in the isolated Alaska-Yukon area as well as in Kamchatka.

29. Range extension for *Lycopodium clavatum* subsp. *monostachyon* to mts NE of Lake Baikal according to map 16 in MALYSHEV 1972. Type locality at Smoking R., 62°N. in The Rocky Mts was omitted in the Circumpolar map.

Range extension to the Baikal district according to SIVILIVINSKY in Nov. Syst. Pl. Vasc. 10, 1973 p. 347.

30. Range extension of *Lycopodium alpinum* to the Richardson Mts W of the Mackenzie Delta (north of area marked on the map in the Alaskan flora) according to CODY in Canad. Field Nat. 1969 p. 412.

31. *Selaginella selaginoides* was reported from southeasternmost Chukotka by JURTSEV et al. in 1972.

31. *Selaginella sibirica* was reported by JURTSEV et al. in 1973 from Penkignei in easternmost Chukotsk Peninsula.

34. Add the synonym *Hippochaete hiemalis* (L.) BRUHIN subsp. *affinis* (ENGELM.) HOLUB in Preslia 44 p. 128.

36. *Equisetum fluviale* was reported by JURTSEV et al. in 1972 from Utavaem in easternmost Chukotsk Peninsula (as *E. limosum*).

37. *Equisetum palustre* was reported from several localities in eastern Chukotka by JURTSEV et al. 1973.

38. *Equisetum pratense* was reported from easternmost Chukotka by JURTSEV et al. 1973.

40. WAGNER & LORD in Bull. Torr. Club 83, 1956 pp. 261—280 point out that what has been called *Botrychium minganense* VICT. in western America seems essentially to be related to *B. lunaria*, mainly differing in colour and size. LÖVE et al. 1971 p. 141 proposed to regard it as *B. lunaria* subsp. *occidentalis* on account of its small size and yellowish-green colour. This taxon is said to also occur in Alaska. Alaskan specimens are by no means small, many rather unusually tall and the yellowish-green colour is characteristic of *B. lunaria* all over its range. There seems to be no reason to accept subsp. *occidentalis*.

40. Very remarkable range extensions of *Botrychium boreale* to the northern part of Lake Baikal according to MALYSHEV 1972 map 6 and to Argun R. according to specimen in the Leningrad Herbarium; also occurs in Colorado according to WEBER, Add. Fl. Colorado.

41. Range extension of *Botrychium multifidum* to SW Greenland (Bot. Tid-skr. 66: 4, 1971 p. 358).

43. *Mecodium Wrightii*. Range extension to Vancouver I. according to TAYLOR 1970 p. 33.

45. *Cryptogramma Stelleri* was reported from Penkignei in southeasternmost Chukotka by JURTSEV et al. 1972 p. 767.

45. According to HOLUB in Preslia 38, 1966, p. 79, the name of *Thelypteris limbosperma* should be *Lastrea limbosperma* (ALL.) HOLUB.

On a map in Lavori della Società Italiana di Biogeographica N.S. 1, 1970 p. 117, PICHI SERMOLLI refers the Alaskan plant from Prince William Sound eastwards to "*Oreopteris limbosperma*", while the Aleutian plant is referred to *Oreopteris quelpartensis* (CHRIST.) CHING. There is no reason to separate the Alaskan material in that way. Alaskan specimens agree exactly with European ones. Compare with the discussion in HULTÉN, Fl. Alaska & Yukon I, 1941 p. 27.

45. In the above-mentioned paper by PICI SERMOLLI p. 116, *Thelypteris palustris* is shown on a map as occurring on the Alaska Peninsula and in the western Aleutian Islands. This plant has, to the writer's knowledge, never been reported from Alaska or collected there. It certainly does not occur there.

46. According to HOLUB in Preslia 38, 1966, p. 79, the name of *Thelypteris phaegopteris* should be *Lastrea phaegopteris* (L.) BORY.

This fern was reported from the Senjavin Hot Springs in easternmost Chukotka by JURTSEV et al. in 1972 (as *Phaegopteris connectilis*).

47. According to the map in TAYLOR 1970, the range of *Asplenium viride* in western America is divided into a coastal and an interior range.

47. The correct author-names should be *Athyrium distentifolium* TAUSCH subsp. *americanum* (BUTTERS) HULT., based on *A. alpestre* (HOPPE) RYLANDS var. *americanum* BUTTERS in Rhodora 19, 1917 p. 204.

49. The scale of the drawing of *Cystopteris fragilis* subsp. *fragilis* is 3/4, not 1/3 as indicated.

50. According to JURTSEV et al. 1973 *Cystopteris montana* occurs in eastern Chukotka.

52. According to TAYLOR 1970 *Matteucia struthiopteris* also occurs in two localities on the eastern Kenai Peninsula. It also occurs at Lynx Creek, Lake Nerka; at Rocky R., Kenai Penins.; and at Nuchek R., Prince William Sound, all collected by ROBERSON.

54. *Polystichum Braunii* var. *alaskense*. Range extension to Lake Kulik, north of Dillingham, collected by ROBERSON. Determination kindly controlled by VIREECK & MURRAY.

55. *Dryopteris spinulosa* was reported from Uelen in easternmost Chukotka by JURTSEV et al. 1973 under the name *D. carthusiana*. As the specimen is sterile and as the locality is very unexpected, a confirmation might be necessary.

55. What has long been named *Dryopteris dilatata* includes two taxa: the European, slightly more southern *D. dilatata* (HOFFM.) GRAY and a circumpolar taxon differing from the European one in having pale brown spores with acute tubercles and with the fronds divided somewhat differently. The latter is tentatively named *D. assimilis* S. WALKER. See Amer. Journ. Bot. 48, 1961 p. 607.

57. *Polypodium vulgare* L. is a polymorphic complex. Practically every author dealing with it arrives at his own conclusions. Only a world-wide monographic study can settle these differences.

In Bot. Zhurn. 49, 1964 p. 542 A. E. BOBROV differentiates Alaskan coastal plants occurring west of Sitka as *P. aleuticum* A. BOBR., characterized by segments broader towards the apex, remotely dentate and less pubescent on the veins. It is a synonym of what is called var. *commune* MILDE in HULTÉN 1968. Very similar specimens have been called *P. hesperinum* MAXON. It is true that in most specimens west of Sitka the segments of the frond are blunt or subacute, but specimens with very acute segments also occur far westwards on Atka and Attu. This is the reason why the writer did not give the western population a higher rank than variety. Aleutian specimens agree very well with the drawing B in TAYLOR, The Ferns and Fern Allies in British Columbia, p. 113.

In Madroño 21, 1971 pp. 235—254 LANG discusses the *Polypodium vulgare* complex in the Pacific Northwest, chiefly from a cytological point of view. His name for the coastal population is *P. glycyrrhiza*. On p. 236 he mentions that the plant from NE British Columbia and Yukon is *P. virginianum* L.

58. A specimen of *Polypodium vulgare* subsp. *occidentale*, collected by ROBERSON at Sadie Cove, Kachemak Bay, fills the gap between the two areas marked on the map.

60. According to ARGUS in *Canad. Journ. Bot.* 49, 1971 p. 573, the valid name for *Pinus Banksiana* is *P. divaricata* (AIT.) DUM. VOSS in *The Michigan Botanist* 11, 1972 p. 26, opposes this view.

60. In his review of the genus *Larix* in *Nov. Syst. Pl. Vasc.* 9, 1972 pp. 4—5, E. G. BOBROV differentiates *L. alaskensis* from *L. laricina* by cones of 10—12 mm (compared with 12—17 mm), cone scales 10—12, 7—8 mm long (compared with 12—15 of 8—10 mm length), and bracts ovate, merely acuminate (compared with bracts with a mucronate projection). The impossibility of keeping the Alaskan Tamarack as a separate species is obvious.

65. In *Preslia* 38, 1969 p. 79 HOLUB gives priority to the name *Juniperus communis* L. subsp. *alpina* (NEILR.) ČELÁK., *Prodr. Fl. Böhm.* 1, 1867 p. 17. This name replaces *J. communis* subsp. *nana* (WILLD.) SYME. Range extension to Chaukuktuli near Tikchik Lake collected by ROBERSON.

69. Range extension of *Sparganium hyperboreum* to the Queen Charlotte I. and St Lawrence I.

70. In *Linnaea* 35, 1867—68 p. 169 already, ASCHERSON distinguished the Alaskan *Phyllospadix* as *Ph. serrulatus* (RUPR.) ASCHERS., differing in 3-nerved leaves, truncate and nearly entire or minutely denticulate in the apex and minutely and densely serrulate. HARTOG in "The seagrasses of the world" 1969 p. 108, followed ASCHERSON. According to HARTOG *Ph. serrulatus* is characterized by having only two roots to each internode of the rhizome, generative axis reduced to a single pedunculate spathe and leaves with 5—7 veins compared with 3 in *Ph. Scouleri*.

That the specimens from the northern-

most localities of a fairly southern plant are reduced to having few roots and a single spathe is what should be expected. The difference in the number of veins has probably been caused through confusion with *Zostera*. As emphasized by CALDER & TAYLOR 1968, sterile specimens of *Zostera marina* can easily be confused with *Phyllospadix*. The leaves of *Zostera*, however, have several veins. The very scanty material of *Phyllospadix* from Alaska does not support the argument that it differs from *Ph. Scouleri*.

71. Range extension of *Potamogeton natans* to South Nahanni R. 61°57'N, 127°13'W, according to CODY & PORSILD 1968.

76. Correct spelling *Potamogeton Bercholdii*.

79. CALDER & TAYLOR (1968 p. 176) declare that only *Ruppia maritima* occurs on the NW coast of America in the collections of Nat. Mus. Canada.

All Alaskan specimens have the long, spirally coiled peduncles of *R. spiralis*, not the short (up to 2 cm long), straight peduncles of *R. maritima* L.

84. The variation and taxonomy of *Hierochloë* taxa have been studied by G. WEIMARCK (*Bot. Notiser* 124, 1971 pp. 129—175). Most of the Alaskan material of *H. alpina* was referred to subsp. *alpina* (map p. 159), but some specimens "with straight untwisted awn, more elongate rhizome internodes etc." were provisionally referred to the Greenland—Eastern American subsp. *orthantha* (SØRENS.) G. WEIM. (map p. 162). WEIMARCK regards subsp. *orthantha* as being an obligate apomict. In *Nov. Syst. Plant. Vasc.* 10, 1973 p. 84, TZVELEV reports this taxon also from Chukotka.

Alaskan specimens might well be included in the natural variation of *H. alpina*.

84. In the above-mentioned paper WEIMARCK splits *Hierochloë odorata* (L.) WAHLENB. into 4 taxa. Acc. to him typical

H. odorata has the lemma of the bisexual floret with appressed or only slightly spreading hairs and the lemma of the male floret awnless, mucronate or with a very thin awn, and with sparse marginal hairs. Alaskan specimens are referred to *H. hirta* (SCHRANK) BORBÁS according to WEIMARCK's key, having the lemma of the bisexual florets with distinctly spreading hairs and the lemma of the male florets with a coarse awn, rarely mucronate, and with dense marginal hairs. WEIMARCK furthermore distinguishes *H. hirta* subsp. *arctica* (PRESL) G. WEIM., based on *H. arctica* PRESL, Rel. Haenk. p. 252. The type specimen was presumably collected at Yakutat Bay.

According to WEIMARCK *H. odorata* and *H. hirta* occur together in both Europe and NE America.

In Nov. Syst. Pl. Vasc. 10, 1973 pp. 81—84, TZVELEV discusses WEIMARCK's conclusions. He refers the Alaskan population to *H. odorata* subsp. *hirta* SCHRANK, differing from subsp. *odorata* in 5 mm long spikelet (4 mm in subsp. *odorata*), lemma of male flower usually not acute, lacking or rarely with thin awn (acute with short awn in subsp. *odorata*) and with pubescence of all scales longer and denser than in subsp. *odorata*.

According to TZVELEV subsp. *hirta* is distributed from Kola Penins. and the Baltic States to Caucasus, Kamchatka and Chukotka in SSSR, also occurring in America, while subsp. *odorata* occurs from Kola Penins., the Baltic States, S. Ural, Altai, Baikal and the Central Asiatic Mts to Tian-shan. As pointed out in the writer's work "The Circumpolar Plants" it is a rule rather than an exception that circumpolar plants consist of a southern, older and a northern, younger taxon, although their areas sometimes overlap to a large extent. This seems to be the case in *Hierochloë odorata*.

85. According to OHWI's Japanese Flora the southernmost area marked on the Circumpolar map of *Hierochloë pauciflora*

belongs to *H. pluriflora* KOIDZ., an endemic, restricted to Mt Yubari in Hokkaido.

89. *Phleum pratense* also occurs introduced on Novaya Zemlya (DOROGASTAJSKAJA 1972) and in South Georgia.

89. *Alopecurus pratensis* has been found at Lake Tustumena, in the Kenai Peninsula by ROBERSON.

98. In Flora of Alaska & Yukon I, 1941 already, the writer realized that the Unalaskan specimens of *Agrostis Mertensii* were identical with *A. borealis*. In the original diagnosis of that species, however, specimens from Chile and Unalaska were mentioned and the name was regarded as a mixture, unfit to be used as a nomenclatural base. Unfortunately the present botanical rules of nomenclature prescribe that one of the components be used as a nomenclatural base. WIDÉN in Fl. Fenn. 5, 1971 p. 52, selected the Unalaskan specimen as the lectotype so that the name *A. borealis* HARTM. of long standing must be replaced by *A. Mertensii* TRIN. in Linnaea 10, 1836 p. 302.

A. Mertensii probably does not occur on the Queen Charlotte Is. Of the specimens reported as *A. borealis* in CALDER & TAYLOR 1968, Nos. 22937 and 36445 are *A. aenea* (= *alaskana*) and No. 22294 is *A. scabra*.

98. A cytotaxonomical study of *A. borealis* (*A. Mertensii*) in Japan, where diploids, tetraploids, hexaploids and octoploids occur, was published by TATEOKA (Bull. Nat. Sc. Mus. 13: 2, 1970 pp. 263—273; 14: 2, 1971 pp. 247—256 and 15: 3, 1972 pp. 455—460).

99. In Fl. Aleut. Is. 1937 p. 72 the writer presents the reason for using the name *Agrostis alaskana*. *A. aenea* TRIN. 1841 cannot be used because of the older *A. aenea* SPRENG. 1827. CHAMBERS in Madroño 18, 1966 p. 251, expresses the opinion that *Agrostis melaleuca* (TRIN.) HITCHC. is a valid name. According to him HITCHCOCK "made the typification by inference from the description, since on his visit to

the TRINIUS Herbarium at St. Petersburg he could not locate the type specimen of *A. canina* var. *melaleuca*". I refrain from deciding if this is permissible according to the nomenclatural rules. Range extension of *A. alaskana* to Copper I. and Paramushir acc. to PROBATOVA 1973 p. 73.

In N. Amer. Fl. 17: 7, 1937 p. 530, HITCHCOCK made *Agrostis canina* var. *melaleuca* TRIN. a synonym of *A. borealis* HARTM. In CALDER & TAYLOR 1968 this view was accepted. Few students of the genus *Agrostis* will agree. *A. borealis*, or *A. Mertensii* as might be the modern name, with its lemma decorated with a long geniculated awn affixed at or below the middle, with anthers 0.6—1.0 mm long and with a broad circumpolar range differs vastly from *A. alaskana* (= *A. melaleuca* TRIN. = *A. aenea* TRIN.) in which the lemma has a short straight awn or often lacks one. Its anthers are 0.5—0.6 mm long and the range is restricted to N America.

100. As regards the name *Agrostis stolonifera* L. see WIDÉN in Fl. Fenn. 5, 1971 p. 52. The plant called *Agrostis palustris* in CALDER & TAYLOR 1968 p. 186 (No 35913) is *A. tenuis* SIBTH. It is not, as stated, a synonym of *A. stolonifera* in Fl. of Alaska.

101. Range extension of *Agrostis exarata* to Mackenzie Mts 61°58'N, 128°15'W, according to CODY & PORSILD 1968.

105. CALDER & TAYLOR 1968 p. 192, report *Calamagrostis crassiglumis* THURB. from the Queen Charlotte Is. This species should have glabrous leaves. The specimen N of Olanda R. No. 35860 has scabrous leaves and is tentatively referred to *C. inexpansa*. This is also the case with the specimen reminiscent of *C. crassiglumis* in HULTÉN 1968 p. 103.

106. According to Á. LÖVE in Taxon 19, 1970 p. 299, the well-known *Calamagrostis neglecta* (EHRH.) G., M. & S. is an illegitimate name. His discussion illustrates the difficulty of applying the present nomenclatural rules exactly.

107. *Calamagrostis Holmii* seems to be a circumpolar taxon. Specimens from Spitzbergen and Prince Patrick I. as well as from Greenland, named *C. groenlandica* (SCHRANK) KUNTH by TH. SØRENSEN, agree well with Alaskan and Siberian specimens. They have glabrous dark glumes. *C. groenlandica* is based on *Arundo groenlandica* SCHRANK, Regensb. Denkschr. 2, 1818 p. 8, and *C. Holmii* was described in 1885. Á. LÖVE in Taxon 19, 1970 p. 299 names the plant *C. stricta* (TIMM.) KOEL. subsp. *groenlandica* (SCHRANK) Á. LÖVE.

C. kolymaensis KOM., cited as a synonym in HULTÉN 1968, is regarded as a hybrid by TZVELEV.

107. Range extension for *Calamagrostis purpurascens* to mts NE Lake Baikal acc. to MALYSHEV 1972 map 28. It also occurs on Wrangel I. and in easternmost Chukotka acc. to JURTSEV et al. 1973.

108. CALDER & TAYLOR 1965 p. 1388, described *Calamagrostis purpurascens* subsp. *tasuensis*. It agrees well with subsp. *arctica* (VASEY) HULT., although the plants are taller, as can be expected in a more southern area. CALDER & TAYLOR compared subsp. *tasuensis* with subsp. *purpurascens* but not with subsp. *arctica*. *C. purpurascens* subsp. *arctica* also occurs on the western shore of the Sea of Okhotsk.

111. *Aira cespitosa* is the original spelling of LINNAEUS.

114. SCHACKLETTE and others (1969 p. 58) considers that *D. beringensis* "cannot be distinguished from *D. caespitosa*". In spite of discussions in Flora of Alaska and Yukon pp. 173—175 and in several European and Siberian treatments it seems that this grass is poorly understood. *D. caespitosa* and *D. beringensis* belong to two different circumpolar complexes with different ranges and history. Frequent hybridization or even introgression where ranges overlap is not a reason for lumping them into one taxon. *D.*

beringensis belongs to a coastal complex with long glumes, mostly three-flowered spikelets and long anthers, while *D. caespitosa* is a continental complex with short glumes, always two-flowered spikelets and short anthers. For discussion see HULTÉN 1962 p. 66.

115. Range extension northwestwards of *Vahlodea atropurpurea* subsp. *paramushirensis* to the Magadan district on the western side of the Sea of Okhotsk.

117. In the discussion of the *Trisetum spicatum* complex in CALDER & TAYLOR 1968, these authors completely depreciate the results arrived at in the author's study of that complex, published in Sv. Bot. Tidskr. 53: 2, 1959 pp. 203—228. Since the writer had tried to elucidate the study very clearly with photographs, both of habit and detail, and illustrated it with maps of the ranges of the different taxa this was a real surprise. Material had been used from the Herbaria in Stockholm (ample Alaskan material), the British Museum, Copenhagen, Gothenburg, Kew Gardens, Leningrad, Lund, Uppsala and Tokyo. One would have expected that at least the easily accessible Alaskan material in Stockholm would have been studied before passing such categoric judgment.

The author willingly admits that the rank of the different taxa can be discussed, but not that the taxa described "are not phytogeographically meaningful".

CALDER & TAYLOR seem to misunderstand the subspecies concept. Characteristic of major races is precisely the fact that they overlap and present transitions in border districts, where they are sympatric. Altitudinal races also occur, and on a map they can appear to be "superimposed", although they don't meet at all or only along a certain altitudinal curve.

The tall plant with glabrous culms reported from Takakia Lake, Queen Charlotte Is as *T. spicatum* was not seen and nothing can be said about its taxonomy.

119. *Trisetum sibiricum* subsp. *litoralis* was reported from Amguem in eastern Chukotka by JURTSSEV et al. in 1973.

120. *Helictotrichon dahuricum* (KOM.) KITAG. was reported from Amguyema and Egvekinot in eastern Chukotka by JURTSSEV et al. in 1973.

122. The writer has maintained that the *Beckmannia* taxa of Asia and America should be regarded as subspecies of *B. erucaeformis* (L.) HOST of Europe. In Fl. Arctica URSS 2 p. 102 TZVELEV gives a key, where these taxa are separated as follows. The European plant has a small bulb at the base of the culm, short runners and anthers 1.2—1.8 mm long, while the Japanese plant, on which *B. syzigachne* (STEND.) FERN. is based, lacks the bulb, is tufted and has anthers 0.4—1 mm long. According to TZVELEV transitions do not occur in Siberia, where the taxa meet.

However, in Nov. Syst. Pl. Vasc. 10, 1973 p. 81, TZVELEV reports a new subspecies, *B. eruciformis* subsp. *borealis* from Vorkuta in the northern Urals, lacking bulb at the base of the culm. He remarks that it seems very probable that it is the result of introgressive hybridization between *B. eruciformis* and *B. syzigachne*. Such specimens were the reason why the writer regards the latter as a subspecies of the former. The taxonomy of the genus *Beckmannia* is still unclear. A plant with short-hirsute glumes was described from Amur R. as *B. syzigachne* subsp. *hirsutiflora* (ROSHEV.) TZVEL. in Nov. Syst. Pl. Vasc. 1968 p. 24.

It should be noted that Japanese specimens have completely glabrous glumes. The keel of the glumes is often slightly scabrous in Alaskan specimens.

123. *Koeleria asiatica* was reported from Pinacul in northeasternmost Chukotka by JURTSSEV et al. in 1972, from Wrangel I. by PETROVSKY 1973 and from Lavrentia (St. Lawrence Bay) by JURTSSEV et al. in 1973.

124. The names *Koeleria cristata* and *gracilis* are both considered to be illegitimate. The writer refrains from trying to find an acceptable name. SKINNERS (Rhodora 58, 1956 p. 94) proposes *K. macrantha* (LEDEB.) SPRENG. based on *Aira macrantha* LEDEB. for *K. gracilis*.

126. A map of the distribution of *Pleurogogon Sabinei* ("Sabini") is given in JURTSEV et al. in 1973 p. 296. The map shows several localities in easternmost Chukotka. It is remarkable that this characteristic plant is unknown from Arctic Alaska, where it must be expected.

129. Several new localities for *Poa alpina* were reported from easternmost Chukotka, where it is common in places, by JURTSEV et al. in 1973.

131. *Poa arctica* subsp. *caespitans* was reported from the Mackenzie delta in CODY & PORSILD 1968 and also from several other localities in Arctic Canada. TZVELEV (Fl. Arctica SSSR 2) regards this taxon as possibly the hybrid *P. arctica* × *glauca*.

137. Range extension for *Poa palustris* to the Seward Peninsula, Pilgrim Hot Springs (ROBERT RAUSCH).

138. Range extension for *Poa lanata* to mts around northern Lake Baikal acc. to MALYSHEV 1972 map 33.

139. NINA PRABATOVA, Vladivostok, who made an extensive study of the genus *Poa* in eastern Asia, includes *Poa Turneri* SCRIBN. in *P. hispidula* VASEY (personal communication). It is hard to find a clear difference between these two taxa and *P. Turneri* can well be regarded as a luxuriant variety of *P. hispidula*.

145. The identity of *Poa leptocoma* TRIN. and *P. paucispicula* SCRIBN. & MERR. was discussed in Fl. Alaska & Yukon 2 p. 215. The writer came to the conclusion that only the type specimen of *P. leptocoma*

from Sitka should be referred to that species. Some 70 specimens now available were examined and the same conclusion was reached. *P. leptocoma* was differentiated from *P. paucispicula* by being slightly taller, having greenish spikelets nearly always lacking any violet tinge and leaves more or less scabrous above. In the Alaskan material only the type specimen of *P. leptocoma* answers to this description. In the Kamchatka material *P. flavidula* KOM. belongs here.

Under such circumstances it might be questioned if the type specimen of *P. leptocoma* really originates from Sitka. The label of the isotype specimen in Leningrad reads: "*Poa stenantha* TRIN. β *leptocoma* TRIN. (Herb. TRINIUS sub. *P. leptocoma* M.) MERTENS 1829". According to kind information received from S. LIPSCHITS the label was not written by TRINIUS but probably by BORODIN. MERTENS visited Sitka from July 24th to 31st, 1827. A safe name for the Alaskan plant is *P. paucispicula* SCRIBN. & MERR. and it is wisest to exclude *P. leptocoma* TRIN. from the Alaskan flora.

146. According to TZVELEV in Fl. Arct. URSS 2 p. 146 the name *Poa pseudoabbreviata* ROSHEV. is three years older than *P. brachyanthera* HULT. The name was misunderstood, as *P. pseudoabbreviata* shows little similarity to *P. abbreviata*. Since examining the type the author accepts TZVELEV's view. The Asiatic range on the map belonging to *Poa* 38 should thus be transferred to *Poa* 36 in the Alaskan Flora.

147. As the name *Poa pseudoabbreviata* ROSHEV. was misunderstood (see above), the plant thus named in the Alaskan Flora (no. 38) should be referred to *Poa Jordalii* PORS. which differs from *P. abbreviata* merely in having lemmas glabrous between the keel and the marginal nerve. It is the Rocky Mountain counterpart to *P. abbreviata* and here regarded as a major race of that species:

Poa abbreviata R. BR. in Suppl. to App. Parry's Voy., 1824 p. 287, **subsp. Jordalii** (PORS.) Hult., **comb. nov.**

Poa Jordalii PORS. in Canad. Field Nat. 79, 1965 p. 82.

It was recently found on Wrangel I., where subsp. *abbreviata* also occurs and extends southwards to the mountains of British Columbia.

148. Range extension for *Colpodium Wrightii* to Karaginskiy I., N Kamchatka, according to VOROSHILOV et al. 1971.

C. Wrightii was transferred to the genus *Puccinellia* by TZVELEV in Fl. Arctica URSS 2, 1964 p. 193. A map of its Asiatic range is given by JURTSEV et al. in 1973 p. 303.

152. In *Rhodora* 54, 1952, CHURCH refers *Glyceria pauciflora* to the genus *Torreya-chloa*, chiefly characterized by open sheaths. His view is accepted in CALDER & TAYLOR 1968. *Glyceria pauciflora* is morphologically extremely similar to other *Glyceria* species. Add the synonym *Torreya-chloa pauciflora* (PRESL.) CHURCH.

155. Range extension for *Puccinellia phryganodes*: Karaginskiy I., N Kamchatka (VOROSHILOV et al. 1971).

157. The locality on Richard I., Mackenzie delta, marked on the Circumpolar map, was omitted in the Alaskan map. Localities between that place and Banks I. were reported by CODY & PORSILD 1968 b p. 265.

158. According to OHWI's Japanese Flora *Atropis kurilensis* TAKEDA is a synonym of *Puccinellia pumila*. TZVELEV agrees with this view. The range should thus be extended from S Kamchatka to N Kyushu and Sakhalin.

160. *Puccinellia sibirica* HOLMB., a west-Siberian plant was found at Pinakul in easternmost Chukotka according to JURTSEV et al. 1973 p. 305. It is very similar to *P. borealis* and the specimens must be carefully compared.

164. Range extension of *Puccinellia borealis* to the Anderson R. and Norman Wells in the Mackenzie district according to CODY & PORSILD 1968 b p. 265. It is said to be an aggressive weed.

164. According to DOROGASTAJSKAJA 1972 *Puccinellia Hauptiana* occurs as a weed along the lower Jenisei, at Khatanga and on the Lena delta.

165. Range extension of *Puccinellia interior* to Fort Simpson according to CODY & PORSILD 1968 b p. 266.

165. According to DOROGASTAJSKAJA 1972 *Puccinellia distans* occurs as a weed along the lower Jenisei and on the Lena delta.

169. *Festuca baffinensis* was reported from northeasternmost Chukotka by JURTSEV et al. 1972.

170. *Festuca ovina* subsp. *alaskensis* HOLMEN seems to be identical with *F. auriculata* DROB. According to the map by TZVELEV (Fl. Arct. URSS 2 p. 220) this taxon extends from the Urals to Anadyr and south to the northern Baikal area, Sichota Alin and Kamchatka. It also occurs on Wrangel I. according to PETROVSKY 1973 p. 115. In Nov. Syst. Pl. Vasc. 9, 1972 p. 45 TZVELEV reports *F. auriculata* subsp. *auriculata* from Alaska.

171. SCHACKLETTE and others (1969 p. 58) writes that *Festuca rubra* subsp. *aucta* "should not be accorded formal taxonomic recognition". It is very remarkable that this taxon is the only segregate of the *Festuca rubra* complex met with in the Aleutians west of Unalaska. It is a very characteristic taxon that possibly merits specific status. Where it meets introduced or mainland taxa of the complex it is, however, less distinct which is why it was given the rank of subspecies.

175. The range of *Bromus Pampellianus* var. *arcticus* should be extended to Pen-shina, the northern Ochotsk area and Kamchatka.

A tetraploid taxon similar to the octoploid *Bromus Pumpellianus* was described as *B. Pumpellianus* subsp. *Dicksonii* by MITCHELL & WILTON in Brittonia 18, 1966 p. 163. According to them it occurs along the Yukon between Kaltag and Ruby.

181. *Lolium temulentum* has been collected at Norilsk, northern Siberia, according to DOROGASTAJSKAJA 1972.

183. According to a personal communication from TZVELEV *Roegneria kamczadolorum* NEVSKI is a synonym of *Agropyron pauciflorum* subsp. *majus* (VASEV) MELDERIS. Its range should thus be extended to Kamchatka.

183. In DOROGASTAJSKAJA 1972 *Agropyron repens* was reported from Khatanga and Provideniya (Port Providence, SE Chukotka).

185. Range extension for *Agropyron macrourum* to Wrangel I. acc. to PETROVSKY 1973 p. 116.

187. Range extension of *Agropyron boreale* subsp. *boreale* to Wrangel I. acc. to PETROVSKY 1973 p. 116.

197. *Elymus sibiricus* also occurs in Peshina and Anadyr, which makes the gap between the Asiatic and American ranges considerably narrower.

199. According to Á. LÖVE (Isl. Ferdafl. 1970 p. 136) *Eriophorum angustifolium* subsp. *triste* has been found once in NW Iceland.

201. *Eriophorum Scheuchzeri* var. *Scheuchzeri* occurs on St Lawrence I. according to YOUNG 1971 p. 40. An earlier report had been regarded as doubtful.

201. An examination of the type of *Eriophorum altaicum* MEINSH. showed that this taxon is not (as had been expected) a synonym of *E. Scheuchzeri* var. *tenuifolium*. The narrow area extending from eastern Siberia to Altai on the Circumpolar map should be removed. The

range will then agree well with that of several other Pacific taxa.

204. *Eriophorum brachyantherum* was reported from several places in eastern Chukotka by JURTSEV et al. 1973.

205. Specimens of *Eriophorum vaginatum* subsp. *spissum* were found in the Leningrad Herbarium from Chukotka, Wrangel I., Anadyr, Peshina and Kolyma westwards to Tixi at the mouth of the Lena R.

207. According to JURTSEV et al. 1972 p. 768 *Scirpus Maximoviczii* occurs at Koolen in northeasternmost Chukotka. Later it was reported from several places in eastern Chukotka by JURTSEV et al. 1973. Map p. 308. It is a very peculiar plant with a broken-up range southwards to the sources of the Indigirka R., Peshina, Dusse Alin, Sakhalin, Ussuri, Korea (Mt Diamants), central and northern Honshu, central Hokkaido and the southern Kuril Islands. It is not known from America.

208. KOYAMA (Canad. Journ. Bot. 40, 1962 p. 927) regards *Scirpus validus*, which he takes as being a subspecies of the Eurasiatic *S. lacustris* L., as a taxon occurring from British Columbia to Nova Scotia and southwards to Mexico and S America, but not occurring in Alaska, Yukon or Mackenzie. He regards the counterpart within the area of the Alaskan Flora as being identical with *S. Tabernaemontani* C. C. GMEL. and names it *S. lacustris* L. subsp. *glaucus* (SMITH) HARTM. with the range Alaska to Nova Scotia south to California and N Carolina. According to him the latter taxon differs from subspecies *validus* in the thinly membranaceous floral scales, papillose on the upper half with dense, reddish gummy spots, considerably fimbriate on the upper margins, and in the slightly larger average size of the achenes. Some specimens, however, such as those from the lower Klondike R., July 21, 1964, collected by myself, have glabrous, nearly nonfimbriate scales,

others have very slightly papillose but fimbriate scales. The scales are much less papillose than in Scandinavian specimens of *S. Tabernaemontani* and the plant should preferably be referred to *S. validus*, which might as well be taken as *S. lacustris* subsp. *validus* (VAHL) KOYAMA. Achenes of Alaskan specimens are 2—2.5 mm long. Compare with discussion and maps 151 and 171 in HULTÉN 1962.

212. In *Rhodora* 70, 1968 p. 207 ARGUS reported *Eleocharis nitida* from Stony Rapids, N Saskatchewan. This locality is situated in the middle of the large gap between the earlier known Alaskan and Eastern American localities.

221. YOUNG (1971 p. 41) reports *Carex Jacobi-Peteri* from two localities on St Lawrence I.

223. *Carex scirpoidea* MICHX. sens. lat. is reported from the Queen Charlotte Is in CALDER & TAYLOR 1968.

224. A map of the distribution in NE Siberia of *Carex obtusata* is presented by JURTSSEV et al. 1973 p. 310.

241. According to NERMES in *Reinwardtia* 1: 3, 1951 p. 444 the type of *Carex canescens* L. is *C. Buxbaumii*. The name of this taxon, for centuries widely known as *C. canescens*, should be changed to *C. curta* GOOD. Cf. MOORE & CHATER in *Bot. Notiser* 124: 3, 1971 p. 325. The botanical nomenclatural rules should provide for the conservation of such old established names.

