Drawings of Scandinavian Plants 75–80

Juncus L.

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75. **Juncus articulatus × bulbosus**

This hybrid is caespitose, with only short and weakly developed rhizomes, often with bulb-like swellings of some straw bases. It is usually only 10—20 cm high. Each well-developed stem has 4—8 leaves and often several short basal internodes. The leaves are unitubulose, perfectly septate, like those of the *J. articulatus* parent. In the upper leaf axils are often new shoots which often give rise to short but distinct rhizomes. The inflorescence usually consists of only 3—8 heads, which are few-flowered at early anthesis but may later become enlarged by continued flowering. Development of shoots in the heads, simulating vivipary, often occurs also. The tepals are all obtuse, though often changed by deformation of their scarious margins, the outer ones usually having a small mucro, the inner ones entire and often longer. The capsule never develops beyond the state of a ripe ovary, but withers and persists after anthesis with depressed sides and remnants of the stigmas, which are not shed in any regular way.

This hybrid has never been found to produce any seeds, not even after free flowering with the parents. Pollen development is also quite irregular. *J. articulatus × bulbosus* is only known from a few localities in NE. Skåne, Sweden. Thus it may represent only one or a few clones. See further SNOGERUP 1960.

76. **Juncus acutiflorus × articulatus**

This hybrid is usually tall and vigorous. Each stem usually has 3—4 leaves. The inflorescence is composed of many, usually 20—40 heads. The heads are usually enlarged by continued flowering, thus comprising a mixture of younger and older flowers. The flowers are small compared with those of the other hybrids, and the tepals are all acute to apiculate, the inner ones usually being longer. The capsule is narrow and tapering, resembling most closely that of *J. acutiflorus,* and is well developed though empty.

J. acutiflorus × articulatus is almost completely seed-sterile, only rarely one or a few seeds forming in some capsules. Probable backcrosses to *J. articulatus* have been found in several places in S. England, and similar occurrences should be looked for (cf. TIMM & CLAPHAM 1940). Only $2n=60$ is known for primary hy-

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[1] NILSSON is responsible for the drawings and SNOGERUP for the text.

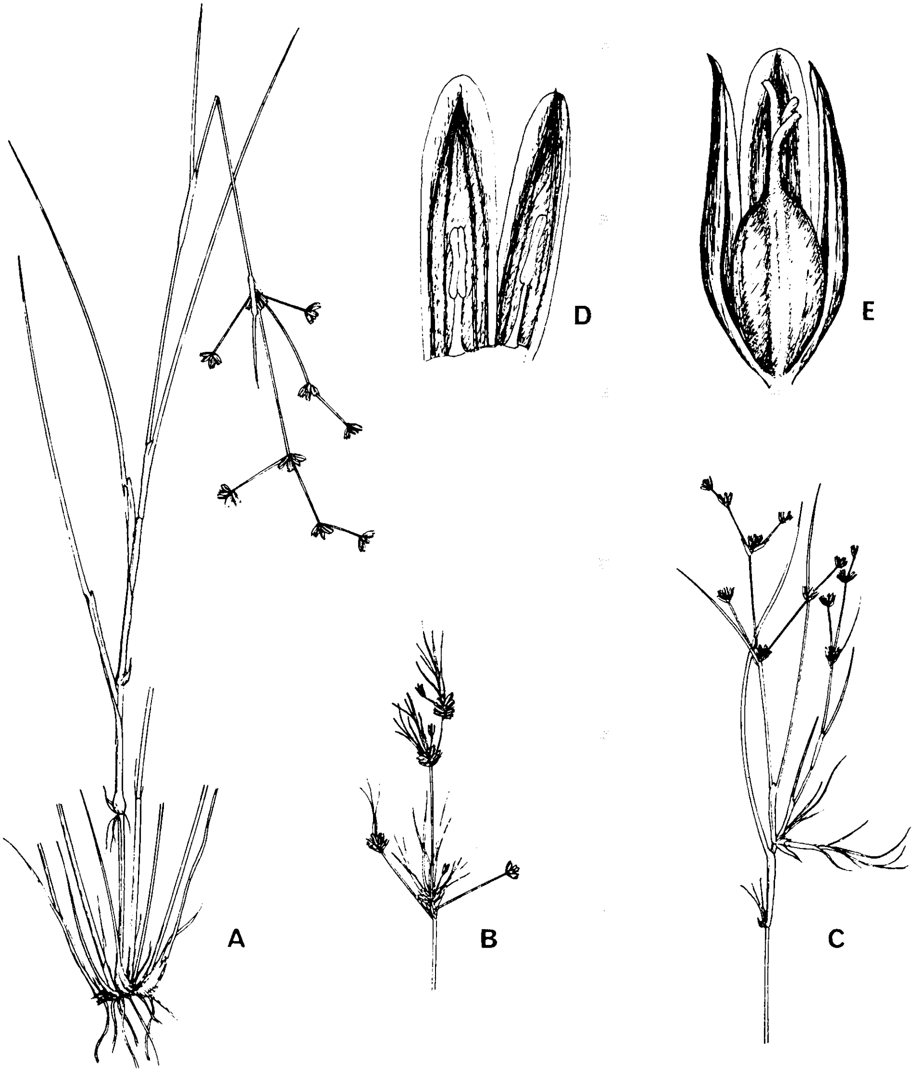

Fig. 75. *Juncus articulatus*×*bulbosus*. — A: Habit, in early anthesis, ×0.5. — B—C: Older inflorescences, ×0.5. — D: Tepals and stamens, ×15. — E: Degenerated ovary, ×15.

brids, 2n=80 for the supposed backcrosses.

This hybrid has been collected on many localities in C. and W. Europe, and even received the name *J. acutiflorus* var. *multiflorus* WEIHE. In Scandinavia, however, it has only been found at one place, at Jylland, par. Seem, near lake Munkesø (MATTISSON 3031).

77. **Juncus anceps × articulatus**

In its general habit this hybrid is most like *J. anceps,* though often laxly caespitose. The stems are comparatively thick,

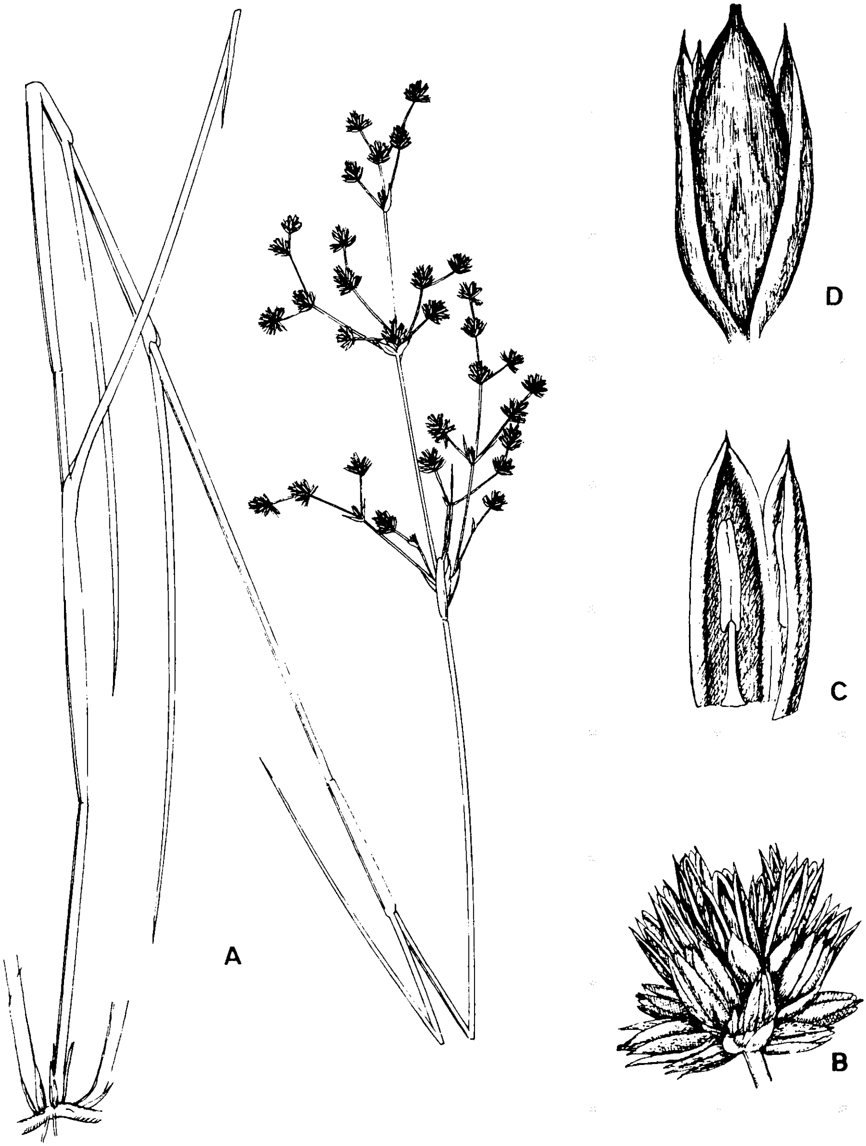

Fig. 76. *Juncus acutiflorus*×*articulatus*. — A: Habit, ×0.5. — B: Head enlarged by continued flowering, ×5. — C: Tepals and stamens, ×15. — D: Capsule, ×15.

with usually 3—4 leaves. The inflorescence is composed of many small, few-flowered heads and is usually contracted. The tepals are dark, obtuse, with broad scarious margins. The capsule is short, broad, but usually acute, often much resembling that of *J. anceps,* though with depressed sides.

J. anceps × *articulatus* is almost completely seed-sterile, only in single capsules are one or a few seeds developed. All chromosome counts give 2n=60, indicating primary hybrids.

This hybrid is often found where the parents occur together. As it is vigorous it propagates vegetatively and is thus often abundant when present.

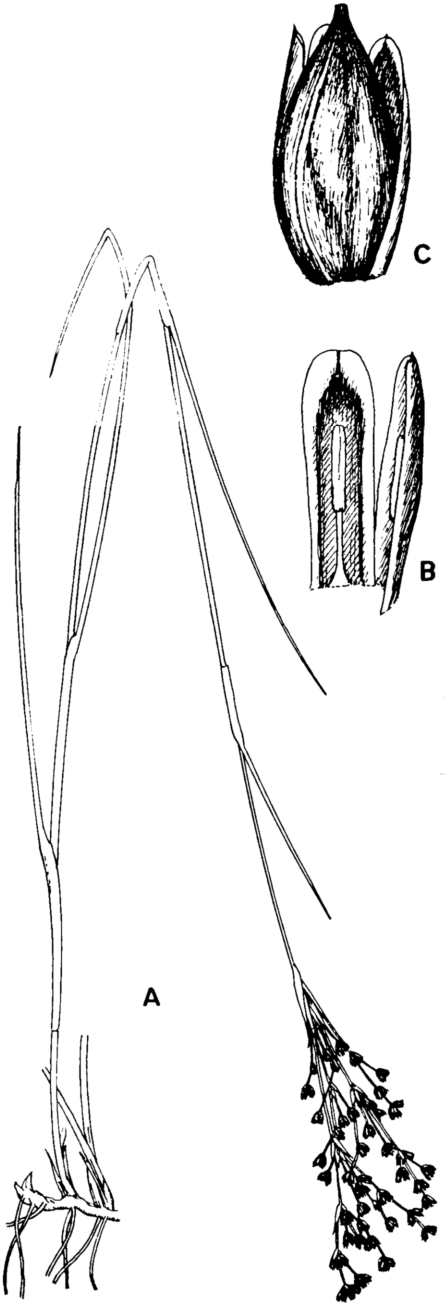

Fig. 77. *Juncus anceps*×*articulatus*. — A: Habit, ×0.5. — B: Tepals and stamens, ×15. — Capsule, ×15.

78. **Juncus alpinus** ssp. **alpinus** × **articulatus**

This hybrid is tall but thin-stemmed and usually not as vigorous as the others in the group. Its rhizome is creeping though often short-noded. The primary branches of the inflorescence are usually patent or almost so. The flowers are dark and usually almost as small as in *J. alpinus*. The tepals are broad and the inner ones, at least, broadly obtuse. The capsule is less obtuse than in the *J. alpinus* parent, usually shorter than the tepals, well developed though with depressed sides. The mucro of the capsule is rather thick.

J. alpinus ssp. *alpinus* × *articulatus* is usually quite seed-sterile, only rarely are one or a few seeds formed in single capsules. F2 specimens from an artificial hybrid have been cultivated, and they proved to have varying higher chromosome numbers. In hybrids from natural localities, however, only 2n=60 has been found, even in specimens deviating in the direction of *J. articulatus*. This probably indicates that only the primary hybrids succeed in establishing themselves in nature.

This hybrid has been collected or observed in a large number of the localities where the parental species occur together. It often produces flowering stems later in the year than the parents, and is thus easily detected in the autumn.

79. **Juncus alpinus** ssp. **nodulosus** × **articulatus**

This hybrid is rather variable in habit, but always apparently vigorous, producing several strong flowering stems from a creeping rhizome. The inflorescence usually consists of few heads and its primary branches are ± erect. The tepals are variable in form and colour, but the inner ones are always obtuse. The capsule is well developed, may even exceed the tepals, but its sides become depressed in the mature state.

J. alpinus ssp. *nodulosus* × *articulatus* is almost completely seed-sterile, only in some capsules are one or a few seeds formed. Such seeds, formed after free flowering with the parents, have germinated well in greenhouse tests. They gave rise to plants of reduced vigour with varying higher chromosome numbers. In specimens collected from natural populations, however, only the number 2n=60 has been found. Thus probably only the primary hybrids have succeeded in establishing themselves.

This hybrid is often found where the parents occur together, and when present it is usually abundant. Because of its vegetative vigour it propagates rapidly and may even out-number the parents in the littoral zone of oligotrophic lakes.

Subgen. **Juncus**

Leaves all basal, terete, nonseptate, pungent, auricles lacking. Stems and leaves mainly filled with a parenchyma of rounded cells, vascular bundles distributed over all or most of the transect. Involucral bracteoles lacking, flowers usually in heads. Seeds with a persistent seedcoat. x=24, but with many reports of divergent chromosome numbers in the literature, chromosomes extremely small and partly heterochromatic.

Subgenus *Juncus* contains 12 species mainly occurring in warm temperate to tropical areas, predominantly in saline environments. In Scandinavia it is only represented by one species.

80. **Juncus maritimus** Lamarck 1789

Perennial, with stems in rows from a creeping rhizome, in some localities laxly caespitose due to more frequent forkings of the rhizome. No intravaginal shoots formed. Stems 50—100 cm high, usually 1.5—2 mm thick, with a few leafless sheaths and 2—4 basal leaves. Leaves

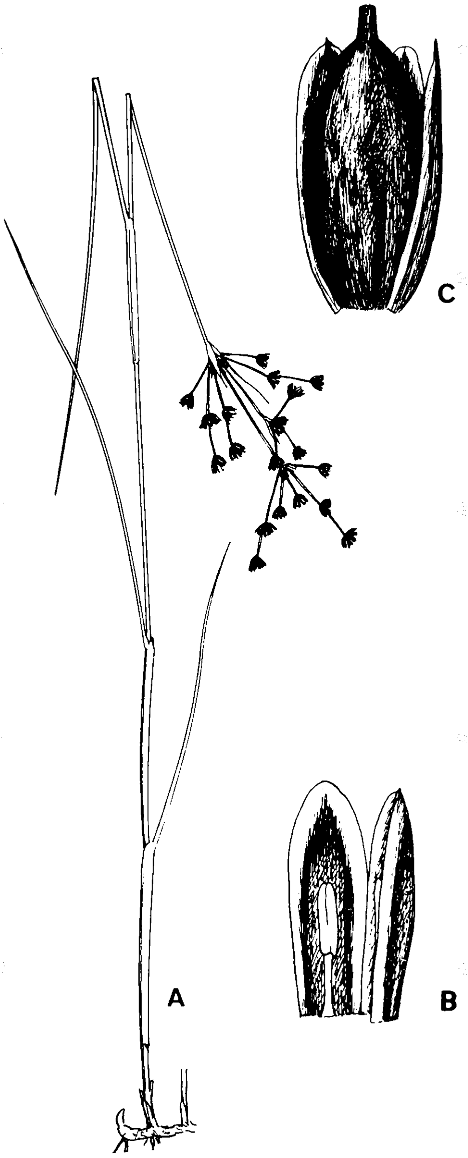

Fig. 78. *Juncus alpinus* ssp. *alpinus*×*articulatus*. — A: Habit, ×0.5. — B: Tepals and stamens, ×15. — C: Capsule, ×15.

terete, nonseptate, pungent, stems and leaves ± striate from subepidermal sclerenchyma bundles, medulla of rounded cells, vascular bundles distributed over all or most of the transect, stomata lowered, auricles lacking. Inflorescence many-flowered, usually lax, rarely contracted to one or a few clusters. Lowest two bracts of the inflorescence stem-like, pungent, the first one forming an apparent prolongation of the stem, the second one usually short. Flowers in few-flowered heads, lacking involucral bracteoles. Tepals unequal, with broad hyaline margins, outer ones boat-shaped, acute, shortly mucronate, inner ones shorter, narrowly elliptic to oblong, obtuse, usually with slightly expanded scarious margins apically. Stamens 6 or rarely 3, about 2/3 as long as the tepals, anthers 0.8—1.2 mm, c. 2 times as long as the filaments. Style c. 1.5 mm, stigmata short, contorted. Capsule 2.5—3.5 mm, trigono-ovoidal, obtuse or broadly attenuate, mucronate, equalling or slightly exceeding the tepals, trilocular. Seeds 0.6—0.7 mm, obliquely ovoidal, including the seedcoat 0.8—1.2 mm, seedcoat forming one short and one longer appendage. 2n=48, chromosomes very small, some of them heterochromatic.

J. maritimus is normally a plant of salt marshes, preferably occuring in their wettest parts. It occurs in W. Europe, the Mediterranean, the Black Sea area and eastwards to Azerbaijan. It was introduced into New York but is now extinct there. In Scandinavia it has been found in a limited number of localities in the southern Baltic area and S. Denmark.

Fig. 79. *Juncus alpinus* ssp. *nodulosus*×*articulatus*. — A: Habit, ×0.5. — B: Tepals and stamens, ×15. — C: Capsule, ×15.

KEY TO THE JUNCUS SPECIES, DRAWINGS 45—80

1. Flowers each with two involucral bracteoles
    2. Leaves terete (Subgen. *Genuini*)
        3. Tall, densely caespitose, with many-flowered inflorescences
            4. Seed fertile pure species
                5. Stem smooth, with c. 50 weak striae .... 50. *J. effusus*
                5. Stem with 10—30 ridges

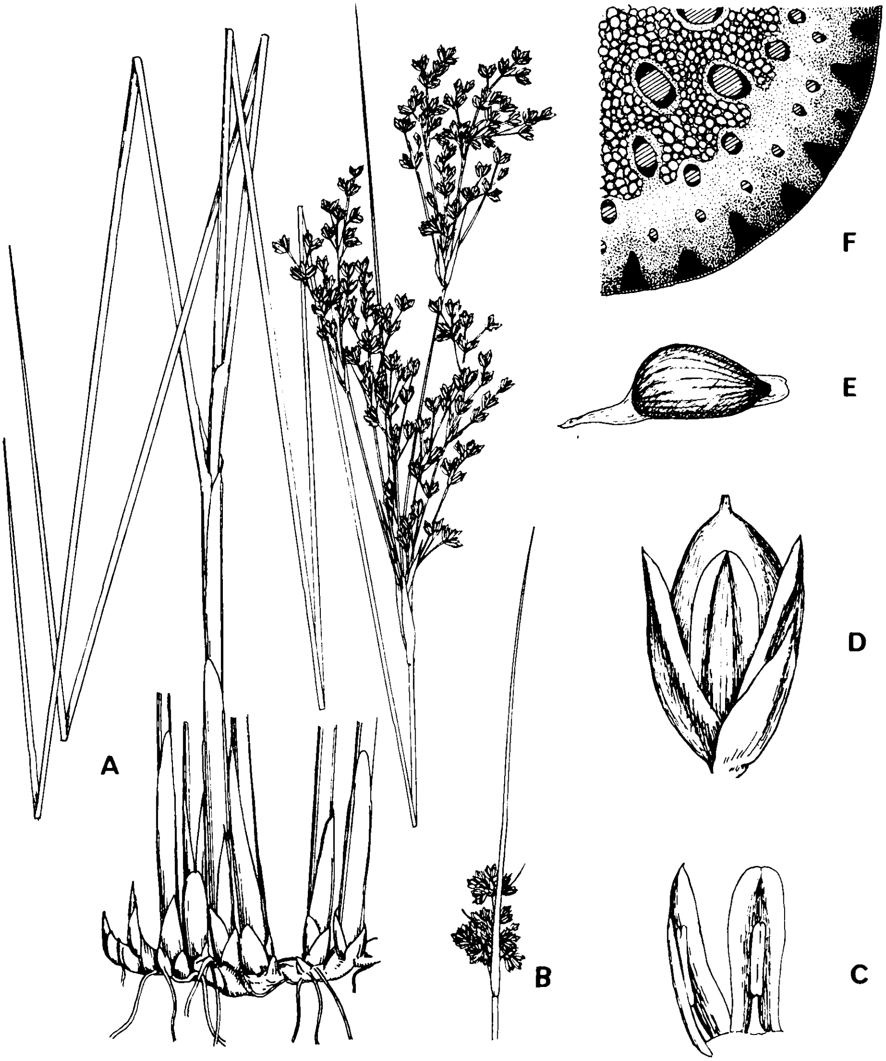

Fig. 80. *Juncus maritimus* LAM. — A: Habit, ×0.5. — B: Deviating form of inflorescence, ×0.5. — C: Tepals and stamens, ×7. — D: Flower with ripe capsule and bract, ×10. — E: Seed, ×30. — F: Leaf transect, ×20.