246. *Carex echinata* MURR. is a very complicated complex not yet well understood. The specimens from Unalaska reported under that name should be referred to var. *angustata* (COREY) BAILEY, in America usually named *C. angustior* MACKENZIE. Alaskan specimens are, however, unusually broad-leaved (mostly 2 mm). *C. angustior* ranges from Newfoundland to British Columbia south to NW N Carolina, northern Michigan, Colorado and California. Russian authors include speci-

mens from Kamchatka to Japan and Korea in this taxon.

255. Both *Carex media* R. BR. and *C. norvegica* RETZ. were reported from easternmost Chukotka in Fl. Arctica URSS 3 (maps pp. 131 and 133), as well as by JURTSSEV et al. 1973 p. 314. Revising the Alaskan material it was found that both specimens with about 2 mm long, dark perigynia, answering to *C. norvegica* RETZ. and such with about 3 mm long, light-coloured perigynia, answering to *C. media* R. BR. occur there, sometimes from the same locality. These two taxa are not very distinctly separated from each other, a fact recognized also by JURTSSEV et al. 1973. This was the reason why the writer proposed to regard *C. media* as subspecies *inferalpina* of *C. norvegica* RETZ. From what is now known, both types are circumpolar. *C. media* is a woodland plant, while *C. norvegica* is subarctic and sub-alpine. They are another example of circumpolar taxa pairs mentioned in HULTÉN 1962 and 1971.

255. *Carex holostoma* was reported by JURTSSEV et al. 1973 from a number of places in eastern Chukotka. It also occurs in the Mts NE of Lake Baikal acc. to MALYSHEV 1972 map 58.

260. The occurrence of *Carex atrata* subsp. *atrosquamea* on the Arctic Slope is verified by MURRAY (in a letter), who collected this taxon at Shublik Springs.

265. *Carex nesophila* HOLM was transformed to a subspecies of *C. microchaeta* HOLM by MURRAY in *Canad. Journ. Bot.* 49, 1970 p. 323.

271. Two small localities for *Carex livida* were discovered on St Lawrence I. by YOUNG (1971 p. 43).

273. *Carex petricosa* was reported from two places in easternmost Chukotka by JURTSSEV et al. 1972 p. 769. A counterpart with more numerous spikes and brownish scales, *C. macrogyna* TURCZ., occurs in eastern Siberia.

274. According to JURTSEV et al. 1972 *Carex Krausei* was found in a few places in easternmost Chukotka.

274. *Carex Ledebouriana* C. A. MEY. ex TREV. was reported from easternmost Chukotka in Fl. Arctica URSS 3, map p. 152. It belongs to the very critical *C. capillaris* complex and is characterized by large, club-like 1—1.5 cm long, 3—5 mm broad, brown-orange male spikes, often overlapping the uppermost female spike. No such specimens were seen in Alaska.

278. *Carex membranacea* also occurs on Wrangel I. acc. to PETROVSKY 1973 p. 116.

281. The leaves of *Lysichiton americanum* are said in the Alaskan Flora to be up to 1 m long. According to EYERDAM in Leaflets Western Bot. 5, 1948 p. 186, they can be much larger, up to 6 feet 2 1/2 inch (2.6 m).

282. Range extension of *Lemna trisulca* to two lakes north of Brooks Range, see map by CH. HOLMQVIST in Bot. Notiser 124: 3, 1971 p. 337.

288. The American component of the *Juncus Mertensianus* complex was divided into six subspecies by HERMANN in Leaflet. Western Bot. 10, 1964 pp. 81—96. The Alaskan plant belongs to subsp. *Mertensianus*.

288. Discussing *Juncus falcatus* CALDER & TAYLOR (1968 p. 267) write: "HULTÉN (1943 p. 427) recognizes subsp. *sitchensis* by its short styles and filaments, but these characters were found to be of no significance in the series of specimens we examined". Alaskan specimens, however, have short styles, and filaments of the same length as the anthers. Specimens from California, where the type of *J. falcatus* came from, for instance KELLOGG & BOLANDER 40, Herb. Junc. Bor.-Amer. Normale ed. G. ENGELMANN from Lone Mt San Francisco, have fairly long styles and filaments much shorter than the anthers. In MUNZ & KECK "A California Flora" *J. falcatus* is said to have anthers longer

than the filaments. In Alaska *J. falcatus* is always single-headed.

289. In HULTÉN 1967 p. 31 it was pointed out that *Juncus castaneus* subsp. *castaneus* and subsp. *leucochlamys* intergrade. Variation is considerable, also the length of the anthers varies between 1 and 2 mm. Russian authors refer specimens with few-flowered heads, pale perianths and capsules and with the lowest bracts long and dilated at base, named *J. castaneus* subsp. *castaneus* var. *pallidus*, to *J. leucochlamys*. They differ from subsp. *castaneus* especially in the bracts. On an average they have long anthers.

Juncus castaneus constitutes a circum-polar complex, not yet well understood. Even in Scandinavia, where it occupies an isolated area in the southern mountains, remarkable variation occurs. In the Dovre Mts most specimens have a long bract, strongly dilated at the base, and few-flowered heads, in contrast with the bulk of the Scandinavian material which has short, narrow bracts and more numerous flowers in the head. The first-mentioned type is similar to those named *J. castaneus* var. *pallidus* in the Alaskan Flora.

292. YOUNG 1971 p. 44 reports a *Juncus* species from St Lawrence I. "which cannot be identified with any species presently known to occur in Alaska". In his description nothing speaks against the view that it is a depauperated form of the very variable *J. alpinus* subsp. *nodulosus* which can be expected to occur on that island. It is very improbable that it belongs to *J. Faurienseis*, with which YOUNG compares it.

293. *Juncus triglumis*, reported in CALDER & TAYLOR 1968 from Moresby I., Upper Victoria Lake, belongs to subsp. *albescens* according to specimens examined. *Juncus triglumis* subsp. *albescens* was reported from easternmost Chukotka in JURTSEV et al. 1973 p. 296.

296. *Luzula rufescens* was reported from eastern Chukotka by JURTSSEV et al. 1973. Range extension to Canoe Lake west of the Yukon delta according to CODY & PORSILD 1968 b.

298. The *Luzula parviflora* complex was discussed by HÄMET-AHTI in Ann. Bot. Fenn. 8, 1971 pp. 368—381. While she referred the eastern American plant, occurring from Saskatchewan and Minnesota eastwards, to subsp. *melanocarpa*, Alaskan specimens were referred to subsp. *parviflora*, the total range of which is left undecided (cf. map 50 in HULTÉN 1962).

A very different opinion was expressed in Fl. Arctica URSS 4 p. 34.

The taxon named *L. parviflora* subsp. *divaricata* in the Alaskan Flora was divided into two taxa: *L. parviflora* subsp. *fastigiata* (E. MEY.) HÄMET-AHTI, ranging from Alaska to California, Utah and Colorado, and characterized by acute, pale to dark brown, not reddish outer perianth-segments, and *L. divaricata* S. WATS., ranging essentially south of the glaciation, from Washington to California (partly sympatric with her *L. parviflora* subsp. *fastigiata*) and characterized by long-acuminate perianth segments with a reddish fringe and with reflexed apex.

These are certainly small differences on which to differentiate taxa with the rank of species. That lowland plants in the north are mountain plants in the south is not rare. The zonal distribution therefore hardly supports taxonomical separation.

HITCHCOCK et al. (Vasc. Pl. Pacific N.W. 1, 1969 p. 215) had apparently not seen Alaskan specimens determined as *L. pauciflora* subsp. *divaricata* when they proposed that the report was founded on specimens of *L. Piperi*.

The specimen from Juskatla TAYLOR 24 and reported as *L. parviflora* "lowland phase" in CALDER & TAYLOR 1968 belongs to *L. parviflora* subsp. *divaricata* as interpreted in HULTÉN 1968. Range extension for that taxon to Amchitka I. (REICH & MCCANN) according to HÄMET-AHTI p. 376.

300. *Luzula nivalis* LAEST. was reported from mts NE of Lake Baikal in MALYSHEV 1972 map 82.

301. In Ann. Bot. Fenn. 8: 2, 1971 p. 156 HÄMET-AHTI reports *Luzula groenlandica* (BÖCHER in Meddel. Grønland. 147: 7, 1950 p. 18 tab. 1) from the Richardson Highway close to mile 200 and from one mile N of Fielding Lake (NW of Paxson). Other collections are from Sourdaugh Creek, about 70 miles NE of Fairbanks, and from Summit Lake, both collected by GALEN SMITH. PORSILD (1972 p. 236) reports it from Ogilvie Mts in Yukon.

L. groenlandica differs from other members of the extremely complicated *L. multiflora* complex, especially from "*L. frigida* sens. lat.", in often having single heads, somewhat shorter perianth segments and seeds usually less than 1.1 mm with a short appendage.

According to CODY & PORSILD 1968 b, *L. groenlandica* is widespread in the continental NW Territories of Canada. It is probably one of the circumpolar components in the *L. multiflora* complex.

In the Greenland Flora by BÖCHER et al. 1968 p. 215 is stated: "Inflorescence a single head, sometimes together with small, shortstalked clusters". Some of the Alaskan specimens determined as *L. groenlandica* on account of the seed character look very different from the drawing in the Greenland Flora fig. 51 d, for instance G. SMITH 2108 from Summit Lake with up to 7 small heads, some on stalks up to 35 mm long.

On examining the Alaskan material referred to *L. multiflora* var. *frigida* specimens with small seeds were found, but no constant correlation with other characteristics could be established.

302. *Luzula tundricola* and *L. multiflora* var. *Kjellmaniana*. The nomenclature of these two very different taxa was discussed by HÄMET-AHTI and VIRRANKOSKI in Ann. Bot. Fenn. 8: 2, 1971 p. 157. The regrettable result is that the plant called *L.*

tundricola GORODKOV in HULTÉN 1968 should, for technical reasons, bear the name *L. Kjellmaniana* MIYABE & KUDO, although its authors had quite a different plant in mind. I refrain from trying to find an acceptable name for the plant called *L. multiflora* subsp. *multiflora* var. *Kjellmaniana* in HULTÉN 1968 p. 302. This taxon can be included in the *L. multiflora* complex until this has been monographically studied.

305. *Zygadenus glaucus* NUTT. is given as a synonym of *Z. elegans* PURSH in the Alaskan Flora. It would, however, be better to regard it as an eastern race of that species:

Zygadenus elegans PURSH subsp. *glaucus* (Nutt.) Hult., comb. nov.

Melanthium glaucum NUTT. Gen. 1, 1818 p. 232.

On the Circumpolar map only the range of subsp. *elegans* is given. Subsp. *glaucus* occurs from Minnesota and Wisconsin to St Lawrence Bay and Mingan I. south to W New York and the mountains of Virginia and N Carolina. Where the ranges overlap intermediates occur or even predominate, cf. FERNALD in Rhodora 37, 1935 p. 257.

306. Range extension for *Veratrum album* subsp. *oxysepalum* along the coast of the Sea of Ochotsk southwards to about 50°N.

309. Range extension for *Smilacina racemosa* to Newfoundland according to information from A. W. H. DAMMAN.

310. For unknown reasons Russian authors use the name *Smilacina trifoliata* DESV. for *S. trifolia* (L.) DESV.

311. *Maianthemum dilatatum* was collected by ROBERSON at Port Dick, Kenai Peninsula.

312. CALDER & TAYLOR 1968 p. 382 maintain that American material of *Streptopus streptopoides* is "quite unlike the few collections we have seen from Asia". It is true that the specimens from

Ajan, the type locality, differ in having the leaf margin sparsely papillose. However, Japanese plants have the same characteristic leaf margin as that shown on pl. 328 fig. n in FASSETT's paper in Rhodora 37, 1935. Japanese specimens are usually branched, as is natural for a more southern, warmer habitat, but small unbranched specimens agree well with Alaskan specimens in all respects.

In Fl. SSSR 4 p. 456 the leaves of *S. streptopoides* are said to have smooth margins or with small, long, linear projections. Both types of leaf margin thus occur in eastern Siberia. In Alaskan specimens only traces of such projections can occasionally be seen. *S. streptopoides* var. *japonicus* (MAXIM.) FASSETT is thus doubtfully distinct from var. *curvipes* (VAIL) FASSETT.

In OHWI's Japanese Flora the note on distribution "W.N. America" should be transferred to var. *japonicus*.

314. A monographic treatment of the *Sisyrinchium* taxa is badly needed as different authors generally arrive at different conclusions in dealing with this genus. MOSQUIN in a paper in Madroño 20 pp. 269—275 lumps the taxa occurring within the range of Flora of Alaska and Neighboring territories together with several others under the name *S. bermudiana* L., a southern plant, the type of which came from Virginia and the Bermuda Is and which is hardly identical with the Alaskan.

318. White-flowered specimens occur in *Dactylorhiza aristata*.

318. To the synonyms of *Amerorchis rotundifolia* add *Ponerorchis rotundifolia* (BANKS) SOÓ in Acta Bot. Hung. 12, 1966 p. 353.

325. *Spiranthes Romanzoffiana* occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

326. *Listera caurina* occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

326. *Listera convallarioides* occurs at Auk Bay in SE Alaska according to Mrs M. WILLIAMS in a letter.

329. *Corallorrhiza trijida* was collected at Cold Bay by Mrs M. WILLIAMS. Reported from E Greenland in Bot. Tidsskr. 66, 1971 p. 72.

330. *Malaxis monophylla* also occurs at Dutch Harbour, collected by Mrs M. WILLIAMS in 1971.

331. The combination *Calypso bulbosa* (L.) RCHB. FIL. (1851) is antedated by *C. bulbosa* (L.) OAKES in THOMSON, Hist. of Vt. 1, 1842 p. 200. OAKES is thus the author of that name.

332. Change name of author for *Populus balsamifera* subsp. *trichocarpa* from (TORR. & GRAY) HULT. to the earlier (TORR. & GRAY) BRAYSHOW in The Canad. Field Nat. 79: 2, 1965 p. 95. This taxon does not occur on the southern islands in the SE Alaskan Archipelago, nor on the Queen Charlotte Is.

333. ARGUS 1973 is a monographical treatment of the genus *Salix* in Alaska and Yukon, giving keys, descriptions and maps of all species known to occur there. It is based on extensive field studies, and herbarium specimens from 15 American botanical museums. It is much to be regretted that the large collection in the Riksmuseum, Stockholm, brought together by the writer, was neglected. It is certainly one of the largest collections from the area in existence. If it had been used, the maps could have been considerably improved. Now the result of the writer's field studies, marked on the maps in HULTÉN 1968, are not included in ARGUS' maps. As ARGUS 1973 was available to the writer after the manuscript of this paper had been given to the printers, only a few comments on that work can be made here.

The experimentally confirmed hybridization within the genus *Salix* is to a very small extent recognized by American authors. This is understandable as the

parent species in the hybrids can often be very difficult to state on the basis of morphological characters. That extensive hybridization exists is, on the other hand, hardly reasonable to deny. Only studies of artificial crossing experiments can shed light on this problem. That the opinions of different authors differ considerably concerning the genus *Salix* is on the above-mentioned grounds natural.

336. In Canad. Journ. Bot. 43, 1965 p. 1021 ARGUS described *Salix reticulata* subsp. *glabellcarpa* from the Queen Charlotte Is (although CALDER & TAYLOR are given as authors on p. 1023). The very young capsules are glabrous but the lower capsules in the catkin are pubescent in no. 21621. A specimen of *S. reticulata* with glabrous adult capsules was found at Juneau (HULTÉN 8299) but on account of the very different state of development it is not comparable with the Queen Charlotte Islands specimens. This is, however, the case with a specimen collected by RAUP & CORELL (no. 10474 S) at Summit Pass, British Columbia. It has glabrous young capsules well matching those of the Queen Charlotte Islands plant and is quite similar to CALDER & TAYLOR no. 36476. It was labelled *Salix* ? *Barclayi* × *reticulata*. ARGUS discusses the possibility of *S. reticulata* subsp. *glabellcarpa* being a hybrid, but rejects this. The very small poorly developed capsules and the abnormal development of the styles, which have 1—3 instead of 4 lobes in many cases in the type specimen, support the hybrid theory as well as the great variation in leaf form. Anyhow, the taxon can hardly be regarded as a subspecies. It is probably a hybrid.

337. Both SKVORTZOV (1968 p. 120) and ARGUS (1973 p. 51) maintain that *Salix polaris* and subsp. *pseudopolaris* are identical. The writer is somewhat reluctant to accept this view. Apart from the differences quoted in the original diagnosis, the taxon named subsp. *pseudopolaris* is a more robust plant, mostly with a thicker,

more woody root. In the description of *S. pseudopolaris* FLODERUS already emphasized its close similarity to *S. polaris*. The case may be worth a closer study.

338. In the Alaskan Flora *Salix Dodgeana* was taken in a narrow sense and only very small specimens, similar to those in the Rocky Mts, were referred to that taxon. PORSILD (Nat. Mus. Canada Bull. 216, 1966 p. 25) adopted a somewhat wider concept and ARGUS (1969 p. 795) included material referred to *S. rotundifolia* in the Alaskan Flora, transferring *S. Dodgeana* to *S. rotundifolia* as a subspecies. Perhaps the Alaskan plant is merely an ecological variety occurring in exposed places. The marcescent leaves at the base of the plant could indicate this.

340. According to LÖVE (Íslensk ferðaflóra) *Salix arctica* occurs in a single locality on Iceland.

341. The type specimen of *Salix torulosa* in the Leningrad Herbarium differs considerably from the Alaskan plant thus named in HULTÉN 1968. SKVORTZOV proposed the name *Salix sphenophylla* SKVORTZ. subsp. *pseudotorulosa* SKVORTZ. (Spisok rast. Herb. Fl. SSSR 91 No 4524, 1966) for the Alaskan plant and this is accepted. It differs from *S. sphenophylla* (*S. cuneata* TURCZ. not NUTT.) in having pubescent capsules. The narrow extension to Altai on the Circumpolar map should be removed.

341. Range extension for *Salix sphenophylla* to Barter Island and Cape Dahlousie according to ARGUS 1973 p. 88.

343. As mentioned in the Alaskan Flora, *Salix glacialis* ANDERSS. is in the writer's opinion the hybrid *S. arctica* × *ovalifolia*. It was transformed to *S. ovalifolia* var. *glacialis* (ANDERSS.) ARGUS in Canad. Journ. Bot. 47, 1969 p. 798.

344. SKVORTZOV (1968 p. 122) treats *Salix nummularia* and subsp. *tundricola* as pure synonyms.

345. *Salix hebecarpa* was regarded as being different from *S. fuscescens* because of its glabrous capsules. The capsules of *S. fuscescens* are pubescent when young, but glabrescent when old. SKVORTZOV (1968 p. 127) takes *S. hebecarpa* FERN. as a synonym of *S. fuscescens*, which should perhaps be accepted. Alaskan specimens agree exactly with those from the Gaspé Penins., and Gaspé should be added to the Circumpolar map of *S. fuscescens* on p. 343.

346. The *Salix ovalifolia* complex is still very obscure in Alaska. ARGUS transferred *S. arctolitoralis* HULT. to a variety of *S. ovalifolia* in Canad. Journ. Bot. 47, 1969 p. 795.

347. *Salix Maccallianae* ROWLEE was reported from Watson Lake in south-eastern Yukon and along Liard R. in adjacent British Columbia in ARGUS 1973 p. 39, map 5. Its range is from Fort Simpson and the Canadian Rocky Mountains to Lake Mistassini in Quebec.

348. Range extension of *Salix brachycarpa* to Oregon and California acc. to MUNZ: Suppl. California Fl. (1968) p. 122.

351. In ARGUS 1973 p. 123 the name *Salix rigida* MÜHL. is preferred before *S. Mackenzieana*, until the complex has been studied closer. Range extension to several localities in SE Yukon is reported.

352. *Salix myrtilifolia* var. *pseudomyrsinitis* is regarded as a distinct species, *S. novae-angliae* ANDERSS. by CRONQUIST (HITCHCOCK et al. 1968). ARGUS in VIERECK & LITTLE 1972 p. 101 accepts this view. According to the map there it is sympatric with *S. myrtilifolia* in Alaska, where hybrids probably occur, but extends to California and S Utah in the Rocky Mts.

352. *Salix pyrifolia* ANDERSS. was reported from Palmer Lake on the western flanks of the Mackenzie Mts in Yukon in ARGUS 1973 p. 147. This is an extreme out-

post locality. Otherwise that species ranges from the vicinity of Lake Athabasca and Little Slave Lake eastwards to northern Labrador and Newfoundland, south to Lincoln Co., Wisconsin, southern Ontario and Maine, with outpost localities in northeastern British Columbia.

353. *Salix amplifolia* COV. was discussed in HULTÉN, Fl. Alaska & Yukon 3, 1943 p. 543, and considered closely related to *S. Hookeriana* BARRATT. ARGUS in VIERECK & LITTLE 1972 p. 106 actually refers it to that species. The taxon was excluded from HULTÉN 1968, as the material available was very poor and not uniform (hybrids with *S. Barclayi*?).

According to ARGUS *S. Hookeriana* is common in Yakutat Bay (from where *S. amplifolia* was described), and also occurs on Middleton I. (apparently reported as *S. Barclayi* by THOMAS). It also occurs on the Queen Charlotte Is and extends to Washington and NW California. Reports from Asia are erroneous according to SKVORTZOV 1968 p. 208. In ARGUS 1973 p. 135 a map of the range in Alaska and N British Columbia is given.

354. *Salix padophylla* RYDB. is called *S. monticola* BEBB by CRONQUIST in HITCHCOCK et al. 1964. This name is accepted by ARGUS in VIERECK & LITTLE 1972 p. 108 and by ARGUS 1973.

356. *Salix Drummondiana* BARRATT, a very doubtful taxon of *S. alaxensis* affinity, was reported by WELSH & RIGBY (1971 b p. 45) from three localities in northern British Columbia. For identity compare with the discussion in RAUP, The Willows of W Amer. p. 91.

358. It is now considered that the old interpretation of *Salix depressa* L. by FRIES and the majority of later authors is erroneous, and that this name is a synonym of the very different *S. lanata*. The combination *S. depressa* subsp. *rostrata* (ANDERSS.) HULT. thus becomes meaningless. It seems evident that *S. Bebbiana* SARG. is a link in a chain of

closely related taxa that should be regarded as subspecies of one species. To find the oldest name for this complex that is acceptable from all points of view seems impossible, as practically every author dealing with the problem proposes a different solution.

SKVORTZOV (1968 p. 173) extends the range of *S. Bebbiana* to northern Scandinavia, a view that hardly seems acceptable. In Fl. Europea 1 p. 51 that taxon is called *S. xerophila* FLOD. Until a better nomenclatural solution can be found it may be better to retain the name *S. Bebbiana* for the very characteristic Alaskan taxon.

On ARGUS's map in VIERECK & LITTLE 1972 p. 117 Kodiak is excluded from the range. *S. Bebbiana*, however, occurs there although not so commonly. See HULTÉN Fl. Alaska & Yukon p. 544 and HULTÉN 1969 p. 64.

Cf. discussion to map 125 in HULTÉN 1971.

359. Together the European—West Asiatic *Salix phyllicifolia* L., the Asiatic—West American *S. pulchra* CHAM. and the American *S. planifolia* form a circumpolar series of very closely related taxa. Transitions occur between them where the ranges overlap. The oldest name for this complex is *S. phyllicifolia*. In HULTÉN 1971 p. 136 the author transferred *Salix pulchra* to *S. phyllicifolia* as a subspecies. ARGUS, however, transferred *S. pulchra* to the later-described *S. planifolia* as a subspecies (Canad. Journ. Bot. 47, 1969 p. 798). In the same place a map of "*S. planifolia* subsp. *pulchra* (with pubescent twigs) var. *yukonensis*" is found (p. 800).

Cf. discussion to map 127 in HULTÉN 1971.

360. In ARGUS 1973 *Salix subcoerulea* PIPER is regarded as a pure synonym to *S. Drummondiana*.

362. In the key p. 334 *Salix boganidensis* and *S. arbusculoides* were separated on pubescence of leaves only. Studying

specimens of *S. boganidensis* from Asia and *S. arbusculoides* from Alaska the writer was unable to find any constant difference in the two populations. Specimens with completely glabrous leaves were not seen from Alaska but occur in Saskatchewan. Specimens with very sparse pubescence also occur in Alaska. An attempt to separate the northeastern Asiatic specimens from the Alaskan on a subspecies basis failed. It therefore seems necessary to regard *S. arbusculoides* ANDERSS. as a synonym of *S. boganidensis* TRAUTV.

The type sheet of *S. boganidensis* contains a mixture of two taxa. The name was therefore discarded and replaced by *S. kolymensis* SEEM. However, according to the present nomenclatural rules the name is valid for one of the components. One of the components is *Salix pulchra* CHAM. (recognized by its persistent stipules), and as for the other component the name *S. boganidensis* is valid. SKVORTZOV (Fl. Arctica URSS 5 p. 99) proposed that *S. boganidensis* should be understood as follows:

S. boganidensis TRAUTV. Fl. Boganid. in Middend. Sibir. Reise 1, 2, Bot. Abt. 1, 1847 p. 154 pro parte: quoad pl. fol. augustis subtus pilosis in tab. 2 (non tab. 3).

363. *Salix lasiandra* also occurs (rarely) on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

364. It is difficult to follow the discussion in CALDER & TAYLOR 1968 concerning *Myrica gale*. Among other differences, the plant from the Pacific coast is undeniably more pubescent than the European one which represents typical *M. gale*, even if single specimens can be found where the variation overlaps. The Pacific plant is therefore referred to var. *tomentosa* in order to account for this fact. It is impossible to agree with the conclusion in CALDER & TAYLOR: "there is no justification for recognizing the Pacific coast population of Western North America as var. *tomentosa*." On the other hand it

should be admitted that the racial conditions within America are far from clear.

Cf. map 199 in HULTÉN 1958 and Fl. Alaska & Yukon 4 pp. 571—572.

364. Concerning the genus *Betula* compare with the discussion to maps 81—82 and 128 in HULTÉN 1971.

368. The taxon called *Alnus fruticosa* RUPR. from easternmost Siberia agrees completely with the inland taxon in Alaska (subsp. *sinuata* excluded). The writer is unable to see any difference between it and *A. crispa* from NE America. Cf. JURTEV et al. 1972 p. 769. The most rational course would be to regard *A. viridis* as a circumpolar species with a fairly large number of subspecies, among which are subsp. *crispa* and subsp. *sinuata*, but the decision should be delegated to the monographer.

369. The valid name for *Alnus oregona* NUTT. should be *Alnus rubra* BONG. in Mem. Acad. St. Petersburg. 6: 2, 1832 p. 162. It has been considered to be a later homonym of *Betula-Alnus rubra* MARSHALL, Arb. Amer. 20, 1785 and therefore not valid. However, at that time *Alnus* had not been separated from *Betula* and the name *rubra* should thus be regarded as belonging to the genus *Betula*. GAERTNER in 1790 was the first to separate *Alnus*, as a genus, from *Betula*. *Alnus rubra* BONG. consequently becomes the valid name. Cf. HITCHCOCK in Vasc. Pl. Pacific NW 2, 1964 p. 74.

371. According to specimens seen *Urtica dioica* L. sens. lat., reported by CALDER & TAYLOR 1968 from the Queen Charlotte Is, belongs to the taxon named *U. Lyallii* in HULTÉN 1968, not to the, in America, introduced European type. Range extension for *Urtica Lyallii* to Lake Nerka (Tikchik & Wood Lake distr.), ROBERSON in Hb Fairbanks, verified by MURRAY.

372. Following KUIJT (Nat. Mus. Canada Bull. 186, 1961 p. 140) the dwarf mistletoe of Alaska was referred to *Arcuthobium campylopodum* f. *tsugense*. In their mono-

graph on the genus "Biology and Classification of Dwarf Mistletoes (*Arceuthobium*)" (US Forest Service Agricult. Handb. No. 401, 1972) HAWKSWORTH & WIENS regard it as a species, *A. tsugense* (ROSEND.) G. N. JONES, ranging along the coast from Alaska to central California and chiefly growing on *Tsuga* species, while *A. campylopodum* is a species essentially occurring south of the glaciation, from N Washington to Lower California and growing on *Pinus ponderosa*. The morphological differences are small, *A. campylopodum* having staminate spikes c. 5 mm long, less than 3 times as long as broad, while they are over 5 mm long in *A. tsugense*. The basal internodes in that taxon are usually rounded. The question can be raised whether these two taxa are not merely ecological races. CALDER & TAYLOR 1968 p. 308 are more categorical, as they "do not recognize f. *tsugensis* GILL., as there seems little justification for recognition of taxonomic entities based entirely on host specificity".

376. Range extension for *Rumex graminifolius* to the St. Elias Mts acc. to MURRAY 1971 b p. 301.

377. The name *Rumex acetosa* L. subsp. *lapponicus* HITONEN, Suomen Kasvio, 1933 p. 298 antedates subsp. *alpestris* (SCOP.) LÖVE 1944 for this taxon.

379. The plant from Tin City (Seward Penins.) described from a single specimen as *Rumex arcticus* var. *perlatus* HULT. (Fl. Alaska & Yukon 4 p. 600) agrees perfectly with the description of *R. acetosa* subsp. *pseudoxyria* TOLM. in Fl. Arct. URSS 5 p. 152. In JURTSEV et al. 1972 p. 770 where a map of its range is presented, it is reported from easternmost Chukotka.

382—383. The maps of *Rumex maritimus* subsp. *maritimus* and subsp. *fuegianus* have regrettably been interchanged.

392. As suspected in the Alaska Flora *P. humifusum* PALL. ex LEDEB. Fl. Ross. 3, 1851 p. 531 is identical with *P. caurianum* ROBINS. according to PETROVSKY in

Fl. Arct. URSS V p. 169. The drawing in Fl. SSSR V, tab. 41: 5 does not represent this taxon. Range extension to the Anderson R. 30 miles above the delta according to CODY & PORSILD 1968. The closest Siberian locality known is Anadyr.

396. The possibility of retaining *Monolepis Nuttalliana* distinct from *M. asiatica* FISCH. & MEY. seems doubtful. Specimens from the Sadlerochit R. (SPETZMAN 1196) are very similar to those from the lower Lena (BULUN, NILSSON-EHLE). The variation of the Siberian plant is unknown, as very little material was seen.

405. Range extension of *Claytonia tuberosa* to the Mackenzie Mts 63°14'N, 127°18'W according to CODY & PORSILD 1968 b.

405. In Canad. Journ. Bot. 50: 9, 1972 p. 1895 MCNEILL described a new species, *Claytonia ogilviensis*, known only from a single locality in the Ogilvie Mts, Yukon. It is very close to *C. umbellata* WATS., a rare plant growing S of the glaciation in Oregon, Nevada and California.

406. In Fl. Alaska & Yukon 4 p. 643 the writer described a fragmentary specimen of an unidentified *Claytonia* and compared it with the description of *C. Vassilievii* KUSEN. PORSILD later described the Alaskan—Yukon plant as *C. Bostockii*. In Bot. Notiser 124, 1971 pp. 90—92 Ö. NILSSON referred both *C. Vassilievii* and *C. Bostockii* to the genus *Montiastrum*, proposed by RYDBERG. Without mentioning this transfer JURTSEV (Bot. Zhurn. 57: 6, 1972 p. 644) created a new genus *Claytoniella*, consisting of these two taxa. NILSSON in his key separates the two taxa in the following way:

Caespitose, with no repent stems. Flowering shoots with one upper leaf. All leaves linear, sessile. Tepals about twice as long as the involucre. Bracts broadly ovate. *M. Vassilievii*
Stems repent with ascending floriferous many-leaved shoots. Basal leaves narrowly oblanceolate ± distinctly petiolate. Tepals about three times as long as the involucre. Bracts ovate *M. Bostockii*

In Bot. Zhurn. 56, 1971 p. 679 PETROVSKI states that, after having compared the type of *C. Vassilievii* and the specimens from Wrangel I. with PORSILD's picture of *C. Bostockii* and the drawing in HULTÉN 1968 p. 406, he had come to the conclusion that the two taxa belong to the same species.

The most important difference between the two taxa in Ö. NILSSON's key is that *C. Vassilievii* is said to be caespitose, while *C. Bostockii* has a repent stem. This is a mistake and agrees poorly with the description of *C. Vassilievii*, which begins: "Perennis, rhizoma tenue, longum, repens, ramosum, caules floriferos et surculos steriles foliosos emittens . . ."

On the type sheet of *C. Vassilievii* runners can also be seen, although disconnected from the flowering stem and mounted in an upright position. Both plants thus have a repent stem.

In Bot. Zhurn. 48: 8, 1963 p. 1192 ALESCHINA presents a picture of the pollen of *C. Vassilievii*. Fine pictures of the pollen of *C. Bostockii* have been published by MCNEILL & FINDLEY in Canad. Journ. Bot. 49: 5, 1971 pl. 1 (opposite p. 714). The pollen is extremely characteristic and there seems to be no major difference in the pollen structure of the two taxa.

This was also the opinion of the Swedish pollen expert, Dr SIVERT NILSSON.

In JURTSEV et al. 1972 p. 770 *Claytoniella Vassilievii* is reported from Koolen in easternmost Chukotka, a locality bridging the gap between the two ranges.

Specimens from Wrangel I. agree very well with alpine specimens of *C. Bostockii* collected by the Kaskawulsh Glacier, in the St Elias Mts by D. F. and M. MURRAY and the writer must regard the two taxa as belonging to a single species, the oldest name of which is *Claytonia Vassilievii* KUSEN. Compare GRICHUK in GITERMAN et al. 1973 pp. 79—80.

407. Range extension for *Claytonia arctica* to St Lawrence I. acc. to YOUNG 1971.

408. Remarkable range extension of *Claytonia sarmentosa* to N Lake Baikal region acc. to MALYSHEV 1972 map 128.

409. A locality of *Claytonia (Crunocallis) Chamissoi* in SW Manitoba is marked on NILSSON's map in Bot. Notiser 123: 1, 1970 p. 139.

412. In Fl. Arctica URSS 6 p. 29 the range of *Stellaria media* is extended to Dudinka (lower Jenisej R.), Khatanga and the SE Chukotsk Penins.

416. None of the specimens reported as *Stellaria calycantha* in CALDER & TAYLOR 1968 p. 332 belongs to that species. They belong to *S. sitchana* var. *sitchana* (e.g. 21857 and 22597) or to var. *Bongardiana* (e.g. 21699 and 36357).

417. A map of the localities of *Stellaria umbellata* from NE Siberia is published in Fl. Arctica URSS 6 p. 19. To this should be added Wrangel I. acc. to PETROVSKY 1973 p. 118. The mark of interrogation on the Circumpolar map in the Alaskan Flora should be replaced by a dot.

418. *Stellaria monantha* was reported from Wrangel I. in PETROVSKY 1973 p. 118.

419. In Bot. Notiser 1943 pp. 251—270 the writer tried to bring some order into the very complicated *Stellaria longipes* complex. Later the American taxa were discussed by BÖCHER (Bot. Tidsskr. 48: 4, 1951 pp. 401—402) and by PORSILD (Bull. Nat. Mus. Canada 186, 1963 pp. 1—35). In Fl. Arctica URSS 6 a very different treatment is presented where the very variable pubescence of the leaves is regarded as a characteristic of superior importance. As is readily seen from the key in that work, this leads to a very bewildering taxonomy, and the writer must refrain from trying to identify the taxa accepted there. A totally new monographic study is needed to coordinate the above-mentioned treatments and to make possible reasonable decisions. It remains to be added that the taxa on both sides

of the Bering Strait are, as far as the writer can see, identical whatever they are named.

421. The high-arctic, densely tufted and densely pubescent phase of *Cerastium Beerlingianum* was distinguished as subsp. *Bialynickii* (TOLM.) TOLM. in Fl. Arctica URSS 6 p. 45. It can possibly be regarded as a poorly differentiated high-arctic race.

425. *Cerastium arvense* was reported from Wrangel I. in PETROVSKY 1973 p. 118.

426. The very unexpected report of *Sagina procumbens* from Queen Charlotte Is by CALDER & TAYLOR (1968 p. 328), also said to be common in cultivated fields along the Pacific coast, could not be checked as the specimens were not available for loan. Compare map 106 in HULTÉN 1958.

426. Acc. to the map in Fl. Arctica URSS 6 p. 55, localities should be added on the Circumpolar map of *Sagina saginoides*, from the lower Olenek R., the lower Lena, Kolyuchin Bay and tributaries of the lower Kolyma R. Also reported from central Honshu, Hokkaido and Sakhalin (OHWI's Japanese Flora) and from the southern Kuril Is.

427. The treatment of *Sagina crassicaulis* by MIZUCHIMA (Journ. Jap. Bot. 35: 11, 1960 p. 335) calls for comment. He refers the entire Pacific population to *S. maxima* A. GRAY, but believes that the plants from Kamchatka and Alaska are annuals. This is certainly not the case, they are at least biennials. The seeds of the northern plant are said to be smooth, not agreeing with the figure in HULTÉN, Fl. Kamchatka 2, 1928 p. 78. That is not so. The seeds of the Kamchatkan and Alaskan plant agree well with the picture. Seen under the microscope the structure can best be observed on the margin of the seed.

The title of MIZUCHIMA's paper is "A preliminary revision of the genus *Sagina* in Japan and its adjacent regions". In the

final revision he may arrive at a different conclusion. Thus, for instance, he also includes inland specimens in *S. maxima*. In the northern Pacific the taxon under discussion is strictly littoral.

In OHWI's Japanese Flora the range of *S. maxima* is given: Hokkaido, Honshu to Korea and Formosa, while the plant occurring from Hokkaido northwards and eastwards is referred to var. *crassicaulis* (S. WATS.) HARA. *S. maxima* must be regarded as a doubtful name of the Alaskan Plant.

432. The occurrences in Siberia of *Minuartia yukonensis* should be removed. They were based on misidentified specimens of *M. arctica*.

433. In Fl. Arctica URSS 6 the name *Minuartia rubella* is reserved for northern single-flowered specimens, while somewhat more southern specimens with branched stems are referred to *M. verna* (L.) HIERN. According to the maps both reach Chukotka. In the key *M. verna* is said to be loosely tufted with a stem up to 10 cm long and 2—3-flowered. The calyx is green, 3 mm long, the fruit is shorter than the sepals and the seeds 0.4—0.5 mm in diam. The petals are longer than in *M. rubella*.

M. rubella is said to be densely tufted with a stem up to 5 cm long and single-flowered. The calyx is purplish, 3—4 mm long, the fruit is longer than the sepals and the seeds 0.6—1 mm in diam. The petals are short. Transitions admittedly occur along the contact line.

In the Alaskan material the writer is unable to find any such correlation between the characters mentioned.

In Scandinavia *M. verna* is usually distinguished on petals longer than the calyx. In the more than 100 collections from Alaska examined no specimen has petals longer than the calyx, rarely as long as the calyx, but some have branched inflorescences. That southern specimens are taller and have more than one flower is not surprising.

The possibility of dividing the Siberian material into two species seems doubtful.

433. In Fl. Arctica URSS 6 p. 64 *Minuartia Rossii* var. *elegans* was transferred to subsp. *elegans* (CHAM. & SCHLECHT.) REBRISTAJA. The reason why the writer does not regard it as a subspecies is that it is ecologically, but not geographically, separated from the common strongly tufted type in Alaska.

M. orthotrichoides SCHISCHK. was erroneously referred to *M. Rossii* as a variety by the writer in the Alaskan Flora. According to Fl. Arctica URSS it belongs to *M. rubella*. The writer was misled by the diagnosis, where the very short stems are said to be subglabrous, by the densely tufted habitus and the northern Arctic locality. The stems of *M. rubella* are glandular.

434. The Arctic race of *Honckenyia peploides*, occurring in northern Alaska, is subsp. *diffusa* (HORNEM.) HULT., Fl. Aleut. Is. p. 173.

435. According to the map in Fl. Arctica URSS 6 p. 77, only the range east of the Kolyma R. refers to *Arenaria capillaris*, characterized by a glabrous stem. The rest of the range marked on the Circumpolar map refers to *A. formosa* FISCH. with a glandular stem. In Alaska some specimens have stems or peduncles with a few glands.

435. JURTSEV et al. 1972 p. 770 report *Arenaria longipedunculata* from Penkignei in southeasternmost Chukotka. A specimen from St Lawrence Bay in the Lenin-grad Herbarium also belongs here.

436. Russian authors refer *Arenaria Chamissonis* to the genus *Stellaria*. The petals are not clearly bifid as in that genus, but reduced and irregularly lobed, or lacking. The seeds were examined by the Swedish seed specialist, GRETA BERGGREN. According to her they have the same form and sculpture as the seeds of *Minuartia biflora*, but are much larger and more distinctly sculptured. The capsule is one-seeded.

The pollen is according to a report from the Palynological Laboratory in Stockholm of *Arenaria* type, not similar to *Stellaria* pollen. The general appearance of the plant is not that of a *Stellaria*, and there seems to be little reason to refer it to that genus.

437. *Moehringia lateriflora* also occurs on the Queen Charlotte Is acc. to CALDER & TAYLOR 1968.

438. In DOROGASTAJSKAJA 1972 *Spergula arvensis* is reported from the lower Ob R. and Khatanga.

440. On the line leading to *Silene Menziesii* subsp. *Menziesii* the "mm" should be cm.

440. Acc. to the map in Fl. Arctica URSS 6 p. 99 *Silene acaulis* (subdivision uncertain) occurs westwards to the Kolyma R. and southwards to Kamchatka and Copper I.

443. *Silene cucubalus* was reported from Alaska by DEARBORN in Weeds 7, 1959 p. 269 as a weed "affecting agriculture". No specimen has been seen by the writer.

444. *Melandrium* is admittedly a heterogeneous genus. In an attempt to better understand the taxa traditionally referred to *Melandrium* authors come to widely differing conclusions. American authors usually refer them to the genus *Lychnis*. In Fl. Arctica URSS 6 they are referred to the genus *Gastrolychnis* (= *Wahlbergella*) according to the key differing from *Silene* in being perennial, monoecious, with petals as long as or somewhat longer than the calyx. CHAWDHURI (Notes R. Bot. Gard. Edinb. 22, 1957 pp. 221—278) unites them with the gigantic genus *Silene*, a policy followed by Flora Europaea and by BOCQUET (Revisio Physolychnidum. — Phanerogam. Monogr. 1, 1969), which involves numerous nomenclatural changes and problems.

As stated in HULTÉN 1967 p. 54, a conservative nomenclature is used in Fl.

Alaska and neighboring territories, pending BOCQUET's treatment.

An attempt to improve the nomenclature and taxonomy so that they correspond with more modern views follows here:

445. The name *Melandrium apetalum* is replaced by *Silene Wahlbergella* CHAWDHURI loc. cit. p. 237 in Fl. Europaea. Synonyms are: *Lychnis apetalata* L., *Melandrium apetalum* (L.) FENZL, *Silene uralensis* (RUPR.) BOCQ., *Gastrolychnis apetalata* (L.) TOLM. & KOZH.

Alaskan specimens belong to *Silene Wahlbergella* CHAWDHURI **subsp. arctica** (Fr.) Hult., **comb. nov.**

Wahlbergella apetalata β *arctica* Fr. in Öfvers. Vet. Akad. Förh. (Stockholm) 1869 p. 133.

They differ from the Scandinavian type in having petals longer than the calyx.

For a review of the conditions see HULTÉN 1971, discussion accompanying map 54.

Melandrium Soczavianum SCHISCHK. (*Silene Soczaviana* (SCHISCHK.) BOCQ.), a plant related to *Silene Wahlbergella* subsp. *arctica* (*Melandrium apetalum* subsp. *arcticum*), was reported from Alaska in Fl. Alaska & Yukon p. 704, but not in Fl. Alaska and neighboring territories. It is a somewhat doubtful taxon, collected only a few times, but no specimen agreeing with its type-specimen has been seen from Alaska. The type has upright flowers and fruits and dark violet petals twice as long as the calyx.

445. *Melandrium macrospermum* receives the name *Silene macrosperma* (PORS.) HULT. 1971 p. 326, with the synonyms *Silene uralensis* subsp. *Porsildii* BOCQ. and *Gastrolychnis macrosperma* (PORS.) TOLM. & KOZH. Apart from Alaska it also occurs in NE Siberia (see map in Fl. Arctica URSS 6 p. 115).

446. The identity of *Silene furcata* RAF. with *Melandrium affine* is most doubtful and possibly erroneous. The name *Silene furcata* RAF. used in Fl. Europaea is

rejected, and *Silene involucrata* (CHAM. & SCHLECHT.) BOCQ. accepted. *Gastrolychnis affinis* (VAHL.) TOLM. & KOZH. is regarded as a synonym. For a review see the discussion to map 10 in HULTÉN 1971.

446. Acc. to BOCQUET the name *Melandrium triflorum* becomes *Silene Sorensenis* (BOIV.) BOCQ., if the taxon is transferred to the genus *Silene*.

In Fl. Arctica URSS 6 it is regarded as the hybrid *Gastrolychnis apetalata* \times *affinis* (= *Silene involucrata* \times *Wahlbergella*). If this is so, its range is most surprising. It is common on Greenland, but known from a few collections in Asia only and is completely lacking in Scandinavia where the two supposed parent species are sympatric. Also morphologically this view seems improbable. The taxon is characterized by tuberculate seeds, lacking membranous margin, and dense tomentose-glandular pubescence in its upper part. It was reported from Wrangel I. in PETROVSKY 1972 p. 119.

447. *Melandrium Taylorae* becomes *Silene Taylorae* (ROBINS.) HULT. 1971 p. 313, if transferred to the genus *Silene*, and *Melandrium taimyrense* becomes *Silene taimyrense* (TOLM.) BOCQ. In Fl. Arctica URSS 6 both these taxa are united under the name of *Gastrolychnis angustifolium* subsp. *tenella* (TOLM.) TOLM. The total ranges are not settled. Specimens belonging to *S. taimyrense* were reported from Wrangel I. by PETROVSKY (1971) as *M. Ostenfeldii*. BOCQUET reports a specimen of *S. Taylorae* under the name of *S. involucrata* subsp. *tenella* from the Black Duck R. in the southern Hudson Bay area.

The key in Fl. Arctica URSS 6 to the genus *Gastrolychnis* clearly illustrates the difficulties involved in distinguishing significant taxa within this much-discussed group.

448. Range extension for *Dianthus repens* to the northern Baikal area acc. to MALYSHEV 1972 map 145.

451. Several new localities for *Ceratophyllum demersum* within the boundaries of the Alaskan map have been reported. In LIKENS & JOHNSON 1968 p. 13 it is reported from Yukon Flats (L. Ohtig). HARMS (1969 p. 253) reports it from Northway and CH. HOLMQUIST gives a map of finds in northern Alaska and Mackenzie in Bot. Notiser 124, 1971 p. 338.

C. demersum is easily overlooked and this is certainly the reason why it has not yet been found in NE Siberia.

452. *Caltha biflora* and *leptosepala*. SMIT & PUNT (K. Nederl. Wetensch. Proc. Ser. C, 72: 1, 1969) came to the conclusion that *C. biflora* and *C. leptosepala* could not be separated as distinct species. Consequently *C. biflora* was reduced to *C. leptosepala* subsp. *biflora* (DC.) P. G. SMIT.

In the Alaskan material no transition between the two quite distinct taxa could be observed. According to CALDER & TAYLOR 1968 all specimens from the Queen Charlotte Is belong to typical *C. biflora*.

Cf. MORRIS in Brittonia 24, 1972 p. 177.

453. Small high-Arctic specimens of *Caltha palustris* such as those from Pt Barrow, agree with the type specimen of *C. arctica* R. BR. in the British Museum, but also with what is called *C. caespitosa* SCHIPCZ. in Fl. Arctica URSS 6. See discussion to maps 75—76 in HULTÉN 1971.

454. Range extension of *Trollius Riederianus* to Lake Baikal acc. to MALYSHEV 1972. The northern part of the range as shown on the map belongs according to Fl. Arctica URSS 6 p. 138 to *T. membranostylis* HULT. and should thus be removed.

458. In the Alaskan Flora *Delphinium brachycentrum* is treated in a broad sense. In Fl. Arctica URSS 6 the *Delphinium* taxa of NE Siberia are divided into six taxa. The name *D. brachycentrum* LEDEB. is reserved for plants with leaves not cleft to the base or close to the base.

After having studied the collections in

the Leningrad Herbarium the writer agrees to separate the plant from the lower Lena R. and Alaska as *D. Chamissonis* PRITZ., differing from *D. brachycentrum* for instance in the deeply cleft leaves with narrow lobes, as seen on the drawing p. 458 of the broad-lobed *D. brachycentrum*, occurring in Kamchatka. Specimens with fairly broad lobes also occur in Alaska, as for instance that collected at Toklat in McKinley Park by MURIE on Aug. 2, 1964 (S). That the variation is considerable in Alaska is evident from the fact that this *Delphinium* has been described from Alaska under three names: *D. Blaisdellii* EASTW., *D. Ruthae* NELS. and *D. alatum* NELS.

The synonym *D. Maydelianum* TRAUTV. belongs to *D. brachycentrum*.

A peculiar dimorphism was observed in some specimens. They have finely cut basal leaves, but broad-lobed stem leaves.

459. Surprisingly, CALDER & TAYLOR are reluctant to recognize any intraspecific taxa of *Aconitum delphinifolium* in central and southeastern Alaska, because they have been unable to distinguish the two subspecies *Chamissonianum* and *delphinifolium* "in all instances". Had it been possible to distinguish them in all instances they would have been treated as species, as REICHENBACH did. The reason why they are treated as subspecies is that the two taxa form geographically differentiated populations, although the morphological variation overlaps, in this case only slightly. The differences are well illustrated in the drawings in the Alaskan Flora.

460. JURTSSEV (Fl. Arctica URSS 6 p. 161) transferred *Aconitum delphinifolium* subsp. *paradoxum* to *A. delphinifolium* subsp. *delphinifolium* var. *paradoxum* (RCHB.) JURTSSEV. This is surprising as Russian authors, approving the KOMAROV school of species concept, usually regard Arctic dwarf specimens not as races, but as distinct species. It is true that subsp. *paradoxum* is not a very well differentiated race, but its dwarfed growth and the

mostly single, large flower makes it a very characteristic taxon which in large parts of its range is not sympatric with other segregates of *Aconitum delphinifolium*.

462. *Anemone Richardsonii* also occurs on Wrangel I. (PETROVSKY 1973 p. 119) and along the lower Yana R.

466. *Anemone Drummondii* has been reported from several localities in Chukotka (as *A. multiceps*) according to Fl. Arctica URSS 6 p. 168. It also occurs at Korf Bay (formerly Baron Korf Bay) N of Kamchatka.

466. A review of the very varying opinions concerning the status and name of the *Pulsatilla patens* complex is given in the discussion accompanying map 140 in HULTÉN 1971. A new view has since been presented by TOLMATCHEV in Fl. Arctica URSS 6 pp. 171—174, where the Alaskan plant is named *P. Nuttalliana* DC. subsp. *Nuttalliana*, differing to a considerable extent from the eastern Siberian subsp. *multifida* (PRITZ.) AICHELE & SCHWEG. in the broadness of the leaves and intensity of the colour of the flowers. In the writer's opinion *P. Nuttalliana* clearly belongs to the *P. patens* complex and should be included in subsp. *multifida*.

469. The drawings have been interchanged. The uppermost one illustrates *R. trichophyllus* var. *hispidulus*, the lower one var. *trichophyllus*.

470. It might be preferable to regard *Ranunculus confervoides* as a segregate of *R. trichophyllus* as in Fl. Europaea. Its name will then be *R. trichophyllus* subsp. *eradicatus* (LAEST.) COOK in Mitteil. Bot. Staatssaml. München 6, 1967 p. 622. On COOK's map this taxon is also marked for the Caucasus and a place that is impossible to identify in Central Asia. Acc. to PETROVSKY 1973 p. 119 it occurs on Wrangel I.

471. *Ranunculus hyperboreus* occurs on the Queen Charlotte Is acc. to CALDER &

TAYLOR 1968. Due to a technical mishap most of the range in Greenland is missing on the Circumpolar map in the Alaskan Flora. The species is common in most parts of unglaciated Greenland, more rare in the southeastern part.

473. *Ranunculus glacialis* subsp. *Chamissonis* is called *Beckwithia Chamissonis* (SCHLECHT.) TOLM. in Fl. Arctica URSS 6 p. 178. The genus *Beckwithia* is separated from *Ranunculus* on account of the persistent sepals.

As reasons for regarding the Atlantic and Beringian taxa as distinct species are given differently cut leaves and the fact that the Scandinavian plant, representing the type of *R. glacialis*, is a high-alpine plant, while the Beringian taxon grows up to 5—600 m only. It should be remembered that the Scandinavian coast is washed by the warm Gulf-stream. In E Greenland, between 70° and 73°30' *R. glacialis* occurs at between 400 and 700 m acc. to SØRENSEN (Meddel. Grønland 101: 3 p. 54) and in its northernmost localities only on the outer, warmer coast.

A good reproduction of the Beringian plant is given in Fl. Alaska & Yukon 4 p. 755.

It is impossible to understand the statement in Fl. Arctica URSS that the Beringian plant is more closely related to the Rocky Mountain *R. Andersonii* A. GRAY than to the Atlantic *R. glacialis*. Probably no specimen of the rare *R. Andersonii* had been seen. It is also stated that the Beringian plant has larger flowers (2—3 cm in diam.) than the Scandinavian one which is supposed to have flowers as small as 1.5—2 cm in diam. Scandinavian specimens of *R. glacialis* with flowers 4 cm in diam. are not rare, very few specimens being small-flowered.

474. Range extension of *Ranunculus reptans* to St Lawrence I. acc. to YOUNG 1971.

475. The gap between the Asiatic and American ranges of *Ranunculus cymbalaria* is partly filled out by finds in the Yana R. basin and on Karaginsk I. in northern Kamchatka.

475. Range extension of *Ranunculus Eschscholtzii* to the Queen Charlotte Islands. According to Fl. Arctica URSS 6 p. 207 *Ranunculus Eschscholtzii* does not occur in Chukotka. The basis for the reports was misidentified *R. nivalis*.

That the race of *R. Eschscholtzii* in Kamchatka was described as subsp. *Hultenianus* by BENSON (Amer. Midl. Nat. 52, 1954 p. 354) has escaped the attention of Russian authors.

476. Range extension for *Ranunculus sulphureus* to the Mackenzie Mts 63°05'N, 128°50'W acc. to CODY & PORSILD 1968 b.

477. Range extension of *Ranunculus gelidus* subsp. *Grayi* to the Udokan Mts NE of Lake Baikal acc. to MALYSHEV 1972 p. 95. A very remarkable find about halfway between the central Asiatic and eastern Asiatic areas of *R. gelidus*.

478. The discussion on *Ranunculus pygmaeus* in CALDER & TAYLOR 1968 p. 354 is most surprising and must depend on lack of familiarity with the Arctic and Scandinavian plants. *R. pygmaeus* is not a very variable plant or "a highly polymorphic species", on the contrary it varies little in its circumpolar distribution. See discussion to map 58 in HULTÉN 1968.

That the writer has taken "occasionally robust plants of this species that occur along the Arctic coast as a distinct race *R. pygmaeus* var. *Sabinei* (R. BR.) KURTZ" is wrong. That real *R. pygmaeus* sometimes has glabrous peduncles is also wrong. Pubescent peduncles is a constant character of the circumpolar *R. pygmaeus*. The plant with glabrous peduncles, which CALDER & TAYLOR have studied, certainly belongs to the still taxonomically unclear *R. Eschscholtzii* complex. CALDER & TAYLOR should read the comments on *R. Sabinei* in BENSON's monograph and

in Fl. Arctica URSS 6 p. 209, where it is strongly argued that *R. Sabinei* is a distinct species. The possibility that *R. Sabinei* is a more or less stabilized hybrid between *R. nivalis* and *R. pygmaeus* is proposed in HULTÉN 1968. The existence of *R. Sabinei* var. *majusculus* TOLM. (Fl. Arctica 6 p. 211) somewhat strengthens this view.

480. *Ranunculus punctatus* JURTSEV was described from western Chukotka (Nov. Syst. Pl. Vasc. 6, 1969 p. 302). It was later reported by JURTSEV et al. 1972 from easternmost Chukotka (Pinakul). It belongs to the, in Alaska, very variable *R. pedatifidus* complex. According to JURTSEV it differs from *R. pedatifidus* (or *R. affinis*) in the linear-lanceolate stem-leaves, in the form of the radical leaves and in the oblanceolate to obovate petals, which are scarcely longer than the sepals. These characters are very variable in the Alaskan population of *R. pedatifidus*, and the taxon belongs to *R. pedatifidus* subsp. *affinis* in a broad sense.

486. *Ranunculus Turneri* was reported from easternmost Chukotka in Fl. Arctica URSS 6 (map p. 223) and from Wrangel I. (PETROVSKY 1973 p. 119). It is closely related to or doubtfully distinct from *R. borealis* TRAUTV. which should be regarded as a northern indigenous race of *R. acris*. In the key in Fl. Arctica URSS *R. Turneri* is said to differ from *R. borealis* in having a dense pubescence, thick peduncles, flowers 2—3 cm in diam. and large seeds 3.5—4 mm long with a 1—1.2 mm long curved beak. At the mouth of the Lena R. it is said to be replaced by *R. Turneri* subsp. *jacuticus* (OV CZ.) TOLM., a tall taxon with a branched, less pubescent stem.

486. *Ranunculus monophyllus* Ovcz. was reported from Utaveem and Penkignei in easternmost Chukotka by JURTSEV et al. 1972 p. 771. It is an Eurasiatic taxon of the very complex *R. auricomus* group with a single cordate-rounded basal leaf. Nothing like it has been seen from Alaska.

486. *Oxygraphis* is undoubtedly a weak genus and it would be wiser to refer *O. glacialis* to the genus *Ranunculus* as many authors have done. The persistent sepals hardly constitutes generic character. Its name then becomes *Ranunculus kamtschaticus* DC.

TUTIN in Fl. Europaea refers this plant, together with *R. glacialis* L. (= *Oxygraphis vulgaris* FREYN), to the section *Cymodes* (A. GRAY) TUTIN of the genus *Ranunculus*.

488. In MELA & CAJANDER, Suom. Kasv. 1906 p. 276 the combination *Thalictrum minus* **kemense* (FR.) MELA & CAJ. is made. If the asterisk is meant to denote a subspecies and not a variety this is an older combination than *Th. minus* subsp. *kemense* HULT. in Fl. Alaska & Yukon 4, 1944 p. 774. The same combination was again made by TUTIN in Fl. Europaea 1 p. 242.

The Asiatic range should be extended northwards to the mouth of the Anadyr R. according to the map in Fl. Arctica URSS 6 p. 229.

490. A very remarkable extension of the range of *Papaver Walpolei* to the Ogilvie Mts, Yukon, was reported in PORSILD 1972 p. 236.

491. *Papaver alboroseum* is a polymorphic plant and practically all specimens seen differ somewhat from one another. The low growth, the white or rose petals with yellow basal spots, the ovate to globose capsule with stiff setae are characters common to them all, while the cutting of the leaves is variable. It was collected on Attu I. by Mrs MAXCINE WILLIAMS and reported from the Sheep Glacier, St. Elias Mts by MURRAY (1971 b), as well as from British Columbia 57°01'N, 127°26'W by WELSH & RIGBY (1971 b).

498. In describing *Thlaspi arcticum* in Sargentia 4, 1943 p. 40, PORSILD remarks that *Th. cochleariforme* DC. "of mountains of Western Siberia" differs from *Th. arcticum* "by the marcescent old leaf-

bases, pubescent flowering stems, and the barely elongated fruiting raceme".

Length of raceme and withering of basal leaves change during the lifetime of a specimen. No conclusion in this respect can be drawn from single specimens. Specimens from Altai as well as those from Tixi at the mouth of the Lena R. have glabrous flowering stems. The description of *Th. cochleariforme* in Fl. SSSR 8 p. 587 begins by stating that the entire plant is glabrous. The Tixi specimens are a perfect match to the Alaskan plant, which should thus be named *Th. cochleariforme* DC. The type came from the Jablonoj Mts in Dahuria. The type specimen in Geneva is a much taller plant than the Arctic ones. *Th. cochleariforme* ranges from Karakorum and Tian-shan to Altai, the Sajon Mts and Dahuria and to the mouth of the Lena R. with an outlying station at Kyshtymski zavod in the southern Urals. In Fl. SSSR it is stated that one pair of the petals in *Th. cochleariforme* is 6—7.5 mm long, the other pair 5—6.5 mm. As only fruiting specimens lacking petals were seen from Tixi as well as from Alaska this character could not be checked.

In Mem. N. Y. Bot. Gard. 21: 2, 1971 p. 64 PATRICIA HOLMGREN discusses *Th. arcticum*. She concludes that additional collecting may show it to be worthy of being accorded varietal rank within *Th. montanum* rather than specific status. She regards *Th. cochleariforme* DC. as a synonym of *Th. montanum* L.

499. In Nov. Syst. Pl. Vasc. 6, 1969 pp. 67—106 POBEDIMOVA presents a revision of the genus *Cochlearia*, where she divides it into 22 species. The circumpolar population is considered to consist of two largely sympatric species, *C. arctica* with 14—16 seeds in each pod, and *C. groenlandica* with 2—6 seeds only. According to the maps both these "species" occur in the northern Bering Sea area.

In Fl. Europaea *C. groenlandica* is distinguished from *C. arctica* (which is

called *C. fenestrata* R. BR. there), on quite another character, a leafless stem. In BÖCHER et al. Fl. of Greenland the Greenland plant is said to have stems with oblong spatulate leaves, and the specimen in the Linnaean Herbarium, which has been considered the type of *C. groenlandica* L., has a leafy stem. *C. groenlandica* merely seems to be the Arctic dwarf form of *C. officinalis* from ecologically unfavourable habitats.

POBEDIMOVA also presents a map of the American range of "*C. oblongifolia*" and a most doubtful map of *C. sessilifolia* ROLLINS. The latter is distinguished from all other *Cochlearias* in having sessile basal leaves. *Cochlearias*, however, produce long-petiolate rosette leaves the first year which die more or less early in the next year. The lowest sessile stem-leaves should not be taken for basal leaves. Specimens with sessile basal leaves were not seen from Alaska.

POBEDIMOVA's treatment hardly contributes to a clarification of the situation within the Bering Sea area.

The writer's conception of the complex is presented in the discussion to map 178 in HULTÉN 1971.

500. Range extensions for *Aphragmus Eschscholtzianus* to Rainbow Mt, the Alaska range (63°68'N, 145°17'W) according to MURRAY 1971 b p. 308.

503. *Sinapis arvensis* is a common weed in Arctic Siberia, occurring in most inhabited places according to DOROGASTAJSKAJA 1972.

507. The American taxa of the genus *Rorippa* were treated monographically by STUCKEY in Sida 4: 4, 1972 pp. 277—430, based on the study of some 6000 specimens. This study has resulted in a number of corrections in the taxonomy and nomenclature of all the Alaskan taxa of this critical genus. Distribution maps are also presented in the study. The following notes on the Alaskan members of this genus are his conclusions. The NW Euro-

pean species were studied by JONSELL (Symb. Bot. Upsal. 19: 2, 1968).

507. STUCKEY excludes the white-flowered water-cress from the genus *Rorippa*. Its name then becomes *Nasturtium officinale* R. BR. In Fl. Europaea this plant is also referred to the genus *Nasturtium*.

508. *Rorippa islandica* (OEDER) BORB., based on *Sisymbrium islandicum* OEDER is according to JONSELL (p. 151, map p. 56) a diploid European plant, different from the tetraploid circumpolar *R. palustris* (L.) BESS.

508. The coastal *Rorippa palustris* population, (*Rorippa* no. 2) in the Alaskan Flora, was divided into two taxa by STUCKEY, subsp. *glabra* (O. E. SCHULZ) STUCKEY var. *cernua* (NUTT.) STUCKEY with siliques mostly shorter than 7 mm and stigma expanded or unexpanded in fruit, and subsp. *occidentalis* (S. WATS.) ABRAMS with siliques mostly longer than 7 mm and stigma unexpanded in fruit.

508. The inland population named *R. islandica* subsp. *Fernaldiana*, (no. 3 in the Alaskan Flora), was referred to *R. palustris* subsp. *palustris* var. *Williamsii* (BRITT.) HULT., differing from *R. palustris* subsp. *palustris* var. *palustris* in the acute apex of the basal leaves, with an angle of c. 40°—80° (—100°), compared with (60°—) 80°—120° in var. *palustris*, and the apex of the middle cauline leaves with an angle of c. 30°—60° (—70°), compared with (40°—) 60°—120° in var. *palustris*, and siliques obtuse at the apex, compared with the acute or pointed apex in var. *palustris*. Var. *Williamsii* is, according to map 15, endemic approximately N of 60°N in western N America. Subsp. *Fernaldiana* is according to STUCKEY confined to eastern America and characterized by having siliques restricted at the middle.

509. *Rorippa hispida* (no. 4 in the Alaskan Flora) was called *R. palustris* subsp. *hispida* (DESV.) JONSELL, Symb. Bot. Upsal. 19: 2, 1968 p. 159. It is characterized by leaves hispid on the lower

surface, and stems hirsute usually up to the terminal raceme. Hybridization between var. *Williamsii* and subsp. *hispida* is regarded as probable by STUCKEY. According to JONSELL this taxon does not occur in Asia. The Asiatic range should thus be excluded from the Circumpolar map.

509. *Rorippa hispida* var. *barbareaefolia* (no. 5 in the Alaskan Flora) is considered to be a distinct species, *R. barbareaefolia* (A. DC.), not very closely related to *R. palustris* subsp. *hispida* by JONSELL (Sv. Bot. Tidskr. 65, 1971 p. 299) and by STUCKEY. Its siliques are 4-, rarely 5-valved, the style in fruit thick, 0.5—1 mm wide, and the stem villous especially in the lower part.

The area in eastern America marked on the Circumpolar map is erroneous due to misidentification. A map of the Asiatic range is given by JONSELL p. 300.

510. Acc. to STUCKEY the name of *Rorippa obtusa* should be *R. curvipes* GREENE. Alaskan specimens were not mentioned by STUCKEY. The Alaskan report is based on a single specimen from Juneau, ANDERSON 6265 (S).

510. STUCKEY (p. 317) refers Alaskan specimens of *R. curvisiliqua* to var. *procumbens* STUCKEY.

512. In HULTÉN 1967 p. 62 a peculiar variation of *Cardamine bellidifolia*, var. *pinnatifida* HULT., was described. It is similar to although not identical with *C. sphenophylla* JURTS. in Nov. Syst. Pl. Vasc. 9, 1972 p. 184, from the type locality in easternmost Chukotka. The possibility of both these plants being hybrid segregates of *C. bellidifolia* and *C. microphylla* should be considered. Other peculiar aberrant specimens from Cape Beaufort in NW Alaska with low fertility strengthens this view. Siliques of *C. sphenophylla* are not known.

516. In the comments to the Alaskan Flora (HULTÉN 1967 p. 62) it was even then admitted that the name *Cardamine*

hyperborea SCHULZ should be replaced by *C. digitata* RICHARDS. By some mistake it was still named *C. hyperborea* in the Alaskan Flora.

516. Russian authors use the name *Cardamine hyperborea* SCHULZ for the plant named *C. microphylla* in the Alaskan Flora. *C. minuta* ADAMS is a distinct taxon, not seen from Alaska.

517. Range extension for *Cardamine purpurea* to Wrangel I. according to PETROVSKY 1973 p. 120.

517. *Lesquerella arctica*, earlier known from Wrangel I., is also reported from eastern Chukotka in JURTSEV et al. 1972. JURTSEV remarks that the siliques can be densely, less densely or not at all pubescent in this plant.

517. From the Ogilvie and Richardson Mts in Yukon Territory MULLIGAN & PORSILD described a new species, *Lesquerella Calderi*. It differs from *L. arctica* in having petals 7—9 mm long, abruptly narrowed below the middle, siliques up to 8 mm long, constricted at the replum, and with stellate hairs on the flowering stem mostly 0.2—0.3 mm in diam. *L. arctica* has 5—6 mm long, gradually narrowed petals, siliques less than 7 mm, not constricted at the replum, and stellate hairs 0.4—0.5 mm in diam. The chromosome number of *L. Calderi* is $n=10$, while that of *L. arctica* is $n=30$. A specimen from "Upper Yukon R. near Eagle", collected by E. H. JONES in 1910 (S), belongs to the new taxon, which is here regarded as a subspecies of *L. arctica*:

Lesquerella arctica (WORMSKJ.) S. WATS. subsp. *Calderi* (Mull. & Pors.) Hult., comb. nov.