6. Capsule trigono-ovoidal, acute, equalling or exceeding tepals .... 52. *J. inflexus*
6. Capsule ovoidal-sphaeroidal, blunt or retuse, shorter than tepals .... 51. *J. conglomeratus*
4. Seed sterile interspecific hybrids
7. Capsule blunt to acute, stem bluish green, inflorescence lax .... 53. *J. effusus×inflexus*
7. Capsule ± retuse, stem green, inflorescence contracted .... 54. *J. conglomeratus×effusus*
3. Usually low, not or laxly caespitose, inflorescence few—20-flowered

8. Seed fertile pure species
9. Capsule equalling tepals, first bract 1/3 of stem or longer 55. *J. filiformis*
9. Capsule exceeding tepals, first bract 1/3 of stem or shorter
10. Flowers 3—8, dark, shining, inflorescence dense ...... 56. *J. arcticus*
10. Flowers 8—20, usually light, inflorescence lax ...... 57. *J. balticus*
8. Completely or almost completely seed-sterile hybrids
11. Thin-stemmed, usually 50—100 cm high ..... 58. *J. balticus*×*filiformis*
11. More rigid, usually 20—40 cm high .... 59. *J. arcticus*×*filiformis*
2. Leaves flat or convolute
12. Annuals without a developed rhizome, lower leaves without auricles .... *J. bufonius* group, not treated in this series
12. Rhizomatous perennials, lower leaves with auricles (Subgen. *Pseudotenageia*)
13. Seeds with appendages, auricles lacerate .... 65. *J. trifidus*
13. Seeds without appendages, auricles entire
14. Tepals apiculate to aristate .... 64. *J. tenuis*
14. Tepals obtuse, rarely mucronate
15. Leaves in many-leaved rosette, semicoriaceous .. 60. *J. squarrosus*
15. Leaves 1—3, cauline
16. Anther 1—2×filaments, capsule exceeding tepals .... 61. *J. compressus*
16. Anthers 2—4×filaments, capsule equalling tepals .... 62—63. *J. gerardi*
1. Flowers lacking involucral bracteoles, in heads
17. Small annual without rhizome, leaves flat .... 49. *J. capitatus*
17. Rhizomatous perennials or annual with terete, septate leaves
18. Leaves and lower bracts pungent, terete, nonseptate .... 80. *J. maritimus*
18. Leaves not pungent, usually septate
19. Leaves not or only apically septate (Subgen. *Alpini*)
20. Capsule distinctly retuse .... 46. *J. biglumis*
20. Capsule obtuse or acute
21. Leaves basal, bitubulose in upper part, capsule dark .... 45. *J. triglumis*
21. Leaves basal and cauline, pluritubulose, 1st bract usually leafy
22. Capsule 6—8 mm, chestnut-coloured, anther 1—1.5 mm .... 48. *J. castaneus*
22. Capsule 5—6 mm, light, pale, anthers 0.4—0.7 mm .... 47. *J. stygius*
19. Leaves terete, septate, uni- or pluritubulose (Subgen. *Septati*)
23. Up to 10 cm, annual, without rhizome or bulbs .... 67. *J. pygmaeus*
23. Perennials with rhizome, bulbs or floating stems
24. Leaves pluritubulose
25. Rhizome thick, one-leaved shortshoots from the rhizome .... 66. *J. subnodulosus*
25. Rhizome lacking, basal bulbs or floating shoots .... 68. *J. bulbosus*
24. Leaves unitubulose, perfectly septate
26. Seed fertile pure species
27. Inner tepals longer, apiculate to cuspidate .... 69. *J. acutiflorus*
27. Tepals equal or outer ones longer, obtuse to acute
28. Caespitose or creeping, at least outer tepals acute .... 74. *J. articulatus*
28. Rhizome creeping, tepals obtuse though often mucronate
29. Capsule usually acute, anther equalling filaments or longer .... 70. *J. anceps*
29. Capsule obtuse, anther shorter than filaments .... 71—73. *J. alpinus*
26. Completely or almost completely sterile hybrids
30. Ovary degenerating, rhizomes none or weakly developed .... 75. *J. articulatus*×*bulbosus*
30. Capsule developing though empty, rhizome well developed

31. Tepals acute to apiculate, capsule ± narrowly tapering .... 76. *J. acutiflorus × articulatus*
31. Tepals ± obtuse, capsule usually blunt
    32. Stem tall, rigid, heads many in dense inflorescence .... 77. *J. anceps × articulatus*
    32. Stem usually thin or low, inflorescence wide or few-flowered .... 78—79. *J. alpinus × articulatus*

FINAL REMARKS ON THE JUNCUS DRAWINGS

With this paper most members of the genus *Juncus* in Scandinavia have been presented in this series. Only Subgen. *Poiophylli* BUCHENAU, in Scandinavia represented by the *J. bufonius* group, has been omitted. We consider that the taxonomy as well as nomenclature of this group have yet not been sufficiently investigated. As it is at present being investigated by SNOGERUP as well as by several other workers we decided to wait until further information can be presented.

Among the hybrids we have only presented those of which we have been able to study material from the area. These are also the only ones we consider definitely occur in Scandinavia. In the subgenera *Genuini* and *Septati* hybridisation is so common that further hybrids can be expected in any combination within each subgenus.

In the literature list of this last contribution we have included a few works of a monographic and floristic nature not cited in the text. These provide additional references and also some essential information on distribution and hybridisation. Works that have already been cited in earlier parts have, however, not been repeated.

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Studies in African Cyperaceae V

Sphaerocyperus K. Lye, gen. nov.

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ABSTRACT

LYE, K. A. 1972. Studies in African Cyperaceae V. Sphaerocyperus K. Lye, gen. nov. — Bot. Notiser 125: 212—216.

A new monotypic genus is established for the African species *Schoenus erinaceus* RIDL. The relationship of this genus is with *Cyperus* and not with *Rhynchospora* or *Actinoschoenus* as stated by some modern authors.

INTRODUCTION

RIDLEY's species *Schoenus erinaceus* RIDL. was based on one of the plants in the WELWITSCH herbarium, viz. WELWITSCH 6788 collected in Angola (cf. RIDLEY 1884). Since that time the plant has been transferred to three other genera. CLARKE (1895) called it *Rhynchospora erinacea* (RIDL.) C. B. CL., KÜKENTHAL (1943) put it in *Cyperus* as *Cyperus erinaceus* (RIDL.) KÜK., while very recently RAYMOND (1971) transferred it to *Actinoschoenus* as *Actinoschoenus erinaceus* (RIDL.) RAYMOND.

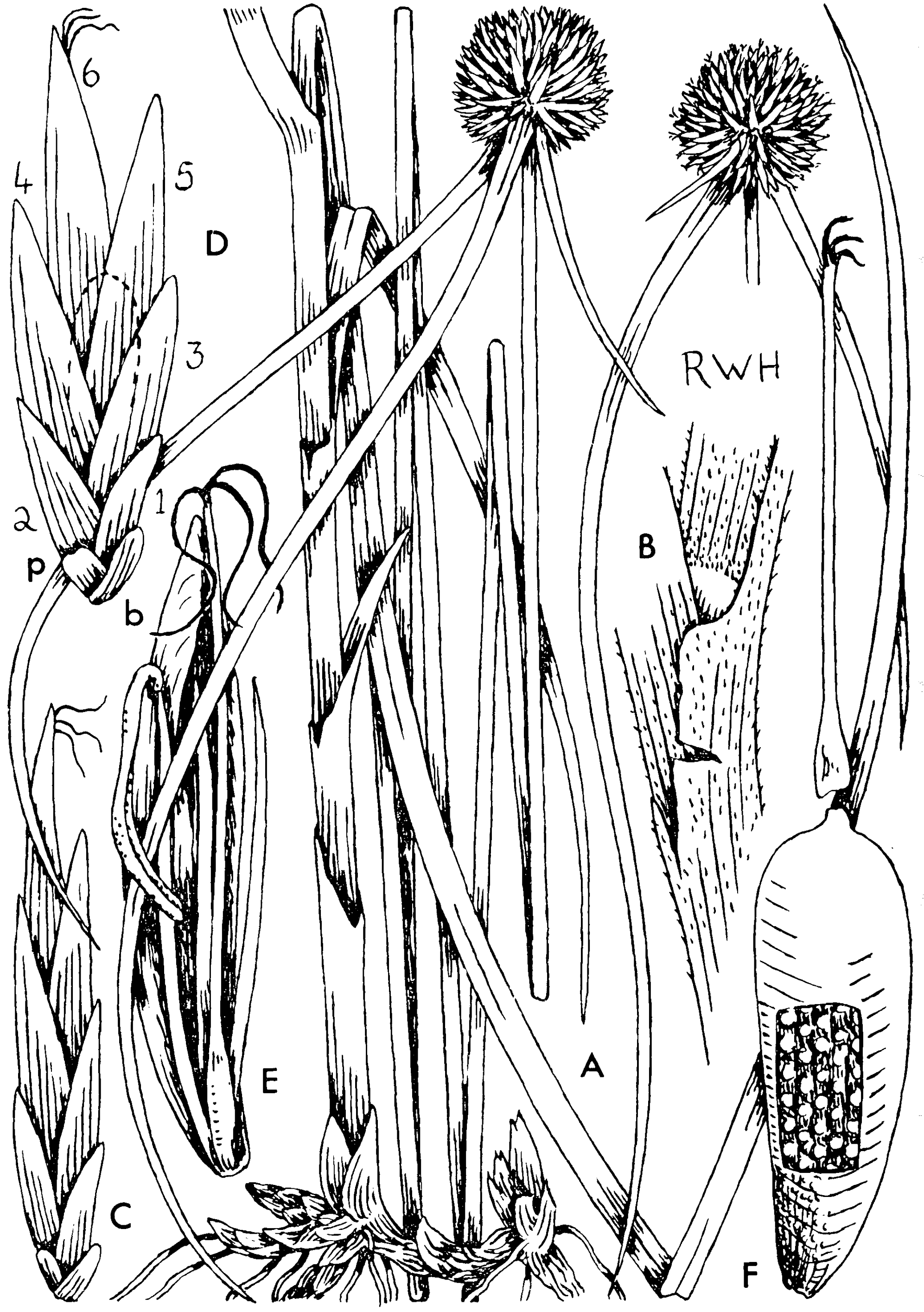
Both *Actinoschoenus* and *Rhynchospora* are, however, typical Rhynchosporoid genera with a *Carex*-type embryo and an eucyperoid stem-anatomy, while RIDLEY's *Schoenus erinaceus* has a *Cyperus*-type embryo and a chlorocyperoid stem-anatomy (cf. VAN DER VEKEN 1965). It is therefore obvious that our plant has no close relationship with *Actinoschoenus* or *Rhynchospora,* and following the taxonomic principle laid down in LYE (1971) and HAINES & LYE (1971) *Schoenus erinaceus* should be placed in the tribe Cypereae and not in Rhynchosporeae.

It is therefore only KÜKENTHAL's view that should be considered here. He transferred the plant to *Cyperus* for the following reasons:

1. The inflorescence bracts are not basally widened or ciliate.
2. The glumes have small lateral nerves.
3. There is no perianth.
4. The style-base is only slightly thickened.
5. The style is 3-parted at the apex.
6. The nutlet is triangular.

When we add that the glumes are distichously arranged, the nutlet is minutely punctulate as in most species of *Cyperus* (cf. Fig. 1), the stem anatomy is chlorocyperoid, and the embryo is of *Cyperus*-type, it is evident that KÜKENTHAL has very strong backing for his views. The only reason for classifying this plant as *Rhynchospora* or *Actinoschoenus* seems to be the fact that the 6—7 lower glumes

Fig. 1. *Sphaerocyperus erinaceus* (RIDL.) K. LYE. — A: Habit, slightly reduced. — B: Throat of leaf-sheath. — C: Young spikelet. — D: Mature spikelet showing bract (b), prophyll (p) and 1—6 glumes. — E: Glume with young flower. — F: Achene. — Drawn from MILNE-REDHEAD and TAYLOR 10366 (near Lipumba, Tanzania). Original by RICHARD WHEELER HAINES.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are sterile. NAPPER (1964), although classifying the plant as *Rhynchospora,* writes: "It is probably necessary to create a new monotypic genus for this very distinctive sedge".

DESCRIPTION

Schoenus erinaceus RIDL. is a robust perennial with creeping scale-covered stolons. Culms 60—120 cm long, triangular; the base slightly swollen, and the lower part covered with leaf sheaths. Stem anatomy chlorocyperoid. Leaves 3—4 mm wide, flat and rather stiff.

Inflorescence bracts 2—3, leafy, spreading or reflexed, the largest up to 20 cm long. Inflorescence an almost spherical head-like anthela, 2.0—2.5 cm in diam., consisting of very numerous crowded whitish spikelets. Spikelets 10—12 mm long, with 7—8 distichously arranged lanceolate glumes with many lateral nerves (the two lowest glumes are the spikelet-bract and the prophyll respectively), only the uppermost glume fertile. Hypogynous bristles absent. Stamens 3, with long filaments. Ovary with a long 3-fid style. Nutlet about 4 mm long, narrowly oblong, minutely punctulate. Embryo of *Cyperus*-type.

Widespread, but uncommon in Angola, Zambia, southern Tanzania, and southern Congo, 900—1800 m. For details of distribution see RAYMOND (1971).

DISCUSSION

When considering whether *Schoenus erinaceus* can be included in *Cyperus* or not, we may do well to study the monotypic genus *Remirea* AUBL., which has traditionally been placed in Rhynchosporeae on account of its spikelets which have a few sterile glumes below, but which was included in *Cyperus* by KERN (1958). KERN has not, however, been followed by recent authors and RAYMOND (1966, p. 314) writes: "In this enumeration, I have followed KERN in including *Diplacrum* in *Scleria,* but I could not bring myself to consider *Remirea* a species of *Cyperus*", and RAYMOND (l.c.) does in fact include *Remirea* among his genera in Rhynchosporoideae. I believe *Remirea* is related to *Cyperus,* but it is sufficiently specialized to be retained as a genus of its own within Cypereae. In the same way I believe *Schoenus erinaceus* is sufficiently different from *Cyperus* to be regarded as a monotypic genus of its own. It differs from *Cyperus* (cf. Fig. 2, which illustrates a habitually very similar species, viz. *Cyperus angolensis* BOECK.) in its larger nutlet and the spikelet which has several sterile glumes below. I suggest *Sphaerocyperus* as a suitable name for this new genus.

Sphaerocyperus K. LYE, gen. nov. *Rhizoma* lignosum stolones duros horizontales emittens. *Culmus* rigidus erectus 60—120 cm altus. *Folia* rigida remota culmo breviora 3—4 mm lata plana. *Bracteae* 2—3, ad 20 cm longae inaequales patentes demum deflexae. *Spiculae* numerosae lineari-lanceolatae acuminatae subcompressae 10—12 mm longae radiantes 1-nucigerae in caput. globosum unicum 2.0—2.5 cm diam. dense congestae. *Squamae* 7—8 distichae a basi accrescentes, inferiores 6—7 vacuae lanceolatae subacutae albo-ferrugineae plurinervosae, summa florem fertilem fovens longissima ommium. *Stamina* 3, filamenta longa, antherae lineares, apice obtusae. *Stylus* longissimus apice trifidus. *Nux* oblonga compresso-trigona 4 mm longa straminea dense punctulata glabra basin versus attenuata (latin description mainly after RAYMOND 1971).

TYPUS GENERIS: *Sphaerocyperus erinaceus* (RIDL.) K. LYE, nov. comb., syn. *Schoenus erinaceus* RIDL. in Trans. Linn. Soc., ser. 2, Bot. 2, p. 165 (1884).

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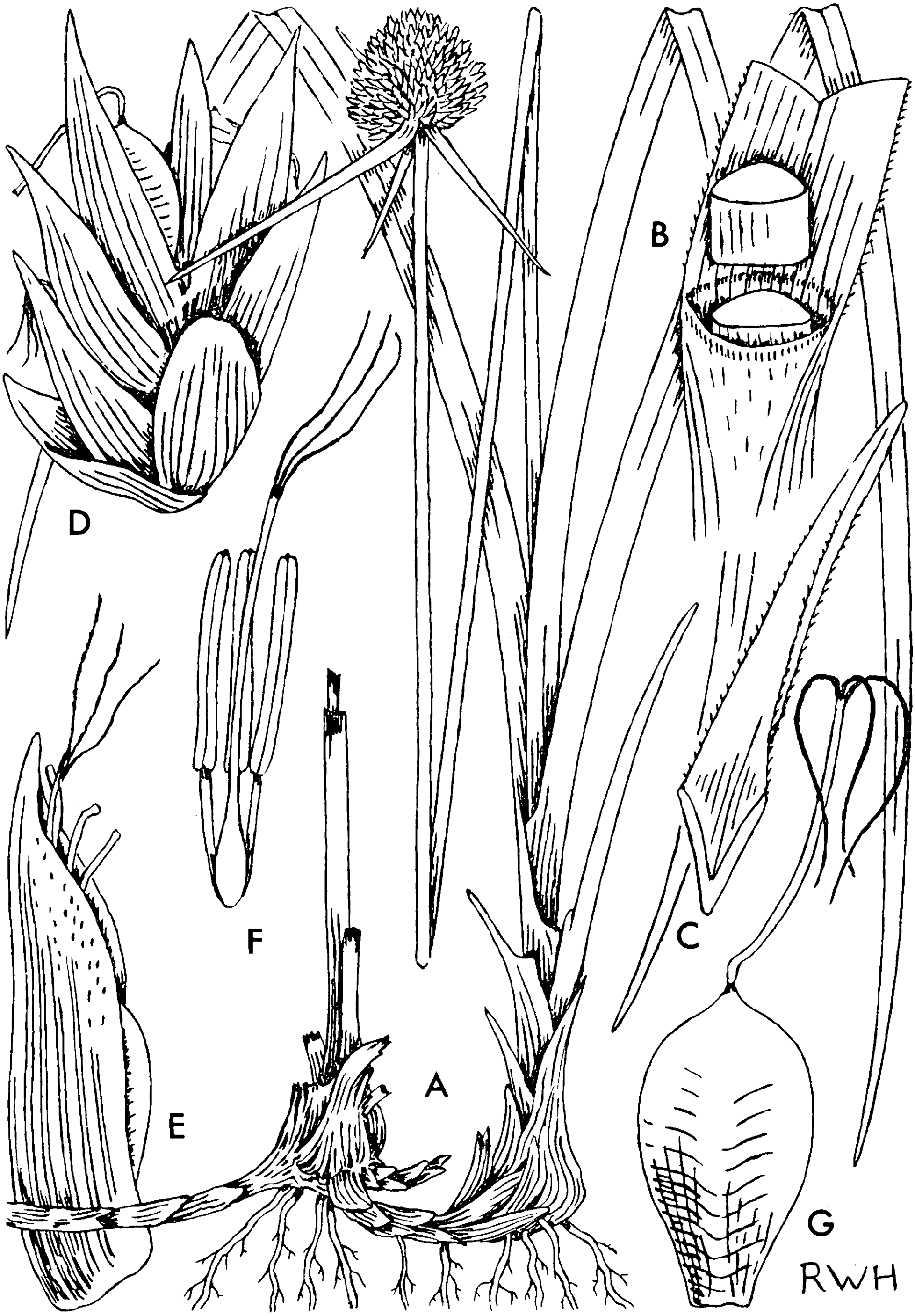
Fig. 2. *Cyperus angolensis* BOECK. — A: Habit, slightly reduced. — B: Throat of leaf-sheath. — C: Leaf-apex. — D: Mature spikelet. — E: Glume with mature flower. — F: Young flower. — G: Achene. — Drawn from LYE 2082 (Mt. Imatong, Acholi, Uganda). Original by RICHARD WHEELER HAINES.