L. Calderi MULLIGAN & PORSILD in Canad. Journ. Bot. 47: 1, 1969 p. 215.

To distinguish the two taxa when petals are not present is very difficult.

522. *Draba crassifolia* was reported from the Kaskavulsh Nunatak, St Elias Mts by MURRAY (1968 p. 107).

523. *Draba lonchocarpa* was reported from Wrangel I. in PETROVSKY 1973 p. 121. A check might be desirable.

524. The identity of *Draba caesia* and *D. Palanderiana* was discussed by PETROVSKY (Nov. Syst. Pl. Vasc. 1971 pp. 140—146). His conclusion is that *D. caesia* ADAMS is a plant very close to *D. nivalis*, known from a single locality at the mouth of the Lena R., where transitions to that species also occur. Under such circumstances the question arises whether or not *D. caesia* is a hybrid. After having examined the type of *D. caesia* the writer agrees with PETROVSKY. *D. Palanderiana* differs from *D. caesia* in having bright yellow petals, less pubescent pedicels and sepals, and somewhat longer styles. The name of *Draba* no. 6 in the Alaskan Flora should thus be *D. Palanderiana* KJELLM.

529. PORSILD (1972 p. 236) reports *Draba barbata* POHLE from the Ogilvie Mts, Yukon, as new to N America. Earlier reports exist but were probably based on *D. barbata* var. *Treleasii* SCHULZ, according to MULLIGAN a synonym of *D. Paysonii*. *D. barbata* is similar to *D. macrocarpa*, but differs in having branched hairs on both sides of the leaves, while *D. macrocarpa* has simple hairs on the upper side.

529. Range extension for *Draba alpina* to the mountains NE of Lake Baikal according to MALYSHEV 1972 map 173.

530. *Draba Paysonii*, *D. ventosa* and *D. ruaxes*. These taxa belong to a group of extremely closely related plants of the Rocky Mountain system. All were reported from Alaska by MULLIGAN (Canad. Journ. Bot. 49, 1971 p. 1456). He separates them as follows:

Long-stalked stellate hairs on both surfaces of the leaves *D. ventosa*
 Only under-surfaces of leaves with long-stalked stellate hairs; upper leaf surface with long, simple or once- or twice-forked hairs; Stem and pedicels with simple, rarely forked hairs, leaves greater than 2 mm broad
 *D. ruaxes*

Stem and pedicels with stellate and forked, rarely simple, hairs; leaves less than 2 mm broad *D. Paysonii*

The possibility of retaining these taxa as distinct species in areas where they are sympatric seems questionable.

MULLIGAN reports *D. Paysonii* MACBR. from Mt Harper in central Alaska, a locality disjunct from southern British Columbia according to his map on p. 1457. The specimens were collected by GJÆREVOLL and have practically no branched or stellate hairs. They agree better with *D. densifolia*, to which they were referred by GJÆREVOLL. They do not fit the description of *D. Paysonii* according to MULLIGAN's key.

D. ruaxes PAYSON & ST. JOHN was reported (as *D. ventosa* var. *ruaxes*) from Mt Crillon by HITCHCOCK in "A revision of the Drabas of Western N America" p. 58, "with considerable doubt". Maps of its distribution were published by MURRAY (1971 b p. 302) and by MULLIGAN (1971 b p. 1457), the latter showing a disjunction from S British Columbia to Yukon—Alaska.

In the above-mentioned paper MULLIGAN published a map of *D. ventosa* A. GRAY, where it is marked from the Rocky Mts in Alberta to Colorado, but not in Alaska. However, in 1970 he determined a specimen collected by the writer at Seward to that taxon. In the Alaskan Flora it is called *D. exalata* EKM.

Too little material of this complex group has been seen by the writer to allow an opinion to be formed as to its Alaskan representation, especially as practically all specimens are incomplete, lacking fruits and flowers.

532. Iceland was omitted from the range of *Draba hirta* on the Circumpolar map.

533. A specimen of *Draba kamtschatica* was collected at Cape Nome, Seward Penins. (LEPAGE 23813, S). *D. kamtschatica* was reported from the mountains NE of Lake Baikal by MALYSHEV 1972 map 175.

534. MULLIGAN in his study of *D. glabella* and its close allies (Canad. Journ. Bot. 48: 8, 1970) gives the following key characters for separating *D. borealis* and *D. hirta* (*glabella* of American authors, *davurica* of Russian authors):

Surfaces of basal leaves mostly with unbranched cruciform stellate hairs *D. borealis*
 Surfaces of basal leaves with branched, cruciform stellate hairs *D. glabella*

This gives a conception of *D. borealis* somewhat different from the usual. In his maps p. 1432 he extends the range of *D. borealis* to the southern Canadian Rockies, the Great Bear Lake and Victoria Land. *D. hirta* is a complex with several puzzling forms, and the plants in the extended range merely belong to that complex. The range of *D. borealis* should, however, be extended eastwards to the Meade R. in Arctic Alaska.

535. As stated in the original description of *Draba maxima*, it is closely related to *D. borealis* and can be taken as a race of that taxon. WELSH & RIGBY (1971 b) transferred *D. maxima* to a variety of *D. borealis* (not quoting the basionym) and at the same time added a locality in N British Columbia.

536. According to MULLIGAN the name *Draba lanceolata* ROYLE was misapplied by SCHULZ, and FERNALD, on writing his paper "Draba in temperate northwestern America" relied on him.

MULLIGAN regards *Draba cana* RYDB. as the correct name for this taxon. He does not quote the difference between *D. lanceolata* and *D. cana*, but remarks: "*D. lanceolata* is from Western Himalaya and thus south of most of the range given for *D. lanceolata* in the Flora of the USSR".

The distributional pattern of *D. lanceolata*, as traditionally accepted, is that of an arctic montane, nearly circumpolar taxon, duplicated by that of many other taxa, and no reason for doubting the identity for phytogeographical reasons should exist.

A careful study of world-wide material,

including specimens from the western Himalayas, the type locality for *D. lanceolata*, is needed for a decision in this case. No Himalayan material has been seen by the writer.

538. *Draba ogilviensis* was reported (as *D. sibirica*) from the Mackenzie Mts 63°13'N, 128°40'W and from 63°05'N, 128°50'W by CODY & PORSILD (1968 b). A map of the range of the closely related *D. sibirica* is found in HULTÉN 1968 map 90.

539. A considerable extension of the range of *Smelowskia calycina* subsp. *integrifolia* to the St Elias Mts in Yukon was reported in MURRAY 1971 b. *S. calycina* shows the same variation on both sides of the Bering Strait. Thus *S. calycina* subsp. *integrifolia* var. *Porsildii* occurs also in Chukotka.

544. Some authors regard the *Arabis* taxa belonging to the section *Cardaminopsis* as a separate genus. They are taxonomically very intricate. The writer realized that material from northern Alaska differs from *Arabis lyrata* subsp. *kamchatica*, but misapplied the name *Arabis arenicola* var. *pubescens* for this taxon. It differs from *A. arenicola* in having uniseriate, narrower siliques and slightly more lobed, not fleshy leaves. A map of *Arabis arenicola* was published by CODY (1971 p. 152).

The northwestern Alaskan plant is identical with *Arabis media* BUSCH, Fl. Sib. Orient. Extrem. 1, 1913 p. 463, fig. p. 464. On a sheet in the Stockholm Herbarium from the middle Penschina R., collected by GORODKOV & TICHOMIROV, which exactly matches the Alaskan plant, ROLLINS wrote: "*Arabis petraea* LAM., probably a variety of it. Not *A. lyrata*". On Alaskan specimens WELSH noted "*A. lyrata* L. (a hairy phase)".

The northern Alaskan plant differs from *A. lyrata* subsp. *kamchatica* i.a. in having spatulate, entire or dentate basal leaves and smaller flowers. It is a member of the *A. petraea* complex and is distributed from the Jenisei R. eastwards.

553. The genus *Braya* presents unusual taxonomical difficulties, not yet even approximately solved. However, nothing indicates that the taxa differ on both sides of the Bering Strait.

554. *Braya purpurascens* was reported by MURRAY (1968 p. 302) from the St Elias Mts, near the southern end of Lake Kluane. MURRAY reports that PACKER discovered this plant in the mountains of S Alberta. However, from specimens examined, the Alberta plant belongs to *B. americana* (HOOK.) FERN.

555. *Braya pilosa* was reported from Wrangel I. in PETROVSKY 1973 p. 121.

Braya pilosa was transferred to *B. purpurascens* as a subspecies in HULTÉN 1971 p. 18.

556. JURTSSEV et al. 1972 report *Braya Bartlettiana* as well as *B. Bartlettiana* var. *vestita* from easternmost Chukotka. PETROVSKY (1973 p. 120) reports cfr. *B. Bartlettiana* from Wrangel I.

Braya Thorild-Wulfjii OSTENF. was reported from Mys Dezhnev (East Cape) and from Wrangel I. by JURTSSEV et al. 1972. The writer did not see the specimens.

Plants similar to the decumbent *B. Thorild-Wulfjii* and with quite pubescent fruits occur on the Arctic coast of Alaska (Wainwright, Barter I.) and were referred to *B. purpurascens* in the Alaskan Flora. Their fruits are less pubescent and not broader at the base as in the Greenland plant. In HULTÉN 1971 p. 18 *Braya Thorild-Wulfjii* was transferred to *Braya purpurascens* as a subspecies.

Braya glabella RICHARDS., a very critical taxon, was reported from the northern Ogilvie Mts on the Dempster Highway in PORSILD 1972.

558. On the Seward Penins. specimens of *Parrya nudicaulis* with broad, coarsely toothed leaves occur. Some are very sparsely glandular. They are considered

to represent transitions between subsp. *nudicaulis* and subsp. *septentrionalis*.

In a map of *Parrya arctica* (CODY in Nat. Canad. 98, 1971 p. 152) this taxon is marked for the Richardson Mts, W of the Mackenzie Delta. The specimen collected by BRYANT lacks leaves and is so fragmentary that the writer is unable to classify it. There is no evidence that it does not belong to *P. nudicaulis* subsp. *septentrionalis*.

Specimens with narrow leaves and glandular leaf-margins occur in north-eastern Siberia. Only a few specimens were examined, but they may belong to subsp. *interior*.

A *Parrya* with filiform leaves, glandular on the margin, occurs within an area in NE Siberia extending eastwards at least to Chaun Bay. No such specimens were seen from Alaska.

561. LÖVE et al. 1971 p. 150 claim that the Siberian and American *Sedum rosea* populations differ. The American plant is said to be polygamous, while the Asiatic one is dioecious. In support of this view they quote BORISSOVA in Fl. SSSR, who, however, says that *R. atropurpurea* has dioecious sometimes hermaphrodite flowers. There seems to be no difference in this respect between the two populations, and that the specimens from NE Siberia are identical with the Alaskan ones is clear.

The conditions in Alaska were discussed in Fl. Alaska & Yukon p. 897. It is remarkable that a tall yellow-flowered taxon close to the European type occurs there, although only a single specimen (Nome, THORNTON 314) was seen. CALDER & TAYLOR 1968 p. 375 report a yellow-flowered specimen from Kodiak (TRELEAS 4015). Specimens from the Queen Charlotte Is are yellow-flowered. A review of the very complicated *Sedum rosea* complex is given in HULTÉN 1958, maps 33 and 34. The name should be *Sedum rosea*, not *roseum*, as often seen. LINNAEUS spelt the

name *Rosea*, indicating that it is a generic name, used as a specific name, as in *Saxifraga Geum*, *Saxifraga Cotyledon* and many others.

565. *Saxifraga oppositifolia* L. SIPLIVINSKY (in Novit. Syst. Plant. Vasc. 1972: 9) divides the eastern Siberian taxa belonging to *S. oppositifolia* in a broad sense (=sect. *Porphyrion* TAUSCH) into five species. He considers *S. oppositifolia* L. to be circumpolar, lacking only in the Beringian sector, where according to him it is replaced by *S. pulvinata* SMALL. A general survey showed that specimens from Scandinavia, Iceland, Jan Mayen, Spitzbergen and the Siberian northern coast, west of the Lena R., all have sepals with rather stout ciliae, lacking glandular heads. All specimens from northeastern-most Siberia, from Alaska and Yukon and British Columbia, as well as all those from the Canadian Arctic Archipelago have sepals with slender, mostly capitate glands on the margin. Similar specimens also occur in northern Greenland from about 77° N on the western coast and 80° N on the eastern coast northwards. Greenland specimens south of these latitudes are similar to the Scandinavian ones. In the northern area in Greenland specimens which can be interpreted as more or less intermediate between the two types occur. In the area east of the Lena R. intermediates also occur according to SIPLIVINSKY. More southern American specimens, such as those from the Great Whale R., Lake Mistassini and Newfoundland lack glands. The reason why this difference and its geographical coordination has not been noticed long ago is probably that the sepals in young specimens are concealed by the leaves which always have stiff ciliae, and in old, withered fruiting specimens they disintegrate so that the margin is destroyed. However, IRMSCHER, too, noticed that the sepals were sometimes glandular, but found no geographical correlation, certainly on account of having too little

material (Das Pflanzenreich IV: 117, 1 p. 618). In Alaska two taxa with glandular sepals occur. One is *S. oppositifolia* subsp. *Smalliana* (*S. pulvinata* SMALL, *Antiphylla pulvinata* (SMALL) SMALL, *S. oppositifolia* var. *typica* subvar. *Smalliana* ENGL. & IRMSCH.). Typical specimens (see drawing in HULTÉN 1968 p. 565) are quite distinct, especially when seen growing. The leaves are small and stiff in four very distinct densely packed rows, the petals are short, the stems become prolonged after flowering and lack bracts in the upper part, the sepals are glabrous on the back and distinctly ciliate with capitate, slender glands.

The other taxon has larger, less densely packed leaves, flat, large, and thin when young, in much less distinct rows. The petals are longer, the scapes are short with large bracts to the tip, the sepals are often glandular-dotted or pubescent, on the back also ciliated with capitate glands. The material is, however, not always easy to divide into two distinct groups. The latter taxon is therefore here described as a subspecies which occurs especially in the coastal areas.

Saxifraga oppositifolia L. **subsp. glandulisejala** Hult., **subsp. nov.**

Sepala margine glandulis capitatis munita. Type specimen: Unimak I., False Pass. EYERDAM 1886. Aug. 1, 1932 (S).

It is noteworthy that a specimen from the Queen Charlotte Islands (CALDER & TAYLOR 3196) has less distinctly glandular sepals than Alaskan specimens.

It is apparently impossible to base taxonomical units on single collections, as SIPLIVINSKY did within the extremely polymorphous *S. oppositifolia* complex. A monographic study of the entire complex is needed. Compare with the treatment in Fl. Europaea I p. 377. For total range of the complex see HULTÉN 1971 map 62.

568. According to LÖVE et al. 1971 p. 152 the American—Asiatic *Saxifraga hirculus*, which they call *S. propinqua* R. BR., is diploid, while the European—

Greenlandic counterpart with its var. or subsp. *alpina* is tetraploid. The first one differs from the latter in habit, forming great, loose tufts with branches ending in shoots, and having narrower, ciliated leaves and smaller flowers. An attempt to divide the circumpolar material into two taxa with the geographical distribution proposed, failed. Specimens agreeing well with the Scandinavian ones occur in Alaska as well as in Siberia and *S. hirculus* subsp. *hirculus* thus appears to be a circumpolar taxon. The old population in Alaska is as usual richer in biotypes. All specimens have a rust-coloured pubescence at the base as well as towards the top going more or less far up on the lower part of the leaves. Occasionally single ciliae occur higher up on the leaves, but the leaves cannot be said to be really ciliate.

From map 66 in HULTÉN 1971 of the total range of *S. hirculus*, it is clear that this species occurs in several isolated areas from which no chromosome counts are known.

570. SIDLIVINSKY (Nov. Syst. Pl. Vasc. 8, 1971 pp. 147—158) divides the Asiatic material of the *S. bronchialis* complex (=sect. *Trachyphyllum* GAUD.) into 13 species. He suspects (p. 154) that the northern and southern areas of *S. bronchialis* subsp. *Funstonii*, as shown on the map in the Alaskan Flora, are populated by different races, the southern one characterized by its larger size, longer and broader leaves with large ciliae and large petals with the claw well visible between the sepals. The northern taxon was called *Saxifraga firma* LITW.

The writer was not able to separate the material into a northern and a southern taxon on these grounds. The variation in size, length of ciliation of the leaves and lush or compact growth is very considerable and not geographically, but ecologically correlated. The variation is similar to that in the related, but not critical, *S. tricuspidata*.

570. In the description of *Saxifraga bronchialis* subsp. *cherlerioides* in the Alaskan Flora it is erroneously stated that the leaves have a short, dense, glandular ciliation. The ciliae are actually of the same type as in subsp. *Funstonii*, lacking capitate glands.

A taxon with glandular ciliation of the leaves is *Saxifraga anadyrensis* LOSINSK., described in Fl. SSSR 9 p. 487, and occurring from the Lena R. to Peshina and Anadyr. The following specimens from Alaska were found to have few, but clearly capitate glands on the margins of the leaves: Upper Kobuk R., Lake Selby Aug. 21, 1964, E. HULTÉN, Lake Peters Aug. 24—26, 1960, E. HULTÉN. Although they are very similar to *S. anadyrensis*, the writer hesitates on geographical grounds to refer them to that taxon. Their ciliation somewhat resembles that of *S. tricuspidata*, which can occasionally have entire leaves, similar to those of *S. bronchialis*, but in other respects the specimens do not resemble that species. The possibility that they represent the hybrid *S. bronchialis* subsp. *Funstonii* × *tricuspidata* should be considered.

572. In FEDDE, Rep. Spec. Nov. 69: 12, 1964 p. 153, WEBB pointed out that the type of *Saxifraga punctata* in the Linnaean Herbarium in London is not the plant that traditionally goes under that name, but a very different one which he identified as *Saxifraga davurica* WILLD. sens. lat. The Linnaean specimens are more precisely *S. Redowskyana* STERNB. and not *S. davurica* WILLD. in a narrow sense. A specimen in the Linnaean Herbarium in Stockholm, labelled "Siberia 13 *punctata*" is also that species. LINNAEUS quotes tab. 9. fig. 7 in MORRISON, Plant. Hist. Univ. Oxoniensis III (1699) as a synonym. This drawing shows the same plant. Under such circumstances it is not possible to retain the name *S. punctata* for the plant traditionally bearing that name. WEBB considers *Saxifraga Nelsoniana* D. DON (Transact. Linn. Soc. 13, 1821 p. 355) the

oldest name in the complex. The European—Siberian plant then becomes *S. Nelsoniana* subsp. *aestivalis* (FISCH. & MEY.) WEBB and *S. punctata* subsp. *Nelsoniana* in the Alaskan Flora becomes *S. Nelsoniana* subsp. *Nelsoniana*.

The following new name combinations will be necessary:

Saxifraga Nelsoniana subsp. **insularis**
(Hult.) Hult., comb. nov.

Saxifraga punctata subsp. *insularis* HULT. in Sv. Bot. Tidskr. 30, 1936 p. 524, fig. 5.

Saxifraga Nelsoniana subsp. **pacifica**
(Hult.) Hult., comb. nov.

Saxifraga punctata subsp. *pacifica* HULT. in Fl. Alaska & Yukon 5, 1945 p. 928.

Saxifraga Nelsoniana subsp. **Porsildiana**
(Calder & Savile) Hult., comb. nov.

Saxifraga punctata subsp. *Porsildiana* CALDER & SAVILE in Canad. Journ. Bot. 38, 1960 p. 429.

Saxifraga Nelsoniana subsp. **Charlottae**
(Calder & Savile) Hult., comb. nov.

Saxifraga punctata subsp. *Charlottae* CALDER & SAVILE in Canad. Journ. Bot. 38, 1960 p. 429.

Saxifraga Nelsoniana subsp. **reniformis**
(Ohwi) Hult., comb. nov.

Saxifraga reniformis OHWI in Acta phytotax. et Geobot. 2, 1922 p. 25.

Saxifraga Nelsoniana subsp. **cascadensis**
(Calder & Savile) Hult., comb. nov.

Saxifraga punctata subsp. *cascadensis* CALDER & SAVILE in Canad. Journ. Bot. 38, 1960 p. 425.

577. Range extension of *Saxifraga rivularis* (reported as *S. hyperborea*) to the Lake Baikal region according to map 197 in MALYSHEV 1972.

578. The name of *Saxifraga* no. 28 in the Alaskan Flora should be *S. calycina* STERNB. Rev. Saxifr. Suppl. 2 p. 10 tab. XXI. The picture of *S. calycina* there agrees very well with the drawing in the Alaskan Flora. STERNBERG's rare work was not available when the writer was working up the genus *Saxifraga* for the Alaskan Flora. Under the name *S. grandipetala*

(ENGL. & IRMSCH.) A. LOS. Russian authors mean a different although closely related taxon not occurring in Alaska, with the more branched inflorescence having thin nearly capillary branches. It is merely a northern race or subspecies of *S. davurica*. According to a specimen in Stockholm it is the *S. davurica* f. *gracilis* of KJELLMAN. The type of *S. calycina* came from St Lawrence Bay. The range of *S. davurica* in the map of the total area should be eliminated.

579. *Saxifraga* no. 29 in the Alaskan Flora agrees with *S. unalaschcensis* STERNB. It is merely the coastal race of *S. calycina*, occurring in the Bering Sea area.

Saxifraga calycina STERNB. subsp. **unalaschcensis** (Sternb.) Hult., comb. nov.

Saxifraga unalaschcensis STERNB., Rev. Saxifr. Suppl. 2 p. 9 tab. XXI.

The drawing in Fl. SSSR 9 tab. VII fig. 2 is this taxon rather than *S. calycina* subsp. *calycina*, as seen from the shape of the leaves and the broad, large petals. In *S. calycina* the petals are smaller and narrower, nearly clawless. Intermediates between subsp. *calycina* and subsp. *unalaschcensis* occur in the Bering Strait area, but not on the Aleutian Islands.

579. The taxon described as *Saxifraga tenuis* is accepted as a distinct species, apparently on cytological grounds, by a number of authors. According to PETROVSKY 1973 both this taxon and *S. nivalis* occur on Wrangel I. The same is the case in the Lake Baikal area according to MALYSHEV 1972.

It is remarkable that no specimens agreeing well morphologically with *S. tenuis* were seen from Alaska. Compare discussion to map 37 in HULTÉN 1971.

580. In Canad. Journ. Bot. 50: 11, 1972 pp. 2131—2141 KRAUSE & BEAMISH present a revision of taxa related to *S. occidentalis* in British Columbia, close to the Alaskan border (58°10'N, 132°07'W). *S. occidentalis* is very closely related to *S.*

reflexa. In habit Alaskan specimens of that taxon agree completely with the photograph of *S. occidentalis* Pl. 1, fig. 5 B in KRAUSE & BEAMISH. In the Alaskan specimens the young leaves are pubescent on the upper side, with short more or less viscid projections which in old leaves fall off or are reduced to a few black dots. In *S. occidentalis* the upper side of the leaves are essentially glabrous, although projections of the same type as in the Alaskan plant occur occasionally. The sepals are spreading in young flowers, later reflexed in both taxa. Thus *S. occidentalis* is here transferred to *S. reflexa* as a subspecies:

Saxifraga reflexa HOOK. **subsp. occidentalis** (S. Wats.) Hult., **comb. nov.**

Saxifraga occidentalis S. WATS. in Proc. Amer. Acad. 23, 1888 p. 264.

The specimen from Rose Lapie Pass, PORSILD & BREITUNG 10066, reported as *S. reflexa* in Bot. Mus. Canada Bull. 121 p. 209, belongs to subsp. *occidentalis* as does the specimen reported as *S. occidentalis* var. *rufidula* by WELSH & RIGBY (1971 b) from N British Columbia 56°50'N, 127°18'W. On *S. reflexa* PORSILD writes: "The species is very variable as to stature, degree of pubescence and amount of branching: thus, in most colonies specimens varying in height from 8 to 30 cm may be observed. In dry habitats the leaves are hoary pubescent, whereas in moist places they may be almost glabrous . . . An equal variation was noted by the writer in the type locality (Arctic Coast east of the Mackenzie Delta)".

It would be very natural to also regard *S. Marshallii* GREENE as a subspecies of *S. reflexa* that developed south of the area of glaciation during the ice age.

583. Range extension of *Saxifraga cespitosa* to the Queen Charlotte Is acc. to CALDER & TAYLOR 1968.

584. *Heuchera glabra* was reported by WELSH & RIGBY (1971 b) from northern British Columbia (56°47'N, 127°17'W) at an altitude of about 1500 m.

585. *Tellima grandiflora* was found by ROBERSON at Seldovia. This indicates that the two ranges marked on the map should be united.

586. *Mitella trifida* GRAHAM in New Phil. Journ. Edinb. 1822 p. 185. This species was found at the junction of Chilcot road and Mosquito Creek by Mrs MAXCINE WILLIAMS. New to Alaska and adjacent territories.

M. trifida differs from *M. pentandra* in having whitish petals, palmately trifid at the apex, and stamens opposite the calyx lobes. *M. pentandra* has greenish petals, pectinately dissected into 6—10 filiform segments, and stamens opposite the petals. The range extends southwards to N California and S Montana.

587. In Bot. Zhurn. 57:6, 1972 p. 646 JURTSEV described *Chryso-splenium rimosum* KOM. subsp. *dezhnevii* from easternmost Chukotka, close to Mys Dezhnev (East Cape). It is a plant with opposite leaves not seen from Alaska. It differs from the Kamchatka type in its smaller size, 2—3 cm, and different anthocyanin colouring and is thus an Arctic form of that species.

587. The drawing of *Chryso-splenium tetrandrum* is in natural size, not in half natural size, as indicated. Specimens up to 20 cm tall occur, however, on the southern coast of Alaska.

587. A considerable range extension of *Chryso-splenium Wrightii* to the Mackenzie Mts at 64°45'N, 129°28'W was reported in CODY & PORSILD 1968 b.

589. Range extension for *Parnassia Kotzebuei* to Wrangel I. according to PETROVSKY 1973.

590. *Ribes lacustre* also occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

591. Range extension of *Ribes hudsonianum* to Lake Aleknagik, collected by ROBERSON.

599. The conditions within the *Amelanchier* complex were discussed in HITCHCOCK et al. 1961 p. 93 and in CALDER & TAYLOR 1968. It seems impossible to retain *A. alnifolia* and *A. florida* distinct at species level. The name for *A. florida* in HITCHCOCK et al. is *A. alnifolia* var. *semi-integrifolia* (HOOK.) HITCHC. It is here regarded as a coastal race of *A. alnifolia*.

Amelanchier alnifolia (NUTT.) NUTT. **subsp. florida (Lindl.) Hult., comb. nov.**

Amelanchier florida LINDLEY in Bot. Reg. N.S. 6, 1833, Pl. 1589.

The drawings in the Alaskan flora are not representative of the respective taxa.

604. SINJKOVA (Nov. Syst. Pl. Vasc. 9, 1972 pp. 191—197) discusses the *Rubus idaeus* complex in the Soviet Union. The paper is apparently a preliminary survey. *R. idaeus* subsp. *melanolasius* is divided into two taxa with the names *R. sachalinensis* LÉV. (*R. melanolasius* var. *discolor* KOM.) and *R. Komarovii* NAKAI (*R. melanolasius* var. *concolor* KOM.). They are referred to "Ser. 1 *Strigosi* SINJK.", while *R. idaeus* is referred to "Ser. 2 *Idaei* SINJK."

See discussion to map 121 in HULTÉN 1971.

Range extension to March Mt. near Lake Aleknagik, collected by ROBERSON.

605. Range extension for *Rubus leucodermis* to the SW Kenai Penins. according to VIERECK & LITTLE 1972 p. 177.

606. CALDER & TAYLOR (1968) report two types of *Fragaria chiloensis* from the Queen Charlotte Is, subsp. *pacifica* STAUDT with spreading hairs on the stem and sepals, and subsp. *lucida* (E. VILM.) STAUDT with appressed hairs on the sepals. In the Alaskan material no specimens with appressed hairs occur. The occurrence of hybrids with cultivated strawberries is doubted by CALDER & TAYLOR. A number of specimens from inhabited places in Alaska are probably such hybrids or backcrosses.

612. Range extension of *Potentilla uniflora* to Putoran Mts between lower Jenisei and Khatanga according to Nov. Syst. Pl. Vasc. 10, 1973 p. 281.

615. JURTSEV et al. 1972 report *Potentilla arenosa* (TURCZ.) JUZ. as common in central and eastern Chukotka. *P. Hookeriana* is given as a synonym with a mark of interrogation added. The specimens agree with *P. Hookeriana* subsp. *Hookeriana*.

616. *Potentilla Chamissonis* was reported from Wrangel I. in PETROVSKY 1973 p. 122.

617. According to DOROGASTAJSKAJA 1972 *Potentilla multifida* was collected at Provideniya (Port Providence) in SE Chukotka. Probably anthropochorous there.

624. *Sibbaldia procumbens*. Range extension to Mt. Akuluktok at Lake Nerka, collected by ROBERSON. Determination kindly controlled by VIERECK and MURRAY.

627. CODY & PORSILD (1968 p. 269) report range extensions of *Geum Rossii* to the Richardson Mts and the Mackenzie Mts between 67°57'N and 62°35'N, which thus partly fill the gap between the northern and the Rocky Mts areas.

627. In the writer's opinion *Geum Schofieldii* CALDER & TAYLOR in Canad. Journ. Bot. 43, 1965 p. 1394, figs. 148—150, is one form of the hybrid series *G. calthifolium* × *Rossii*, not rare on the Aleutian Islands. Thus specimens from Unimak I. False Pass, EYERDAM 1882 agree well with the type of *G. Schofieldii* which consequently, even if regarded as a species, is not endemic on the Queen Charlotte Islands.

628. Very remarkable range extension of *Geum glaciale* to the northern Lake Baikal area in MALYSHEV 1972, map 216.

629. The extremes of the *Dryas* taxa in Alaska are certainly very different morphologically, but as more material accumulates, it becomes increasingly clear that

they are joined by forms that can only arbitrarily be referred to the distinct species proposed. In nature 3—4 different types can be observed growing side by side. CODY & PORSILD (1968 b) report *Dryas Hookeriana* Juz. from SE Yukon, thus adding to the polymorphy. *D. Hookeriana* is very closely related to *D. octopetala* subsp. *alaskensis*, differing in shorter scapes, and in leaves more tapering towards the apex and with more incised teeth. Russian authors report *D. Chamissonis* SPRENG. from Chukotka. In the writer's opinion it is a form of the hybrid *D. integrifolia* × *octopetala*. The type came from Kotzebue. Anyhow, similar specimens occur on both sides of the Bering Strait.

JURTSEV believes that *D. octopetala* prefers calcareous soil, while this is not the case with *D. punctata*, taxa treated as separate species by Russian authors. MALYSHEV 1972 pp. 110, 204 admits, however, that many transitions between them, which according to him should be treated as hybrids, occur in the Stanovyje Mts. *Dryas octopetala* var. *kamtschatica*, reported by WELSH & RIGBY (1971 a, b) from northern Yukon and northern British Columbia, does not belong to that taxon but to several other taxa including subsp. *alaskensis* and *D. integrifolia* - *octopetala* hybrids. Cf. discussion to map 45 in HULTÉN 1971.

632. *Sanguisorba officinalis* also occurs on the Queen Charlotte Is, at Elfin Cove in SE Alaska according to Mrs M. WILLIAMS in a letter, in northern British Columbia 58°20'N, 128°45'W according to WELSH & RIGBY 1971 b p. 44 and by Lake Nerka (Tickchik and Wood Lakes), collected by ROBERSON.

634. LÖVE et al. 1971 maintain that *Rosa Sayi* is a well defined species, distinct from *R. acicularis*. In Alaska the differences between the Euroasiatic and the American plants break down completely. The American plant might, however, merit the rank of subspecies as proposed by

LEWIS in Brittonia 11, 1959 p. 19. For discussion see the comments on map 155 in HULTÉN 1971.

642. Range extension for *Trifolium repens* to Amchitka I. (SHACKLETTE et al. 1969). In DOROGASTAJSKAJA 1972 it is reported from the lower Ob R., Khatanga, the lower Lena R., Magadan and E Chukotka. It also occurs on South Georgia.

650. In Rhodora 75, 1973 p. 802 BARNEBY reports that *Astragalus Atlasovi* KOM. is a synonym for *A. polaris* BENTH. The range of *A. polaris* should consequently be extended to southern central Kamchatka. *A. Atlasovii* was also reported from Pekulney Mts in Anadyr by VASSILJEV.

659. *Oxytropis deflexa* var. *dezhevii* was described from easternmost Chukotka by JURTSEV. A collection fitting his description is D. F. & B. M. MURRAY 140 from Kaskavulsh nunatak, 6000 feet. This indicates that this taxon is an arctic-high-alpine ecological variation occurring both in easternmost Asia and in America.

659. Range extension of *Oxytropis arctica* to the St Elias Mts, 1800 m according to MURRAY 1971 b p. 303.

660. A remarkable range extension of *Oxytropis Scammaniana* to the Mackenzie Mts 63°46'N, 127°90'W was reported by CODY & PORSILD (1968 b p. 269).

661. The plant named *Oxytropis nigrescens* subsp. *pygmaea* (PALL.) HULT. agrees very well with the description and plate of *Astragalus pygmaeus* in PALLAS's Species Astragalorum p. 66 and tab. LIV from St Lawrence Bay, Chukotka. PALLAS's specimen was in fruit and the flowers were unknown to him. JURTSEV et al. 1972 p. 773 are of another opinion. They write (translated from the Russian text): "*O. gorodkovii* JURTZ. (*O. nigrescens* subsp. *pygmaea* HULT. non *Astragalus pygmaeus* PALL.). Utaveem; ur. Dezhneva, Pinakul, Penkignej. Dry calcareous mountain

tundra. On acid mountain soil the closely related *O. Tschuktschorum* JURTZ. (? *O. bryophila* /GREENE/ JURTZ.) is found".

The *Oxytropis nigrescens* complex, comprising very closely related taxa, is not yet well understood. Whatever the taxa are named the variation on both sides of the Bering Strait is the same judging from specimens seen.

664. *Oxytropis campestris* subsp. *Jordalii* was reported (as *O. Jordalii*) from Wrangel I. in PETROVSKY 1973 p. 123.

664. *Oxytropis viscida* was reported from northern Yukon in WELSH & RIGBY 1971 a.

667. The type of *Astragalus leucanthus* PALL. was located in the Brit. Mus. and described by WELSH in Taxon 21, 1972 p. 155. According to him it is a non-glandular plant of the *O. campestris* complex. The name *O. leucantha* cited as a possible synonym of *O. borealis* should thus be excluded.

667. In Nov. Syst. Pl. Vasc. 1964 p. 217 JURTSEV described *Oxytropis semiglobosa* (sect. *Orobia*) from Anadyr and central Chukotka. Acc. to JURTSEV et al. 1972 p. 773 it also occurs in SE Chukotka. It was not seen in the Alaskan material.

667. *Hedysarum Mackenzii* was reported from easternmost Chukotka in JURTSEV et al. 1972 p. 773. Its Siberian counterpart *H. dasycarpum* TURCZ. extends to western Chukotka. According to JURTSEV *H. Mackenzii* differs from that taxon in having a keel longer than the standard and in the dark rose-coloured, not saturated, violet-red corolla. The living Alaskan plant has purple flowers becoming paler when dried.

668. The range of *Hedysarum hedy-saroides* should include St Lawrence I., where this plant was collected by FR. KJELLMAN as early as 1879 and reported as *H. obscurum*. Also collected there by YOUNG and reported as *H. alpinum* in YOUNG 1971.

672. Concerning races and nomenclature of *Lathyrus maritimus* see P. W. BALL in HEYWOOD in FEDDE, Rep. 79: 1—2, 1968 pp. 45—46 and HULTÉN, Circumpolar Plants II, map 176.

675. *Geranium Robertianum* was collected at Kodiak by Mrs M. WILLIAMS.

676. Concerning *Linum perenne* subsp. *Lewisii* see HULTÉN 1971, discussion to map 168.

677. According to monographic studies by SCHOTSMAN (in JOVET, Fl. France 1, 1967, p. 78) the name of the taxon that has long been known as *Callitriche verna* L. should be *C. palustris* L. Sp. Pl. 1 1753 p. 969. Range extension to St Lawrence I. according to YOUNG 1971.

678. *Callitriche anceps* has wingless, orbicular, sessile fruits, while *C. subanceps* has wingless, obovate, short-pedunculate fruits. KOZHEVNIKOV reports *C. anceps* FERN. from western Chukotka in Bot. Zhurn. 58: 2, 1973 p. 297. See also discussion by SCHOTSMAN in JOVET, Fl. France 1, 1967 p. 82.

682. Range extension of *Viola Selkirkii* to Putoran Mts between lower Jenisei and Khatanga according to Nov. Syst. Pl. Vasc. 10, 1973 p. 282.

683. Reports of *Viola palustris* (for instance in CALDER & TAYLOR 1968 p. 431) must be due to lack of familiarity with that European plant. It is an acidophilous plant, characterized by leaves broader than long, not in pairs, but 3—4 together, thin rootstock, small, pale lilac flowers, and bracts below the middle of the stem. See for instance drawing in LID, Norsk og Svensk Flora 1963 p. 492. It does not at all resemble ANDERSON 6316 from Juneau, which CALDER & TAYLOR quote as *V. palustris*. The plant from the northern Pacific is *Viola epipsila* subsp. *repens*, by Russian authors treated as a species, *V. repens* TURCZ. Cf. discussion to maps 103 and 104 in HULTÉN 1958.

688. Range extensions of *Epilobium palustre* to St Lawrence I. according to YOUNG 1971 and to the Queen Charlotte Is according to CALDER & TAYLOR 1968.

693. *Circaea alpina* subsp. *pacifica* is regarded as an ecological response to the coastal climate as similar specimens occur in other coastal areas than those of the Pacific. See discussion to map 86 in HULTÉN 1971.

694. HARMS (1969 p. 254) reports *Myriophyllum spicatum* subsp. *exalbescens* from Palmer and Katmai. He considers that specimens from SE Alaska and the western Aleutians belong to subsp. *spicatum*. A map with range extensions northwards of *M. spicatum* is presented by CH. HOLMQUIST (Bot. Notiser 124: 3, 1971 p. 339).

694. Range extension of *Myriophyllum verticillatum* in Eastern Siberia to Ajan, Ochotsk, Anadyr and northern Kamchatka. The report from Iceland is based on an old unreliable statement.

695. K. L. CHAMBERS has pointed out (by letter) that *Echinopanax* is not a valid genus name as proposed in Fl. SSSR 16, 1950 p. 18. Compare the discussion in HULTÉN 1967 p. 88. If *Echinopanax* had been based on the combined description of a new genus and a new species, it would have been valid as a genus-description, but in this case it was based on the description of an earlier described species and is therefore not valid. See Articles 41 and 42 in the International Code of Botanical nomenclature. *Oplonanax horridus* (SM.) MIQ. should thus be the valid name of this species.

698. Range extension of *Bupleurum triradiatum* subsp. *arcticum* to the Lake Baikal area acc. to MALYSHEV 1972 map 241. Both subsp. *arcticum* and subsp. *triradiatum* are reported to occur there.

702. *Ligusticum Calderi* (MATHIAS & CONSTANCE in Bull. Torr. Club 86, 1959 p. 374) was found on a mountain top

near "Amara Lake" 57°19'N, 154°36'W within the unglaciated part of Kodiak I. The specimen was erroneously reported as *Conioselinum chinense* in HULTÉN 1969 p. 70. Immature specimens lacking fructifications are very similar. The best distinguishing character is the fibrous root-crown of *L. Calderi*. In *Conioselinum chinense* (*C. pacificum*) it consists of scale-like structures. The latter is a sea-shore plant, while *Ligusticum Calderi* is an alpine, inland plant.

L. Calderi is thus not an endemic of the Queen Charlotte Islands as originally supposed.

703. A study of the Siberian material of *Pachypleurum alpinum* LEDEB., the base for the combination *Ligusticum mutellinoides* subsp. *alpinum*, showed that the Alaskan plant does not belong to that taxon. The plate 344 in Ledeb. Icon. Fl. Ross. IV, as well as the drawing of *Pachypleurum alpinum* in Fl. SSSR 16, tab. 37:2, shows a plant with more dissected leaves with narrow lobes. In the arctic branch of the range specimens with leaves having much broader lobes occur, and such specimens were the reason why the Alaskan plant was referred to *Ligusticum mutellinoides* subsp. *alpinum*. The name of the Alaskan plant is *Podistera Macounii* (COULTER & ROSE) MATH. & CONSTANCE in Bull. Torr. Club. 69, 1942 p. 247, if that genus is accepted as being different from *Pachypleurum* and *Ligusticum*. The localities in easternmost Chukotka belong to the Alaskan taxon, while the easternmost locality for the Siberian taxon is in western Chukotka according to KOZHEVNIKOV in Bot. Zhurn. 58:2, 1973 p. 297. Thus only the range given on the Alaskan map belongs to *Podistera Macounii*.

705. Modern American authors agree that the population of *Angelica* no. 1 in eastern America and in the Pacific cannot be separated morphologically and that its name should be *Angelica lucida* L. This is also the opinion of WEINERT (Flora

159, 1970 map p. 421), who names the plant *Archangelica Gmelini* DC. subsp. *Gmelini*.

Russian authors, following PIMENOV (Nov. Syst. Pl. Vasc. 1965 p. 199) separate the Pacific plant as *Angelica Gmelini* (DC.) PIMENOV without mentioning the difference from the eastern American population. HARA (Journ. Fac. Sc. Tokyo, Sect. III, VI: 2, 1952 p. 91), too, quotes no difference when he suggests the name *Coelopleurum lucidum* var. *Gmelini* (DC.) HARA for the Asiatic plant, while both the eastern and western American populations are called *Coelopleurum lucidum*. That the western American and the eastern Asiatic coastal populations are identical can not be doubted. A new inland locality in northern British Columbia is reported in CALDER & TAYLOR 1968 at 57°20'N, 123°51'W.

707. According to BRUMMITT in *Rhodora* 73, 1971, pp. 578—584, *Heracleum lanatum* MICHX. is a synonym of *H. sphondylium* L. subsp. *montanum* (SCHLEICH.) BRIQ. That the *Heracleum* taxon occurring in Alaska and Kamchatka differ from all types of *H. sphondylium* in Scandinavia is clear. GOVOR on the other hand maintains that the Asiatic and American taxa are specifically different (Zontichnye Primorja i Priamurja, 1966 p. 210). The mericarps are said to be different in anatomical detail. The writer, who has field experience from both Kamchatka and Alaska, finds the two populations very similar. Russian authors consider the Kamchatka plant an endemic, *H. dulce* FISCH., described from a doubtful cultivated specimen. Cf. HULTÉN, Fl. Kamchatka 3 p. 173 in note. It is probable that the range of *H. lanatum* should be extended to China and the Himalayas.

BRUMMITT's paper illustrates the insoluble problems created by the present Botanical rules of nomenclature.

708. CODY & PORSILD (1968 b p. 271) report a very remarkable range extension for *Cornus suecica* to Munn Lake 63°35'N,

110°02'W. It should be regarded as a relict from a moister period when the Pacific and Atlantic populations were joined along the northern coast of the continent.

709. In HULTÉN 1967 p. 91 the hybrid nature of *Cornus unalaskensis* LEDEB. was discussed. CALDER & TAYLOR (1968) still insist on treating it as a separate species not of hybrid origin, in spite of its reduced fertility and obvious morphological variation. CALDER & TAYLOR (p. 451) state that it can tolerate many diverse ecological niches. That is why it has a somewhat larger range than *C. suecica* today. See map in CALDER & TAYLOR 1965 p. 1396. The above-mentioned find of *C. suecica* in the northcentral part of the continent, showing that *C. suecica* once had a wider range, strongly supports the writer's views.

Compare with the case of *Circaea alpina* × *lutetiana* in Great Britain, reported on by RAVEN in *Watsonia* 5: 5, 1963 p. 266.

710. Range extension for *Chimaphila umbellata* subsp. *cisatlantica* to central and western Newfoundland according to personal communication from A. W. DAMMAN.

711. Concerning the variation in the genus *Ledum* compare the discussion to map 71 in HULTÉN 1971.

712. Russian authors still use the name *Rhododendron parvifolium* ADAMS not only for the fairly tall more southern plant of eastern Siberia, but also for the prostrate plant of Chukotka. Specimens from Chukotka agree exactly with the common Alaskan plant as well as with the Scandinavian one. Specimens up to 70 cm tall were seen from central Alaska, Inuvik in Yukon, and from central British Columbia.

713. *Rhododendron camtschaticum* subsp. *camtschaticum* was collected at March Mt, N of Dillingham by ROBERSON, which

means a somewhat closer approach between the two subspecies in Alaska.

724. In VIERECK & LITTLE's map (1972 p. 219) the range of *Cassiope tetragona* covers the whole of Alaska, north of approximately 60°N. It was not seen during fieldwork at Kotzebue, the lower Yukon R., the mts of Scamman Bay, the lower Kuskokwim R. and in the mountains surrounding Kilbuck and Kisaralik Lakes.

729. Add the synonym *Arctostaphylos adenotricha* (FERN. & MACBR.) LÖVE, LÖVE & KAPOOR to *A. uva-ursi* var. *adenotricha*. See the discussion to map 149 in HULTÉN 1971. According to PACKER in Canad. Journ. Bot. 45, 1967 p. 1767 var. *adenotricha* has $2n=26$ chromosomes, while var. *uva-ursi* has 52.

730. The map of *Arctostaphylos alpina* in VIERECK & LITTLE 1972 p. 230 does not show the gap between a northern and a southern area, as does the map in the Alaskan Flora. The species probably occurs all over interior Alaska.

734. *Vaccinium alaskensis* should be changed to *Vaccinium alaskense*.

734. In a paper with the title "On the taxonomy and distribution of *Vaccinium uliginosum*" in Rhodora 72, 1970, YOUNG reports subsp. *pubescens* (WORMSKJ.) YOUNG, subsp. *pedris* (HARSHB.) YOUNG, subsp. *gaultherioides* (BIGEL.) YOUNG, subsp. *occidentale* (GRAY) HULT. and subsp. *occidentale* var. *salicinum* (CHAM.) HULT. from Alaska. Maps of the ranges of these taxa are also presented. The writer is unable to divide the material rationally according to this study. Compare the discussion to map 70 in HULTÉN 1971.

741. Range extension for *Primula egalikensis* to Eyja Fjörður on northern Iceland (found once) according to LÖVE in Ízlenzk Ferðaflóra, 1970 p. 336.

749. The *Dodecatheon* drawings have unfortunately been interchanged. The

lower one represents *D. frigidum* and the upper one *D. Jeffreyi*.

751. The differences between *Trientalis europaea* subsp. *europaea* and subsp. *arctica* are well illustrated in Flora of Alaska p. 751. As geographical races they are obvious, where they meet they merge into each other and should not be taken as species. That CALDER & TAYLOR cannot see the difference between the Pacific and the European plants must be due to lack of familiarity with the latter. See the discussion to map 148 in HULTÉN 1971. For a photograph of subsp. *arctica* see HULTÉN, The Plant cover of Southern Kamchatka in Ark. f. Bot., ser. 2, 7:3, 1972 p. 202.

752. In CALDER & TAYLOR 1968 the more or less obtuse-leaved specimens of *Glaux maritima* are regarded as a subspecies, as proposed by BOIVIN (Bull. Soc. Bot. Belg. 88, 1955 p. 10). From a study of world-wide material it becomes obvious that obtuse-leaved specimens occur in many different places, often together with more acute-leaved ones. The variation within the Alaskan population can be illustrated by a collection from Eagle R., Juneau, ANDERSON 6356. Some specimens have very obtuse rounded leaves 13×17 mm, while others have quite acute leaves 12×3.5 mm. Specimens from alkaline inland localities (Alaskan Highway mile 945) have leaves that are only 1.5 mm broad. Compare the discussion to map 182 in HULTÉN 1971.

753. It has become customary, for instance in Fl. Europaea 3, to separate *Gentianella* (lacking appendages between corolla lobes, and usually with throat and corolla lobes ciliate) as a genus from *Gentiana*. In the writer's opinion *Gentianella* is best regarded as a section of the genus *Gentiana*, which has many characteristics that speak for its unity.

If *Gentianella* is regarded as a separate genus consistency requires the rest of the genus *Gentiana* to be split up into a

number of genera (*Gentianopsis*, *Comastoma*, *Gentianodes*, and others). The desirability of such a development can be discussed.

754. To the synonyms of *Gentiana algida* add *Gentianodes algida* (PALL.) LÖVE & LÖVE in Bot. Notiser 125: 3, 1972 p. 256.

757. Range extension for *Gentiana glauca* to the mountains NE of Lake Baikal according to MALYSHEV 1972 map 265. Thus *G. glauca* goes approximately as far east as west of the Bering Strait, which is the case with numerous other species.

758. Russian authors use the name *Gentiana nutans* BUNGE for the Siberian *G. prostrata*. According to Fl. SSSR it differs from the European low *G. prostrata* HAENKE in being 5—10 cm tall with nodding or drooping, always pentamerous flowers.

In Alaska flowering specimens occur from up to 15 cm and down to 2 cm (in the mountains). Tetramerous flowers are not rare, often growing together with pentamerous ones. Small specimens have erect flowers, in tall specimens they are often nodding. The Alaskan plant agrees well with the European one, as well as with those from NE Siberia.

758. Range extension for *Gentiana auriculata* to St Lawrence I. according to YOUNG 1971.

759. *Gentiana amarella* subsp. *acuta* also occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

761. *Gentiana propinqua* subsp. *arctophila* was reported from several places in eastern Chukotka by JURTSSEV et al. 1972 and also from Wrangel I. in PETROVSKY 1973 p. 123.

761. *Lomatogonium rotatum* has been found in eastern Chukotka according to JURTSSEV (personal communication).

762. *Swertia perennis* occurs at Lake Beverly, north of Dillingham, according

to ROBERSON (in letter). It also occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

762. In Canad. Journ. Bot. 46, 1968 pp. 92—96 GILLETT separates the Japanese population of *Fauria crista-galli* from the American as subsp. *japonica* (FRANCH.) GILLETT. The Japanese plant is considered to be tetraploid, while the American is hexaploid. According to GILLETT minor quantitative differences also occur between the Asiatic and the American populations.

764. JURTSSEV et al. 1972 p. 774 report *Phlox sibirica* from two places in easternmost Chukotka.

765. Range extension of *Phlox sibirica* subsp. *Richardsonii* to the Steele Glacier in the St Elias Mts according to MURRAY 1971 a (as *Ph. Richardsonii*).

768. A map of the distribution of *Polemonium boreale* var. *villosissima* was published by MURRAY in Arctic 21: 4, 1971 p. 303.

769. *Polemonium pulcherrimum*. Range extension to N of Dillingham, collected by ROBERSON. Determination kindly controlled by VIERECK & MURRAY.

771. In a review of Flora of Alaska and neighboring territories in Madroño 20 p. 79, CHAMBERS remarks that *Romanzoffia sitchensis* and *unalaschkensis* should merely be regarded as subspecies, as they chiefly differ in pubescence. The writer prefers to keep them as separate species as they are quite different in habit as can be seen from the drawings in the Flora, and as real intermediates were not seen.

773—774. *Eritrichium aretioides* and *Chamissonis*. Misled by the key in WIGHT, *Eritrichium* in North America (Bull. Torr. Club 29, 1902 p. 408), the writer accepted the name *E. Chamissonis* for the plant with the flowers scarcely exceeding the cushion. As seen from the drawing in Fl. SSSR 19 tab. XXV, fig. 1, that taxon is called *E. aretioides* there. The original description also confirms this view. The

type specimen of *E. Chamissonis* shows that this taxon has a long stem. The distinction between the two taxa is unclear, variation is considerable, but if they are distinguished as different taxa the one lacking a stem at flowering should be named *E. aretioides* and that with long stem *E. Chamissonis*. In Fl. SSSR p. 520 *E. Chamissonis* is proposed to represent the hybrid *E. aretioides* × *villosum*. However, *E. villosum* is unknown from Alaska, while its counterpart in the supposed hybrid is common there. A study of the fruits may help to elucidate conditions, but ripe fruits are rare in herbarium specimens. A drawing of *E. aretioides* with the fruit also represented is found in SEEMAN, Bot. Voy. Herald, Pl. VIII.

775. Range extension of *Eritrichium splendens* to Horne Lake, the Richardson Mts 67°45'N, 136°01'W according to CODY in Canad. Field Nat. 1969 p. 412.

777. The very isolated population from Mission Bluff, Eagle area, passing for *Cryptantha spiculifera*, was described as *C. Shacklettiana* by L. C. HIGGINS in Great Basin Naturalist 29: 1, 1969 p. 28. According to him it differs in having longer and narrower leaves, inconspicuously pustulate hairs, a subcapitate inflorescence, longer and narrower nutlets and a weaker stem, i.e. in quantitative characters only. In such a small isolated population the variation must be very small, containing few or single biotypes only. The variation should be checked on the spot and compared with the variation within its main area.

781. Range extension of *Mertensia maritima* subsp. *maritima* to Wrangel I. according to PETROVSKY 1973 p. 124.

783. *Mertensia kamezatica* does not occur within the area of the left-hand map in the Alaskan Flora according to personal information from B. A. JURTSEV and should thus be excluded from the Flora.

788. *Lamium purpureum* L. was reported from Alaska by DEARBORN in Weeds 7, 1959 p. 269, as a weed "affecting agriculture". No specimen was seen by the writer.

789. The single specimen of *Stachys Emersonii* from Alaska (Annette Island, EDITH A. PURER 7689), has a corolla tube 9 mm long and is thus correctly referred to that species according to EPLING in Madroño 4, 1938 p. 272. An older name of the species is *S. mexicana* BENTH. (although the plant does not occur in Mexico). CALDER & TAYLOR 1968 p. 481 suggest that the Alaskan plant is *S. Cooleyae*, a plant with a corolla tube 15—25 mm long.

793. *Linaria vulgaris* also occurs at Ivigtut, S Greenland.

794. *Collinsia parviflora* also occurs on the Queen Charlotte Is according to CALDER & TAYLOR 1968.

796. In Canad. Journ. Bot. 43, 1965 p. 1398 CALDER & TAYLOR described *Mimulus guttatus* subsp. *haidensis* from the Queen Charlotte Is. It was characterized by the acute leaves, pubescence on the veins underneath and puberulous pedicels. No such specimens were seen in the Alaskan material.

The pedicels have a patent, sometimes nearly glandless pubescence, in a few cases they are nearly glabrous.

796. A specimen of *Mimulus Lewisii* PURSH was collected on Douglas I. by Mrs M. WILLIAMS according to information in a letter.

797. *Limosella* taxa similar to *L. aquatica* occur in the southern hemisphere, southwards to the Antarctic islands, but the identity of that species with *L. aquatica* is uncertain.

805. Remarkable range extension for *Lagotis glauca* subsp. *minor* to the mountains NE of Lake Baikal according to MALYSHEV 1972 map 276. Add the synonym *Lagotis minor* (WILLD.) STANDL.

807. *Castilleja miniata* was found at Gustavus, Glacier Bay, by Mrs M. WILLIAMS.

814. SELL & YEO (Bot. Journ. Linn. Soc. 63: 3, 1970 p. 210) treat *Euphrasia disjuncta* FERN. & WIEG. in a narrower sense than the authors of that taxon did. SELL & YEO reserve the name for the plant from Newfoundland to Lake Mistassini which they include in the series *Minutiflorae* PUGSL. The Alaskan plant differs according to them in having "usually" more or less numerous glandular hairs, less rounded leaves and a smaller corolla (it is surprisingly referred to the series *Grandiflorae* WETTST.). In Fl. Alaska & Yukon p. 1398 the Alaskan plant was reported as *E. subarctica* RAUP and that is the name adopted by SELL & YEO for the plant distributed from Alaska to Lake Athabasca.

824. Add the synonym *Pedicularis sudetica* δ *bicolor* WALP. Rep. 3, 1845 p. 422 to *P. sudetica* subsp. *albolabiata*.

825. Range extension for *Pedicularis capitata* to the Mts NE of Lake Baikal according to MALYSHEV 1972 map 277.

827. The name *Pedicularis lanata* PALL. that has long been used was changed to *P. Kanei* because *P. lanata* CHAM. & SCHLECHT. was considered a later homonym of *P. lanata* PALL. ex STEVEN, quoted as a synonym of *P. Langsdorffii* var. *lanata* (HULTÉN 1967 p. 121). K. L. CHAMBERS has pointed out (in a letter) that the *P. lanata* PALL. was not validly published as it was merely cited as a synonym. *P. lanata* was earlier used as a synonym of *P. verticillata* by PURSH (Fl. N. Amer. 2, 1814 p. 426). It is very satisfactory that the old name *Pedicularis lanata* CHAM. & SCHLECHT. in *Linnaea* 2, 1827 p. 584 can be used for *Pedicularis* no. 21 in the Alaskan Flora.

Pedicularis no. 22 will then be named:

Pedicularis lanata CHAM. & SCHLECHT.

subsp. *Adamsii* (Hult.) Hult. stat. nov.

P. Adamsii HULT. in K. Vet. Akad. Handl. Ser. 3, 8: 2, 1930 p. 117 in adn., Pl. 5 c.

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Two other taxa regarded as races of *P. lanata* will need new name combinations.

Pedicularis lanata CHAM. & SCHLECHT.
subsp. *Pallasii* (Vved.) Hult. stat. nov.

P. Pallasii VVED. in Fl. SSSR 22, 1955 p. 817.

Pedicularis lanata CHAM. & SCHLECHT.
subsp. *dasyantha* (Hadač) Hult. stat. nov.

P. dasyantha HADAČ in Norges Svalbard og Ishavsunders. skr. no. 87, 1944 p. 57.

Cf. discussion to map 13 in HULTÉN 1971.

831. There was no specimen of *Utricularia intermedia* from Chukotka in the Leningrad Herbarium.

831. *Utricularia minor* was reported from one locality in western Chukotka by KOZHEVNIKOV in Bot. Zhurn. 58: 2, 1973 p. 298.

833. *Plantago maritima* was collected at Providenie (Port Providence) in SE Chukotka according to DOROGASTAJSKAJA 1972 p. 136. It is probably an anthropochor there.

833. *Plantago canescens* was reported by JURTSEV from Chaun Bay, a locality situated in the middle of the gap between the Alaskan and the Eastern Siberian ranges.

835. Range extension for *Plantago major* to Igarka, Dudinka, Norilsk and SE Chukotka according to DOROGASTAJSKAJA 1972 p. 136.

839. Range extension for *Galium kamtschaticum* to the Queen Charlotte Is according to CALDER & TAYLOR 1968 and to Hyndman Lake, 68°14'N, 131°06'W (West of the Mackenzie delta) according to CODY & PORSILD 1968 b p. 272, a most remarkable find. A sterile specimen only.

844. WELSH & RIGBY 1971 b p. 21 report *Linnaea borealis* var. *longiflora* from the interior of northern British Columbia. The specimens from Cold Fish Lake, RIGBY & CUDDY 171 and 193, belong to subsp. *americana*.

851. A very remarkable range extension for *Campanula uniflora* to the Stanovoye Mts NE of Lake Baikal is reported in MALYSHEV 1972 map 291. The locality is situated in the middle of the large Asiatic gap in the range of this characteristic species.

In Alaska *C. uniflora* was found on March Mt., N of Dillingham by ROBERSON.

851. *Lobelia dortmanna* L. occurs according to CALDER & TAYLOR 1968 on the Queen Charlotte Is, just south of the boundary of the left-hand map in the Alaskan Flora. As it is easily overlooked it should also be sought in southern Alaska. The species has a peculiar range. See map 192 in HULTÉN 1958, to which can now be added a single locality in Central Saskatchewan, reported by BREITUNG.

851. *Grindelia integrifolia* DC. occurs on the Queen Charlotte Is. CALDER & TAYLOR 1968 p. 535 remark that "although this plant has been reported from Alaska by a number of authors, it was not included by HULTÉN in his Flora of Alaska & Yukon". The basis for the reports is apparently PRESL's report in Reliquiae Haenkeanae from Port Mulgrave (Yakutat Bay), repeated in DC. Prodrum.

The plants reported in this publication were either from Yakutat Bay or from Nootka Sound on Vancouver I. In the case of *Grindelia* it was apparently from Nootka Sound as no *Grindelia* was later collected in Alaska. CRONQUIST in HITCHCOCK et al. 1955 came to the same conclusion. On the map of the genus *Grindelia* by STEYERMARK (Ann. Missouri. Bot. Gard. 24, 1937 p. 232) this genus is marked for SE Alaska and Yakutat Bay. *Grindelia* is, to the writer's knowledge, not known to occur in Alaska.

852. The range of *Solidago multiradiata* var. *arctica* should be extended to the Commander Is, as shown by the type specimen of *S. cuprea* JUZ. from Copper I., which is this taxon.

864. Range extension for *Erigeron eriocephalus* to Karaginsk I., N Kamchatka, according to VOROSHILOV et al. 1971 and to the mountains NE of Lake Baikal according to MALYSHEV 1972 map 293.

864. *Erigeron pallens* CRONQU. was reported from three places in the Mackenzie Mts, NW Terr., within the boundary of the Alaskan map in Fl. Alaska and neighboring Territories.

865. Range extension of *Erigeron hyperboreus* to the Mackenzie Mts and Coronation Gulf according to CODY & PORSILD 1968 b p. 273 and to three places in easternmost Chukotka acc. to JURTSSEV et al. 1972 p. 774 (as *E. alaskanus*).

865. A new Alaskan *Erigeron* species closely related to the polymorphic *E. grandiflorus* was described by SPONGBERG in Rhodora 75, 1973 p. 801 as *Erigeron Hultenii*. The type comes from Campbell Creek Valley, 11 miles north of Anchorage. SPONGBERG regards it as transitional between *E. peregrinus* and *E. grandiflorus*.

866. The author of the synonym *Erigeron angulosus* should be GAUD., not GANDOGER.

873. A very remarkable range extension for *Antennaria monocephala* to the mountains NE of Lake Baikal was reported in MALYSHEV 1972 p. 141 and map 296. *A. dioiciformis* KOM. and *A. Komarovii* JUZ., described from Kamchatka are here regarded as synonyms of *A. monocephala*.

876. *Antennaria subviscosa* FERN. was reported from the Steele Glacier in the St Elias Mts in MURRAY 1971 a. It was earlier reported from Canol Road by PORSILD and included in the variation of *A. isolepis* in Fl. Alaska and neighboring territories.

877. *Antennaria Friesiana* subsp. *compacta* also occurs in easternmost Chukotka. A specimen in Stockholm from the head of St Lawrence Bay, Cape Krause, collected by JURTSSEV, belongs here. Re-

ported from Penkignei in JURTSEV et al. 1972 p. 774 (as *A. compacta*).

888. CALDER & TAYLOR 1968 p. 524 give *Achillea borealis* and *A. lanulosa* as synonyms of *A. millefolium* L., a taxon introduced into America. The indigenous and not weedy *A. borealis* BONG. is clearly distinct from *A. millefolium* in Alaska. *A. borealis* or *A. lanulosa* do not occur in Asia. In parts of America where the introduced *A. millefolium* is common introgression between the native American taxa and the European one probably occurs.

889. In DOROGASTAJSKAJA 1972 p. 142 *Matricaria matricarioides* was reported from the lower Ob R. (Salechard), the lower Jenisei R. and from Providenie in SE Chukotka. One specimen was even found on South Georgia in 1964 acc. to LONGTON.

892. *Chrysanthemum bipinnatum* subsp. *huronense* was reported from the Queen Charlotte Is by CALDER & TAYLOR (as *Tanacetum huronense*). It also occurs on Vancouver I.

897. A taxon similar to *Artemisia globularia* var. *lutea* was described from the Anjui Mts in Chukotka as *A. flava* by JURTSEV (1969 p. 317). It is said to differ from *A. globularia*, apart from the yellow corolla, in the more glabrous leaves, the broad petioles and the long inflorescence.

The variation in these respects is great in *A. globularia*. Specimens from Wales show a similar type of pubescence to that of *A. flava* and the inflorescence is up to 15 cm long. *A. flava* is hardly a taxon at species level.

905. Range extension for *Artemisia alaskana* to the Yukon—Mackenzie border 67°57'N, 136°27'W acc. to CODY & PORSILD 1968 b p. 272.

910. Specimens from the Kaskawulch Glacier in MURRAY 1971 a, reported as *Artemisia hyperborea*, agree exactly with specimens from McKinley Park, named *A. furcata* var. *heterophylla* in the Alaskan

Flora. *A. hyperborea* is an arctic-alpine plant. The leaves are usually more strongly dissected with shorter lobes. As no clear distinction could be found between this taxon and *A. furcata* it was treated as a segregate of this plant.

The taxa of this affinity are treated very differently by Russian and American authors, although the variation on both sides of the Bering Strait is very similar. POLJAKOV in Fl. SSSR regards *A. furcata* (1819), *A. trifurcata* (1826) and *A. heterophylla* (1832) as synonyms. PORSILD on the other hand separates the hoary-villous *A. Richardsoniana* BESS. (1836) and the appressed silver-grey, silky pubescent *A. hyperborea* (1916) as distinct species. The variation in type and density of pubescence is wide, and the range of the proposed taxa partly overlap (see maps 317 and 319 in PORSILD, III. Fl. Canad. Archipel.). It seems impossible to distinguish *A. Richardsoniana* from *A. furcata*, while *A. hyperborea* belongs to var. *heterophylla*, which could possibly be regarded as an arctic-alpine race of *A. furcata*.

913. CALDER & TAYLOR (1968 p. 538) regard *Petasites nivalis* GREENE as an older name for *P. hyperboreus* RYDB. The type of *P. nivalis* was not seen, but the description in Pittonia 2, 1889 p. 18 agrees well with *Petasites* no. 4 in the Alaskan Flora, the name of which should be changed to *P. nivalis* GREENE.

No proper understanding of the Alaskan *Petasites* taxa can be expected unless hybridization is taken into account. From the study of extensive material hybridization is obvious. CODY (1971 p. 155) presents a map of *P. arcticus* PORS. In the writer's opinion it is the hybrid *P. nivalis* (*hyperboreus*) × *palmatum*.

914. *Petasites sagittatus* was collected at Soldotna, Kenai Peninsula, by ROBERSON.

919. CALDER & TAYLOR (1968 p. 527) maintain that *Arnica amplexicaulis* subsp.

prima MAGUIRE should not be recognized. The writer cannot agree. Subsp. *prima* was described on specimens from Kodiak I., and Kodiak specimens differ from subsp. *amplexicaulis*, as stated by MAGUIRE and in the key of the Alaskan Flora. A specimen from the Queen Charlotte Is in Stockholm, CALDER & TAYLOR 36935, does not belong to subsp. *prima*. The specimen from the Kenai Peninsula with strongly serrulated leaves, mentioned by CALDER & TAYLOR, indicates that the range of subsp. *amplexicaulis* should be extended to that peninsula.

923. Specimens from Chukotka named *Arnica Iljinii* (MAGUIRE) ILJIN can hardly be distinguished from *A. alpina* subsp. *angustifolia* from Alaska. The specimen from Konyam Bay, marked on the map of *A. alpina* subsp. *angustifolia* and collected by KJELLMAN, is one such specimen.

927. *Senecio fuscatus* is, as far as the writer can see, the oldest name for a complex of very similar taxa with the arctic-alpine range given on the Circumpolar map. If the Alaskan taxon is regarded as distinct its name should not be *S. Lindstroemi* PORS. (1945) but *S. tundricola* TOLM. (1928). The taxon in question is exactly the same on both sides of the Bering Strait.