D
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Studies in African Cyperaceae VI

New Species and Combinations in Kyllinga

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ABSTRACT

LYE, K. A. 1972. Studies in African Cyperaceae VI. New species and combinations in Kyllinga. — Bot. Notiser 125: 217—219.

Three new species of *Kyllinga* are described from East Africa, viz. *K. microbulbosa* K. LYE, *K. tanzaniae* K. LYE, and *K. songeensis* K. LYE.

Six new combinations are made, viz. *Kyllinga ugogensis* (PETER & KÜK.) K. LYE, *K. nervosa* STEUD. var. *flava* (C. B. CL.) K. LYE, *K. nervosa* STEUD. var. *ruwenzoriensis* (C. B. CL.) K. LYE, *K. colorata* (L.) DRUCE var. *lurida* (KÜK.) K. LYE, and *K. polyphylla* KUNTH var. *elata* (STEUD.) K. LYE.

Kyllinga microbulbosa K. LYE sp. nov.

Herbae perennes. *Culmi* dense caespitosi, 7—20 cm alti, gracillimi triangulares sulcati laeves basi breviter bulboso—incrassata. *Folia culmo* breviora longirave perangusta 0.5—2.0 mm lata carinato—plana, vaginae brunneae. *Bracteae* 2—3. *Spica* 1, globosa, 3—8 mm diam. *Spiculae* undique patentes ovatae 2.0—3.0 mm longae, compressae, 1—3 nucigerae. *Squamae* ovatae, albae. *Stigmatae* 2. *Nux* 1.0—1.2 mm longa et 0.4—0.5 mm lata.

TYPUS SPECIEI: VESEY-FITZGERALD 4926, 6.IV. 1966. Tanzania, S. Masailand 0503S: 3725E, Kaitokoi pools, 1150 m (EA holotype).

Kyllinga microbulbosa K. LYE (cf. Fig. 1) is a slender perennial with a 2 mm thick swollen brown stem-base, sometimes with the previous year's base persisting beside the new, or several new stem-bases loosely connected and forming dense colonies. Culms 7—20 cm long and 0.3—0.9 mm thick, triangular. Leaves to 12 cm long and 0.5—2.0 mm wide, flat, scabrid on margin and midrib.

Inflorescence a globose white anthela (but sometimes rather irregular in outline) 3—8 mm in diam. Inflorescence bracts 2—3, leafy, spreading or reflexed; the largest 1—6 cm long. Spikelets 2.0—3.0 mm long, 1—3-flowered. Glumes 2.0—2.5 mm long, white. Nutlet 1.0—1.2 mm long and 0.4—0.5 mm wide, elliptic, compressed (but only immature fruit seen).

On shallow sandy soil in damp places of rock basin edge, 1150 m (3800 ft). Only known from the type collection from Tanzania.

This species is most closely related to *K. ugogensis* (PETER & KÜK.) K. LYE, from which it differs in its white (not golden) spikelets and slightly larger anthela with more numerous spikelets.

Kyllinga tanzaniae K. LYE sp. nov.

Herbae perennes. *Rhizoma* horizontaliter repens lignosum percrassum. *Culmi* 15—40 cm alti. *Folia* 2—5 remota culmo breviora 1—4 mm lata. *Bracteae* 2—3, ima ad 2—4 cm longa, reflexae. *Spica* 1, ovata, 5—8 mm longa, densa, alba. *Spiculae* numerosae patentes ovato-oblongae 2.5—3.5 mm longae compressae 1—2 florae. *Squamae* 2.0—3.5 mm longae. *Nux* 1.8—2.0 mm longa et 0.9—1.2 mm lata, obovato-oblonga biconvexa dense punctulata.

TYPUS SPECIEI: E. A. ROBINSON 4783, 28.XII. 1961. Tanzania, Sumbawanga district, Rukwa Escarpment, Namwele, c. 2000 m (K holotype).

Kyllinga tanzaniae K. LYE is a medium-sized perennial with a thickish horizontal or curved rhizome and solitary or somewhat crowded stems. Culms 15—40 cm long and 4—8 mm thick, triangular, glabrous. Leaves 2—5 pr. culm, 3—8 cm long and 1—2 mm wide, flat, scabrid on margin and midrib, otherwise glabrous.

Inflorescence a single ovate to spherical white or cream (but often drying dirty greyish white) spike 5—8 mm long and 5—7 mm wide. Inflorescence-bracts 2—3, leafy, the longest 2—4 cm, reflexed or spreading. Spikelets 2.5—3.5 mm long, 1—2-flowered. Glumes 2.0—3.5 mm long, whitish with 3—5 nerves on each side of the smooth and unwinged midrib; apex acuminate. Nutlet 1.8—2.0 mm long and 0.9—1.2 mm wide, obovate with truncate apex, compressed, dark brown to blackish; surface minutely punctulate.

In well-drained grassland, often in *Brachystegia*-country. Uncommon. Only recorded from the Sumbawanga, Songea and Njombe districts in Tanzania.

Kyllinga tanzaniae K. LYE is related to *K. merxmuelleri* PODLECH, but differs in having a thicker rhizome and in the absence of long slender stolons.

Kyllinga songeensis K. LYE sp. nov.

Herbae perennes. *Rhizoma* horizontaliter repens lignosum percrassum. *Culmi* 5—40 cm alti, 0.4—1.0 mm lati. *Folia culmo* breviora 1—2 mm lata. *Bracteae* 3—4 divergentes, ima ad 7 cm longa. *Spica* 1, globosa 6—12 mm diam. compacta alba. *Spiculae* numerosae 4.0—4.5 mm longae 1—2 florae. *Squamae* 3.5—4.5 mm longae.

TYPUS SPECIEI: MILNE-REDHEAD & P. TAYLOR 10106, 6.V. 1956. Tanzania, Songea district, R. Luhimba, about 28 km N of Songea, 970 m (K holotype).

Kyllinga songeensis K. LYE is a small to medium-sized perennial with bulbous stem-bases often crowded on a horizontal rhizome, more rarely the "bulbs" connected by a short stolon. Roots numerous, the old ones reddish, the young ones white. Culms 5—40 cm long and 0.4—1.0 mm thick, glabrous, rounded to angular, the basal part covered by pale to dark brown leaf-sheaths splitting into fibres. Leaves 5—15 cm long and 1—2 mm wide, flat or enfolded, scabrid on margin and midrib, otherwise glabrous.

Inflorescence a single spherical white to cream spike 6—12 mm in diam., the spikelets set on a narrow cylindrical receptacle. Inflorescence-bracts 3—4, leafy, the longest 1—7 cm, reflexed or spreading. Spikelets 4.0—4.5 mm long, 1—2-flowered. Glumes 3.5—4.5 mm long, whitish, with about 5 nerves on each side of the smooth and unwinged midrib; apex acuminate. Nutlets only seen immature.

In sandy or black cotton soil in *Brachystegia*-woodland or seasonally waterlogged grassland. Rare. Only recorded from Upland Kenya and the Songea district in Tanzania.

Kyllinga songeensis K. LYE is related to *K. crassipes* BOECK., but differs in having a spherical spike, larger spikelets and glumes, and in having a rhizome which is less distinctly moniliform.

NEW COMBINATIONS

The following new combinations of *Kyllinga* are needed for "The sedges of Uganda and Kenya":

Kyllinga ugogensis (PETER & KÜK.) K. LYE, comb. nov.; syn. *Cyperus ugogensis* PETER & KÜK. in Das Pflanzenreich IV. 20 (101): 572 (1936).

Kyllinga nervosa STEUD. var. *flava* (C. B. CL.) K. LYE, comb. nov.; syn. *Kyllinga flava* C. B. CL. in Fl. Trop. Afr. 8: 281 (1902).

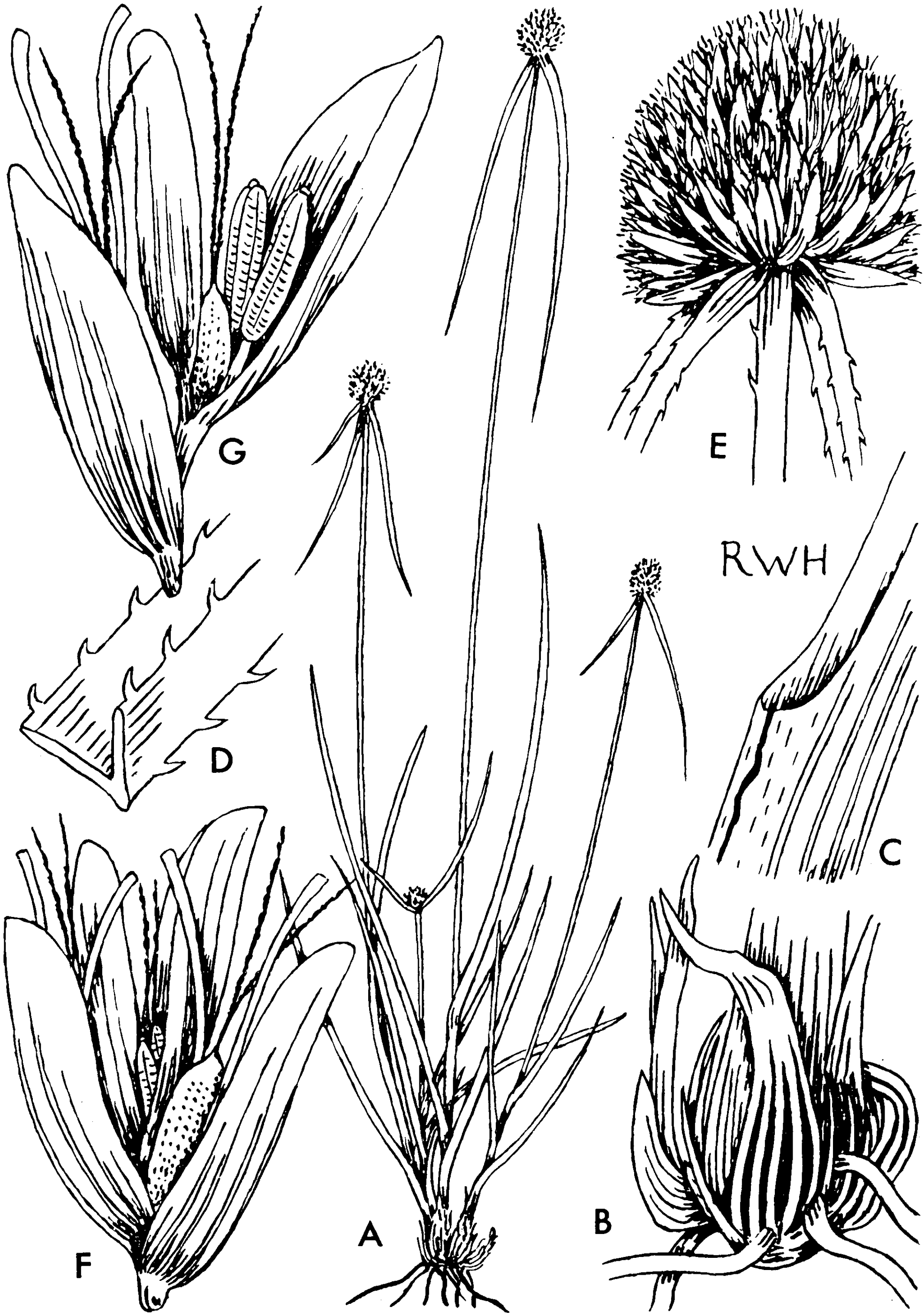
Kyllinga nervosa STEUD. var. *ruwenzoriensis* (C. B. CL.) K. LYE, comb. nov.; syn. *Kyllinga ruwenzoriensis* C. B. CL. in Fl. Trop. Afr. 8: 283 (1902).

Kyllinga colorata (L.) DRUCE var. *aurata* (NEES) K. LYE, comb. nov.; syn. *Kyllinga aurata* NEES in Linnaea 10: 139 (1835).

Kyllinga colorata (L.) DRUCE var. *lurida* (KÜK.) K. LYE, comb. nov.; syn. *Kyllinga erecta* SCHUMACH. var. *lurida* KÜK. in Notizbl. Bot. gart. Berl. 9: 300 (1925).

Kyllinga polyphylla KUNTH var. *elata* (STEUD.) K. LYE, comb. nov.; syn. *Kyllinga elata* STEUD. in Synops.: 70 (1855).

Fig. 1. *Kyllinga microbulbosa* K. LYE. — A: Habit-drawing, slightly reduced. — B: Culm-base. — C: Leaf-sheath with the throat. — D: Leaf-section. — E: Anthela. — F and G: Spikelets. — Drawn from VESEY-FITZGERALD 4926 (S. Masailand, Tanzania; the holotype). — Original by RICHARD WHEELER HAINES.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A New Species of Iphigenia Kunth, Liliaceae, from Mysore

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ABSTRACT

AREKAL, G. D. & SWAMY, S. N. R. 1972. A new species of Iphigenia Kunth, Liliaceae, from Mysore. — Bot. Notiser 125: 220—222.

Iphigenia mysorensis AREKAL & SWAMY sp. nov., collected in Ranganathittu near Mysore City, Mysore State, India is described as a new species. It is allied to *I. indica* (A. GRAY) KUNTH in having the chromosome number 2n=22, n=11 and dark purple flowers, but differs from it in several important morphological characters.

In a plant-collecting trip during September, 1965 at Ranganathittu, an island in the Cauveri River near Mysore City, the authors collected a slender species of *Iphigenia* which is markedly different from all the other three species viz. *I. indica* (A. GRAY) KUNTH (HOOKER 1892), *I. stellata* BLATTER (BLATTER & MCCANN 1928) and *I. pallida* (BAKER 1879; SANTAPAU 1957) so far reported from India, and also from species of New Zealand (BENTHAM 1878) and Africa (BAKER 1898). It is allied to *I. indica* in having dark purple flowers and the chromosome number 2n=22 (n=11) but differs from it in having a smaller corm, longer internodes, narrow acicular leaves, filiform perianth, cordate anthers with prominent extended connectives, 3 free styles, conspicuously longer fruiting pedicels and smaller obovoid fruits.

Iphigenia mysorensis AREKAL & SWAMY sp. nov.

Valde *I. indicae* affinis at differt cormis tenuibus, internodiis longioribus, foliis tenuibus, perianthiis filiformibus, connectivis antherarum prolongatis, pedicellis fructuum longioribus seminibusque minoribus.

Herba cormo perennis. *Cormus* tenuis, vagina pallida brunnea, facie priorum cormorum paulo applanatus, 0.9—1.0 cm diam. *Caulis* tenuis usque 20 cm longus, 0.1 cm diam., internodiis 3.0—4.5 cm longis. *Folia* generaliter 3 (quandoque 2 vel 4) acicularia, usque 13.0 cm longa, 0.1—0.15 cm lata, plerumque crassa. Inflorescentia terminalis, racemosa, 2—4-flora, quandoque inflorescentia axillari et secundaria praedita — tunc usque 7-flora. *Flores* pedicellis longioribus porcatisque muniti; perianthium 6 lobis filiformibus, 0.6—1.0 cm longis instructum, minus quam 0.05 cm latis, atropurpureis. *Stamina* 6, antheris cordatis longitudinaliter dehiscentibus, plerumque 0.2 cm longis, connectivis prominenter prolongatis. *Gynoecium* 3 stylis libris munitum. *Capsulae* generatim 2—4, quandoque usque 7, parvae, obovoideae, loculicidae, pedicellis 6.0—7.0 cm longis. *Semina* multa, 0.1—0.15 cm diam. trigona, verrucosa, raphibus minoribus albidis. Numerus chromosomatum 2n=22, n=11.

Holotypus prope Ranganathittu, in distr. Mysore ab AREKAL et SWAMY die 20-10-1965 lectus, in herbario sectionis botanicae, Manasa Gangotri, Mysore, sub numero 120-A positus est. Isotypi vero ibidem sub numeris 120 B—F positi sunt.

Iphigenia mysorensis AREKAL & SWAMY is a perennial slender corm-bearing plant. Corm 0.9—1.0 cm in diameter, bulb-like with pale brown sheath and somewhat flattened on the side, associated with remains of the old corms. Stem up to 20.00 cm long, slender, 0.1 cm thick; internodes

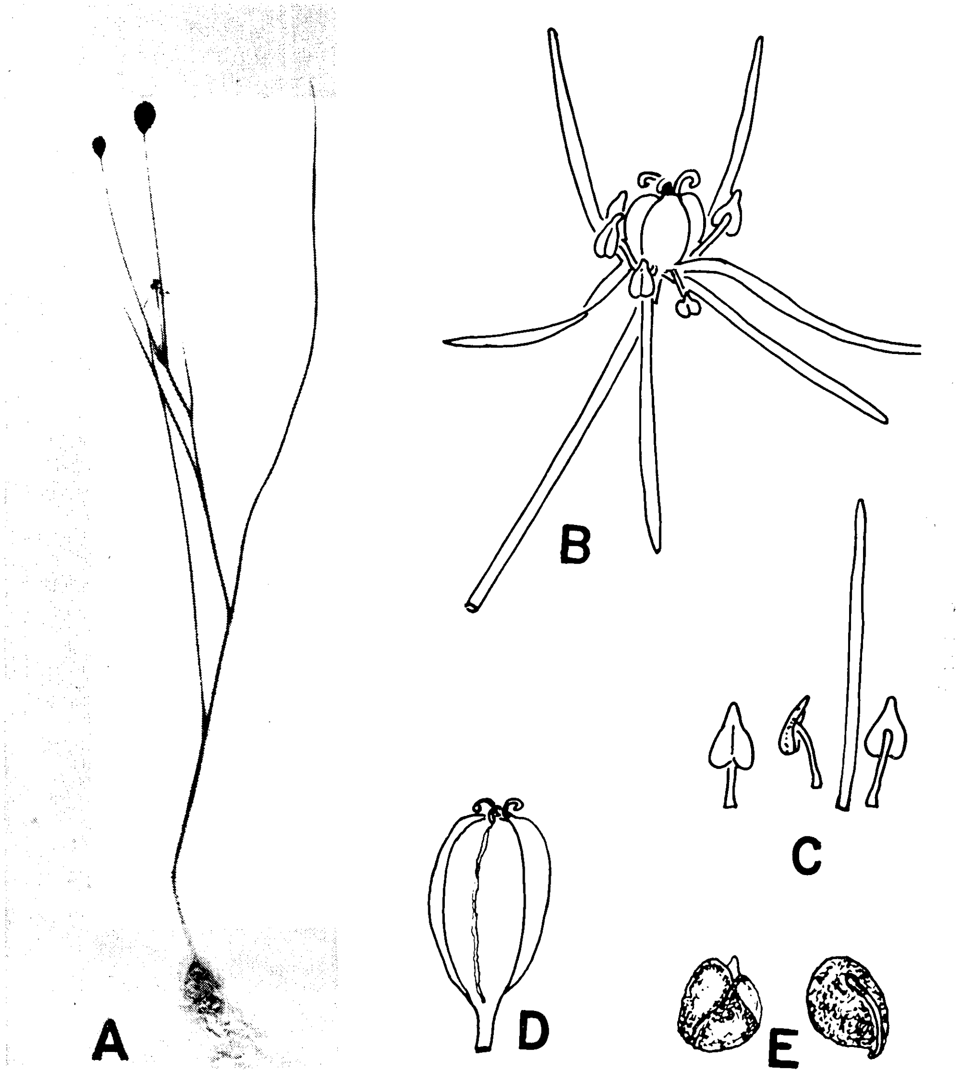

Fig. 1. *Iphigenia mysorensis* AREKAL & SWAMY — A: Fruiting plant with corm and roots, ×0.55. B: Flower, ×3.5. — C: Stamen in different views and a tepal, ×4. — D: Old fruit, ×5. — E: Two views of a seed, ×8.

3.0—4.5 cm long. Leaves usually three (sometimes 2 or 4), acicular, up to 13.00 cm long, 0.1—0.15 cm broad, generally thick. Inflorescence a terminal raceme with 2—4 flowers, occasionally a second axillary inflorescence is also produced — the plant then bearing up to seven flowers. Flowers with longer-ridged pedicels; perianth of 6 free filiform lobes 0.6—1.0 cm long, less than 0.05 cm broad, dark purple. Stamens 6, anthers cordate with a prolonged prominent connective dehiscing by lateral longitudinal slits, usually 0.2 cm long. Gynoecium with three free styles.