927. *Senecio* no. 4—6 in the Alaskan Flora, taken as segregates of *S. atropurpureus*, constitute in the writer's opinion a complicated complex which should be studied monographically. In particular the limitation of subsp. *atropurpureus* compared with subsp. *frigidus* is obscure. Russian authors readily divide the complex into clear-cut species, but provide no key to the different taxa. The drawing of *Senecio* no. 4, *S. atropurpureus* subsp. *atropurpureus* in the Alaskan Flora is not typical. See the drawing in Fl. SSSR tab. XXXV. The range of this taxon should be extended to central Alaska. Specimens agreeing with the type of *S. Tichomirovii* SCHISCHK. were collected at Wales, the

Bering Strait, by the writer. A good representation of *S. frigidus* is tab. XII in HOOKER, Fl. Bor. Amer. I.

929. The type specimens of *Senecio resedifolius* from St Lawrence Bay, Chukotka, show a small plant with short, crenate to indistinctly lobed basal leaves, small, acute, nearly entire stem leaves and a single, large head. They correspond to the drawing in the Alaskan Flora. *S. resedifolius*, as understood in the Flora, is a critical complex comprising specimens up to 25 cm high, such as Naknek, NORBERG; 20 miles above Russian Mission, HULTÉN, similar to *S. cymbalarioides* subsp. *moresbiensis* CALDER & TAYLOR (1968 p. 540, fig. 178), as well as others similar to *S. Newcombei* GREENE from the Queen Charlotte Is (CALDER & TAYLOR 1968 fig. 182), Nelson I., Nightmute, HULTÉN. Some specimens even have reddish ligulae (Lake Peters and the Sadlerochit R., SPETZMAN; Craig, NORBERG).

PACKER recently published a revision of the *S. resedifolius* group, mainly from a cytological point of view (Canad. Journ. Bot. 50: 3, 1972 pp. 507—518). He regards all Rocky Mountain material earlier referred to *S. resedifolius* as *S. cymbalarioides*, but does not discuss the above-mentioned critical types in Alaska, nor does he include *S. resedifolius* var. *columbianus* GRAY, *S. Newcombei* or *S. cymbalarioides* subsp. *moresbiensis* in his study. In one case PACKER suspects hybridization.

Hybridization and apomixis in the hybrid populations may be responsible for part of the polymorphy.

929. PACKER states that specimens of *Senecio conterminus* from the Rocky Mts have 160+ chromosomes, while two collections of the corresponding Alaskan population have 46 (Canad. Journ. Bot. 50: 3, 1972 pp. 507—518). He therefore describes the Alaskan plant as a new species, *S. ogorukensis*. The morphological differences quoted are extremely weak and

hardly provide a good basis for separating the two taxa at species level. Both *S. conterminus* and *S. ogorukensis* can be distinguished from the glabrous *S. resedifolius* and *S. cymbalarioides* (*S. streptanthifolius*) by their woolly pubescence. One high-Alpine specimen of *S. conterminus* in Stockholm from the Wrangell Mts (Copper Glacier, JIM HENNINGS) is white-woolly throughout. The chromosome number of such a specimen would be of interest to state. Alpine, single-headed specimens, such as those from Mt McKinley Park, are morphologically extremely similar to the Rocky Mountain specimens.

930. JURTSEV et al. (1972 p. 775) report *Senecio hyperborealis* from Utaveem in northeasternmost Chukotka. It was also reported from Wrangel I. by PETROVSKY (1971 and 1973).

931. The name *Senecio cymbalarioides* NUTT. cannot be used, as there is an earlier *S. cymbalarioides* BUCK. PACKER reserves this name for a population south of the area of glaciation (see map in Canad. Journ. Bot. 50:3, 1972 p. 517, fig. 14). For *S. cymbalarioides* NUTT. the name *S. streptanthifolium* GREENE in Erythraea 3, 1895 p. 23, has been proposed. After renewed study of the Alaskan material of *Senecio* no. 11, called *S. cymbalarioides* NUTT. in the Flora, the writer is inclined to unite it with no. 12, *S. pauperculus* MICHX.

940. CALDER & TAYLOR 1968 p. 530 report *Cirsium brevistylum* CRONQU. from the Queen Charlotte Is. It might therefore be expected that the single Alaskan specimen reported as *C. edule* (Hyder, Mrs E. G. MEYER), belongs to that very closely related taxon. Judging from the study by MOORE & FRANKTON (Canad. Journ. Bot. 40:2, 1962) it should, however, be referred to *C. edule* as its anthers are about 6 mm long and the style is long extruding.

943. According to CHAMBERS in Contrib. Dudley Herb. 4:7, 1955 p. 214, *Apargidium boreale* should be referred to the

genus *Microseris*. Its name then becomes *Microseris borealis* (BONG.) SCHULTZ-BIP.

CHAMBERS regards it as the single member of *Microseris* subgen. *Apargidium*, differing in being scapose, rhizomatous and perennial. (Contrib. Dudley Herb. 5:2, 1957 p. 57).

945. Range extension for *Taraxacum ceratophorum* to S Japan and the western State of Washington. The range in northernmost Greenland should be eliminated and replaced by an area in central E Greenland.

948. Range extension for *Taraxacum phymatocarpum* to easternmost Chukotka according to JURTSEV et al. 1972 p. 775 and to Wrangel I. according to PETROVSKY 1971.

950. Remarkable range extension for *Taraxacum carneocoloratum* to the Ogilvie Mts, NE of Dawson, collected by A. T. PORSILD according to note in "The Beaver" 1971 p. 19. Examination of the type specimen of *T. Soczavae* TZVEL. in Nov. Syst. Pl. Vasc. 1966 p. 232 from Kamenskoje at the mouth of the Penzhina R. showed that it is identical with *T. carneocoloratum* A. NELSON. This remarkable plant thus occurs on both sides of the Bering Strait. *Taraxacum* species with pink ligulae occur in the Caucasus (*T. porphyranthum* BOISS.), in Central Asia (*T. pseudoroseum* SCHISHK., *T. lilacinum* KRASSN.), in Transbaikalia (*T. pseudo-nivale* MALYSH.) and in China, but are unknown in America outside Alaska—Yukon.

953. In *Rhodora* 50, 1948 p. 32 CRONQUIST states that *Agoseris gaspensis* FERN. falls within the variation of *A. aurantiaca*. Gaspé should thus be added to the map of the total area.

954. *Crepis tectorum* also occurs as a weed in SW Greenland and on Iceland.

956. Range extension for *Crepis nana* var. *lyratifolia* to the St Elias Mts, the Steele Glacier, according to MURRAY 1971 a p. 181.

958—959. *Hieracium triste* and *H. gracile*. The Alaskan material very clearly belongs to two different types, although more or less intermediate specimens sometimes occur. *H. triste* has large, strongly blackish-grey, villous pubescent heads with a more or less rounded base, dark involucreal scales, little or not at all floccose stem, and leaves pubescent with hirsute hairs at least on the margin. *H. gracile* var. *alaskanum* has smaller heads with a funnel-shaped base, often lighter-coloured involucreal scales, distinctly floccose stem, and leaves glandular on the margin, but otherwise glabrous. CALDER & TAYLOR (1968 p. 536) decide that the collections cited by HULTÉN as belonging to *H. gracile* var. *alaskanum* should all be transferred to *H. triste* subsp. *triste*, but this must be due to their not having examined the specimens in question.

On the contrary, most of the material referred to *H. gracile* var. *alaskanum* is very close to typical *H. gracile*. They agree exactly with specimens from, for instance, the State of Washington. *H. gracile* var. *alaskanum* is not a very marked taxon. It is founded on part of FUNSTON 107 from Yakutat Bay. It is described as having slightly pilose leaves, stems pilose above, a darkish involucreum with broad scales and dark hairs, as well as long and blackish glands on the involucreum, pedicels and upper stem. *H. gracile* and *H. triste* are so different that they are best retained as species. The variation in *H. triste* can be studied in Kamchatka, where *H. gracile* does not occur. The variation in *H. gracile*, on the other hand, can be studied south of British Columbia, where *H. triste* does not occur, as well as in S America.

PHYTOGEOGRAPHICAL NOTES

From a study of the maps alone in Flora of Alaska and Neighboring Territories it is apparent that the Transberingian floristic affinities are very close. In this paper several taxa earlier known from

only one side of the Bering Strait have also been shown to occur on both the Asiatic and the American side of the Strait. This is not surprising as the Strait was dry as recently as about 12,000 years ago.

Leaving out introduced or very critical taxa, the following list enumerates the American species (27), that reach the Seward Peninsula but are unknown from Chukotka — as far as our present knowledge goes:

Hordeum brachyantherum
Zygadenus elegans
Cypripedium passerinum
Populus balsamifera
Polygonum alaskanum (?)
Delphinium glaucum
Aphragmus Eschscholtzianus
Draba longipes
Boykinia Richardsonii
Saxifraga spicata
S. reflexa
S. adscendens subsp. *oregonensis*
Potentilla virgulata (?)
Dryas octopetala subsp. *alaskensis* (?)
Lupinus arcticus
Astragalus polaris
Hedysarum alpinum subsp. *americanum*
Cicuta mackenziana
Androsace chamaejasme subsp. *Andersonii*
Polemonium pulcherrimum (?)
Mertensia paniculata
Veronica Wormskjoldii
Viburnum edule
Achillea borealis
Artemisia alaskana
Senecio conterminus (?)
S. lugens

Several of these, as for instance those marked with a mark of interrogation, will probably be found on the Asiatic side when the Flora there is better known. Others, such as *Astragalus polaris* and *Aphragmus Eschscholtzianus* are inconspicuous and may thus have escaped notice.

On the other hand, it can hardly be expected that plants as conspicuous as *Boykinia Richardsonii*, *Saxifraga spicata*, *Lupinus arcticus*, *Mertensia paniculata*, *Viburnum edule* and *Senecio lugens* will be found on the Asiatic side.

In the following list those Asiatic species (21) that reach easternmost Chu-

kotka but are not known from America are enumerated:

Helictotrichon dahuricum
Elymus interior
Carex melanocarpa
C. Ledebouriana
Juncus Leschenaultii
Salix saxatilis
S. nummularia
Polygonum tripterocarpum
Silene stenophylla
Cardamine Victoris
Christolia parryoides
Chrysosplenium kamschatcicum
C. rimosum subsp. *desznevii*
Potentilla fragiformis
Androsace filiformis
Gentiana auriculata
Eritrichium villosum
Pedicularis amoena
P. villosa
Petasites glacialis
Saussurea Tilesii

Of these at least *Juncus Leschenaultii*, which occurs near hot springs only, could be expected to occur in Alaska. There are several hot springs, but their Flora is not known. Most of the others probably don't occur in Alaska.

The present situation in the Bering Strait Area can be interpreted as follows: The Flora of Northern Beringia was identical on the Asiatic and the American sides at the time of the last landbridge, presumably only 12,000 years ago. Since then a few American taxa have penetrated westwards to the Straits but not further, and some Asiatic species have in the same way spread eastwards until their migration was stopped by open water.

JURTSEV (1972 p. 19) admits a very close floristic relationship between easternmost Asia and westernmost America, but in spite of this he regards the Bering Strait as constituting a boundary between two provinces. It is impossible to accept this view.

The forests of Siberia and those of America have been isolated from each other since the Miocene. They should certainly be referred to different floristic provinces. They are, however, separated from each other by a broad forestless

area in the northern Pacific with a very uniform flora, now divided into an Asiatic and an American half. During the time of the landbridge they were connected. This forestless area cannot be divided into two floristic provinces.

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ADDITION

Epilobium ciliatum RAF. In *Blyttia* 31, 1937 pp. 19—28 HONDA revised the *E. glandulosum* group occurring introduced in Scandinavia. What has been called *E. rubescens* there is *E. ciliatum* (*E. glandulosum* var. *perplexans* FERN.). On examining the seeds of Alaskan *Epilobium* Miss GRETA BERGGREN found two collections of *E. ciliatum* there. They were from Fairbanks (POLUNIN) and from Circle Hot Springs (J. P. ANDERSON). The plant is new to Alaska.

Some Early *Vaucheria* Descriptions

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ABSTRACT

CHRISTENSEN, T. 1973. Some early *Vaucheria* descriptions. — Bot. Notiser 126: 513—518.

The names *Vaucheria bursata* (O. F. MÜLL.) C. AG., *V. dillwynii* (WEB. & MOHR) C. AG., *V. velutina* C. AG. and *V. subsimplex* CROUAN FRAT. are shown to be earlier legitimate names of the plants mostly referred to as *V. sessilis* (VAUCH.) DC., *V. pachyderma* WALZ, *V. thuretii* WOR. and *V. sphaerospora* NORDST.

Vaucheria bursata (O. F. MÜLL.)

C. AG. 1812

Conferva bursata O. F. MÜLL. 1788, cf. 1779

?*Conferva vesicata* O. F. MÜLL. 1788

Ectosperma sessilis VAUCH. 1803

Vaucheria sessilis (VAUCH.) DC. in LAM. & DC. 1805

This species is based on a plant collected in August 1777 at Bad Meinberg 74 km southwest of Hannover in Germany. MÜLLER visited this spa and the neighbouring Bad Pyrmont for his arthritis, and during his stay also studied the algal flora of the places. Two of his finds were siphonous threads, one later named *Conferva bursata* by him, the other *C. vesicata*. Back in Copenhagen, he refound the latter, or a close ally of it, and set up an article on "invisible water-mosses", expanding in his peculiar manner on the supposed rarity of his finds. The article was published both in German (1779) and in French (1784). It gives a description and a small-scale illustration of each of the siphonous algae but only names them in German, resp. French. In addition he wrote a different paper with nearly the same title in Latin, here giving Latin names and formal diagnoses for these

plants as well as others found during his stay in Germany. This paper was submitted to the Academy of Sciences of St. Petersburg in 1779, and was published by that society in 1788. The illustrations of *Conferva bursata* and the German *C. vesicata*, more carefully made than those in the German and French journals, are rendered as Fig. 1 A, resp. B and C of the present account.

MÜLLER's figure of *C. bursata* is seen to fit with the alga currently called *Vaucheria sessilis* (VAUCH.) DC., cf. Fig. 1 F—G. The characteristics of the oogonia are rendered quite well except that the various deviations from a spherical shape are much exaggerated so as to make the oogonia look emaciated, probably due to the poor quality of MÜLLER's optical equipment. The antheridium is not shown. This is common in early *Vaucheria* illustrations, VAUCHER failed to see the antheridium in one of the groups of sexual organs illustrated by him, antheridia are also missing in DILLWYN's illustrations of the same species, cf. Fig. 1 D and E, and the two following species dealt with in the present paper were pictured without antheridia by DILLWYN and C. A. AGARDH, respectively.

The species is abundant at Bad Meinberg today, growing in the brook, die Werre, that runs into the pond of the Kurpark, and in the effluent of this pond down in the town. The culture material shown in Fig. 1 F—G was reared from a sample taken on 1 Aug. 1971 in die Werre in the park extension called Silvaticum.

MÜLLER's *Conferva vesicata* as illustrated by Fig. 1 B and C was found in the same place as *C. bursata* according to the German and French papers; in the Latin text, the station is said to be Bad Pymont. Obviously this is a *Vaucheria* grown from a zoospore or an aplanospore (though one filament has been drawn with two swellings), most probably the same species as his *C. bursata*, as this forms such germlings much more frequently than any other species.

DILLWYN (1806) found filaments very similar to *Conferva bursata* mingled with filaments that were obviously *C. vesicata*, and with a little doubt united the two under the name of *C. vesicata*. SMITH & SOWERBY (1807) united DILLWYN's plant with *Vaucheria sessilis* (VAUCH.) DC. under the name of the latter, and DILLWYN (1809) agreed in this synonymy, being inclined to go even further in lumping together. C. A. AGARDH (1812), reporting MÜLLER's *Conferva bursata* from Sweden, combined this epithet with the generic name *Vaucheria*. Later he appears to have changed his mind repeatedly. After (1817) reporting *V. sessilis* as a species separate from *V. bursata* and introducing his *V. ornithocephala* as a new name for what he thinks is *Conferva vesicata* sensu DILLWYN, he then (1822) doubts whether the two last-mentioned species are identical, and finally (1824) lists the following three as independent species: (2) *V. bursata* with *C. vesicata* MÜLLER as a synonym, (11) *V. sessilis*, and (12) *V. ornithocephala* with *C. bursata* MÜLLER as a synonym. Later authors avoided this confusion by simply neglecting MÜLLER's species. WALZ in his monograph (1866) declared it most probable that MÜLLER's *C. bursata* was

identical with *V. sessilis*, but said there were other possibilities too, giving *V. sericea* LYNGB. as an example. Today no other possibility is to be seen. *V. sericea* must be rejected because the oogonia of that species as conceived by WALZ (= *V. fortinialis* (L.) T. CHRISTENSEN) point largely in the same direction and do not form symmetrical pairs. So the specific name given by MÜLLER must be taken up again.

***Vaucheria dillwynii* (WEB. & MOHR)**

C. AG. 1812

Conferva dillwynii WEB. & MOHR 1803

Conferva frigida sensu DILLWYN 1802, non *Conferva frigida* ROTH 1797

Vaucheria pachyderma WALZ 1866

This species was first described and illustrated by DILLWYN (1802), who identified it with *Conferva frigida* ROTH. WEBER & MOHR (1803) pointed out that this was a misidentification, and introduced the epithet *dillwynii* for DILLWYN's plant. DILLWYN's illustration, rendered here as Fig. 1 H, is rather poor and shows no antheridium, but apart from some brackish-water species there is no alga known today that fits with it except for that later called *Vaucheria pachyderma* by WALZ (1866), and this species is found "on the ground in moist shady places" in the colder seasons, just like DILLWYN's plant is said to be. WALZ says DILLWYN's plant may be a *Vaucheria* with aplanospores, but aplanospores are never sessile in a lateral position.

Typification of *V. dillwynii* by herbarium material is difficult. The terrestrial specimen in the DILLWYN herbarium in Cardiff (cf. DIXON 1966) has been used up except for a few sterile filaments. These filaments agree with *V. pachyderma* WALZ in thickness; the soil contains a good deal of *Microcoleus vaginatus*. A badly preserved aquatic specimen entered underneath appears to have been taken in brackish water to judge from the diatoms on it, and must be regarded as a later addition, then assumed to be the same

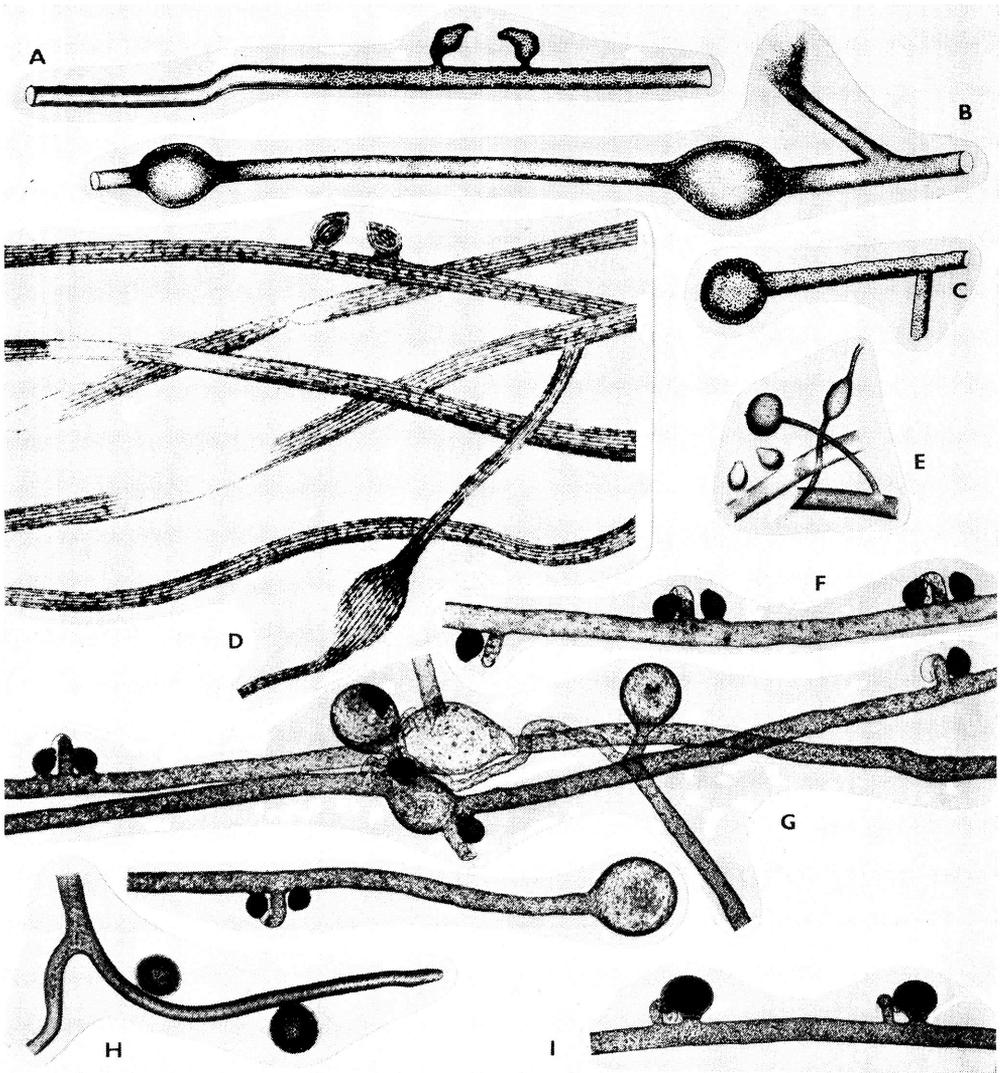


Fig. 1. A—G: *Vaucheria bursata*. — A: Type illustration, material from Meinberg, Germany. From MÜLLER 1788. — B—C: *Vaucheria vesicata* from the same region, probably the same species. From MÜLLER 1788. — D—E: Illustrations from DILLWYN 1806. — F—G: Photomicrographs, unialgal culture reared from sample from Meinberg, Germany. — H—I: *Vaucheria dillwynii*. — H: Type illustration, material from England. — I: Photomicrograph, crude culture reared from a sample from the Geneva region, Switzerland. — Photomicrographs $\times 50$. Scale of older illustrations adapted to fit with the micrographs in size.

species. HEERING (1907 pp. 151 and 191) mentions "das Original exemplar von MOHR" kept in Kiel. This is probably one of the samples collected by WEBER &

MOHR near Göttingen, as they say "an einem Orte ganz demjenigen ähnlich, wo Hr. TURNER und Hr. DILLWYN dieselbe bemerkten". Unfortunately, the specimen

seems to have been in the type herbarium destroyed during World War II, so probably it will never be known with certainty whether it was collected by DILLWYN or by MOHR. In any case, HEERING confirms its identity with *V. pachyderma*, and says its filaments were 60 μm thick. As DILLWYN's specimens have been scattered among a great number of herbaria, authentic DILLWYN material may still turn up somewhere. Even without type material, however, the epithet *dillwynii* must be retained. As to the plant studied by DILLWYN no species fits with it except that which by unbroken tradition is called *V. dillwynii* in England, and also partly called so elsewhere, e.g., in the monograph by DANGEARD (1939). As to MOHR's plant its identity has been witnessed by a specialist of this century. So the name given by WEBER & MOHR holds, regardless of whether it might be typified by "material cited" or their "material at hand".

***Vaucheria velutina* C. AG. 1824**

Vaucheria thuretii WOR. 1869

This species was established by C. A. AGARDH (1824 p. 312), and the type material is kept as no. 14700 in the AGARDH herbarium in Lund. Most of the material, collected "in lacunis exsiccatis ad Graen Aug Sept 1824", is mounted on a sheet of paper. A pencil note on the paper says there is mica material belonging with it and this, too, is still present. On the paper with the dried alga there is also a rough pencil sketch. Fig. 2 A shows a part of this sketch and Fig. 2 B—F a number of fruiting organs from the dried sample. Obviously the plant is the same as that later described by WORONIN (1869) as *V. thuretii*, cf. Fig. 2 G and H. Such identity has previously been indicated by NORDSTEDT (1878), but NORDSTEDT's observation, though recorded by HEERING (1907), has been generally disregarded as to its nomenclatural consequences.

***Vaucheria subsimplex* CROUAN FRAT. 1867**

Vaucheria sphaerospora NORDST. 1878

When NORDSTEDT (1878) introduced *Vaucheria sphaerospora* as a new species he said its closest ally was *V. piloboloides* THUR. Immediately after publishing this he realized that P. L. & H. M. CROUAN (1867) had described a plant under the name *V. subsimplex* which agreed with his own except for details that were probably unimportant. He made a footnote about this in his next paper (1879) saying, in English translation: "It seems very probable to me that *V. subsimplex* CROUAN (Florul. du Finistère, Paris 1867) is identical with *V. sphaerospora*, but since the former species is shown (l.c. tab. 10, Fig. 76) with obovate oospores and without any empty cell under the very antheridial cell, it might possibly be a species separate from the latter."

Fig. 3 of the CROUAN brothers, rendered as Fig. 2 J in the present account, shows a plant with its sexual organs turned obliquely forwards. The outline of the dark body seen would be abnormal for an oospore of NORDSTEDT's species if it is true, but it may well represent an unfertilized oogonium. The drawing shows only a single wall under the antheridium, but the double septation may be difficult to see when the antheridium is directed towards the observer. In addition the entire oogonial part of the tube is evenly dotted instead of showing an isolated mass of cytoplasm (presumably with surplus nuclei) in the middle, but clumping of the cytoplasm may have been taken for an artifact, or perhaps only the outlines were drawn at once and the schematic indication of cytoplasm added after inking. As long as the *Vaucheria* flora of the European west coast was badly known one might perhaps allow for the possible existence of two slightly different species, one covered by the CROUAN, one by the NORDSTEDT description. Today plants of this general type have been found on many localities, and all agree with NORD-

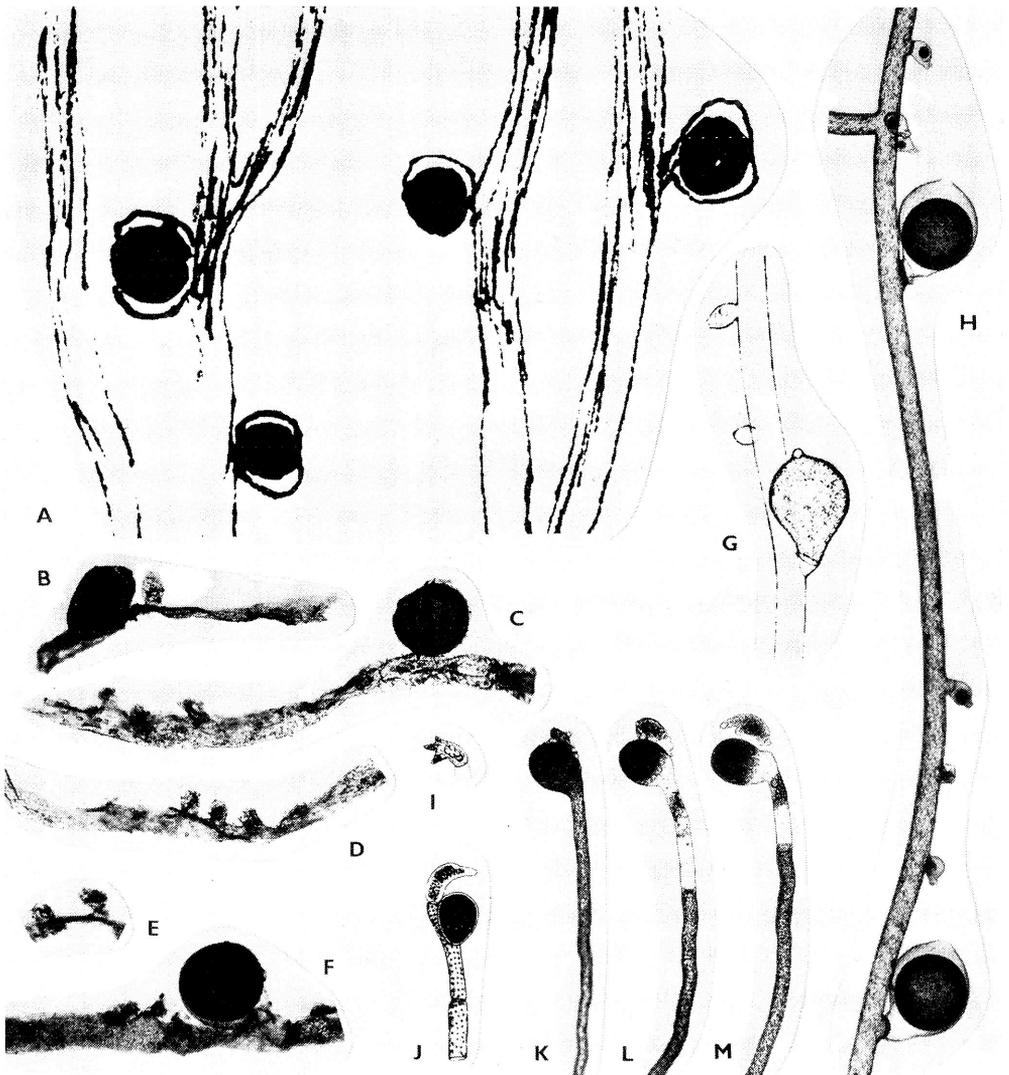


Fig. 2. A—H: *Vaucheria velutina*. — A: Part of sketch by AGARDH on paper with type material. — B—F: Photomicrographs, type material, from Gråen at Landskrona, Sweden. Stained with ruthenium red. — G: Sketch by THURET kept in Paris with his find from the Cherbourg region mentioned by WORONIN when describing *V. thuretii*. — H: Photomicrograph, unialgal culture reared from a sample from the Stornoway region, Scotland. (Most oogonia strongly bent like in THURET's drawing, some little bent as in the illustration published by WORONIN.) — I—M: *Vaucheria subsimplex*. — I—J: Type illustrations, material from the Brest region, France. — K—M: Photomicrographs, crude cultures reared from samples from the Stornoway region, Scotland (K and L) and the Holbæk region, Denmark (M). — Photomicrographs $\times 50$. Scale of older illustrations adapted to fit with the micrographs in size.

STEDT's description. So the slight differences are undoubtedly due to inaccuracies on the part of the CROUAN's.

FELDMANN (1958) expresses the hope that things will be settled by an examination of CROUAN type material. The present author has looked for such material in the two CROUAN herbaria without success. A specimen may still exist, as there is much unsorted material (cf. DIXON 1967). Even without such a specimen, however, the identity of the two species is obvious.

ACKNOWLEDGEMENTS

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Some Electron Microscopical Methods for Solving Wood Anatomical Problems¹

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ABSTRACT

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Various preparatory methods suitable for plant anatomical studies with different types of electron microscopes have been tried. Some of the more promising methods are described. Already by studying relatively thick microtomed wood sections, as well as hand-made ones, in the transmission electron microscope, the presence or absence of pit membranes can be ascertained. Simple preparation makes it possible to obtain good 3-dimensional depth of wood structure with the scanning electron microscope.

Although the chief objective was to perfect methods, some wood anatomical results were also obtained. There are two types of scalariform series of large pits in *Geissoloma* — those with true perforations and those with persisting membranes. The perforations in *Geissoloma* are of the bordered type, whereas in *Betula* borders are absent or extremely reduced. In *Geissoloma*, the marginal zones of the pit membrane persist in the periphery of the perforations.

INTRODUCTION

With the light microscope it is possible to study wood anatomy, except for very fine details. The world beyond the resolution power of the light microscope is, of course, impossible to reach with this instrument. However, already at an earlier stage difficulties arise owing to several factors. Considerable difficulty is associated with obtaining a sufficiently sharply focused image of the detail in question or of its optical section. These problems are related to the thickness, as well as other properties, of the material above, below and adjacent to the detail of interest; the absence of sufficient contrast; the difficulties to recognize relatively thin, convex or otherwise bent membranes or plane

membranes that are not perpendicularly disposed in the slide.

When studying the secondary wood of the genus *Geissoloma* LINDL. ex KUNTH., the senior author once more became troubled by these difficulties. VAN TIEGHEM (1893), SUPPRIAN (1894), SOLEREDER (1908) and DAHLGREN & RAO (1969) have given very few and only brief notes about *Geissoloma* wood, but have reported the presence of vessels with scalariform perforation plates. The senior author is, however, now of the opinion that the published reports are not entirely correct, and was initially uncertain if vessels and perforation plates were actually present in *Geissoloma* wood. The micrographs that we obtained employing conventional methods were not convincing. Further, the senior author obtained a vague impression with the light microscope that the perforations

¹ This work is dedicated to Professor Vivi Täckholm on her 70th birthday.

or the large pits with persisting membranes were bordered. *Betula* L., as well as most other higher plants possessing scalariform perforation plates, has (cf. METCALFE & CHALK 1950) non-bordered perforations. However, more or less distinct borders are described in a few families with scalariform perforation plates, *inter alia*, in the Hamamelidaceae (TIPPO 1938). The presence especially of those with broad borders is regarded as more primitive than the absence. Hence, it is of special interest to know where these different types are really represented and where they are absent. It is highly problematical if this can be determined with the light microscope. With this instrument, the relevant structures are only visible when conditions are particularly favourable, and even then are often very indistinct. Under such circumstances, it must be acknowledged that it is almost impossible to detect variations if they exist in the same material. Later, the senior author, with a special, not yet published method, was able to demonstrate, also with the light microscope, true perforation plates in *Geissoloma* and that the perforations may be of the bordered type. This has, however, only been possible in a very few points of the slides studied. If this is due to very favourable conditions in the relevant regions or if there is a variation, it eludes judgement when the light microscope is employed.