Capsules usually 2—4, sometimes up to 7 per plant, small, obovoid, loculicidal; fruiting pedicels 6.0—7.0 cm long. Seeds several, 0.1—0.15 cm in diameter, trigonous, verrucose; raphe whitish and smaller. Chromosome number 2n=22 (n =11) (Fig. 1 A—E).

Holotype was collected by AREKAL and SWAMY at Ranganathittu in Mysore District on 20-10-1965 and has been deposited in the Herbarium, the Department of Botany, Manasa Gangotri, Mysore-6, under No. 120 A. The isotypes are in the same herbarium under numbers 120 B—F.

Habitat: On fine sandy loam associated with *Iphigenia indica* (A. GRAY) KUNTH, *Urginea indica* KUNTH, *Lophopogon tridentatus* HACK., *Sporobolus diander* BEAUV. and *Blepharis molluginifolia* PERS., etc.

The same species has been subsequently collected in two other localities in Mysore State — on open grass land with sandy loam near Boovanahalli and Mavinakere of Hassan District.

ACKNOWLEDGEMENTS

We are deeply grateful to the Director, Royal Botanical Gardens, Kew, Surrey, England and Dr. K. SUBRAMANYAM, Director, Botanical Survey of India, Calcutta for valuable opinions and suggestions on the taxon. To Rev. Fr. CECIL SALDANHA, Professor of Botany, St. Joseph's College, Bangalore we are also deeply grateful for the Latin diagnosis.

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Experimental Studies in Hieracium pilosella L.

II. Taxonomy and Differentiation

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ABSTRACT

TURESSON, B. 1972. Experimental studies in Hieracium pilosella L. II. Taxonomy and differentiation. — Bot. Notiser 125: 223—240.

Cultivated material of a great number of Swedish *Hieracium pilosella* collections, representing various levels of polyploidy and amphimictic as well as apomictic strains, has been taxonomically examined and referred to different species and subspecies, mainly by comparisons with the rich collections in the Botanical Department, Naturhistoriska Riksmuseet, Stockholm. Much attention is paid to phenotypic variation, habitat conditions, and distribution patterns. The reproductive systems and their bearing on the variation are discussed.

INTRODUCTION

In part I of this study, with the subtitle "Reproduction, chromosome number and distribution", the late Professor G. TURESSON and the present author also reported on certain morphological differences between groups with different chromosome numbers, and on methods, collection years, collectors, and, to a certain extent, also on the embryology (TURESSON & TURESSON 1960).

It now remained for us, however, to try to identify our collections with previously named subspecies. For this task, we had the good fortune to have among our colleagues at the Institute of Systematic Botany and Genetics, Uppsala, a Latvian botanist, Mrs. BERTA RUDZITE, who took on this work. I would like to thank her here for a very carefully and expertly executed job.

Financial aid was given by Statens Naturvetenskapliga Forskningsråd for the publication of this paper.

EXAMINATION OF THE COLLECTIONS

Since there is no Swedish flora with a synopsis of the subspecies of *Hieracium pilosella,* it is necessary to go direct to the papers on *Hieracium* published by various research workers, if one wishes to find descriptions of their different subspecies. The foremost Swedish expert within this area, HUGO DAHLSTEDT, who has named more than two-thirds of the known Swedish Pilosellas, has unfortunately only published about 40 of his subspecies and varieties — the remainder (over 100) he has left undescribed. Thus, in order to be able to examine the collections, we were obliged to turn to the *Hieracium pilosella* herbarium (800 sheets) at Naturhistoriska Riksmuseet, Stockholm, containing DAHLSTEDT's *Hieracium* exsiccata as well as his "Herbarium Hieraciorum Scandinaviae". After very tedious and time-consuming labour, BERTA RUDZITE succeeded in determining 216 of our 312 *Pilosella* collections.

MORPHOLOGICAL DIFFERENCES BETWEEN DIFFERENT CYTOTYPES

The diploid *Hieracium macrolepideum* is sexual; at higher chromosome levels, aposporous. In the early rosette stage, it is tightly appressed to the ground, having the appearance of a regular, multipointed star. The lower surface of the leaves is bright white owing to the presence of a dense, short tomentum of stellate hairs. The midrib is very prominent. The stolons are very short and stout, bearing a few homophyllous leaves. At the apex of the stolon, there is a dense cluster of leaves that forms a rooting rosette very early. The plant has a rather low habit, the capitula are more robust, and the flowers are somewhat larger and a paler yellow than *H. pilosella*. The bracts are broad and acute. The outer bracts are quite often loosely appressed.

It grows on open, grass-covered hills forming dense mats. The amphi-apomictic tetraploids and pentaploids are larger and more robust than the diploids. They have considerably longer stolons, but are otherwise characterized by the distinctive marks of *Hieracium macrolepideum*. The tomentum of the lower surface of the leaves is looser and coarser than in the diploids. They are rather rare in nature and grow as scattered individuals without forming dense mats, preferably in crevices and on open stony ground.

We have not found specimens of *Hieracium pilosella* s. str. having a lower chromosome number than 2n=36. This tetraploid type is amphimictic; the types with higher chromosome numbers are aposporous. In *H. pilosella* the rosette is more irregular, the innermost leaves are often turned somewhat upwards. The stellate hairs on the lower surface of the leaves are coarser, sparser and more greyish-white than in *H. macrolepideum*. In the types with higher chromosome numbers the green colour of the leaf often shows through. The midrib is frequently conspicuous in the tetraploids only. They have long slender stolons bearing small, distant leaves that decrease in size towards the apex of the stolon, where a rooting rosette is eventually formed. The involucres are less robust and the bracts are narrower, the tips are long attenuate, and frequently reddish. The flowers are somewhat smaller and a darker yellow, and the scape is longer than in *H. macrolepideum*. The long slender stolons are still longer in plants with higher chromosome number. The scapes also increase in height and the pubescence on the lower surface of the leaves becomes coarser and looser.

Hieracium pilosella also tolerates somewhat damper soil conditions. The tetraploid occurs exclusively in Skåne. The pentaploid is the commonest type within the country, being common throughout southern and central Sweden. In contrast to the other types within the group, it is also found in wooded areas inland. The long stolons and the tall scapes, especially marked in the fruiting stage, make the pentaploids better fitted for occupying somewhat taller vegetation than the other types.

The types with 2n=54 and 2n=63 are rare, and usually occur as isolated individuals. They have a robust habit but develop slowly; they flower late and their seed dispersal is limited.

Hieracium macrolepideum NORRL.

Very few subspecies of *Hieracium macrolepideum* have been described. Since the majority of the types within this species are sexual (with 2n=18) they must be regarded as segregants resulting from allogamy and of little systematic interest. The aposporous types with the high chromosome numbers 2n=36 and 2n=45 are rare. We have therefore deemed it pointless to attempt to name our collections of *H. macrolepideum*. However, within Sweden three form groups can be distinguished: a very robust bristly-haired type that occurs in northern Bohuslän and adjacent parts of Norway, designated by DAHLSTEDT by its old name, *H. peleterianum* MERRAT. It is gradually replaced by the somewhat less stiff-haired form, *H. subpeleterianum* N. & P., which follows the coast southwards to Skåne thence up to Blekinge, where it is in turn gradually replaced by the more gracile *H. sabulosorum,* distinguished by DAHLSTEDT. This taxon then predominates the entire way northward.

Hieracium pilosella L.

On the systematic side, this paper will accordingly deal with *Hieracium pilosella* s. str. Research workers agree that this species is extremely polymorphic and is well able to adapt itself to different environments. For example, OMANG, in the introduction to his paper (1936) regards the species complex *H. pilosella* as being positively chaotic with its abundance of subspecies and varieties, their diverse interrelationships and numerous transitional forms. As the *Pilosella* species are in addition particularly sensitive to external environmental conditions, in particular to the nature of the habitat, it is obvious that difficulties, at times virtually insurmountable, are met with in delimiting the various subspecies and assembling them into natural groups for the sake of clarity. Both OMANG (1936), and NÄGELI & PETER (1885) attempt a grouping of the subspecies, whereas DAHLSTEDT (1890) and NORRLIN (1884), because of the many intermediate forms, avoid actually dividing them into groups. Instead, they indicate in certain cases which they consider to be either similar or related subspecies, a practice that is not very clear.

In the introduction to his main work (1890) DAHLSTEDT writes that he had found a surprising wealth of constant forms in Sweden, and points out thereafter the importance of discriminating and delimiting these constant forms to gain points of reference in their systematic treatment.

He admits here that in certain cases he has perhaps gone farther in separating taxa than what is in agreement with the true conditions in nature, but he considers that such mistakes can easily be rectified through further investigation.

With his trained eye DAHLSTEDT (1890) has noted that "while a number of forms exist that build form groups of extremely close, but in nature constant types; also other groups of forms occur whose most extreme terminal segments are joined with each other by a continuous series of transitional forms, as well as forms that are considerably isolated and distinct. It has thus developed that the forms do not have the same degree of constancy — that the forms can be closely related on the one hand and yet be well differentiated, on the other hand extremely well marked but still through intermediate series united in multitudinous ways, or that some form groups, in appearance at least, build a chaos of forms in which the differentiation appears to proceed at a maximum and where the numerous intermediate forms still do not, by no means, appear to be undergoing extinction." (Translated from Swedish.)

To judge by the last sentence DAHLSTEDT apparently considers *Hieracium pilosella* to be a young species that is still evolving and that the intermediate forms will disappear with time so that the species can stabilize itself.

Without being aware that the species comprises both apomictic and sexual forms, he gives an excellent description here of the constant character of the apomictic forms apart from the modifications and of the swarm of segregants in the sexual species.

ENVIRONMENTAL CONDITIONING AND PHENOTYPIC VARIATION

Concerning the sensitivity of *Hieracium pilosella* to external agents, NORRLIN (1884) reported that his *H. coalescens,* a very distinct form with a wide distribution in Finland, has larger flowers in the north, and in poor, dry localities paler and softer, more poorly developed hairs due to a deficiency in nutrients. The latter observation has also been made by DAHLSTEDT. But it was only NÄGELI and PETER

(1885) who treated this problem more fully. They had no less than 2,000 Piloselloids in cultivation in Munich. How many of these belonged to *H. pilosella* s. str. is not clear. They describe, however, about 200 subspecies and varieties. They described and dried vouchers of their collections when they were newly collected and before specimens were planted, and could later compare them with the same collections after they had been growing for a few years in culture. Many forms that displayed great differences in different natural habitats — and that had often been given different subspecific names — lost many of their habitat-conditioned characteristics when grown under uniform conditions, and thus proved to belong to the same subspecies. Through careful observation, they found that certain characters remained constant in spite of changes in environment; others, on the other hand, were easily modified. Under cultivated conditions, the plants became more luxuriant and robust, and were able to develop all innovation shoots, which they were unable to do in nature in poorer localities. They developed larger leaves, longer and more numerous stolons, and produced flagellae more often than plants in the natural habitat where they have to compete with the surrounding vegetation. On the other hand, cultivation had no effect on the distribution of the internodes and their relative lengths, the length of the peduncle, nor the absolute size and shape of the involucre, the width and shape of the bracts, and the colour of the flower and leaf, the relationship between leaf dimensions, and the length and distribution of pubescence. All of these characters are inherited unchanged from generation to generation and can with full justification be used to delimit subspecies.

Hieracium pilosella, as mentioned previously, is very sensitive to changes in the external environment and is able to form rather distinctive modifications that are conditioned by the habitat. NÄGELI and PETER (1885) mention that even critical authors often made serious mistakes by assigning variety names to such modifications. For example, luxuriant specimens that developed flowering flagellae, receive the name var. *flagellare* or *stoloniflorum.*

Unfortunately, DAHLSTEDT has been too zealous in delimiting closely similar forms and in giving them separate subspecific names. Several of these have proved to be identical when grown under uniform conditions. BERTA RUDZITE has therefore been obliged to give several of our collections double, or should we say alternative names.

DAHLSTEDT (1890), in his main work, has some closely related forms that he considers to be distinct subspecies: *Hieracium favillicolor, H. venustum* and *H. laxisquamum.* Yet he has a variety under *favillicolor* that, according to him, is nevertheless perhaps an environmental modification of *favillicolor.* Under *laxisquamum* he names a variety *subfavillicolor,* and claims, moreover, that there are numerous intermediate forms.

We have no less than 11 collections that belong to this group. They are all sexual with 2n=36, and are difficult to distinguish from one another when grown under uniform conditions. These three "subspecies" with their "varieties" and intermediate forms thus must be regarded as segregants after cross-fertilization between sexual biotypes, and should not have received separate names. One may ask how many new subspecies DAHLSTEDT would have been able to describe if he had raised progeny from seed. Under natural conditions, we have not found plants of the sexual group north of the borders of Skåne. We have one plant from a railway embankment north of Norrköping, another from a roadside in Gränna in Småland. This points to dispersal by artificial means.

How is it then that DAHLSTEDT (1890) came to describe these forms from the region of Linköping in Östergötland? As it turns out, he collected them from lawns in parks in the city. He also collected some from built-up areas in Berg, in Vreta parish, north of the city. The fact is that the firms that sell lawn seed are all in Skåne, and there may well have been *Pilosella* seed in the grass seed. There are several other cases like this reported by DAHLSTEDT and by STENSTRÖM, NORRLIN, and NÄGELI & PETER.

APOSPORY AND VARIATION

The aposporous forms of *Hieracium pilosella* seem, however, to be constant. After emasculation, the flowers set seed without fertilization but in every capitulum, however, there are always some florets that do not develop seed. We presumed, as did OSTENFELD, that these were sexual florets that were unable to set seed without being fertilized. But we found that there have been approximately the same number of undeveloped flowers both after free pollination and after artificial fertilization.

We have taken offspring after free pollination where the plants have been grown together with all our other collections as well as after crossing with morphologically strongly deviating pentaploid forms with good pollen. But the progeny has always been matroclinous. Embryological investigation has shown that the florets initially form a fully normal sexual embryo-sac in which the egg cell has undergone meiosis. As soon as the embryo-sac is fully developed, an apomictic embryo-sac starts to grow downwards from the nucellus and suppresses and destroys the sexual embryo-sac. This process occurs at approximately the same time in all florets, when the capitula are still very young, so that the sexual embryo-sacs have no opportunity to be fertilized.

In *Hieracium pilosella*'s northern distributional area the early summer can come very suddenly with high temperatures, low humidity and intense insolation. Flowering then occurs almost explosively. Theoretically it could be expected that the apomictic embryo-sacs had not had time to suppress the sexual embryo-sacs and that fertilization could take place.

The above seems, however, only to apply to the apomictic Piloselloids with even genome numbers. SKALIŃSKA (1971) described attempts to cross different aposporous forms of *Hieracium aurantiacum* (very closely related to *H. pilosella*) that have the same chromosome numbers as *H. pilosella:* 2n=36, 45, 54 and 63. However, here the tetraploid is also aposporous. With plants having an even number of genomes as the maternal parent, SKALIŃSKA has succeeded in obtaining a few hybrids, whereas her embryological investigations reveal that the sexual embryo-sac of the pentaploid, after irregular meiosis, dies at a very early stage. This accords well with my own embryological investigations of the pentaploid *H. pilosella* in which the sexual embryo-sac had already shrivelled and died when the aposporous embryo-sac began to grow down from the nucellus. This is in contrast to ROSENBERG's (1908) micrographs of embryogenesis in Piloselloids with even genome numbers in which it can be clearly seen how the still living and sound sexual embryo-sac is suppressed and destroyed by the downward-growing aposporous embryo-sac.

The undeveloped florets in the pentaploid have thus not died because fertilization has not taken place, as OSTENFELD suggests, but rather because the apomictic embryo-sac has not had time to develop before the plant flowers. The pentaploid has, however, in spite of aberrant chromosome numbers, excellent pollen.

Since the constant pentaploid forms within a given area usually belong to the same phenotype, for example, robust plants with black hairs in one locality and slenderer types with pale hairs in another, workers have been inclined to believe that the formation of new forms within a particular area occurs by means of hybridization between these aposporous apomicts. But since this seems to be ruled out, the alternative remains that they have arisen by mutation. — These unsuccessful attempts at crossing involve, however, only the pentaploid types of *Hieracium pilosella* s. str.

OSTENFELD, who began his experiments in 1904 by crossing different aposporous Piloselloids with even chromosome numbers, got partly different results. To make it easier to discern putative hybrids, he often used the red-flowered *Hieracium aurantiacum* in his crosses. When he used this species as female parent, he obtained no hybrids, however, whereas when he used a form of "*H. pilosella*" as female parent and *H. aurantiacum* as male parent one hybrid was produced; and in the cross *H. excellens* × *H. aurantiacum,* he got no fewer than six hybrids.

OSTENFELD sent his material to ROSENBERG (1908, 1917) in Stockholm for cytological investigation. The three species mentioned above were all aposporous. *Hieracium aurantiacum* and *H. pilosella* both had 2n=36, whereas the peculiar, totally male sterile *H. excellens* had 2n=42. ROSENBERG considered this species to be of hybrid origin. Thus all of OSTENFELD's experimental plants had an even number of chromosomes which facilitated the formation of hybrids.

As regards the development of the embryo-sac, he found the same thing as we ourselves found later — the apomictic embryo-sac suppresses and destroys the normal one. But on odd occasions (in *Hieracium excellens*), he found that the apomictic embryo-sac grew down beside the sexual one without destroying it, and as a consequence the latter was able to produce hybrids. For many years after OSTENFELD's and ROSENBERG's investigations *Hieracium pilosella* was then claimed to be aposporous with 36 chromosomes.

From his observations in nature, G. TURESSON came to the conclusion that the abundance of forms pointed to the possibility of the existence of several different cytotypes. He also considered that in certain localities the variation was that of sexual segregants. He began, then, to collect living material, which he grew at Uppsala. After emasculating and determining the chromosome numbers of the plants, we could confirm his assumption. There were both sexual and apomictic biotypes, as well as many different chromosome numbers. To our surprise, we found that all our tetraploid plants of *Hieracium pilosella* s. str. were sexual. But the tetraploid *H. macrolepideum* was apomictic like OSTENFELD's "*H. pilosella*". In the Botanical Museum in Copenhagen, there are carefully numbered voucher specimens of the plants that OSTENFELD had used and sent to ROSENBERG. It was thus easy to establish that OSTENFELD's "*pilosella*" was typical tetraploid *H. macrolepideum.*

OSTENFELD had collected these specimens in the lawn of the Botanical Gardens. How they ever got there is a mystery. According to RAUNKIAER (1922) *Hieracium macrolepideum* is commonest on Bornholm, but also occurs on the west coast of Jylland. But both GÖTE TURESSON and HEDDA NORDENSKIÖLD have looked for Hieracia just there. They have never found *macrolepideum,* only sexual, tetraploid *H. pilosella* s. str. But in the lawns of botanical gardens it is not uncommon to find many extraneous and unusual plants.

On a later excursion (1970), a single plant of *Hieracium macrolepideum* was observed. From its appearance, it was presumably diploid. Also the types of *H. macrolepideum* from Bornholm appear to be diploids. That they have the very short stolons characteristic of diploids, is evident from STENSTRÖM's descriptions (1896 b) as well as from his herbarium material.

GEOGRAPHICAL DISTRIBUTION

Hieracium pilosella is particularly local in occurrence. Of the 145 subspecies and varieties that OMANG (1936) described from Norway and the more than 250 that occur in Sweden, there are only 11 that are common to both countries. Finland's *H. pilosella* are also pronouncedly endemic. Of the 150 named Finnish forms, only about five occur in Sweden.

But even within the various countries, the subspecies groups have a definite geographical distribution. In Norway, OMANG distinguishes three distinct groups of forms: one north of Dovrefjället, one west of and one south-east of Langfjellen. In Sweden there are no similar mountain borders, but according to DAHLSTEDT, the great lakes form barriers between regions with different forms, and the provinces north of these lakes constitute a single region. He found that the provinces in the west near the Norwegian border have forms that do not occur in the east and vice versa. The area that he covers in his paper of 1890 comprises part of Östergötland, Gotland, and the greater part of Småland. In the north the area is delimited by the lakes that cut across Östergötland, and in the south it extends over the southern parts of the South Scandinavian Highlands into Blekinge and northern Skåne. In the west, Lake Vättern forms a natural border. But in the south-west the border is more indefinite since south-western Småland, Halland and Västergötland were then (1890) practically uninvestigated with regard to Hieracia. In northern Östergötland, which should be considered as a transitional area, and even more so in Södermanland, Uppland and Gästrikland begins a divergent area characterized by the more general occurrence of certain forms, the presence of new forms and the absence of others. We too have found that in central Sweden there is a mixture of northern and southern forms.

DAHLSTEDT considered that Öland, the south-eastern part of the coastal regions of Småland, Blekinge and some parts of Skåne form a single region. He also considers that Gotland, with its endemic forms and the deviating appearance of the mainland forms found there, could be treated as a special area, but since the species are similar to those in Östergötland and northern Småland, he prefers to see these areas as a single unit.

DAHLSTEDT admittedly divides the Pilosellas into different geographical groups within Sweden, but he does not describe the morphological differences between the groups. BERTA RUDZITE has, on the other hand, with the aid of the herbaria from Naturhistoriska Riksmuseet, Stockholm, attempted a survey of the dominating morphological types within each area.

In the northernmost provinces, the plants have consistently dark involucres with black glands and stellate hairs. The tips of the bracts are a dirty reddish-violet with stellate hairs. This northern area can be further divided into an eastern and a western group. The eastern group (Västerbotten and Ångermanland) is characterized by plants with rather large growth and having long, large leaves and large capitula. Towards the south, in Hälsingland, transitional forms occur to plants being smaller with more rounded leaves.

In the western group (Jämtland and Härjedalen), both plants and leaves are smaller. In the south, in Dalarna, the Pilosellas become more robust and, above all, more bristly. If the Norwegian border is followed southwards, smaller forms are met with in Värmland. They are less bristly and often have bluish-green leaves, which is also true of the biotypes east of Värmland, in Västmanland, where in addition they are extremely glandular. Further south in Dalsland, one finds partly somewhat larger plants with involucres with stout black glands having dark yellow knobs that give them a piebald appearance, partly paler, slenderer forms. Farthest south, towards the west coast of Bohuslän, the forms are rather divergent. They are densely bristly on the involucres, leaves and stolons. Because of the pubescence the leaves are not so green. Even subspecies that also occur in other areas are here more pubescent. Even *Hieracium macrolepideum* is more bristly here than in other districts. Since none of these plants lose their pubescence when grown under other conditions, they cannot be regarded as habitat modifications. In Bohuslän, with its barren, rocky, windswept conditions, apparently only these strongly pubescent forms are able to survive, all the others are excluded by natural selection. Hence, we have here a typical ecotype formation of species that show hereditary adaptation to an extreme environment.

In Västergötland the plants are rather robust, often dark in colour, and some of them are bristly. Naturhistoriska Riksmuseet in Stockholm has practically no material from Halland. Our own plants from the sloping beach meadows and grassy hills of this province are rather robust and dark in colour, but are not bristly pubescent.

If we now return north and follow the east coast southwards, we find in Uppland large, robust plants, dark in colour due to the presence of black glands, but less bristly. South of Lake Mälaren in Södermanland, the plants have a low habit and have more rounded leaves which are rather weakly pubescent. But already here the central Swedish confluence region, which DAHLSTEDT mentions, starts gradually.

In Östergötland, and above all in Småland, many different forms are found together. On Öland both tall and very short forms occur. They are mostly black-glandular and some are pubescent. On Gotland the majority is very short, black-glandular and small-leaved, and some material is pubescent.

In the southernmost provinces, rather robust types occur in Blekinge, whereas in Skåne the biotypes are small and very slender. This is not surprising, since it is here we find the sexual tetraploid forms which have one genome less than the northern forms and are smaller in size. That the tetraploids have not spread northwards is due perhaps to the fact that topography and climate are of a different character here. On the other hand, it is found in the west in Denmark and England. All our Danish collections, as well as the two from Sussex, England, belong to this tetraploid type. Strangely enough one of these English types agrees in detail with NORRLIN's Finnish subspecies *Hieracium jodolepis.* NORRLIN reports that it is very difficult to determine as there are so many very closely related forms and also many intermediates. A better description of a sexual type with all its segregants is hardly possible. Thus, even though in Sweden the tetraploid sexual form does not occur at latitudes north of Skåne in natural habitats, it obviously does in southern Finland.

AURICULA HYBRIDS

FRIES' *Hieracium auriculaeforme* is a classical example of a species hybrid. As regards habit it is intermediary between its parents, *H. macrolepideum* and *H. auricula,* and is practically sterile, as a true species hybrid should be. In the floras it is often reported to occur where the two parents grow in close proximity to each other, but we have never found it. Fortunately, a colleague sent us a plant from Södermanland, so that we were able to determine the chromosome number. Like both of the parents it was a diploid with $2n=18$.

As mentioned above, we have a number of specimens in our collections with bluish-green leaves. They also often display other features reminiscent of *Hieracium auricula.* Here, above all, belongs NORRLIN's (1884) tetraploid, apomictic subspecies *H. suivalensis.* He considers this to be intermediary between *H. auricula* and *H. pilosella,* though not a species hybrid because of its perfect seed-setting. He refers it to FOCKE's concept "Blendart". FOCKE (1881) writes that he gives the name "Blendart" to species that he considers to be the offspring of hybrids but that they now behave as normal species (i.e. they set seed abundantly). He does not say how he presumes they have arisen. Presumably these "Blendarten" are hybrids that have become apomictic in the same way as the diploid sexual *H. macrolepideum,* by chromosome duplication, and thus have evolved a good capacity of seed-setting.

SUMMARY

During the 1880's and the following decades a considerable number of botanists took up the study of apomictic species. For example, they devoted themselves to the genus *Hieracium,* to the aposporous *Pilosella* but chiefly to the diplosporous *Archieracium.* They found that these apomicts form an endless number of distinguishable, constant microspecies, to which they gave subspecific and varietal names. Many members of the Archieracia have been well investigated and described by DAHLSTEDT, K. JOHANSSON, and others, but as regards the *Pilosella* group little has been published. Under *Pilosella* in the Swedish floras first comes *H. macrolepideum* NORRL. with its easily recognized slenderer subspecies *sabulosorum* DAHLST. and its hybrid with *H. auricula, H. auriculiforme* FR. Then comes *H. pilosella* (coll.) with the remark that it comprises hundreds of microspecies. No further information is given. To assign a subspecific epithet to a specimen that has been collected, it is necessary first of all to search through the various *Pilosella*-hieraciologists' original publications where about one-fifth of the *Pilosella* forms are described. The remainder are found only in the form of DAHLSTEDT's exsiccata in botanical museums and lack descriptions. For the amateur they are difficult of access, and even for the professional botanist troublesome and extremely time-consuming to go through, on account of their great number.

The reason why DAHLSTEDT left the enormous work of classifying this material untouched was probably that he had not succeeded in finding a satisfactory key to the natural classification. He found the Pilosellas so chaotic that he gave up and turned his attention to the subgenus *Archieracium,* which because of its striking obligate apomixis was easier to work with.

Many botanists today do not agree with the old hieraciologists' habit of giving specific or varietal names to all these constant apomictic microspecies. They regard it to be entirely meaningless, as the names do not serve any function. It is a rather hopeless enterprise to attempt to find a subspecific name for any given *H. pilosella.* Most collectors must content themselves with naming their specimens *Hieracium pilosella* coll.

In the following list, in which our collections are referred to subspecies of *Hieracium pilosella,* some of DAHLSTEDT's names are published for the first time. Latin descriptions are not added to the names, which therefore become *nomina nuda.* However, my aim when publishing the list is not to publish new taxa within *H. pilosella,* which I do not find desirable, but to connect our experimental studies with the herbarium material kept at Naturhistoriska Riksmuseet in Stockholm. I hope that both botanical museums and private persons in possession of *Hieracium pilosella* belonging to subspecies mentioned here may derive interest from information on chromosome number and mode of reproduction given in the list.

APPENDIX 1.

Localities of the Experimental Material of Hieracium pilosella

Field no.	Locality	Province or country	Subspecies
AMPHIMICTIC HIERACIUM PILOSELLA (2n=36)			
1	Ljungbyhed	Skåne	*favillicolor* DAHLST. — *venusticeps* DAHLST.
6	Hylla	»	*distantilingua* var. *oblongiceps* NORRL.
11	Gunnarp	»	*granulosum* STENSTR.
12	Sätaröd	»	*linguatum* DAHLST. — *hypochlorum* STENSTR.
14	Kungsmarken	»	*favillicolor* DAHLST. — *venusticeps* DAHLST.
15	Ludvigsborg	»	*ermineum* N. & P. — *erminellum* STENSTR.
16	S. Rörum	»	*linguatum* DAHLST.
20	Östarp	»	*stenostictum* STENSTR. — *stenophyton* DAHLST.
21	Stenestad	»	*venustum* DAHLST.
38	Tunbyholm	»	*stenophyton* f. *floccosior* DAHLST.
122	Kaffatorp 3	»	*favillicolor* DAHLST. forma — *venustum* DAHLST.
134	Broby 4	»	*favillicolor* DAHLST. forma — *venustum* DAHLST.
147	Landskrona 2	»	*vankivense* STENSTR.
150	Landskrona 5	»	*subvenustum* DAHLST. — *venustum* DAHLST.
183	Hallands Väderö	»	*tenuistolonum* DAHLST.
278	Axelvold 1	»	*stenostictum* STENSTR. (*stenophytoides* DAHLST.)
280	Knutstorp 1	»	*venustum* DAHLST.
281	Knutstorp 2	»	*venustum* DAHLST.
293	Högestad 1	»	*favillicolor* DAHLST. forma?
295	Falsterbo 1	»	*venusticeps* DAHLST. — *robusticeps* DAHLST.
296	Falsterbo 2	»	*subvenustum* DAHLST.
312	Broby D	»	*venustum* DAHLST. — *favillicolor* DAHLST.
315	Broby G	»	*stenophyton* DAHLST.
318	Broby K	»	*stenophyton* DAHLST.
329	Sånekulla	»	*robusticeps* DAHLST. forma
336	Sjöbo	»	*robusticeps* DAHLST.
343	Viktorshög	»	*venusticeps* DAHLST. (*robusticeps* DAHLST.)
346	Domsten 1	»	*tenuistolonum* DAHLST. forma
347	Domsten 2	»	*tenuistolonum* DAHLST. forma
445	Hohög	»	*laxisquamum* DAHLST. forma
446	Frostavallen	»	*tenuistolonum* DAHLST. forma
450	Vankiva 3	»	*polychorum* STENSTR. forma
488	Båstad 1	»	*pachytrichellum* DAHLST.
489	Båstad 2	»	*pachytrichellum* DAHLST.
33	Gränna	Småland	*vulgare* TAUSCH forma
467	Forserum 1	»	*brachytrix* f. *acutifolia* DAHLST.
291	Österild	Denmark	*venusticeps* DAHLST.?
257	Sussex 1	England	*jodolepis* NORRL.
AMPHIAPOMICTIC HIERACIUM PILOSELLA (2n=45)			
3	Gyllebo	Skåne	*baliocephalum* DAHLST.
10	Nybroån	»	*atrocanum* OMANG
114	V. Ströö	»	*leptacinum* DAHLST. — *epipyrrhum* DAHLST.
127	Kaffatorp 8	»	*porati* DAHLST. — *subcrassescens* DAHLST.
132	Broby 2	»	*atrocanum* OMANG forma
133	Broby 3	»	*atroëpilosum* ADLERZ — *atrovillosulum* DAHLST.
136	Broby 6	»	*atrovillosulum* DAHLST. forma

Field no.	Locality	Province or country	Subspecies
137	Broby 7	Skåne	*atroëpilosum* Adlerz
153	Skälderviken	»	*tenuistolonum* Dahlst. ? or *polyadenium* Dahlst.?
155	V. Ströö 2	»	*trichoscapoides* Dahlst. forma?
162	Kungsmarken	»	*baliocephalum* Dahlst.
184	Hallands Väderö 2	»	*firmistolonum* Dahlst.
309	Broby A	»	*polyadenium* Dahlst.
310	Broby B	»	*atrovillosulum* Dahlst.
313	Broby E	»	*atroëpilosum* Adlerz — *atrovillosulum* Dahlst.
314	Broby F	»	*epipyrrhum* Dahlst. forma
319	Broby L	»	*leptaleum* Dahlst. modif. — *leptaloides* Dahlst.
337	Bollerup	»	*subcrassescens* Dahlst. forma
344	Sibbarp	»	*subcrassescens* Dahlst. ?
452	Vittsjö	»	*leptacinum* Dahlst. — *leptaleum* Dahlst. modif.
453	Osby	»	*epipyrrhum* Dahlst. forma
283	Bräkne-Hoby 2	Blekinge	*firmistolonum* Dahlst. forma
284	Karlskrona	»	*trichoscapoides* Dahlst. v. *obtusiusculum*
525	Tjurkö 1	»	*leptaleum* Dahlst. — *leptaloides* Dahlst.
342	Tolarp	Halland	*leptaloides* Dahlst.
349	Skrea strand 1	»	*leptaleum* Dahlst. — *leptacinum* Dahlst.
350	Skrea strand 2	»	*leptaleum* Dahlst. — *leptacinum* Dahlst.
351	Skrea strand 3	»	*epipyrrhum* Dahlst. forma
352	Steninge 1	»	*leptacinum* Dahlst.
353	Steninge 2	»	*leptacinum* Dahlst. — *leptaleum* Dahlst.
355	Åsa	»	*baliocephalum* Dahlst.
490	Tönnersjö	»	*leptaloides* Dahlst.
37	Visingsö	Småland	*atrovillosulum* Dahlst.
218	Vassmolösa 1	»	*semicrassescens* Dahlst. — *crassescens* Dahlst.
219	Vassmolösa 2	»	*semicrassescens* Dahlst. forma
274	Jönköping	»	*semicrassescens* Dahlst. — *subcrassescens* Dahlst.
275	Tånnö	»	*atrocanum* Omang
276	Tånnö	»	*atrocanum* Omang
411	Hornsborg	»	*subcrassescens* Dahlst.
432	Råshult	»	*multistolonum* Dahlst. forma
455	Pataholm	»	*trichoscapoides* Dahlst. v. *obtusulum* Dahlst.
457	Urshult	»	*leptaleum* Dahlst. modif.
458	Rävamåla	»	*semicrassescens* Dahlst.
460	Lenhovda	»	*granulatum* Dahlst.
462	Oskarshamn 1	»	*acrophylloides* Dahlst. modif.
463	Oskarshamn 2	»	*leptaloides* Dahlst. forma
465	Vimmerby 2	»	*candescens* Dahlst.
466	Eksjö	»	*atroëpilosum* Adlerz
469	Bankeryd	»	*atroëpilosum* Adlerz forma
491	Vrå	»	*epipyrrhum* Dahlst. forma
492	Ljungby	»	*candescens* Dahlst.
494	Bellö	»	*crassistolonum* Dahlst.
495	Svinhult	»	*praepilans* Dahlst. forma
515	Västervik, Gränsö 1	»	*stenophyton* Dahlst. f. *floccosior*
516	Västervik, Gränsö 2	»	*trichoscapoides* Dahlst. (or *poliochlorum* Dahlst.)
518	Västervik, Segersg. 1	»	*svedalense* Stenstr.

Field no.	Locality	Province or country	Subspecies
519	Västervik, Segersg. 2	Småland	*tynnophyton* Dahlst. modif.
520	Västervik, Kuggviken	»	*tynnophyton* Dahlst. forma
521	Oskarshamn, Gunnarsö	»	*aeruginicolor* Dahlst. — *furviceps* Dahlst.
119	Vickleby	Öland	*aerophyllum* Dahlst. modif.
425	Resmo 3	»	*poliochlorum* Dahlst.
431	Böda	»	*subcrassescens* Dahlst.
511	Djupvik, Föra	»	*aeruginicolor* Dahlst. forma
41	Råby träsk	Gotland	*pauxillum* Dahlst. forma
181	Fårösund	»	*firmistolonum* Dahlst. modif.
542	Hoburg 3	»	*trichadenium* N. & P. ?
545	Vike 1	»	*coloreum* Dahlst. forma
546	Vike 2	»	*leucopsarum* Dahlst. ?
89	Ringstad 1	Östergötland	*laetevirens* Dahlst.
112	Omberg 1	»	*epipyrrhum* Dahlst. forma
178	Grensholmen	»	*vagans* Dahlst.
217	Borghamn	»	*atrovillosulum* Dahlst.
496	Åtvidaberg	»	*crassistolonum* Dahlst. forma
499	Nakna 1	»	*stenophyton* Dahlst.
500	Nakna 2	»	*stenophyton* Dahlst.
4	Göteborg	Västergötland	*hypochlorum* Stenstr. — *hypochlorellum* Dahlst.
115	Läckö	»	*drodantale* Norrl. forma
202	Hindås	»	*epipyrrhum* Dahlst. forma
203	Alingsås	»	*epipyrrhum* Dahlst.
265	Tivägsboda	»	*semicrassescens* Dahlst.
300	Falköping	»	*furviceps* Dahlst. forma
301	Mösseberg 1	»	*hypochlorum* Stenstr.
302	Mösseberg 2	»	*acrophyllum* Dahlst.
303	Kleva 1	»	*aeruginicolor* Dahlst.
305	Kleva 5	»	*firmistolonum* Dahlst. forma
374	Trollhättan 4	»	*pachytrichellum* Dahlst.
375	Trollhättan 5	»	*subcrassescens* Dahlst. ?
471	Bjurum 2	»	*leptaloides* Dahlst.
476	Undenäs	»	*trichoscapoides* Dahlst.
477	Granvik	»	*drodantale* Norrl. forma
56	Munkedal	Bohuslän	*epipyrrhum* Dahlst. forma
362	Stenungsund	»	*tynnophyton* Dahlst. forma
364	Hårleby, Orust 1	»	*barycephalum* Dahlst.
365	Hårleby, Orust 2	»	*barycephalum* Dahlst.
367	Svälte 1	»	*tynnophyton* Dahlst. forma
368	Svälte 2	»	*tynnophyton* Dahlst. forma
369	Uddevalla 1	»	*subcrassescens* Dahlst. v. *breviceps* Dahlst.
370	Uddevalla 2	»	*leucodes* Dahlst.
269	Laxarby	Dalsland	*acrophyllum* Dahlst. — *acrophylloides* Dahlst. — *baliocephalum* Dahlst.
270	Ed, Stora Le	»	*trichoscapoides* Dahlst.
377	Mellerud 2	»	*atrovillosulum* Dahlst. — *trichoscapoides* Dahlst.
382	Bengtsfors 2	»	*baliocephalum* Dahlst. ?
383	Bengtsfors 3	»	*acrophylloides* Dahlst. — *baliocephaloides* Dahlst.
266	Säbylund	Närke	*aeruginicolor* Dahlst. forma
271	Degerfors	»	*drodantale* Norrl.
478	Olshammar	»	*epipyrrhum* Dahlst.