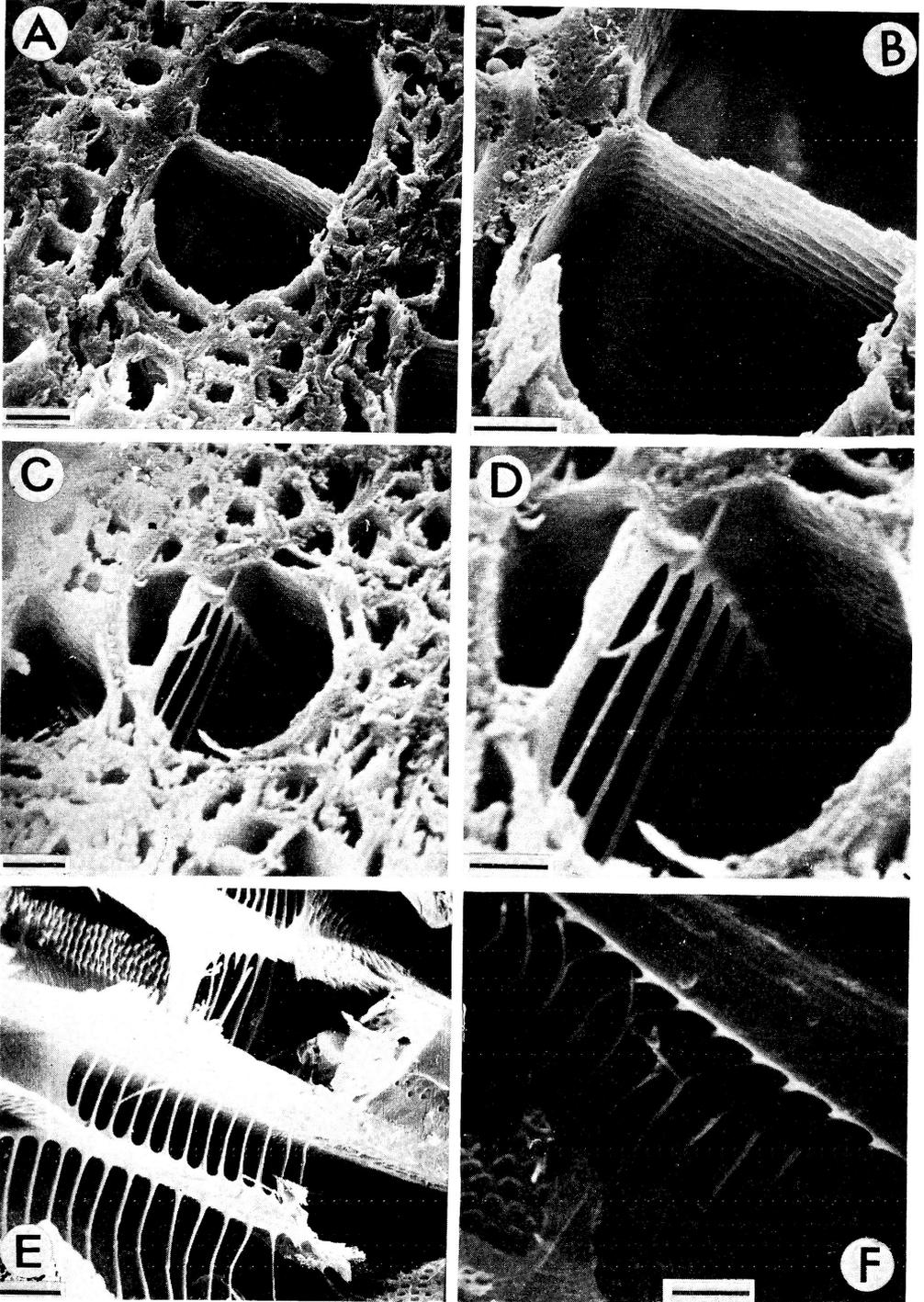
The examples mentioned above of indiscernable wood anatomical details in the light microscope can surely be added to. Electron microscopy certainly offers opportunities to check such a situation and it perhaps should supplant light microscopy. Since mature secondary wood, as is well known, consists predominantly

of dead and empty cells, such investigations may not need to be preceded by a more complicated technical treatment. Any dried wood fragment can be coated with gold-palladium alloy directly in the current way and then immediately be studied in the scanning electron microscope. The true perforations of the plates in the xylem and, on the assumption that the pit membranes are not too thick, also the membrane-bearing large pits should be observable in the transmission electron microscope without prior fixation, embedding, contrasting, etc. when the sections are thin or moderately thick. More elaborate pretreatment may, however, be required before studies of other features can be undertaken employing the transmission electron microscope. Actually, in such instances the additional preparatory work can be expedited quite quickly and is a relatively simple procedure.

EXPERIMENTS WITH TRANSMISSION ELECTRON MICROSCOPE

The objects studied here were mainly secondary wood of *Geissoloma emarginata* (L.) A. JUSS., but *Betula* L. and *Hamamelis* L. have also been used. Thin sections or somewhat thicker ones but with thinner marginal zones and thin fringes were made by hand or with a microtome. In the latter case, paraffin- or methacrylate-embedded material as well as non-embedded wood was employed. After sectioning, the embedding material was removed with xylene and slightly heated in amylacetate, resp. The material was either untreated or fixed in FAA (by our associate KÅRE BREMER) and osmium-contrasted or not contrasted. The initial material included fresh wood and dried wood from

Fig. 1. Wood details of *Betula verrucosa* as seen under the scanning electron microscope. — A, B: Original material fresh, transversely split surface, slightly trimmed locally. Elements belonging to two different vessels dominate in the pictures. — C, D: Original material FAA-fixed, transversely split surface, lightly trimmed locally. Perforation plate and vessel walls exposed in the opened vessel. — E, F: Original material fresh, radially split surface after light trimming. Perforation plates and vessel walls exposed in the opened cells. — The bars equivalent to 1 μ .



herbarium sheets. In the latter case, experiments were conducted with untreated material and with material that had undergone imbibition in a warm teepol solution. The results that were obtained were more or less equivalent in all cases. The herbarium material likewise yielded almost the same detail as the other series.

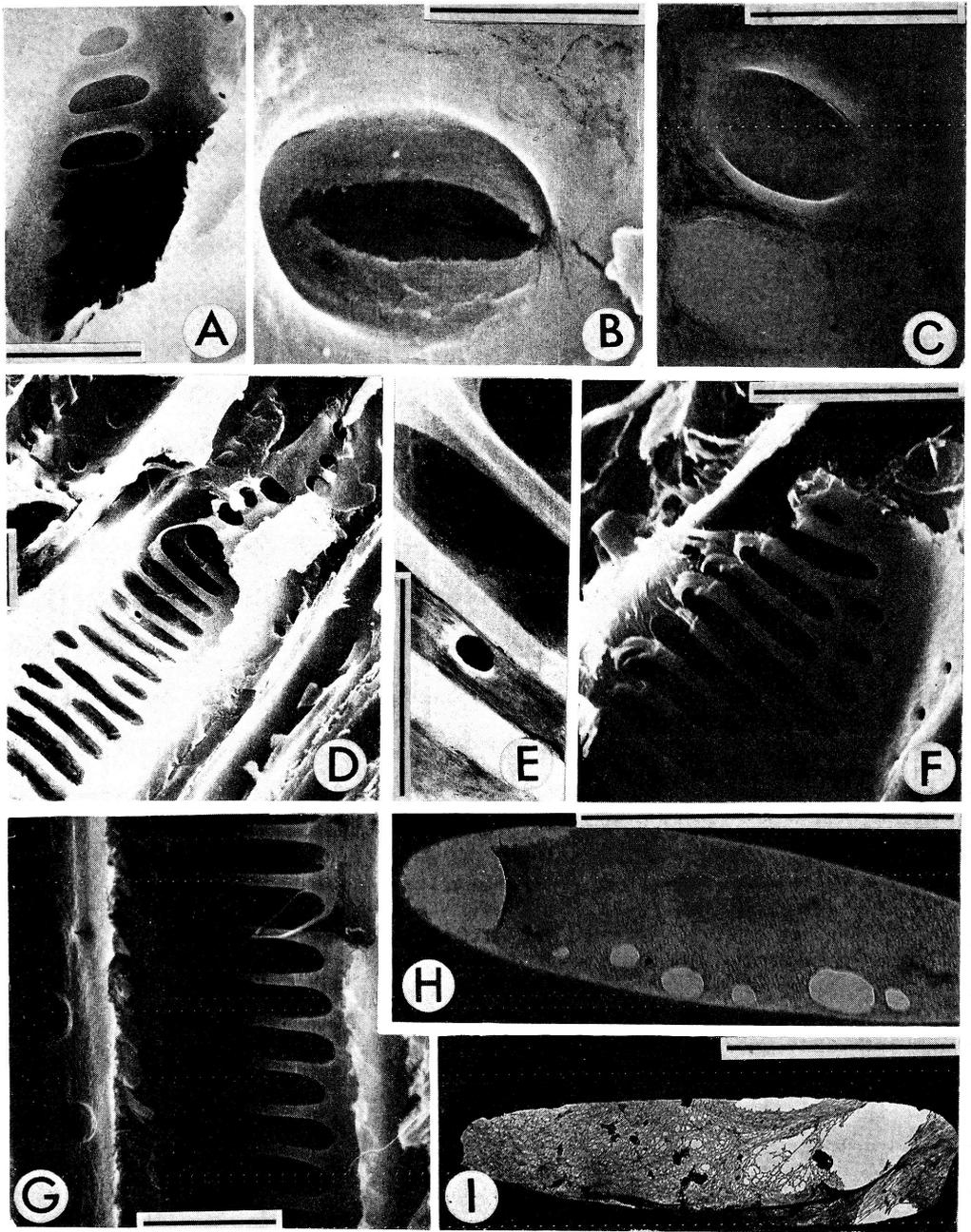
The sectioning procedure can obviously be extremely simple. Hand-prepared sections were quite adequate if they included thin margins or fringes. After the embedding material that might have been present was removed, the sections were rinsed with ethanol and chloroform, then air-dried and placed directly between two grids, each with a single central aperture. Insufficient rinsing caused a disturbing "boiling" phenomenon in the projected image in the transmission electron microscope. The sections were placed between the grids so that they could be attached as securely as possible and with the thinner areas overlapping the grid apertures. The orientation of the specimen can be checked in the light microscope. It is important to be certain that the detail for study is freely exposed, viz. unobscured by material projecting above or below it. The specimens were observed to cant in the transmission electron microscope, although they had been carefully rinsed. These movements, however, could be arrested somewhat by infiltrating the material with a small amount of glycerine or lutrol before drying (Fig. 2 H). To select the right emission dosage is, however, still a problem. The tilting or canting movements did not prevent examination, but were generally an incubus when attempt-

ing to take good electron micrographs. However, adequate stability was often obtained if the material was first exposed 5—10 minutes in the transmission electron microscope, after which sufficiently sharply focused micrographs were obtainable (Fig. 2 I).

As expected, most of the material appeared in the transmission electron microscope to be very black. In *Geissoloma* some scalariform series appeared, however, as composed of wholly electron-transparent, structureless gaps in the black mass. This, of course, signified the presence of true perforations. Other scalariform series exhibited highly transparent areas with irregular cloudlike formations, with a more or less reticular pattern (Fig. 2 I) or with a moderately dark ground substance amply interrupted by lighter spots with darker margins (Fig. 2 H). We deemed all of these partially transparent areas as representing persisting pit membranes. Superpositional effects in these parts of the studied material could be excluded. The reason why these membranes displayed different aspects and the possibility of contamination are not elucidated as yet. The pit membranes often showed a tendency to have one or more open gaps (Fig. 2 H, I). We consider these to be artefacts. Sometimes these gaps appeared to enlarge during the canting movements of the material during observation.

Normally, all the members of each scalariform series either have a pit membrane or lack one. However, occasionally we have observed a series of perforations that are locally interrupted by one or two

Fig. 2. Wood details of *Geissoloma* as seen under the scanning electron microscope (A—G) and the transmission electron microscope (H, I). — A: FAA-fixed material, part of a fringe of a radially split specimen. The end of a scalariform series of membrane-bearing large pits, as well as a few smaller, isolated pits. — B: FAA-fixed material, radially split surface. A membrane-bearing large pit from a scalariform series; the membrane is broken during the preparation work. — C: FAA-fixed material, radially split surface. A membrane-bearing large pit from a scalariform series, and at the base a rather vestigial one in the same series. (The picture has been slightly retouched). — D: FAA-fixation, part of a fringe of a radially split specimen. A scalariform series dominates in the picture. (See further the text!). — E: Detail of Fig. 2 D at a higher magnification. — F: FAA-fixation. Part of a scalariform perforation plate with fragmented bars. — In the right upper corner,



a partially damaged, circular bordered pit. — G: FAA-fixed material, radially split surface. A scalariform perforation plate to the right; bordered pits in the fractured fibre wall to the left. — H, I: Handmade sections. Membrane-bearing, large pits from scalariform series. — The bars equivalent to 1 μ .

pits with membranes or a perforation series with a series of pits with persisting membranes that continue on without interruption. We believe that most of the scalariform series of real perforations belong to the very obliquely oriented "end walls" of the vessel elements and that the series with intact pits belong to the wall systems between the vessels and the rays.

Apart from the rays, the *Geissoloma* wood lacks parenchyma cells. The predominant part of the wood is composed of fibre-tracheids with bordered pits. The transition mentioned above from one type of scalariform series to another probably occurred because the total series belonged to a zone where an obliquely oriented end wall was continued by the wall between one of the engaged vessel elements and a ray. The fact that membranes of large pits are disclosed in the transmission electron microscope confirms that they are really very thin. It is therefore quite understandable why it is so difficult to discriminate between membrane-bearing pits and perforated pits in the light microscope. The absence of a distinct margin around both of the observed pit types favours the absence of borders or of electron-opaque overhanging wall material.

Besides the electron-transparent areas corresponding to perforations and the moderately dense areas corresponding to the members of the larger pits, transmission electron microscopy in *Geissoloma* also reveals narrow, light fissures against a black background. These may be other pit types, which are seen, however, in such perspective that an analysis is not possible. The electron beam may never or very seldom be oriented straight into the narrow pit channel, which in the fibre-tracheids is very deep in relation to the shortest diameter. In *Geissoloma* the two pit apertures of the fibre-tracheids are also shaped like narrow slits that cross each other. This alone may, as mentioned above, make an analysis unfeasible.

In *Betula* and *Hamamelis*, the transmission electron microscopic study has disclosed the presence of scalariform perforation plates, but the bars were considerably narrower than in *Geissoloma*. We have not yet observed any parallel structures with persisting pit membranes. In *Betula* in one case a few intact, large pits at the end of a normal perforation plate were observed.

The observations above indicate that the method described has only a limited range. It may be of utility in making rapid determinations of the presence or absence of scalariform perforation plates or other types of larger perforations or membrane-bearing pits. If all the more or less unnecessary steps (see above) are excluded, the investigation can, indeed, be performed very rapidly: A longitudinal radial section with a thin margin is prepared using a razor blade, then rapidly rinsed with ethanol and chloroform, air-dried for a few seconds and finally mounted directly between the two grids. The entire treatment sequence takes only a few minutes.

EXPERIMENTS WITH SCANNING ELECTRON MICROSCOPY

The scanning electron microscope, as already mentioned, should be an excellent instrument for wood anatomical analysis. We have begun trials of suitable pretreatments of material and, to some extent, a wood anatomical study with the scanning electron microscope. In the beginning, we believed that we were pioneers. We were unaware that the IAWA Bulletin has carried studies during the past 2 years with the same objective (JUTTE & LEWY 1971, 1972; KEITH 1971; ANTOINE, AVELLA & VAN EYSEREN 1971; BUTTERFIELD & MEYLAN 1972). JUTTE and LEWY (1971) also cited some earlier publications on the same subject matter. The authors mentioned have clearly shown that the scanning electron microscope offers good resolution with 3-dimensional depth of

field of a number of wood details. This has been very beautifully shown, *inter alia*, in *Betula* by JUTTE and LEWY (1971).

Up to now, we have only used secondary wood of *Geissoloma* and *Betula* — of *Geissoloma* because of reasons apparent above, of *Betula* to include a well-known material as well as to be able to compare the scalariform-arranged pit and aperture series of *Geissoloma* with the corresponding well-known conditions in *Betula*. The apertures of *Betula* are said to be of the non-bordered type. In the light microscope, bordered pits and apertures are perceived, though very faintly, in *Geissoloma* that are similar to those described in Hamamelidaceae by TIPPO (1938).

Our material included fresh wood (*Betula*), FAA-fixed material (*Geissoloma* and *Betula*) and material from herbarium sheets (*Geissoloma*). At first, relatively thick, transverse, radial and longitudinal sections were made by hand using razor blades. After air-drying, these sections were attached to a dural holder with a drop of glue and coated with a thin film of evaporated gold-palladium alloy. The specimens were then examined on the screen of a Stereoscan Mk LLa (Cambridge Scientific Instrument So.) up to a maximum magnification of 30,000. After learning from JUTTE and LEWY (1971) that splinter sections are better than hand-cut sections, the following series was also made: specimens with transversely fractured surfaces, obtained by simply breaking off slender wood splinters; radially and tangentially fractured surfaces, obtained by first making a very light cut in the desired cleavage plane followed by bending the razor blade upward. All the split surfaces appeared to be rather rough. Some of them were trimmed with a single glancing swipe with a razor blade. This procedure was especially favourable for radially split sections. Here, the fractured surface runs mostly through the rays. In the rays, as well as in non-ray tissue, the fracture surface is mostly in the wall system. Hence, the scalariform perforation

plates are only occasionally exposed after radial splitting, but a great number of them are exposed after trimming. This is possible to confirm in a preparatory microscope at a magnification of $\times 50$.

To remove surface residual fragments, a brief, light contact with adhesive tape is recommended by JUTTE and LEWY (1971). We have found that blowing with compressed air also works very well. To reduce the roughness of the surfaces as much as possible, some of the wood splinters were embedded in methacrylate (methylmethacrylate 90 %, butylmethacrylate 10 %). Paraffin, which was tried, was unsuitable. After the sections were made (both by hand with razor blades and with the microtome), the methacrylate was rinsed out with warmed amylacetate followed in turn by chloroform and ethanol. The material was then air-dried and mounted on dural holders. The results obtained from the various methods and modifications did not differ appreciably from one another nor was there a great difference between herbarium material and other types of material. However, in the herbarium material it is often difficult to identify the rays, and these are, indeed, important when it is necessary to ascertain conditions of orientation inside the material. A further reduction, or best of all, an elimination of the surface fringes seems to be a desideratum. We believe that the results will be much better if the methacrylate method is combined with a smoothing of the investigative surfaces with a glass or diamond knife in an ultratome. Another possibility would be a fine polishing of the surface of wood splinters while embedded in a material that is suitable for such a procedure, followed by removal of the embedding substance. We are presently continuing our work along these lines.

BUTTERFIELD and MEYLAN (1972), working on *Knightia* R. BR. wood, made sections with a razor blade and obtained surfaces that were practically devoid of fringes. We believe that this favourable

result is more or less due to special characteristics of the wood studied. The pre-adjustment of a split surface with a single surface section, as we have practised on *Geissoloma*, would have otherwise resulted in a similar effect as the sectioning method of the above-cited authors. Hence, we believe that the success of one method will vary according to the material under investigation.

ANTOINE & VAN EYSEREN (1971) and ANTOINE, AVELLA & VAN EYSEREN (1971) seem to have really found a method to eliminate all the surface fringes. They pretreated the material with gamma rays. After breakage in various planes, the material displayed no fringes: it was instead very smooth. The surfaces were remarkably uniform, without structural variation. There were, for instance, no differences between the wall centre and the wall periphery. Owing to this, it is possible that the treatment caused some morphological changes — not just a rupturing of the cellulose chains.

Parts of our results are presented as electron micrographs; Fig. 1 is of *Betula*, Fig. 2 A—G, 3 and 4 are of *Geissoloma*. Some remarks on the micrographs will be presented below.

REMARKS ON BETULA

In *Betula verrucosa* (Figs. 1 E, F), the effects of radial splitting with surface trimming are shown. The pits of the scalariform-patterned plates are always perforated. Borders seem to be lacking. It is often possible to recognize details in the background wall between the bars of the perforation plate (Fig. 1 E). All the bars are strikingly narrow. Most of these impressions are confirmed by the transverse surfaces in Fig. 1 C, D, where the perforation plate appears to be strongly obliquely oriented. Each bar is provided here with a vague, dark streak (Fig. 1 D) on its upper side, that is the side that is turned towards the perforation. Possibly this represents the middle lamella or per-

haps a very shallow depression — namely a border of a very vestigial type. The marginal zones of the intact perforation plates seem to have a somewhat uneven surface.

The longitudinal walls of the vessel elements can be observed directly in the opened cells (Fig. 1 B, D), or through the apertures of the perforation plates in the cells that are still closed. In those parts of the vessel that are surrounded only by wood tissue with narrow cells, it is not possible to make reference to radial and tangential walls. Here, the transverse sections of the vessel elements approach the shape of a circle. However, more sharply tangentially oriented walls occur between elements belonging to different vessels and occurring in more or less radially oriented pairs and in small groups. The opposite tangential wall and the radial walls are, however, still grading successively into each other, provided that the former wall only borders on wood cells of the narrow type. Our preliminary studies give the impression that the wall pitting is the same in all of these cases.

As in the light microscope, in the scanning microscope the pits convey the impression as occurring very closely together in one or more closely lying helical lines (Fig. 1 B, C). The wall surfaces are taken up practically completely by the pits. Our scanning electron microscope study gives the impression that the pit opening towards the lumen of the vessel has a rather broad elliptical outline and that the pit channel then constricts to a narrow fissure that widens trumpet-shaped into the almost circular border periphery adjacent to the pit membrane. This impression is not incompatible with the conditions that seem to be perceived in the light microscope. That *Knightia* (Proteaceae) has pits with this shape seems to be certain as shown by the excellent scanning electron microscope micrographs of BUTTERFIELD and MEYLAN'S (1972). Our own micrographs may perhaps give the impression that these

pits have a variable shape. This impression is due mostly to the change in perspective relationships. To obtain a clear picture of the relevant detail of the cell wall with the scanning electron microscope, it seems imperative to study the same spot of the specimen, including the actual detail, from different visual angles. This is possible to do in the scanning electron microscope. However, we have tried this method in a very few cases only.

In the middle part of the left edge in Fig. 1 E, in the left-hand basal corner in Fig. 1 F, and possibly also at some other sites in our *Betula* micrographs, longitudinally fractured vessel walls can be seen. Here, the pits are visible as round areas or cavities, with or without a central dark line. The cavities appear to be the dilated pit chambers; the central line, the maximally narrow part of the pit canal. The absence of the central line may be because the pit canal is obscured by the pit membrane, which in that case has not followed along with the broken-off material, but also may be due to an unfavourable perspective.

JUTTE and LEWY (1971) have shown in *Picea* A. DIETR. and *Abies* MILL. that no one-sided distribution of the pit membranes occurs during the longitudinal splitting of the walls. The interpretation above corresponds also very well with JUTTE and LEWY's *Betula* micrograph (1971). With respect to the parts of the wood tissue with narrow cells in *Betula*, longitudinal sectioning — and even more in longitudinal splitting — but also in transverse sectioning and splitting, results in such great tissue teasing that the surfaces can hardly be studied. However, the transverse surfaces, here and there, exhibit somewhat less disruption. A thin central zone, perhaps the middle lamella, is diffusely perceived against the other wall material. But it could be the result of an extrusion of part of the material as a result of the treatment. The teasing of the surface material could be the

reason why we have not for sure found any longitudinally opened pit canals. That such ones are possible to observe in a more favourable material or after special treatment is evident from the work of BUTTERFIELD and MEYLAN (1972) and ANTOINE, AVELLA and VAN EYSEREN (1971).

REMARKS ON GEISSOLOMA

The surfaces of the radial sections show, *inter alia*, a scalariform series of fenestrate pits. In these cases, it is often very difficult to discriminate if true perforations or pits with persisting membranes are involved. In Fig. 2 G and F, the former type is surely present. The assessment is, however, very difficult in such a case, as illustrated in Fig. 2 D. It appears that there is some kind of substance that has filled up the central part of the pit. This may possibly represent a pit membrane; but belongs most likely to a cell wall in the background. The uniformly outlined perforation, Fig. 2 D, E, visible in one of the filled areas, speaks in favour of the latter opinion, and if this interpretation is correct the presence of a true opening in the actual series is confirmed. The perforation plates of *Geissoloma* are all obliquely disposed, often at such an angle that the vertical plane is approached (light microscopy studies by the senior author). Hence, the distance between the plate and the wall behind it is variable and often very small. Because of the perspective, part of the background often will be projected into the perforations. The scalariform system in Fig. 2 D is in the upper part of the micrograph running obliquely down into the 3-dimensional system. Thus, the corresponding upper part of the relevant cell is only present in the upper third of the micrograph. There appears to be broadly elliptical to more circular perforations, similarly shaped grey areas, as well as transitional types. The light microscopy studies of the senior author disclosed that they are rather broad pits

(fenestrate pits) belonging to a wall in the vessel/ray border. During the splitting of the material, some of the pit membranes may have been completely or partly disrupted.

A part of a scalariform series with rather broad elements can be seen in Fig. 2 A; details of another part of the same series in Fig. 2 B, C. Pit membranes are present here. Experience from the light microscopy substantiates that that type of scalariform series always belongs to walls between vessels and rays. The pit membranes are of a different thickness and as a consequence they are placed in the bottom of more or less shallow wall depressions. Fig. 2 B shows a large pit composed of a relatively deep depression and a very thin pit membrane that has been broken during the preparation work. Fig. 2 C shows, beside a still quite distinct larger pit, also a smaller, scarcely perceivable, vestigial one. The membrane of the former is rather thick but not at all as thick as the membrane of the latter.

As regards radial longitudinal sections, the above-mentioned scalariform series runs a great risk of being damaged mechanically during the preparatory work. This is not surprising since they are practically situated in the wound surface. The membranes and bars may be cracked, flapped or even eliminated. The fissures that result often continue into the surrounding parts of the wall (cf. Fig. 2 B).

The longitudinal sections and cleaved splinters also display smaller pits. Small, round, intensely black areas (Fig. 2 E, F, G) may be the apertures on the vessel side of pits belonging to the walls between the vessel and the fibre-tracheids.

The structures present to the right in Fig. 2 D and G may be pits in the walls between fibres. The differences appear here to be due to different conditions of perspective and because the cleaved plane has had a somewhat zigzag course in the wall.

The radial sections and radial splinters display scalariform plates more or less from in front. The tangential sections, on the other hand, display plates more or less in profile. The bars of the latter are generally broken to such a degree that the plates are worthless as study objects. At the margin of the tangentially sectioned specimens, where, of course, the tangential orientation is very far from perfect, more laterally oriented, less fragmented plates appear. This provides some possibility for a study. The risk of confusing the perforation series with the series of wide-type pits with membranes is mostly eliminated. Fig. 3 E—G shows different zones of scalariform perforation plates and different perspectives. If the micrographs are combined with one another and with our other illustrations, it is evident that the bars are always provided with a rather deep furrow on the side turned towards the perforation. This signifies perforations with well-developed borders. From the bottom of the furrow, a relatively low, central lamella, or ridge, arises. This may represent a marginal zone that remained when the other parts of the earlier present pit membrane was broken down. The perforation plates differ also from the ones in *Betula* by their obviously broader bars.

Possibly Figs. 2 F and 3 G show that the lateral edges of the bars of the per-

Fig. 3. Wood details of *Geissoloma* as seen under the scanning electron microscope. — A: FAA-fixation, transversely split surface, lightly trimmed. Vessel elements; in front of these as well as behind them ray cells. Perforation plate between the vessel elements as well as a series of large, membrane-bearing pits in the wall between one of the vessel elements and ray cells. In the perforations the borders as well as the marginal parts of the earlier present membranes are distinctly seen. — B—D: More or less the same as in Fig. 3 A; the material is, however, in B and C embedded in methacrylate before cutting, in D the material is from a herbarium sheet. — E—G: FAA-fixed material; half-tangentially split surface. Parts of different scalariform perforation series. — The bars equivalent to 1 μ .

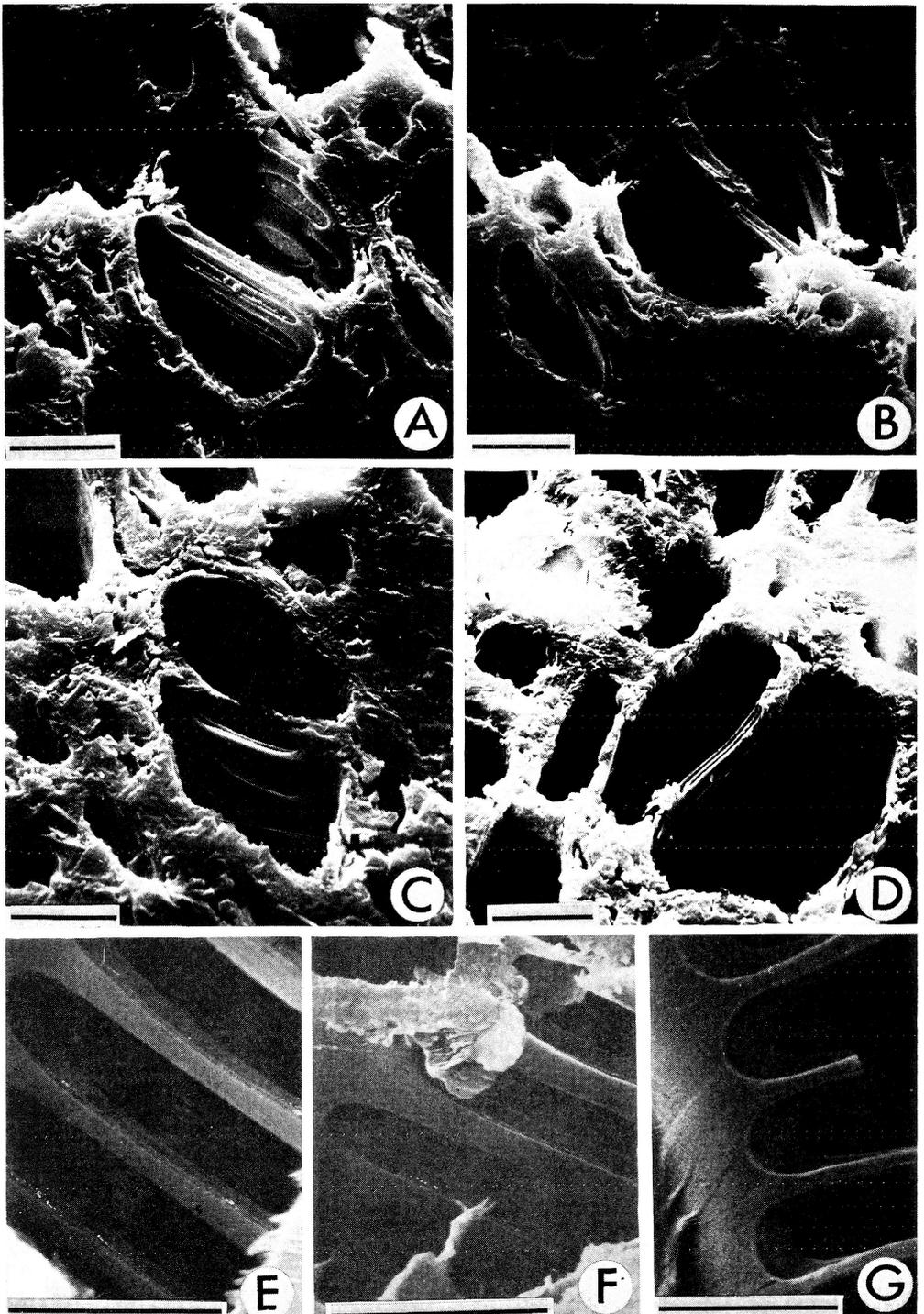


Fig. 3.

foration plates do not have perfectly smooth surfaces. But contamination cannot be excluded here either. In the bottom right-hand corner (Fig. 2 F), a small series of pit apertures can be seen. They probably belong to a wall in a vessel-fibre border. Visible in the upper right-hand corner is a pit chamber with an intact distal aperture, and possibly a proximally fragmented, bent pit membrane above.

The central ridge mentioned above does not seem to be something that is unique for *Geissoloma*. A corresponding condition is illustrated in BUTTERFIELD and MEYLAN's *Knightia* electron micrograph (1972). However, they did not comment on it in their text. *Knightia* and *Geissoloma* have been placed in quite different parts of the angiosperm taxonomic classification system. The perforation plate of *Knightia* has a single perforation, whereas *Geissoloma* has a scalariform perforation plate. Thus, there is justification in assuming that the ridge is not a special phenomenon, but a common one.

The possibility to see the "dilated pit chambers" and their morphological details and the "borders" is different in Figs. 2 D—F and 3 E—G. Of course, the reason for this is the different perspective conditions. In Fig. 2 F, where the dural holder has been turned so that the plate is seen practically from in front, there is no possibility to observe the pit chambers and the borders in the undamaged parts. In the damaged parts, however, there arises sometimes a possibility to see also a little of the borders. The pictures favour a stronger overarching of the border material in the end poles than longitudinally. Similar conditions have been reported by light microscope microscopists in the wood of many different higher plants.

The transversely cut sections and the transversely split sections turned out to be much more favourable for studying the various details than the longitudinal sections. This was due to the possibility of being able to look down into the opened vessels, and in spite of the fact that *Geissoloma* has very narrow ones. Consequently, there are possibilities also to observe undamaged areas. The transverse section exhibits (Fig. 3 A, B) still more distinctly than the longitudinal sections that the vessels of *Geissoloma* have two types of scalariform perforation plates — one with no pit membranes as far as to the marginal zone and a second type with persisting membranes. It is possible to immediately confirm that the former series belongs to the obliquely oriented planes between the elements of one and the same vessel, the latter series to walls in the vessel/ray border. It is also possible in the light microscope to show that this is the case but only after very much labour. Most suitable for such a light microscopic study are indeed sections that are intermediate between transverse and longitudinal sections. The reported experiences show that the scalariform series discussed on page 527 really consists of perforations and that the seeming "filling material" here belongs to the opposite wall.

In our cross sections, we have, up to now, only directly observed the perforations in smaller parts of the represented series. In the remaining portions the perforations themselves have been more or less obscured owing to the perspective. However, very often the presence of the perforations is also in these parts clearly revealed by the central ridge in the chamber zone (Figs. 3 A—D, 4 A—C, E, F).

The margins of the apertures of the pits

Fig. 4. Wood details of *Geissoloma* as seen under the scanning electron microscope. — A: Detail of Fig. 3 A at a higher magnification. — B: Detail of Fig. 3 B at a higher magnification. — C: Detail of Fig. 3 A at a higher magnification. — D: Detail of Fig. 4 A at a higher magnification. — E: Detail of Fig. 3 B and Fig. 4 B at a higher magnification but seen from another projection angle. — F: Details of the same series but seen from a third projection angle. — The bars equivalent to 1 μ .