Field no.	Locality	Province or country	Subspecies
479	Askersund	Närke	*furviceps* DAHLST. forma
58	Kila 1	Södermanland	*acrophyllum* DAHLST.
91	Tystberga	»	*firmistolonum* DAHLST. — *acrophyllum* DAHLST.
182	Sjösa	»	*baliocephalum* DAHLST.
259	Vaxåker 2	»	*epipyrrhum* DAHLST. forma
273	Vaxåker	»	*poliochlorum* DAHLST. forma
307	Römora, Trosa archip.	»	*tenuistolonum* DAHLST. forma
433	Sparreholm	»	*poliochlorum* DAHLST. ?
434	Sparreholm	»	*poliochlorum* DAHLST. ?
501	Simonstorp	»	*trichoscapoides* DAHLST.
502	Simonstorp	»	*granulatum* DAHLST.
503	Klastorp	»	*aeruginicolor* DAHLST. var.
234	Noppen	Värmland	*baliocephalum* DAHLST.
386	Valnäs	»	*baliocephalum* DAHLST.
387	Karlstad	»	*multistolonum* DAHLST.
389	Saxå	»	*atrovillosulum* DAHLST.
390	Hjulsjö	Västmanland	*baliocephalum* DAHLST.
482	Arboga	»	*multistolonum* DAHLST.
27	Bäcklösa	Uppland	*crassescens* DAHLST.
46	Lidingö	»	*porati* DAHLST.
48	Ärna	»	*aeruginicolor* DAHLST.
185	Hummedal	»	*aerophyllum* DAHLST.
186	Torslunda	»	*aerophyllum* DAHLST.
189	Hjälstaviken	»	*longiscapum* DAHLST. modif.
190	Uppsala 1	»	*stereodes* DAHLST. modif.
205	Bogesund 1	»	*baliocephalum* DAHLST. forma
207	Bogesund 2	»	*subcrassescens* DAHLST.
215	Funbo 2	»	*aerophylloides* DAHLST. forma
216	Gårdskär	»	*firmistolonum* DAHLST.
220	Hammarby 1	»	*firmistolonum* DAHLST. — *leucopsarum* DAHLST.
256	Biludden	»	*aerophylloides* DAHLST.
308	Ultuna	»	*leucopsarum* DAHLST.
320	Ultuna	»	*vagans* DAHLST. forma
321	Vittinge 1	»	*trichoscapum* N. & P.
322	Vittinge 2	»	*trichoscapoides* DAHLST.
324	Månkarbo 1	»	*trichoscapoides* DAHLST.
325	Österbybruk	»	*baliocephalum* DAHLST.
326	Älvkarleby	»	*acrophylloides* DAHLST.
406	Norrtälje	»	*leucopsarum* DAHLST. modif.
407	Frötuna	»	*lautumiarum* DAHLST.
409	Gottröra	»	*leptaleum* DAHLST.
413	Grisslehamn	»	*lamproglossum* DAHLST. — *leucopsaroides* DAHLST.
416	Väddö Huvud	»	*longiscapum* DAHLST. var. — *acrophylloides* DAHLST.
418	Väddö Huvud	»	*leptaleum* DAHLST. modif.
419	Gottsunda	»	*epipyrrhum* DAHLST. forma
396	Storvik 1	Gästrikland	*porati* DAHLST. — *subcrassescens* DAHLST.
61	Säter	Dalarna	*subpraestans* DAHLST.
165	Hedemora	»	*fimbrilliferum* NORRL. forma
392	Rämshyttan 1	»	*tenuilingua* NORRL.
393	Rämshyttan 2	»	*tenuilingua* NORRL.
395	Hosjö	»	*firmistolonum* DAHLST.
72	Ånge	Medelpad	*tenuilingua* NORRL.
75	Norrhassel	»	*tenuilingua* NORRL.

Field no.	Locality	Province or country	Subspecies
174	Åre	Jämtland	*adpressum* NORRL.
63	Nåtö, Åland	Finland	*coalescens* NORRL.
AMPHIAPOMICTIC HIERACIUM PILOSELLA (2n=54)			
528	Tjurkö 4	Blekinge	*melanochroum* DAHLST. forma
304	Kleva 2	Västergötland	*prasaeum* DAHLST.
414	Väddö Huvud 1	Uppland	*longiscapum* DAHLST. forma — *acrophylloides* DAHLST.
415	Väddö Huvud 2	»	*longiscapum* DAHLST. forma
166	Hedemora 2	Dalarna	*longiscapum* DAHLST.
97	Gånsvik 1	Ångermanland	*belfragei* MAGNUSSON forma
98	Gånsvik 2	»	*belfragei* MAGNUSSON
AMPHIAPOMICTIC HIERACIUM PILOSELLA (2n=63)			
131	Broby 1	Skåne	*praepilans* DAHLST.
531	Stenshuvud	»	*praepilans* DAHLST.
AMPHIAPOMICTIC HIERACIUM PILOSELLA WITH SOME DISTINCT CHARACTERS OF H. AURICULA (2n=36)			
493	Vrigstad	Småland	*vagans* DAHLST. forma
497	Norsholm	Östergötland	*suivalense* NORRL. forma
263	Berga Färed 1	Västergötland	*suivalense* NORRL.
264	Berga Färed 2	»	*suivalense* NORRL. forma
172	Virå	Södermanland	*suivalense* NORRL.
391	Hjulsjö 2	Västmanland	*suivalense* NORRL.
248	Stockacher Bach, Innsbruck	Austria	*suivalense* NORRL.
249	Stockacher Alm, Innsbruck	»	*suivalense* NORRL.

APPENDIX 2.

Subspecies studied of Hieracium pilosella

After the name of the subspecies is the literature and the herbarium material that we used for making the determination of the plants, and our collections that belong here along with the province and field number.

DAHLSTEDT's Hieracia Exsiccata are grouped into fasces, abbreviated here to Exsic. Fasc.; his Herbarium Hieraciorum Scandinaviae is divided up into centum groups, abbreviated here to Cent.

AMPHIMICTIC HIERACIUM PILOSELLA (2n=36)

H. brachytrix DAHLST. f. **acutifolia.** — Sine descript. — Småland, Oskarshamn 1903 leg. KÖHLER, det. DAHLST.; Västergötland, Göteborg 1915 leg. PALMÉR, det. DAHLST. — Småland 467.

H. distantilingua NORRL. v. **oblongiceps.** — NORRLIN 1895 p. 19. — STENSTRÖM 1896 a p. 20. — Exsic. Fasc. I—6, Östergötland, Lindekull 1886; Skåne, Skäralid 1890 leg. STENSTR. — Skåne 6.

H. erminellum STENSTR. — STENSTRÖM 1896 a p. 8. — Skåne, Rönneholm 1890 leg. STENSTR. Skåne, Skäralid 1889 leg. STENSTR. — Skåne 15.

H. ermineum N. & P. — N. & P. 1885 p. 68. — STENSTRÖM 1896 a p. 27. — Skåne, Svedala 1890 leg. STENSTR. — Skåne 15.

H. favillicolor DAHLST. — DAHLSTEDT 1890 p. 31. — Exsic. Fasc. I—10, II—12, Östergötland, Linköping 1889. — Skåne 1, 14, 122, 134, 293, 312.

H. granulosum STENSTR. — STENSTRÖM 1896 b p. 220. — Skåne, Svedala 1890 leg. STENSTR. — Skåne, Rönneholm 1890 leg. STENSTR. — Skåne 11.

H. hypochlorum STENSTR. — STENSTRÖM 1896 a p. 13. — Cent. XVIII—12. — Skåne 12.

H. jodolepis NORRL. — NORRLIN 1884 p. 82. — Herb. Pilos. Fenn. nr. 17. — England 257.

H. laxisquamum DAHLST. — DAHLSTEDT 1890 p. 32. — Exsic. II—10. Cent. VI—88, Östergötland, Vreta 1981 legi ipse. — Skåne 445.

H. linguatum Dahlst. — Dahlstedt 1893 p. 5. — Exsic. Fasc. IV—5, Skåne, Hallandsås, Båstad 1890 leg. Stenstr. — Skåne 12, 16.

H. pachytrichellum Dahlst. — Sine descript. — Cent. XVI—31, Stockholm 1903 leg. Dahlst. — Skåne 488, 489.

H. polychorum Stenstr. — Stenström 1896 a p. 32. — Skåne, Stehag 1890 leg. Stenstr. — Skåne 450.

H. robusticeps Dahlst. — Dahlstedt 1890 p. 24. — Exsic. Fasc. II—9, Småland, Nybro 1897 leg. O. G. Köhler. — Skåne 295, 329, 336, 343.

H. stenophyton Dahlst. — Sine descript. — Cent. VIII—5, Östergötland, Linköping 1890 legi ipse. Cent. VI—96, Östergötland legi ipse. — Skåne 20, 38, 315, 318.

H. stenostictum Stenstr. — Stenström 1896 a p. 21. — Skåne, Bökebergsslätt 1890 leg. Stenstr. Skåne, Svedala 1890 leg. Stenstr. — Skåne 20, 278.

H. subvenustum Dahlst. — Sine descript. — Cent. VI—89. Cit. Adlerz 1903 p. 151. Cit. Stenström 1896 a p. 10, 12. — Skåne 150, 296.

H. tenuistolonum Dahlst. — Sine descript. — Cent. VI—94, Västmanland, Kungsör 1891 leg. von Porat. Cent. VIII—7, Östergötland, Linköping 1890 legi ipse. — Skåne 183, 346, 347, 446.

H. vankivense Stenstr. — Stenström 1896 a p. 26. — Skåne, Vankiva 1890 leg. Stenstr. — Skåne 147.

H. venusticeps Dahlst. — Sine descript. — Småland, Gårdsby 1899 leg. Köhler, det. Dahlst. — Skåne 1, 14, 295, 343, Denmark 291.

H. venustum Dahlst. — Dahlstedt 1890 p. 30. — Exsic. Fasc. I—7, Östergötland, Linköping 1885—1889. Skåne, Malen 1913 leg. Segerström, det. Dahlst. — Skåne 21, 122, 134, 150, 280, 281, 312.

H. vulgare Tausch — Dahlstedt 1890 p. 27. — Exsic. Fasc. I—6, Småland, Växjö 1894 leg. Köhler, det. Dahlst. — Småland 33.

AMPHIAPOMICTIC HIERACIUM PILOSELLA ($2n=45$)

H. acrophylloides Dahlst. — Adlerz 1903 p. 159. — Cent. VI—98, Dalsland. Cent. XVI —44, Gotland. — Småland 462, Dalsland 269, 383, Uppland 326, 415.

H. acrophyllum Dahlst. — Dahlstedt 1890 p. 34. — Exsic. Fasc. IV—3, Östergötland 1890. — Västergötland 302, Dalsland 269, Södermanland 58, 91.

H. adpressum Norrl. — Norrlin 1888 p. 18. — Jämtland 174.

H. aerophylloides Dahlst. — Sine descript. — Cent. VI—98, Dahlstedt 1890. — Kungsör, Västmanland 1890 leg. von Porat, det. Dahlst. — Uppland 215, 256.

H. aerophyllum Dahlst. — Sine descript. — Exsic. Fasc. IV—3, Östergötland, Linköping 1890 legi ipse. Cent. VI—97, Östergötland, Linköping 1886 legi ipse. Cent. XVI—44, Gotland, Visby 1897. — Öland 119, Uppland 185, 186.

H. aeruginicolor Dahlst. — Dahlstedt 1890 p. 43. — Exsic. Fasc. II—2, 3. — Småland 521, Öland 511, Västergötland 303, Närke 266, Södermanland 503, Uppland 48.

H. atrocanum Omang = **paraleucum** Omang. — Omang 1936 p. 80. — Cent. XVIII—9. — Skåne 10, 132, Småland 275, 276.

H. atroëpilosum Adlerz — Adlerz 1903 p. 162. — Cent. XVI—52, Småland, Källvik 1902 leg. Adlerz. — Skåne 133, 137, 313, Småland 466, 469.

H. atrovillosulum Dahlst. — Dahlstedt 1890 p. 39. — Exsic. Fasc. I—13, Östergötland 1886. Exsic. Fasc. II—6, Östergötland 1886. Cent. VI—82, Östergötland 1890 legi ipse. — Skåne 133, 136, 310, 313, Småland 37, Östergötland 217, Dalsland 377, Värmland 389.

H. baliocephaloides Dahlst. — Sine descript. — Dalsland, Vibergsön leg. P. A. Larsson. — Dalsland 383.

H. baliocephalum Dahlst. — Omang 1936 p. 59. — Cent. VII—11, Dalsland 1894. Cent. XX—8, Värmland 1890. — Skåne 3, 162, Halland 355, Dalsland 269, 382, Södermanland 182, Värmland 234, 386, Västmanland 390, Uppland 205, 325.

H. barycephalum Dahlst. — Sine descript. — Bohuslän, Stenungsön 1906 leg. Liljeholm, det. Dahlst. Bohuslän, Bäve 1905 leg. Palmér, det. Dahlst. — Bohuslän 364, 365.

H. candescens Dahlst. — Dahlstedt 1890 p. 35. — Exsic. Fasc. I—16, Östergötland, Linköping. — Småland 465, 492.

H. coalescens Norrl. — Norrlin 1884 p. 80. — Herb. Pilos. Fenn., nr. 16. — Finland 63.

H. coloreum Dahlst. — Cent. VIII—2, Gotland, Fårö 1894 leg. K. Johansson. — Gotland 545.

H. crassescens Dahlst. — Dahlstedt 1890 p. 37. — Uppland, Djurgårdsfresk. 1903 leg. Dahlst. Uppland, Lagnö leg. Lindegren, det. Dahlst. — Småland 218, Uppland 27.

H. crassistolonum Dahlst. — Sine descript. — Östergötland, Linköping 1890 leg. Dahlst. — Småland 494, Östergötland 496.

H. drodantale Norrl. — Norrlin 1895 p. 23. — Närke, Tysslinge 1894, Exsic. Fasc. II—11, 23, leg. Adlerz. Småland, 1901 leg. Köhler, det. Dahlst. Västergötland 115, 477, Närke 271.

H. epipyrrhum Dahlst. — Sine descript. — Cent. XVI—18, Värmland 1897. Cent. XVI—17, Södermanland 1902. — Skåne 114, 314, 453, Halland 351, Småland 491, Östergötland 112, Västergötland 202, 203, Bohuslän 56, Närke 478, Södermanland 259, Uppland 419.

H. fimbrilliferum Norrl. — Norrlin 1888 p. 24. Omang 1934 p. 86. — Ångermanland 1885 leg. Holm. — Dalarna 165.

H. firmistolonum Dahlst. — Dahlstedt 1890 p. 26. — Exsic. Fasc. IV—2, Linköping 1890 legi ipse. Cent. XIII—11, Hort. Bergian. 1904 legi ipse. — Skåne 184, Blekinge 283, Gotland 181, Västergötland 305, Södermanland 91, Uppland 216, 220, Dalarna 395.

H. furviceps Dahlst. — Dahlstedt 1890 p. 44. — Exsic. Fasc. I—11, 12. Cent. XVI—8, Södermanland 1903. Cent. VI—65, Södermanland 1890. — Småland 521, Västergötland 300, Närke 479.

H. granulatum Dahlst. — Dahlstedt 1890 p. 22. — Exsic. Fasc. I—3, Östergötland 1886. Cent. XVIII—6, Östergötland 1890. — Småland 460, Södermanland 502.

H. hypochlorellum Dahlst. — Sine descript. — Cent. XVIII—12, Bohuslän, Stenung, Norum 1903 leg. Liljeholm. — Västergötland 4.

H. hypochlorum Stenstr. — Stenström 1896 a p. 13. — Cent. XVIII—12. — Västergötland 4, 301.

H. lactevirens Dahlst. — Adlerz 1903 p. 148. — Cent. VI—95, Östergötland. — Östergötland 89.

H. lamproglossum Dahlst. — Sine descript. — Cent. XX—20, Stockholm 1906. Cent. XX—21, Stockholm 1906. — Uppland 413.

H. lautumiarum Dahlst. — Sine descript. — Cent. VII—17, Stockholm, Östermalm 1894 legi ipse. — Uppland 407.

H. leptacinum Dahlst. — Omang 1936 p. 93. — Cent. XVI—7, Bohuslän 1903. — Skåne 114, 452, Halland 349, 350, 352, 353.

H. leptaloides Dahlst. — Sine descript. — Dalsland, Öjersbyn 1907 leg. Larsson. — Skåne 319, Blekinge 525, Halland 342, 490, Småland 463, Västergötland 471.

H. leptaleum Dahlst. — Sine descript. — Cent. XVI—15, Södermanland 1902 leg. Dahlst. Cent. XVI—7, Bohuslän 1903. — Skåne 319, 452, Blekinge 525, Halland 349, 350, 353, Småland 457, Uppland 409, 418.

H. leucodes Dahlst. — Dahlstedt 1890 p. 35—36. — Bohuslän 370.

H. leucopsaroides Dahlst. — Sine descript. — Södermanland, Taxinge sn, Näsby 1901 leg. Samuelsson, det. Dahlst. Strängnäs 1900 leg. Samuelsson, det. Dahlst. — Uppland 413.

H. leucopsarum Dahlst. — Dahlstedt 1890 p. 22. — Cent. VI—85, Östergötland 1890 leg. Dahlst. Cent. XX—15, Uppland 1906 leg. Dahlst. — Gotland 546, Uppland 220, 308, 406.

H. longiscapum Dahlst. — Sine descript. — Cent. XXIV—2, Dalarna 1907 leg. Samuelsson. — Uppland 189, 416.

H. multistolonum Dahlst. — Sine descript. — Cent. VII—11, Dalsland 1890. — Södermanland, Byringe 1900 leg. Köhler, det. Dahlst. — Småland 432, Värmland 387, Västmanland 482.

H. pachytrichellum Dahlst. — Sine descript. — Cent. XVI—31, Stockholm 1903, leg. Dahlst. — Västergötland 374.

H. pauxillum Dahlst. — Sine descript. — Cent. XX—2, Gotland 1892 leg. K. Johansson. — Gotland 41.

H. poliochlorum Dahlst. — Dahlstedt 1890 p. 25. — Småland 516, Öland 425, Södermanland 273, 433, 434.

H. polyadenium Dahlst. — Sine descript. — Cent. XVI—47, Södermanland 1902 leg. Dahlst. — Skåne 153, 309.

H. porati Dahlst. — Dahlstedt 1890 p. 45. — Exsic. Fasc. II—4, Västmanland 1889 leg. von Porat. Cent. VI—68, Västmanland 1892 leg. von Porat. — Skåne 127, Uppland 46, Gästrikland 396.

H. praepilans Dahlst. — Sine descript. — Cent. XVI—25, Småland 1902 leg. Köhler, det. Dahlst. — Småland 495.

H. semicrassescens Dahlst. — Sine descript. — Cent. VI—76, Småland, Jönköping 1892 leg. von Porat. Småland 218, 219, 274, 458, Västergötland 265.

H. stenophyton Dahlst. — Sine descript. — Cent. VIII—5, Östergötland, Linköping 1890 legi ipse. Cent. VI—96, Östergötland, Linköping legi ipse. — Småland 515, Östergötland 499, 500.

H. stereodes Dahlst. — Sine descript. — Cent. XX—23, Uppland, Solna 1906 leg. Dahlst. — Uppland 190.

H. subcrassescens Dahlst. — Dahlstedt 1890 p. 38. — Exsic. Fasc. II—5, Östergötland 1889. Cent. VI—74, Östergötland 1890 legi ipse. — Skåne 127, 337, 344, Småland 274, 411, Öland 431, Västergötland 375, Bohuslän 369, Uppland 207, Gästrikland 396.

H. subpraestans Dahlst. — Sine descript. — Ångermanland, Sollefteå 1907 leg. Rönnblad, det. Dahlst. — Dalarna 61.

H. svedalense Stenstr. — Stenström 1896 a p. 23. — Skåne, Svedala 1890 leg. Stenström. — Småland 518.

H. tenuilingua Norrl. — Norrlin 1884 p. 75. — Cent. XXIII—1, Medelpad, Ånge 1904 leg. Johansson. — Dalarna 392, 393, Medelpad 72, 75.

H. tenuistolonum DAHLST. — Sine descript. — Cent. VI—94, leg. VON PORAT. — Skåne 153, Södermanland 307.

H. trichadenium N. & P. — NÄGELI & PETER 1885 p. 165. — Gotland, Hessle 1881 leg. LÖNNROTH, det. DAHLST. — Gotland 542.

H. trichoscapoides DAHLST. — DAHLSTEDT 1890 p. 20. — Exsic. Fasc. I—2, 1886. — Cent. VI—87, Östergötland, Vreta 1891 legi ipse. Cent. VI—84, Östergötland, Linköping 1890 legi ipse. — Skåne 155, Blekinge 284, Småland 455, 516, Västergötland 476, Dalsland 270, 377, Södermanland 501, Uppland 322, 324.

H. trichoscapum N. & P. — NÄGELI & PETER 1885 p. 133. — Södermanland, Strängnäs 1900 leg. SAMUELSSON. — Uppland 321.

H. tynnophyton DAHLST. — Sine descript. — Småland, Oskarshamn 1904 leg. O. KÖHLER, det. DAHLST. — Småland 519, 520, Bohuslän 362, 367, 368.

H. vagans DAHLST. — Sine descript. — Cent. XVI—12, Uppland 1903 leg. DAHLST. Cent. XVI—11, Södermanland, Ornö 1902 leg. DAHLST. — Östergötland 178, Uppland 320.

AMPHIAPOMICTIC HIERACIUM PILOSELLA (2n=54)

H. acrophylloides DAHLST. — ADLERZ 1903 p. 159. — Cent. VI—98, Dalsland. Cent. XVI —44, Gotland. — Uppland 414.

H. belfragei MAGNUSSON. — Sine descript. — Ångermanland, Härnösand 1908 leg. JOHNSSON, det. DAHLST. Hälsingland, Söderhamn 1892 leg. MAGNUSSON. — Ångermanland 97, 98.

H. longiscapum DAHLST. — Sine descript. — Cent. XXIV—2, Dalarna 1907 leg. SAMUELSSON. Dalarna 1902 leg. SAMUELSSON, det. DAHLST. — Uppland 414, 415, Dalarna 166.