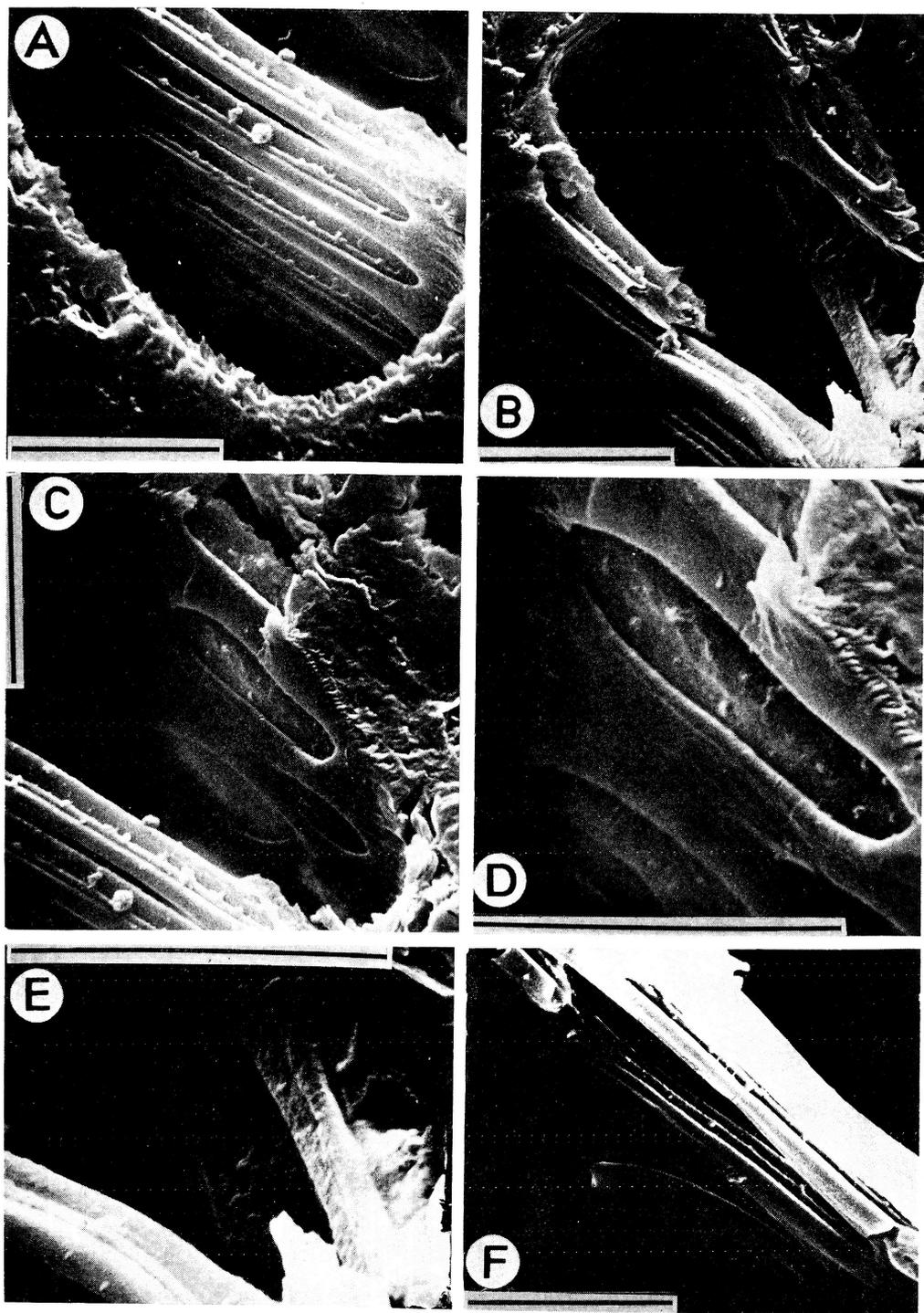


Fig. 4.

in the scalariform series belonging to the vessel/ray border seem to be rounded off (Fig. 4 C, D) and appear, though still more faintly, to project a bit over the pore membrane. This could be construed as representing a slight nuance of chamber formation. The light microscope studies convey the impression that such formations do occur. SUPPRIAN (1894), however, remarked that the pits of the walls in the vessel/parenchyma borders are simple. To draw conclusions here in the light microscope is, however, very difficult. The pit has a certain depth. If the view is not straight down into the pit in the light microscope, the oblique projection creates a risk that bordered pits will be interpreted, although they are really simple pits.

The series of transverse sections give the impression of the presence of strikingly shorter, broader and more scattered pits in the scalariform series, with membrane-bearing pits, than in the perforation series. Light microscope studies confirm that this is usually the case. With exception to a variation in the number of bars and perforations, the series of the latter type is somewhat uniform; the series of the former type is extremely variable. The picture may become very similar to the one that characterizes the perforation series, but passes through a congeries of intermediate types to more or less irregular systems with almost circular pits. The intact parts of the vessel walls, the bars, the plate margins, the pit membranes, the remaining pit margins, etc., all display great unevenness, more or less global aggregates, waves, and so forth, in the scanning electron microscope. We report this, but defer assessments until later.

As in *Betula*, the transverse sections of *Geissoloma* locally show a very dark central streak in the broken longitudinal walls. In this case, it involves the walls in the fibre as well as in the vessel/fibre borders. However, this streak gives primarily the impression of being the result

of mechanical breakage. Locally, just as in the section surface, radial passages are also visible in the walls of the borders between fibres. Occasionally, they verily give the impression of being pits. They suffer, however, so much damage from breakage that an unequivocal identification is impossible. Irregular, rather small cavities appear to be very common in the transverse broken walls, and possibly correspond to the fringes in the removed material.

SOME CONCLUDING REMARKS

Our results indicate that the scanning electron microscope is an excellent instrument for wood anatomical studies. The possibility to obtain a direct view in the 3-dimensional system signifies something novel for the wood anatomist. However, it is obvious that there are risks for erroneous interpretations if different perspectives are not employed. When taking cognizance of perspective, the instrument will be maximally exploited and interpretational errors will be reduced to a minimum.

Some wood elements are easy to identify in the scanning electron microscope. Difficulty arises with others. Prerequisites for solving relevant problems using this instrument are previously acquired, basic knowledge of the specific wood structure under consideration from light microscope studies. The scanning electron microscope thus stands out as a very important complementary instrument. Scanning electron microscopy can also settle questions that were only possible to approach partially with the light microscope.

The transmission electron microscope studies, reported on page 520, show that the transmission electron microscope is also an important complementary instrument for the wood anatomist. We are, however, convinced that the importance of the transmission electron microscope

is not at all limited to such special occasions as the one we illustrated. Instead, transmission electron microscopy may become of very great importance for the wood anatomist in a number of different situations once the technical difficulties of preparation are solved.

The greatest problem, based on our experience, is to deem if the detail under consideration is being identified properly in the transmission microscope, and how it is oriented. The difficulties are extraordinarily great ones when a more complicated tissue is involved. For the most part, there are greater or smaller opportunities to make an arbitrary identification by guessing, but this is, of course, less recommendable.

Many of the difficulties could be obviated if there were possibilities to employ, what we call, "etapp sectioning" and "etapp study". Here, we mean the possibility to make preparations for light microscope studies first, choose from this material, identify and take micrographs of the relevant details, cut this portion out of the primary slide preparation, orient it in the most desirable way, section it again in an ultratome and then study it in the transmission electron microscope. The senior author has, for a number of years, worked with these technical problems — mostly with other plant materials than wood — and has made some attempts employing the above procedures with some progress being enjoyed. Our present technical work on wood also includes such

experiments. These are, however, only in the initial stages.

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Current Topics

Xeromorphy in Plants as a Possible Basis for Migration between Arid and Nutritionally-deficient Environments¹

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ABSTRACT

SMALL, E. 1973. Xeromorphy in plants as a possible basis for migration between arid and nutritionally-deficient environments. — *Bot. Notiser* 126: 534—539.

Xeromorphic features are frequently present in plants adapted to conditions of nutrient deficiency. Apparently such characteristics have evolved independently in response to aridity and nutrient deficiency. It is suggested that physiological properties inherent in xeromorphy are adaptive to both circumstances, and that accordingly there is a degree of overlap in the ecological amplitude of xeromorphs adapted either to arid or to nutritionally-deficient environments. The hypothesis is discussed that such preadaptation may facilitate occupation of the reciprocal habitat, both as a flexible response within the range of plasticity of a species, and as an evolutionary change.

INTRODUCTION

Botanists have recognized the considerable morphological convergence frequently present in plants adapted to dry habitats. It is not so generally known, however, that these recurrent features of plants adapted to arid environments are often also found in plants adapted to nutritionally-deficient environments (FIRBAS 1931, SÆBØ 1970, SMALL 1972 c). Such features include limited stature, reduction in internode length, perenniality, and leaf modifications, such as small size, small cells, compaction of tissues, thick cuticle, narrowed shape, glaucescence, pubescence, and the development of strengthening features. This paper examines the possibility that these common characteristics allow ecological exploitation of one habitat by plants adapted to the other, and that such

preadaptation has facilitated the evolution of specialized xerophytes and "oligotrophophytes" from each other. The evidence to be given is circumstantial, and the hypothesis is presented primarily in the hope of provoking further examination of the adaptive role of xeromorphy.

THE CORRELATION OF XEROMORPHY AND NUTRIENT-DEFICIENT HABITATS

SCHIMPER (1898) recognized that xeromorphous plants frequently occurred in habitats receiving a large supply of moisture. He interpreted this as an indication that the habitats were in fact arid, and listed seven classes of environment which he described as "physiologically dry". Several of these, including peat bogs, solfataras, the surfaces of bark and rocks, and coarse-textured soils, are all substrates which are poor in nutrients.

¹ Plant Research Institute Contribution No. 822.

Serpentine soils are especially exemplary. Such soils usually are characterized by very low levels of available calcium, are generally occupied by plants of xeromorphic appearance, and a characteristic set of "serpentinomorphoses" consisting of narrow leaves, glabrescence, and glaucescence is frequently present (KRUCKEBERG 1969 a). Moreover, there are numerous examples of plant species of mesophytic appearance which have varietal xeromorphs occupying serpentines (KRUCKEBERG 1969 b).

A particularly widespread sub-set of xeromorphic features is included in the rather subjective concept of "sclerophylly". Sclerophylly refers to the "hardness" of leaves, and is conditioned by cutinization, sclerification, silicification, and perhaps also by hydration. The occurrence of sclerophylly has been correlated with levels of essential elements in the substrate. BEADLE (1966) found that sclerophyllous-leaved species increase and nonsclerophyllous species decrease toward the west across the Australian continent. He attributed this to a corresponding decrease of phosphorus in the soil, and reinforced his argument by demonstrating that the xeromorphs are extremely resistant to mineral starvation (BEADLE 1968). LOVELESS (1961, 1962) examined the leaves of many species from Jamaica, North America, Africa, and India, and found a negative correlation between degree of sclerophylly and phosphorus content. He also noted that phosphate deficiency was characteristic of soils carrying sclerophyllous vegetation.

PHYSIOLOGICAL BASES OF MUTUAL ADAPTATION THROUGH XEROMORPHY IN PLANTS OF ARID AND NUTRITIONALLY-DEFICIENT HABITATS

There may be a close physiological kinship between drought tolerance and tolerance to low availability of nutrients. Low levels of nitrogen strongly increase

the drought resistance of plants as measured by a variety of criteria (PHARIS & KRAMER 1964, BEADLE 1966, ETTER 1969), and xeromorphic features often appear to be increased both by drought (SHIELDS 1950, STOCKER 1960, OPPENHEIMER 1960) and by low levels of nutrients (MOTHES 1932, MÜLLER-STOLL 1948, MILLER 1963, BEADLE 1966; see MARTHALER 1939 for a contradictory viewpoint). MOTHES (1932) has in fact attributed the increase in xeromorphy of plants grown under low nitrate levels to a developmental response to actual drought brought on by the high osmotic pressures induced in tissues by low nitrogen.

Moreover there is reason to believe that the adaptations evolved to meet one environment are also partly suited for the other. A prime function of sclerophylly in true xerophytes is probably the ability to tolerate, through high mechanical strength, the great tissue water potentials developed when water becomes limiting and stressful pressure gradients are developed. It is well-known that extreme pressures are frequently found in sclerophylls (SCHOLANDER et al. 1965), and that such pressures cause plasmolysis of the cells of leaves of mesophytes. Additionally, small cells, common in xerophytes and plants deficient in nutrients, appear relatively resistant to plasmolysis (STOCKER 1960 p. 132). ILJIN (1957) has emphasized the mechanical aspects of drying injury, ascribing desiccation damage particularly to mechanical rupture of the protoplast. Cutinization and compaction of tissues also decrease water loss and so improve water economy. Accordingly, sclerophylly resulting from adaptation to low nutrient levels should also be of utility in an arid environment.

The converse, why xeromorphy due to aridity should be adaptive under conditions of limited nutrient availability, is more difficult to rationalize, and in fact an adaptive basis for xeromorphy in plants of nutritionally-deficient habitats is unclear. However, the observations that

genetically-fixed xeromorphic traits are common in plants native to nutrient-deficient substrates, and that nutrient deficiency enhances a plastic xeromorphic response, combine to suggest that canalization (genetic assimilation) occurs, and therefore that xeromorphy may indeed be adaptive to nutrient deficiency. There is a reduced proportion of nitrogen and phosphorus, thus of protein, in sclerophyllous leaves, which accordingly use less nutrients to construct and maintain a unit of dry matter. SMALL (1972 b, d) has suggested that sclerophyllous leaves may therefore be relatively efficient utilizers of the limited nutrient resources of nutritionally-deficient substrates. Another factor may be related to the observation that many sclerophyllous xeromorphs are evergreen. MONK (1966) found that evergreenness in Florida forest communities is predominant on sterile soils, and explained this observation on the basis of a closed nutrient conservation cycle in which the slow decomposition of evergreen litter (compared to deciduous litter) provides a continuous supply of nutrients from year-round leaf fall.

A consideration of the biology of arid and nutritionally-deficient habitats also leads one to predict that a degree of adaptive convergence should be present between types of plants suited to each habitat. Limited moisture and limited nutrients both reduce productivity and so limit the life form. Annuals are generally absent from low-fertility soils, probably because they are unable to compete with perennials which survive on much smaller nutrient uptake on the basis of maintaining a given unit of biomass. (Annuals store food only in the seeds, whereas perennials store it in various organs). Annuals are present in arid environments but they are generally drought-evaders which do not possess xerophytic adaptations, and do not enter into the discussion. Because of limited productivity, arid and nutritionally-impoverished communities are often sparse and open, hence subject

to intense insolation and high temperature. These factors have both been suggested as possible causes of xeromorphy (SHIELDS 1950, WARDLE 1965) and they might therefore intensify xeromorphic features in both kinds of environments, causing further convergence.

It should be noted that plants may alternatively adapt to drought and to mineral deficiency by a variety of cryptic mechanisms which are quite divorced from the xeromorphic syndrome. Adaptation to limited nutrients can be had by lower nutritional requirements, by superior ability to extract from the substrate, and by efficient mechanisms of redistribution and utilization of limited elements. Drought tolerance may simply be a physiological property of the protoplasm. One should therefore not be surprised to find that xeromorphic characters are frequently absent from plants of arid and nutritionally-deficient habitats, and often do not indicate pronounced adaptation to either habitat. It has long been realized that many xeromorphs are not xerophytes (MAXIMOV 1929) and in particular it has been found that many nutritional xeromorphs are physiologically mesophytic (BEADLE 1966).

EVIDENCE FOR PREADAPTION OF XEROMORPHS OF ARID AND NUTRITIONALLY-DEFICIENT HABITATS FOR THE RECIPROCAL ENVIRONMENT

If there is a degree of overlap in the ecological amplitude of plants adapted to arid and to nutritionally-deficient environments, then one should expect to find (a) examples of species which have the ability to exploit both habitats, (b) species in one kind of habitat phylogenetically related to species in the other kind of habitat, and (c) an especially pronounced development of xeromorphy in habitats which are both arid and infertile.

With respect to (a) the acid bog habitat is exemplary. Many acid bog plants are

exceptionally xeromorphic, showing such characteristics as small, thick, heavily-cutinized, revolute leaves, with sunken stomates, and a covering of hairs, and short internodes. For a considerable period after SCHIMPER put forth his theory of "physiological drought" it was thought that some form of aridity existed in bogs. However it has been shown that bog plants do not experience limitation of water supply (SMALL 1972 b), but rather that nutrient restriction is the major ecological factor. The bog substrate is extremely deficient in nitrogen and phosphorus and bog xeromorphs have comparatively low leaf contents of these elements (SMALL 1972 a). Of importance to this discussion is the fact that many of the plants found in bogs are also found in dry habitats such as dunes, sand ridges, and dry fields (SMALL 1972 b).

Another kind of drought is experienced by evergreen plants of very cold climates. During the dormant season, when water freezes and is no longer available, such plants must be resistant to desiccation (GATES 1914). LEVITT (1956) has concluded that there is a close correlation of the hardiness of plants to frost and drought because of a common resistance to dehydration. It is interesting to note, therefore, that a number of cold-climate conifers and Ericaceae are dominant in edaphically poor substrates in New England pine barrens (STERN & BUELL 1951, TEDROW 1952).

With regards to (b), the occurrence of phyletically related species in the different habitats, an outstanding example is found in BEADLE's (1966) analysis of xeromorphy in the Australian flora. BEADLE found that all but one of the common sclerophyllous desert genera also occur in coastal, high-rainfall, low-soil-fertility regions. The desert species are probably derived from species of the low fertility regions, as the desert is of comparatively recent origin. Not one of the many sclerophyllous rain-forest genera of Australia is related to the desert genera, suggesting a high degree

of preadaptation by low soil fertility for a xeric environment in the latter.

The xeromorphic Ericaceae perhaps are the family of plants most specialized to low nutrient availability, and they are very prominent, for example, in nutrient-deficient bogs. It is significant therefore that ericads appear adapted to many arid habitats. PISEK and WINKLER (1953) found that evergreen alpine dwarf bushes of *Arctostaphylos*, *Rhododendron*, and *Vaccinium* showed extreme desiccation resistance.

With respect to (c), it may be noted that habitats are frequently both arid and infertile, especially when the substrate is coarse-textured, simultaneously lowering cation exchange capacity and available water. An especially arid and infertile habitat was investigated by SHIELDS (SHIELDS 1951, SHIELDS & MANGUM 1954), who examined numerous xeromorphic plants in the nutrient-deficient gypsum of the White Sands of New Mexico. Another example is seen in the sclerophyllous associations dominating Mediterranean climates. These associations are often found on infertile soils (SPECHT 1969). Serpentine soils provide an additional example. WALKER (1954) has noted that the physical characteristics of serpentine soils contribute to aridity. However WHITTAKER (1954) points out that comparatively xeromorphic serpentine vegetation often occurs adjacent to non-xeromorphic, non-serpentine vegetation receiving a comparable supply of water.

EVOLUTIONARY SIGNIFICANCE

Ease of movement between arid and infertile environments may play a significant role in plant evolution. Drought and soil infertility are ubiquitous selective forces requiring adaptation from all plants. The geographical mosaic of environments in which plants occur often involves differential adaptation to drought and to soil fertility. A minor degree of xeromorphy may therefore play an important

though inconspicuous role in movement between environments which differ only slightly with respect to aridity and nutrient status. The opportunity to migrate between arid and nutritionally-deficient environments probably occurs frequently and preadaptation by xeromorphy may often expedite entry into the new adaptive zone.

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Botanical Literature

RECHINGER, K. H. (ed.): *Flora Iranica*. Lfg. 90—100. — Akademische Druck- u. Verlagsanstalt, Graz 1972.

The ninetieth fascicle of 'Flora Iranica' deals exclusively with *Cousinia*, the next largest genus of flowering plants in that area. With 355 species in the actual region, the genus is surpassed in number only by *Astragalus*. Professor RECHINGER, who has long taken a keen interest in *Cousinia*, now presents a masterly revision of an almost monographic character. Only the solicitude for the progress of the flora has prevented him from treating the whole genus, which very clearly has its evolutionary centre in the 'Flora Iranica' area. Altogether 307 species, or 86 % of those occurring in the area, are endemic there. No less than 61 species are described as new in the present treatment and about 65 further species have already previously been described by the author. In other words, more than one third of the species in the area have been established by RECHINGER! Only 32 earlier species are put into synonymy.

RECHINGER divides the genus into about 60 sections, partly on new criteria and partly based on the grouping presented by TSCHERNOVA in the 'Flora of the U.S.S.R.' Many sections are monotypic and a number of species cannot yet be attributed to sections, mainly because of the insufficient knowledge of fruit characters.

The sequence chosen is based on life form and duration of the species, starting with the strongly lignified, perennial species and ending with the annuals.

In spite of the extreme polymorphism in the genus, even the larger sections seem to constitute natural groups. The largest section is *Cynaroideae*, comprising 57 species with a fairly constant and characteristic combination of morphological

characters and with a western distribution within the generic area. On the other hand, sect. *Alpinae* with 22 species presents quite a different combination of characteristics and occurs in the eastern and north-eastern mountain regions.

A detailed phytogeographical analysis of the genus would no doubt give important clues to the history and evolution of the flora in the area. In *Cousinia* there is a high percentage of local endemics and only a limited number of more widely and evenly distributed species. Some species have a complicated distribution pattern with disjunctions or otherwise broken or even mosaic ranges. In some groups hybridization seems to have obliterated the borderlines between once distinct taxa and thus contributed to the polymorphism and the complexity of distribution.

The polymorphism in the genus is, indeed, striking, even when considering its size. There is an astonishing variety in, e.g., habit, leaf shape and morphology of the involucre. The certainly considerable and taxonomically useful variation in achenes and pappus is still, however, largely unknown.

The *Cousinia* volume is exceptionally well illustrated. In addition to the 329 text pages there are 184 pages of illustrations, which greatly enhance the usefulness of the work. They include a great number of accurate photographs of herbarium specimens, several good drawings adopted from one of RECHINGER's previous publications, and about thirty especially artistic and elegant new drawings by H. LAUTH. Finally, 16 excellent colour photographs of *Cousinias* in natural habitats conclude this fine volume.

The other families now treated are in \pm decreasing size, Solanaceae (E. SCHÖNBECK-TEMESY), Zygophyllaceae (M. NABIL

EL HADIDI), Amaranthaceae (P. AELLEN), Thymelaeaceae (B. PETERSON), Betulaceae, Corylaceae and Hippocastanaceae (all by K. BROWICZ), Frankeniaceae (J. CHRTEK), Pyrolaceae and Monotropaceae (both by B. KRÍSA).

Points of interest include SCHÖNBECK-TEMESY's treatment of *Hyoscyamus*. She recognizes a new subgenus named *Dendrotrichon*, comprising eight species, confined to the Saharo-Sindian floristic region. Five of these are endemic to the 'Flora Iranica' area and no less than four are described as new.

BROWICZ in his treatment of *Betula* recognizes two new endemic species, both from the mountainous eastern parts of the area.

Another genus of special phytogeographical interest is *Hypericopsis* (Frankeniaceae), which is monotypic and restricted to southern Iran.

'Flora Iranica' is now rapidly approaching the stage of half completion. This amazing progress of the immense undertaking has only been possible thanks to RECHINGER's unrivalled capacity and devotion to the task. The parts so far published are naturally varying, not only in size, but also in quality and detail. It seems to be the editor's policy to treat the genera with pronounced centres within the area with special care and thoroughness. *Cousinia* is one good example, others to come are e.g. *Astragalus* and *Acantholimon*.

Among the large families still remaining are Compositae (except *Cousinia*), Leguminosae (with the formidable genus *Astragalus*), Labiatae, Caryophyllaceae and Chenopodiaceae. On the other hand, it is reassuring to know that families as for instance Gramineae, Cruciferae and Boraginaceae have already been successfully dealt with, as well as such crucial genera as *Cousinia* and *Allium*.

One of the important outcomes of the 'Flora Iranica' project is the correlation of Soviet taxonomy with that of the western world. In this respect the flora constitutes a pioneer work of great signi-

ficance, viz. the first synthesis of two often contrasting views on the circumscription and naming of taxa, especially on the level of species.

The botanical world, already deeply indebted to RECHINGER for his fundamental contributions to the flora of Eurasia, looks forward to the further progress and the successful completion of this outstanding flora.

BERTIL NORDENSTAM

HORIKAWA, Y. Atlas of the Japanese Flora. An introduction to plant sociology of East Asia. — Gakken Co. Ltd., Tokyo 1972. 12+8 pages, 500+1 maps.

This atlas (actually vol. I) contains results of fifty years of research performed by Emeritus Prof. Y. HORIKAWA, Hiroshima, on the distribution of plants in Japan and its neighbouring areas: the southern Kuril Islands, Sakhalin, Manchuria, Korea, Taiwan and the Pacific Islands. This great work presents the distribution of 440 flowering plants, 30 pteridophytes and 30 bryophytes (the flora of Japan comprises nearly 7000 species of flowering plants, 600 pteridophytes and 1500 bryophytes). Almost all the records are based on Prof. HORIKAWA's personal field observations and collections, only a minor part on specimens in other herbaria, on monographs or on local floras.

Every taxon in this atlas has been presented by the "three-dimensional method" devised about ten years ago by Prof. HORIKAWA himself. In addition to a traditional map of the horizontal distribution there are two profiles on each map that show the vertical distribution, one from west to east and the other from south to north. The map of the horizontal distribution is based on a grid method, with a dot for the occurrence of a plant in each square of 10' of latitude by 15' of longitude, which means ca. 18.5×22.82 km at

lat. 35°N. For the sake of comparison it may be mentioned that in HULTÉN's N.W. European atlas a dot represents occurrence in an area 16 km in diameter, PERRING & WALTER's Flora of the British Isles has 10-km squares, and Atlas Florae Europaea 50-km squares. Of the total of 7210 squares in the grid, 1379 relate to Japan and 5831 to other areas. The symbols used for occurrence in Japan are black dots and open circles, the latter representing extinct localities. The records in the neighbouring areas are marked with crosses; however, areas outside Japan are treated (and explored) rather incompletely. — Grids are also used with the profiles, each square covering 100 m of altitude.

Every map has a short text, which besides the scientific name contains important synonyms, the Japanese name (written in Japanese katakana and Roman letters) and data on the general habit, life-form, month of flowering and fruiting or spore maturation in the median area of the Japanese range, the distribution outside Japan, habit, habitat, ecology, taxonomy, and possible utilization by man.

A separate colour map of the potential vegetation in Japan compiled and revised by HORIKAWA is also included in the atlas.

The three-dimensional maps are extremely illuminating. In Japan the differences in altitude are great, and the traditional maps cannot give adequate information on the zonal distribution of plants in mountain areas, but the present maps show distinctly in which life zone a taxon occurs. For instance, some mapped moss species common in Fennoscandia (*Ptilium crista-castrensis*, *Hylocomium splendens*, *Rhytidiadelphus triquetrus*) and boreal dwarf shrubs (*Empetrum nigrum* var. *japonicum*, *Vaccinium vitis-idaea* coll.) seem to have fairly extensive horizontal distribution in Japan, but in fact they may occur at sea-level only in Hokkaido; in Honshu they are confined to the medium and upper levels on mountains. So-called arctic-alpine plants (*Diapensia*

lapponica var. *obovata*, *Loiseleuria procumbens*) are found only in the uppermost parts of the mountains in both Hokkaido and Honshu. The ranges of these species agree with their known ecology, but the map of *Hedwigia ciliata* is surprising, since this moss species seems to be commonest in the warm-temperate zone in Japan. Bioclimatically this corresponds to the Mediterranean region in Europe, where, however, the species is also common at latitudes and altitudes above this region. This map is one of those which call for further taxonomic studies.

It is specially interesting to examine the natural distributions in Japan of plants cultivated as ornamentals elsewhere. For instance, *Magnolia obovata*, *Aralia elata*, *Hydrangea petiolaris* and *Actinidia kolomikta* occur in Hokkaido up to 600—1000 m above sea-level and from those extreme localities we might perhaps be able to obtain more hardy provenances of ornamentals for Northern Europe and Canada (the present ones presumably mainly derive from the temperate regions of Honshu).

It is obvious that HORIKAWA's excellent atlas inaugurates a new era in the mapping of the distributions of plants, an activity that has grown considerably in importance since the publication of HULTÉN's inspiring first atlas about twenty-five years ago. Earlier, range studies were primarily employed in the fields of taxonomy and phytosociology, but nowadays the use of distribution maps is increasing.

For all purposes the three-dimensional maps are more useful and valuable than the traditional ones. The provision of information on altitude in distribution maps could be facilitated by the inclusion of altitude records in all future herbarium labels and field notes.

The reader who has only a limited acquaintance with the Japanese flora is not able to find any real defects. There are some cases in which the Russian literature is overlooked (*Vaccinium vitis-idaea*

coll. occurs in the area of Ussuri; the seeds of *Pinus koraiensis* are also very important as food in the area of Amur and Ussuri, etc.), but, considering the scope of the atlas, such omissions are of no great significance. The selection of the taxa presented is obviously the result of careful consideration by the author, but the European reader hopes that next volume may also contain examples of wide-ranging ("cosmopolitan") weeds.

Used together with the Distribution maps of flowering plants in Japan by HARA and KANAI it gives readers outside Japan a good idea of many distributional types in the Japanese flora and of the ranges of many important taxa used as climatic indicators. We are most grateful to Prof. HORIKAWA for this admirable atlas, which will enable us to understand and use Japanese botanical papers much better than earlier. We are eagerly awaiting the next volumes!

LEENA HÄMET-AHTI

NORDHAGEN, R.: Norsk Flora. Illustrasjonsbind. Del 1. — Aschehoug & Co., Oslo 1970. 638+XVIII pp., 772 fig. Drawings by MIRANDA BØDTKER. Price Nkr 75:—.

This book is a very beautiful and useful newcomer among Scandinavian floristic handbooks. It is the first of two volumes of illustrations intended to accompany NORDHAGEN's Norsk Flora of 1940. The illustrations can, however, very well be used separately as they are quite independent of NORDHAGEN's text. Apart from the legends, the only text is a two-page preface (in Norwegian), the remaining 636 pages being drawings.

The book consists of three parts bound together, dealing with, respectively, pteridophytes and conifers, monocotyledons, and dicotyledons up to and including the Papaveraceae in ENGLER-DIELS' system. The first two parts appeared in 1944 and 1948, the third not until 1970. This fact should

have been stated somewhere in the compound edition, in particular as it explains the great differences in nomenclature between the three parts. One is somewhat surprised at finding names such as *Dryopteris Linnaeana*, *Juncus macer*, and *Carex gracilis* in a book dated 1970, and at not even finding the currently used names as synonyms: *Gymnocarpium dryopteris*, *J. tenuis*, and *C. acuta*. The third part is up to date in this respect, and follows the nomenclature in Flora Europaea I (1964) fairly closely.

All species native to, or naturalized in Norway have been illustrated, and a great number of casuals, for instance in *Chenopodium*, are included. As a rule, different subspecies of polytypic species are illustrated separately. For each species, trees and shrubs excepted, there is at least one drawing of a complete specimen including its subterranean parts. Parts of the plant are shown in enlarged detail. The details selected are on the whole relevant, however, some items that could perhaps have been expected in a book like this are missing, e.g. anthers of *Poa annua* and *supina*, spikelets of the adventitious *Phalaris* species, and capsules of *Arenaria serpyllifolia* and *leptocladus*. — The drawings of *Rumex palustris* and *maritimus* have been exchanged, as have the ligule drawings of *Carex "Pairaei"* and *contigua*.

MIRANDA BØDTKER's drawings are quite admirable, and each illustration is a little masterpiece in composition as well as in accuracy. With its richness of detail, her style approaches LINDMAN's in Bilder ur Nordens Flora (1901—1905). Much of the good impression the book makes is due to her efforts.

Unfortunately, the printer has not done full justice to MIRANDA BØDTKER's fine work: the paper used is rather too thin, so that the pictures on the next two pages show through. In some cases, the original drawings have been too much reduced, so that the finest lines appear to be broken: the illustration of *Luzula pilosa*

is partly spoilt for this reason. These remarks apply only to the part dealing with monocotyledons; the 1970 part on dicotyledons is satisfactory in both respects.

To make full use of page space, the scale of the habit drawings has been varied, even between closely related taxa. The scale has, however, been given in the legends (except in the pteridophyte—gymnosperm part).

In the monocotyledon section, the enlargement of the detail drawings is clearly indicated. This good custom has been abandoned in the section on dicotyledons, which the reviewer regards as a serious shortcoming. There can have been no valid reason for substituting an exact statement with a word like "forstørret" (enlarged). In this way there is an unnecessary loss of important information, and one could in some instances be quite misled: in *Selaginella* and *Isoëtes* the microspores are drawn almost as large as the macrospores, and there is no indication that the scales are different!

Anyone with a special interest in a taxonomically intricate group would perhaps not get maximum information from illustrations of the type presented in this book (an exception might be the *Papaver* drawings, which seem very instructive). But this applies at least equally well to any other illustrated flora of comparable size known to the reviewer.

Indeed, the book has proved to be extremely useful in practical floristic work. It is strongly bound and stands up to extensive use in the field. It can be strongly

recommended as a guide to Scandinavian botany, equally valuable for beginners and for experienced taxonomists.

THOMAS KARLSSON

OHNSORGE, J. & HOLM, R.: Raster-elektronenmikroskopie. Eine Einführung für Mediziner und Biologen. (Scanning Electron Microscopy. An Introduction for Physicians and Biologists.) — Georg Thieme, Stuttgart 1973. ISBN 3-13-502-301-X. X+121 pp. Price DM 68:—.

The volume is intended to give an orientation in basic techniques and modes of interpretation. The descriptive text, consisting of parallel texts in German and English, takes up less than half the book. This together with considerable areas of blank space left, regrettably restricts the amount of information given, especially with a view to the high price of the book. The text is clear and easy to understand, avoiding more complicated technical matters. More than half the book comprises good reproductions of scanning electron micrographs of various subjects exemplifying the scope of the microscope. A fairly extensive list of literature completes the volume.

To sum up, I am afraid that the authors' efforts to make the book intelligible to all has had the result that little of added interest has been given the somewhat more advanced reader, such as the majority of physicians or biologists.

GUNNAR WEIMARCK