H. melanochroum DAHLST. — Sine descript. — Cent. XVI—4, Värmland 1898 leg. FRÖDING. Småland 1901, leg. KÖHLER, det. DAHLST. — Blekinge 528.

H. prasaeum DAHLST. — Sine descript. — Cent. XVI—29, Uppland 1903 leg. DAHLST. — Västergötland 304.

AMPHIAPOMICTIC HIERACIUM PILOSELLA (2n=63)

H. praepilans DAHLST. — Sine descript. — Cent. XVI—25, Småland, Oskarshamn 1902 leg. KÖHLER. Västergötland 1898 leg. ANDERSSON, det. DAHLST. — Skåne 131, 531.

AMPHIAPOMICTIC HIERACIUM PILOSELLA WITH SOME DISTINCT CHARACTERS OF H. AURICULA (2n=36)

H. suivalense NORRL. — NORRLIN 1884 p. 84. — DAHLSTEDT 1890 p. 41. — Cent. VIII—1, Östergötland 1895 leg. DAHLSTEDT. Exsic. Fasc. I—14, Östergötland 1889. — Östergötland 497, Västergötland 263, 264, Södermanland 172, Västmanland 391, Austria 248, 249.

H. vagans DAHLST. — Sine descript. — Cent. VVI—12, Uppland 1903 leg. DAHLST., Cent. XVI—11, Södermanland, Ornö 1902 leg. DAHLST. — Småland 493.

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Morphology and Embryology of Scaevola frutescens K. and Affinities of the Family Goodeniaceae

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ABSTRACT

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The morphology and embryology of *Scaevola frutescens* K. have been investigated and the data collated with the presumed allies of the family Goodeniaceae. *S. frutescens* is a shrub with cymose inflorescence. Flowers are pedunculate, bisexual, and zygomorphic. The calyx and corolla are five each and are fused. The petal lobes are equal and spread like a fan. There are five epipetalous stamens. The ovary is inferior, bilocular with one ovule in each locule.

The ontogeny of anther wall follows the Dicotyledonous type. The middle layers are ephemeral and tapetum is of the secretory type. The microspore tetrads are tetrahedral. Pollen grains are triporate and are shed at the two-celled stage. The ovule is anatropous, unitegmic, and tenuinucellate. There is prominent hypostase. The innermost layer of the integument forms a well-developed endothelium. The archesporial cell functions directly as the megaspore mother cell. The development of the embryo-sac conforms to the Polygonum type. Double fertilization occurs. The endosperm is cellular, the embryogeny follows the Solanad type.

The morphological and embryological features indicate that the Goodeniaceae should be placed in the separate order Goodeniales very close to the Campanulales. Goodeniaceae differ from the families centred around the Campanulales in many important features such as the absence of haustoria, the presence of indusium, the presence of hypostase, the persistence of both the inner and outer epidermes of the seed coat to form the testa; endothelium although differentiated not enclosing the extremities of the embryo sac, and the presence of calcium oxalate crystals in the seed coat.

INTRODUCTION

The Goodeniaceae, largely an Australian family, consists of herbs and shrubs with about 14 genera and 300 species (VAN STEENIS 1958). *Scaevola* with 80 species, 60 restricted to Australia and the rest to Polynesia and tropical coasts, is specially interesting since it has zygomorphic flowers and an indusium covering the stigma. RILEY (1963) observed that throughout South Africa, *Scaevola* is the only genus representing the family Goodeniaceae.

Scaevola frutescens, a shrub, sometimes becoming an undersized tree, grows at an altitude of 400 to 500 metres, and is distributed in Ceylon, South India, Mauritius, Madagascar, tropical America and Africa (BRIZICKY 1966). However, the embryological data on the genus are meagre and that of the family are not only scarce but also doubtful being restricted to only two genera. Further, the affinities of the family are disputed and in recent years taxonomists have even set up a separate order, Goodeniales, to accomodate this family (HUTCHINSON 1959). The present investigation on *Scaevola frutescens* was, therefore, undertaken to furnish detailed embryological data and to evaluate the affinities of the Goodeniaceae on a comparative basis.

MATERIAL AND METHODS

The material of *Scaevola frutescens* was collected by one of us (U.M.) from the botanical gardens, the University of Peradeniya, Ceylon in June, 1969. Buds, flowers, and fruits of different developmental stages were fixed in F.A.A. Usual methods of dehydration, infiltration, and embedding were followed. A few fruits, after scarification and prior to dehydration were treated with picric acid for about 10 days, washed in water, and immersed in a solution of lithium carbonate. Later they were dehydrated in the butyl alcohol series. The sections were cut between 5 and 15 microns thick and stained either with safranin-fast green or iron-alum haematoxylin. Acetocarmine squashes of the pollen mother cells were also observed.

OBSERVATIONS

EXTERNAL MORPHOLOGY

Scaevola frutescens is a shrub with simple, spirally arranged leaves. The inflorescence is a cyme (Fig. 1 A) with pedunculate, bisexual and zygomorphic flowers (Fig. 1 B—D). The calyx is gamosepalous and is covered with unicellular hairs. The corolla is gamopetalous, the petals spread like the fingers of an open hand. The lobes are provided with very thin membranous wings which are equal and sharply folded inward in bud. The stamens are five in number, alternating with the petals. The anthers are basifixed, introrse and have a long filament (Fig. 1 E, F). The gynoecium is bicarpellary, syncarpous, with a slightly lobed, hairy stigma and is subtended by an indusium (Fig. 1 G—I). The style is solid and hairy at the base. The ovary is inferior, bilocular with one ovule in each loculus. The fruit is a drupe (Fig. 1 J—L).

MICROSPORANGIUM

The pre-archesporial anther is oval in cross section and consists of parenchymatous cells with a well-developed epidermis (Fig. 2 A, C). A single large hypodermal archesporial cell, with dense cytoplasm and prominent nucleus differentiates (Fig. 2 B, D, Table 1). As the anther develops it divides periclinally to form an outer primary parietal cell (*ppl*) and an inner primary sporogenous cell (*sp*). The primary sporogenous cell undergoes a few mitotic divisions along different planes and forms the sporogenous tissue. The primary parietal layer divides periclinally resulting in secondary parietal layers (spl_1 and spl_2; Fig. 2 E, F). The inner one of the two parietal layers (spl_2) develops into the tapetum whereas the outer one (spl_1) divides periclinally to form the middle layer and the endothecium (Fig. 2 F). The cells of the middle layer divide again resulting in two layers (Fig. 2 G). Thus in the mature anther there are 5 wall layers including the epidermis (Fig. 2 H). Table 1 summarizes the ontogeny of the anther wall but does not show the development of the tapetum towards the connective side. The development of the anther wall thus follows the Dicotyledonous type (DAVIS 1966). The epidermal cells are small and undergo anticlinal divisions to keep pace with the developing anther. The endothecium at maturity consists of large cells with radial fibrous thickenings and possess stellate crystals which disappear at maturity (Fig. 2 J, K). A few cells of the connective adjacent to the endothecium also develop thickenings.

The cells of the two middle layers degenerate when the microspore mother cells are still in prophase (Fig. 2 I). The innermost layer of the anther wall is the tapetum and its cells in early stages are

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Fig. 1. *Scaevola frutescens*. — A: Part of cymose inflorescence. — B, C: Buds of various sizes. — D: Flower with indusium surronding the stigma. — E, F: Dorsal and ventral view of the stamen. — G, H: Face and lateral view of the carpel. — I: Longisection of the stigma showing indusium. — J—L: Fruits of various ages. — A—L ×2.

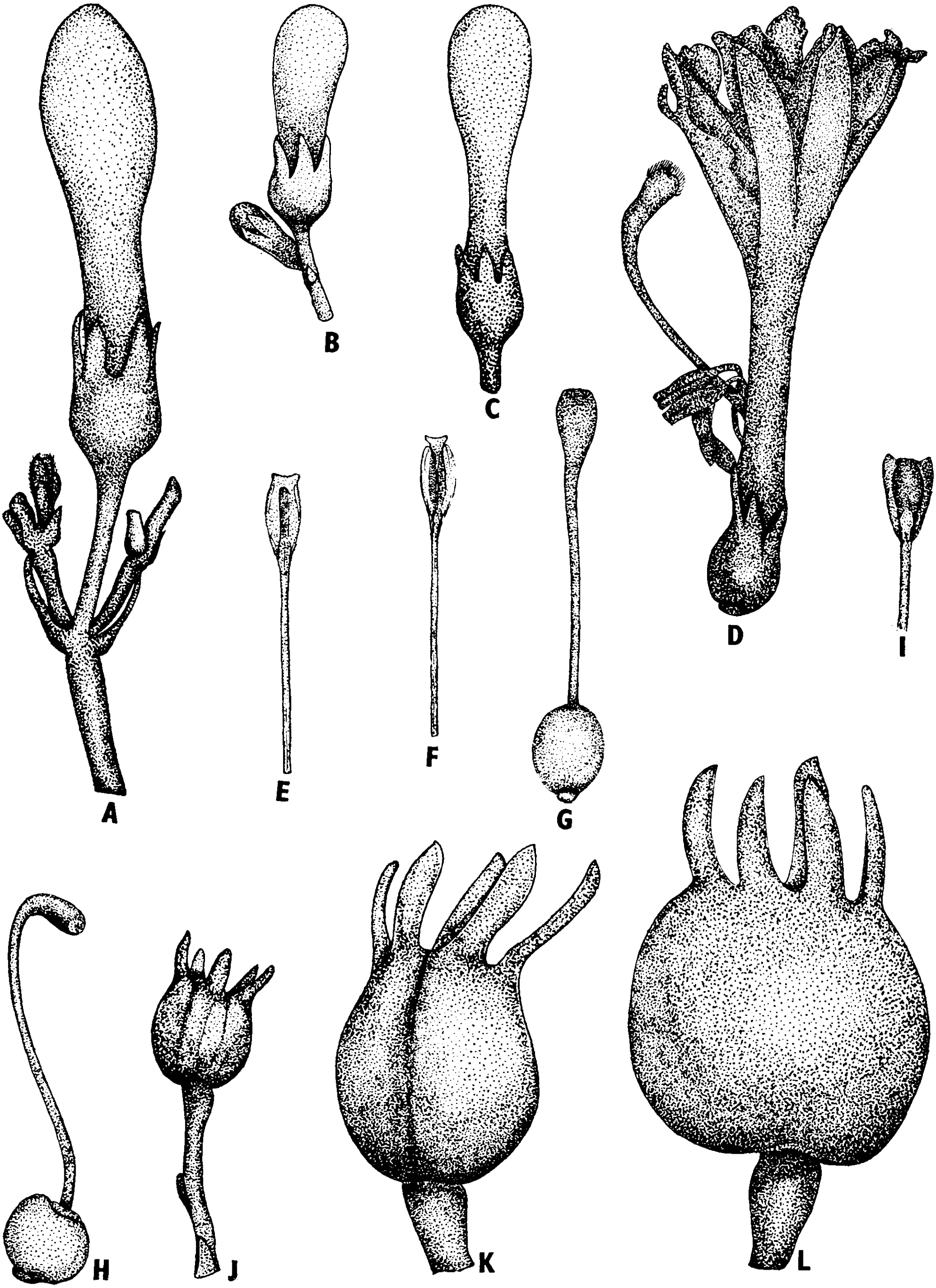
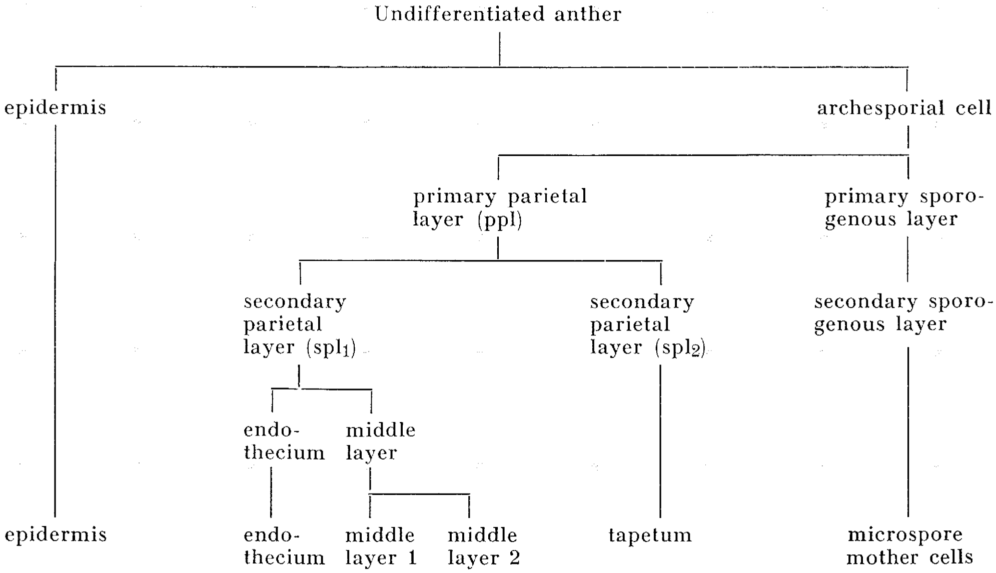


Fig. 1.

Table 1. Ontogeny of the anther in *Scaevola frutescens.*



uninucleate, with dense cytoplasm. Later the tapetal cells enlarge considerably, become vacuolate and binucleate (Fig. 2 L, M). Nuclear divisions and fusion in the tapetal nuclei are common resulting in polyploid nuclei (Fig. 2 N, O). The tapetum has a dual origin, being partly derived from the wall layers on the abaxial side and partly from the cells of the connective on the adaxial side.

MICROSPOROGENESIS AND MALE GAMETOPHYTE

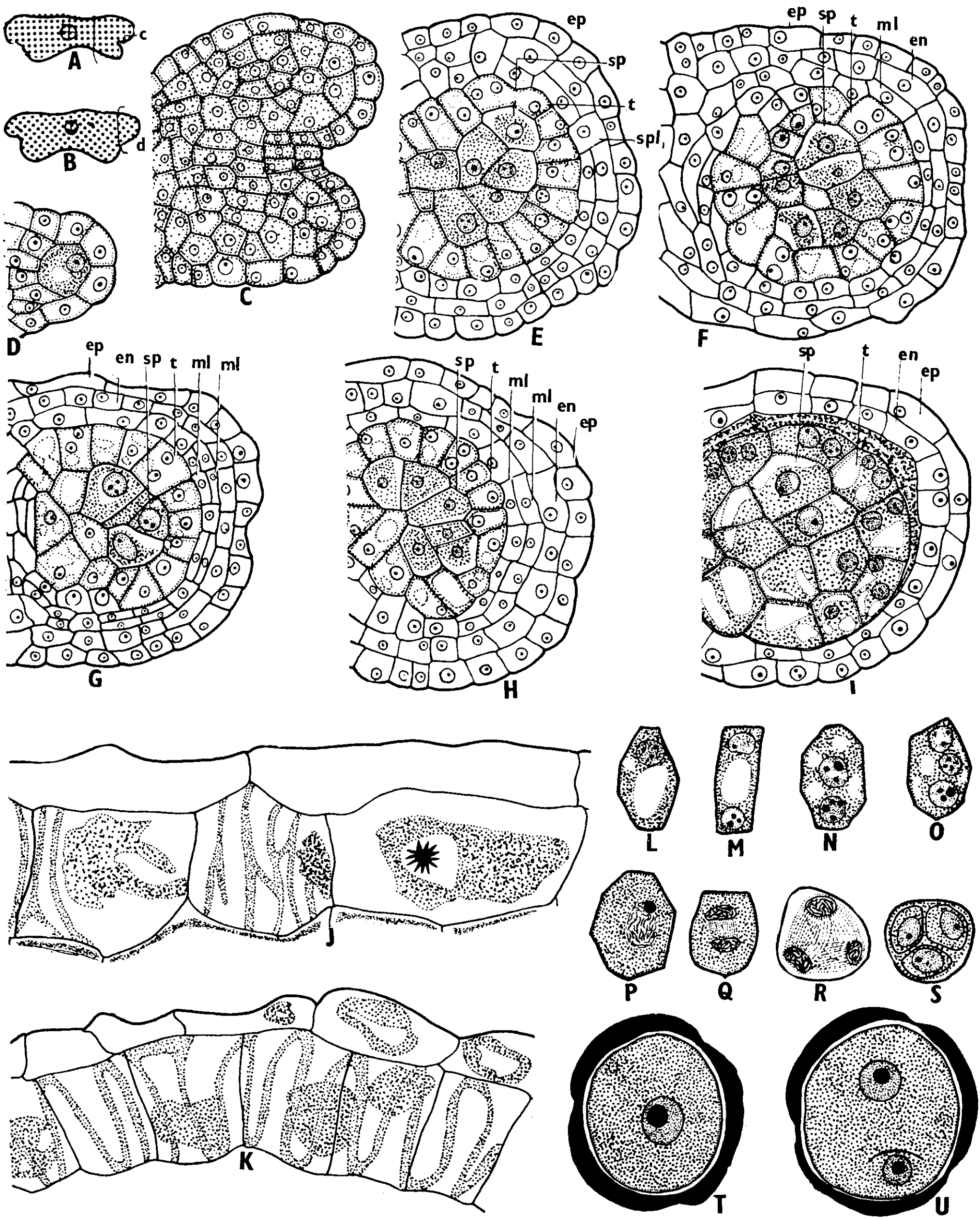
Meiosis in the microspore mother cells is of the simultaneous type resulting in tetrahedral tetrads (Fig. 2 P—S). The pollen grains are triporate with a thick exine and thin intine (Fig. 2 T, U). The microspore nucleus divides to form a large vegetative and a small generative cell. The pollen grains are shed at the 2-celled stage (Fig. 2 U).

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

There are two anatropous, unitegmic, and tenuinucellate ovules. The ovular primordium arises from the placenta as a tiny protuberance which soon begins to curve. The integument appears soon after the differentiation of the archesporium, and the ovule becomes completely anatropous at about the megaspore tetrad stage. During this stage cells of the innermost layer of the integument become transversely elongated, envelope the nucellus and act as the integumentary tapetum.

At the 2- or 4-nucleate stage of the em-

Fig. 2. *Scaevola frutescens* (en, endothecium; ep, epidermis; ml, middle layer; sp, sporogenous cell; spl_1, secondary parietal layer 1; t, tapetum). — A, B: Transverse section of anthers at different stages of development. — C, D: Enlarged portions marked *c* and *d* in A and B to show undifferentiated anther and hypodermal archesporial cell respectively. — E: Portion of an anther showing periclinal divisions in secondary parietal layer 1. — F: Part of an anther lobe showing four wall layers. — G, H: Portion



of an anther showing some of the cells of the middle layer in division forming two layers. — I: Anther lobe showing degeneration of middle layers, binucleate tapetum, and sporogenous cells. — J, K: Portion of anther showing fibrous endothecium. — L—O: Tapetal cells at various stages of development. — P—R: Meiosis in microspore mother cells. — S: Tetrahedral tetrad. — T, U: Uni- and binucleate pollen grains. — A, B: ×56, C—I ×350, J—U ×513.

bryo-sac, a few cells of the nucellus lying immediately below the gametophyte become densely cytoplasmic, show prominent nuclei and constitute the hypostase. During the globular stage of the pro-embryo the cells of the hypostase are highly stretched.

A single hypodermal archesporial cell (Fig. 3 A) functions direct as the megaspore mother cell (Fig. 3 B). The latter undergoes meiosis resulting in a linear tetrad of megaspores (Fig. 3 C). The three micropylar megaspores degenerate and the chalazal one functions. The functional megaspore enlarges and its nucleus divides to form two-, four-, and eight-nucleate embryo-sacs of the Polygonum type (Fig. 3 D—G).

The mature embryo-sac consists of an egg, two synergids, two polar nuclei and three antipodal cells (Fig. 3 G). The synergids and antipodal cells degenerate soon after fertilization (Fig. 3 H, I).

ENDOSPERM AND EMBRYOGENY

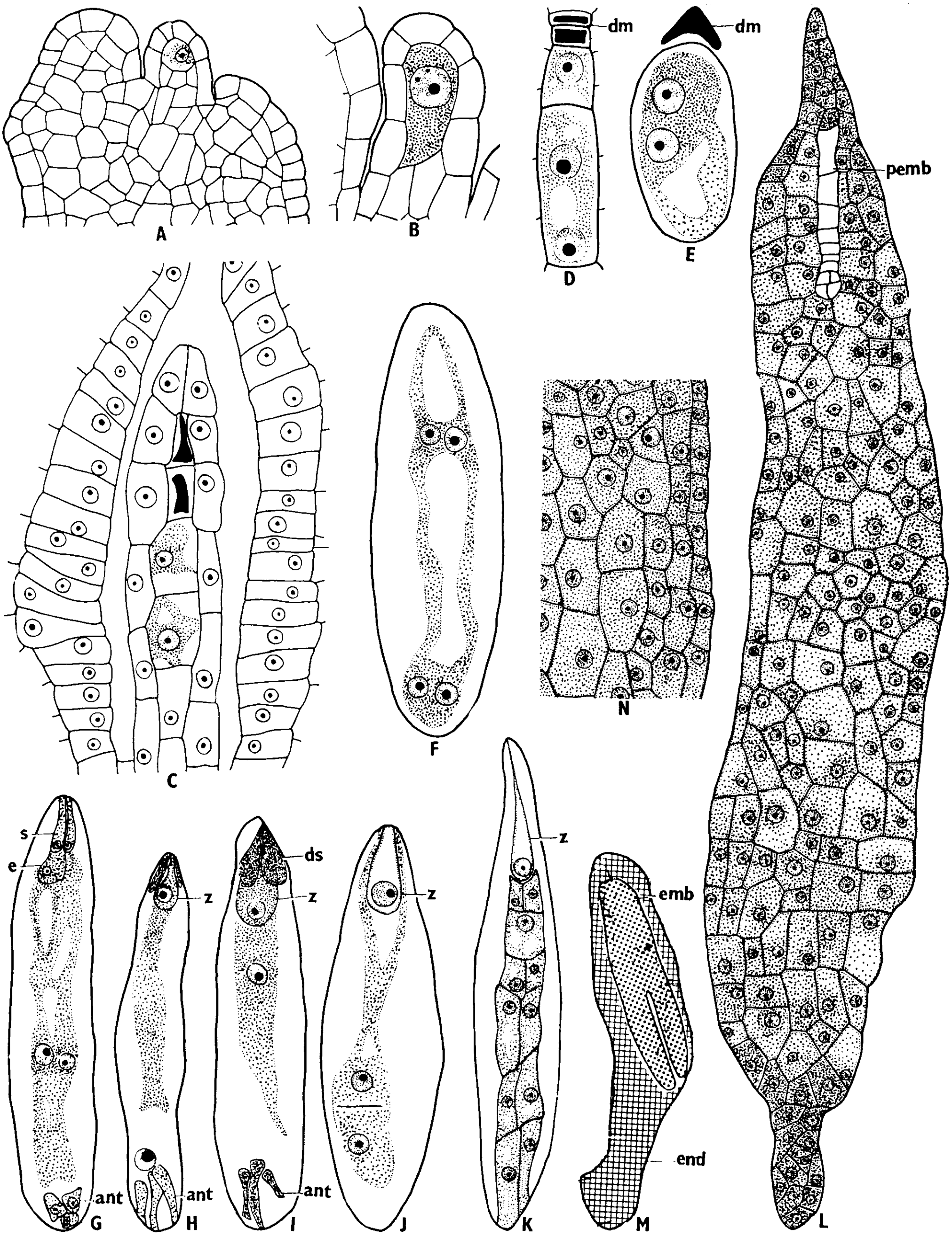
The primary endosperm nucleus divides before the zygote and the division is followed by a transverse wall resulting in a large micropylar chamber and a small chalazal one (Fig. 3 J). Further divisions in both the chambers occur in various planes (Fig. 3 K). The development of the endosperm is very rapid and occupies almost the whole of the embryo-sac (Fig. 3 L). At the micropylar and chalazal ends the cells of the endosperm stain deeply and even form pouch-like structures (Fig. 3 L). Later the cells of this pouch degenerate. During the globular and dicotyledonous embryo stages the cells of the endosperm are irregular with prominent nuclei and are devoid of any reserve food material (Fig. 3 M, N).

There is a considerable time lag between fertilization and the division of the zygote. During this time the zygote elongates (Fig. 4 A). At about the 12-celled stage of the endosperm the zygote divides transversely resulting in a small terminal cell *ca* and a large basal cell *cb* (Fig. 4 B). The basal cell divides and re-divides to form a many-celled suspensor (Fig. 4 C, D). The terminal cell undergoes transverse division. This then divides by vertical walls oriented at right angles to each other to form the octants (Fig. 4 D). Subsequent divisions in the octant give rise to a mass of cells and the pro-embryo becomes large and globular in shape (Fig. 4 E—G). The suspensor starts degenerating from the top (Fig. 4 F, G). The mature embryo is large, straight, and has two cotyledons (Fig. 4 H). The embryogeny follows the Solanad type (MAHESHWARI 1950).

TESTA

At the megaspore tetrad stage the integument comprises 13 to 15 layers of cells, many of them containing crystals of calcium oxalate (Fig. 5 A, D). The innermost layer of the testa differentiates into the endothelium. The testa at the two- or four-nucleate embryo-sac stage comprises 15—18 layers of cells (Fig. 5 E, F) while at the mature gametophyte stage it becomes 18—20-layered (Fig. 5 B, G). At the dicotyledonous stage of the embryo the seed coat is 7—14-layered, and is comprised mainly of thin-walled vacuolate cells with a few crystals (Fig. 5 C, H).

Fig. 3. *Scaevola frutescens* (ant, antipodal cells; e, egg; dm, degenerating megaspore; ds, degenerating synergids; emb, embryo; end, endosperm; pemb, proembryo; s, synergids; z, zygote). — A, B: Longitudinal section of the nucellus showing hypodermal archesporial initial and megaspore mother cell. — C: Linear tetrad of megaspores, the nonfunctional megaspores degenerate in basipetal manner. The endothelium is well developed. — D—F: Two- and four-nucleate embryo-sacs. — G: Mature embryo-sac. — H, I: Embryo-sac showing zygote, degenerated synergid and antipodal cells. The primary endosperm nucleus lies near the antipodal cells in H. — J: Two-celled endosperm. — K, L: Multi-



celled endosperm; note the 'pouch' at both the ends and the cells at micropylar and chalazal ends stain deeply and are tapering. — M, N: Endosperm at Dicotyledonous embryo stage; in N a portion of the endosperm is enlarged. — A—F: ×550, G—I ×250, J ×385, K, L ×130, M ×22, N ×260.

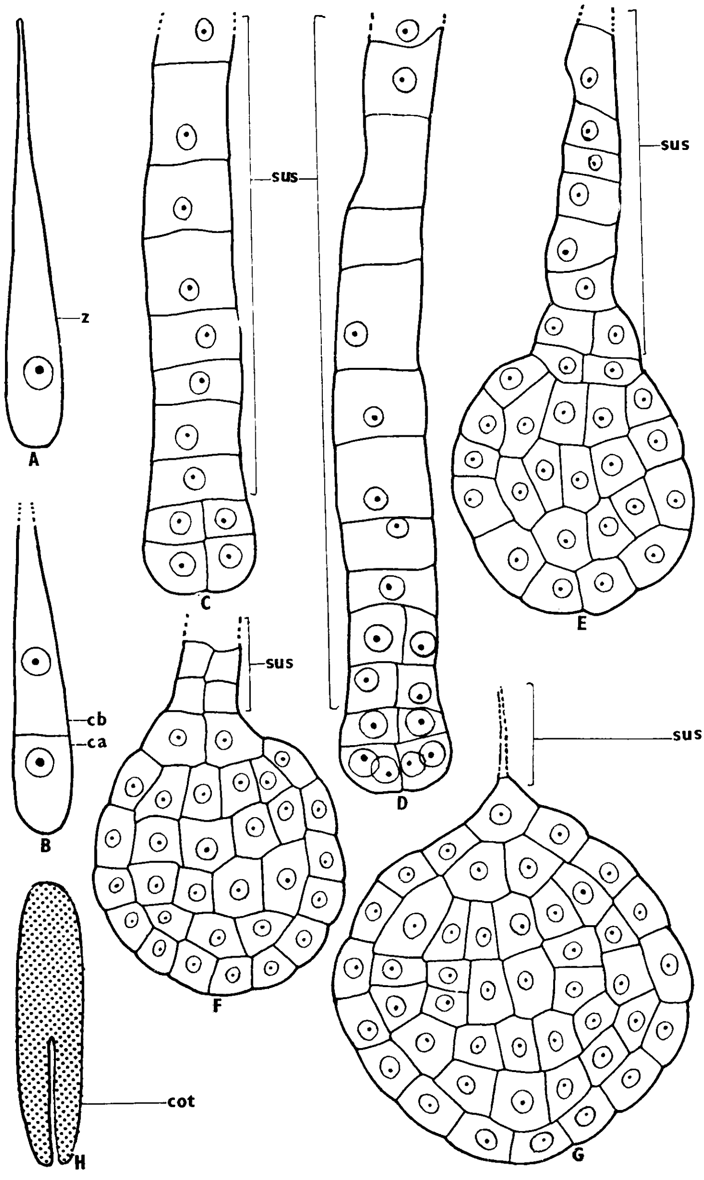
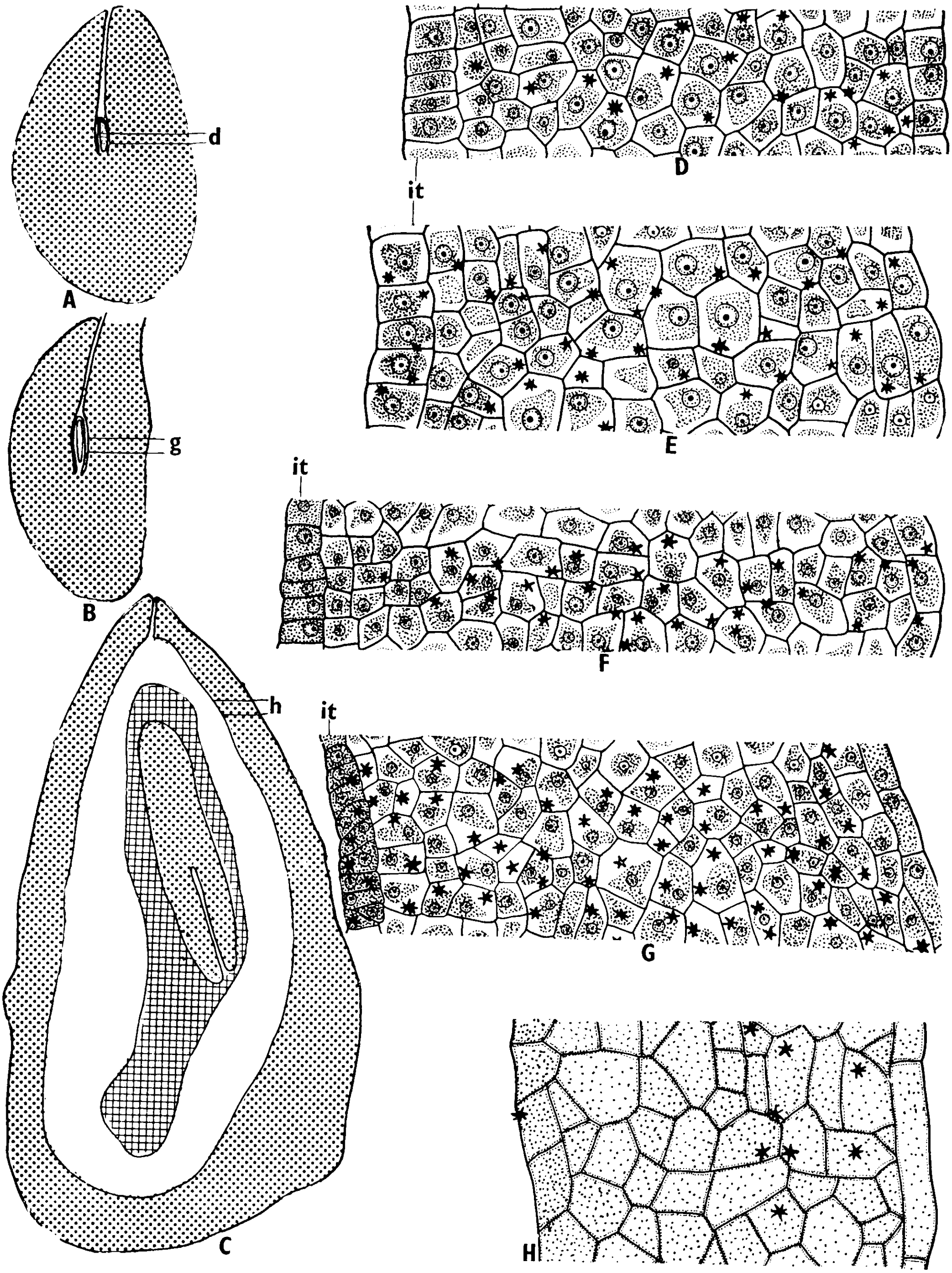


Fig. 4. *Scaevola frutescens* (cot, cotyledon; sus, suspensor; z, zygote). — A, B: Zygote and two-celled proembryo. — C—G: Stages leading to the formation of a globular embryo. — H: Dicotyledonous embryo. — A, B ×375, C—G ×770, H ×45.

Fig. 5. *Scaevola frutescens* (it, endothelium). — A—C: Longitudinal sections of the ovules (diagrammatic). — D: Portion marked *d* in A enlarged to indicate testa at tetrad stage. There are 13 to 15 layers of cells which contain calcium oxalate crystals. — E, F: Testa at two- and four-nucleate embryo-sac stage. — G: Enlarged view of the portion marked *g* in B to show the testa at mature embryo-sac stage. The outer and inner



epidermes persist and the latter forms the endothelium. — H: Magnified view of the portion *h* in C showing the seed coat at the dicotyledonous stage of the embryo. The outer epidermis is tangentially elongated. — A, B ×40, C ×30, D—F ×513, G, H ×350.

Table 2. Comparative embryological data of Goodeniaceae, Brunoniaceae, Campanulaceae, Lobeliaceae and Stylidiaceae.

Character	Goodeniaceae	Brunoniaceae	Campanulaceae	Lobeliaceae	Stylidiaceae
Indusium	Present	Absent	Absent	Absent	Absent
Endothecium	Fibrous, calcium oxalate crystals present	Not known	Fibrous crystals absent	Fibrous, crystals absent	Fibrous, crystals absent
Middle layer(s)	1 or 2 layers, ephemeral, calcium oxalate crystals present	Not known	1 layer, ephemeral, crystals absent	1 layer, ephemeral, crystals absent	1 layer, ephemeral, crystals absent
Tapetal cells	Binucleate, polyploid but finally fuse to form uninucleate	Not known	Binucleate, polyploid	Binucleate, polyploid	Binucleate, polyploid
Microspore tetrads	Tetrahedral or isobilateral	Not known	Usually tetrahedral sometimes isobilateral	Tetrahedral	Tetrahedral
Shedding stage of pollen	2-celled, occasionally tetrads	Not known	3-celled rarely 2-celled	2-celled	3-celled
Nectary	Absent	Not known	Present	Present	Present
Ovule	Anatropous, unitegmic, tenuinucellar, integumentary vascular bundle may or may not be present	Anatropous, unitegmic, tenuinucellar, integumentary vascular bundle absent	Anatropous, unitegmic, tenuinucellar, integumentary vascular bundle absent	Anatropous, unitegmic, tenuinucellar, integumentary vascular bundle absent	Anatropous, unitegmic, tenuinucellar, integumentary vascular bundle absent

Hypostase	Present	Absent	Absent	Absent	Absent
Embryo-sac	Polygonum type, starch absent	Polygonum type	Polygonum type, starch present	Polygonum type, starch present	Polygonum type, starch present
Antipodal cells	3, uninucleate and ephemeral	3, uninucleate and ephemeral	3, uninucleate and ephemeral	3, uninucleate and ephemeral	3, uninucleate and persist after fertilization
Endosperm development	Cellular*	Not known	Cellular	Cellular	Cellular
Endosperm haustoria	Absent	Not known	Well developed micropylar and chalazal present, may be 1-, 2- or 4-celled	Both micropylar and chalazal well developed	Micropylar haustorium more aggressive than chalazal
Embryogeny	Solanad type	Not known but multinucleate suspensor haustorium present	Solanad type	Solanad type	Solanad type
Polyembryony	Absent	Not known	Present	Present	Absent
Testa	7—14 layers, both the outer and inner epidermes persist	Not known	1—4 layers, only outer epidermis persists	1—4 layers, only outer epidermis persists	1—4 layers, only outer epidermis persists

* The report of nuclear endosperm in *Dampiera stricta* (BROUGH 1927) needs confirmation.

DISCUSSION

The available data on the morphology and embryology of the family Goodeniaceae are discussed in the light of the present work on *Scaevola frutescens*.

MICROSPORANGIUM, MICROSPOROGENESIS AND MALE GAMETOPHYTE

The present detailed investigation on the development of the anther wall in *Scaevola frutescens* is the first report for this family. It is revealed that the endothecium and the two middle layers are sister layers while the tapetum is derived direct from the secondary parietal layer II. Thus the wall of the microsporangium is made up of 5 layers and the development conforms to the dicotyledonous type (DAVIS 1966). In *Dampiera stricta,* however, only one middle layer is present and the wall of the microsporangium is composed of four layers (BROUGH 1927). In *S. frutescens,* the endothecium develops the usual fibrous thickenings, the middle layers are ephemeral and the cells of the tapetum become binucleate. According to BILLINGS (1901) in *S. lobelia* the uninucleate condition of the tapetal cells is restored by fusion of the nuclei. Crystalliferous idioblasts found in the endothecium of S. *frutescens* have not been reported for any other genus of this family. The pollen grains are shed at the two-celled stage as in other genera of the family. *Leschenaultia* is an exception in that they are shed in permanent tetrads (MARTIN & PEACOCK 1959).

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

SCHNARF (1931) reported bitegmic ovules in Goodeniaceae. In contrast to this the unitegmic condition is met with in *Scaevola attenuata, S. koenigii* (BILLINGS 1901), *Dampiera stricta* (BROUGH 1927) and *S. frutescens* (present work). BILLINGS (1901) further reported that the vascular bundle runs completely around the flattened ovule, thereby indicating integumentary vascular bundles. In *S. frutescens* no such integumentary vascular bundles were seen, and the supply ended at the chalazal end of the ovule. The development of the embryo-sac conforms to the Polygonum type. According to BROUGH (1927), in *Dampiera stricta* the synergids are elongated and devoid of filiform apparatus; the antipodal cells remain active after fertilization and even function as a medium for passing nourishment from the chalazal end of the ovule into the embryo-sac. In *S. frutescens,* however, the antipodal cells degenerate before fertilization and the synergids although elongate are devoid of filiform apparatus. HAVILAND (1914) observed cross-pollination and porogamy in *Goodenia.* In *S. frutescens* the entry of the pollen tube is also porogamous.

ENDOSPERM AND EMBRYOGENY

The primary endosperm nucleus in *Scaevola frutescens* divides transversely followed by wall formation. The endosperm development is cellular in contrast to the nuclear endosperm in *Dampiera stricta* (BROUGH 1927). ROSEN (1937) reported cellular endosperm in *Scaevola* and the present work confirms his findings. BILLINGS (1901) observed the presence of a weakly developed micropylar haustorium in *Scaevola attenuata* and *S. koenigii.* Although in *S. frutescens* the endosperm cells at the micropylar and chalazal ends were deeply stained, their nuclei did not show hypertrophy and the tissue centred around these deeply stained cells was healthy. It is therefore concluded that these cells do not act as haustoria (present work). The embryogeny in *S. frutescens,* as in *Dampiera stricta* (BROUGH 1927), is of the Solanad type.

TAXONOMIC CONSIDERATIONS

HUTCHINSON (1959) placed Goodeniaceae in the order Goodeniales along with Brunoniaceae and Stylidiaceae. MANNING

(1965) also placed Goodeniaceae in the order Goodeniales. GUNDERSEN (1950) and TAKHTAJAN (1959) placed Goodeniaceae in Campanulales.

Table 2 enumerates the embryological characters of the families Goodeniaceae, Brunoniaceae, Campanulaceae, Lobeliaceae and Stylidiaceae (for the literature see BENTHAM 1869, HOOKER 1894, BROUGH 1927, CORE 1955, DAVIS 1966, ENGLER 1964, KAUSIK & SUBRAMANYAM 1946, 1947, ROSEN 1937, 1946, 1949, SOUÈGES 1938, SUBRAMANYAM 1951; and present work).

Goodeniaceae differs from Campanulaceae, Lobeliaceae and Stylidiaceae in the shedding-stage of pollen, absence of nectary, presence of hypostase, absence of endosperm haustoria, presence of indusium, absence of polyembryony, and the presence of calcium oxalate crystals in seed coat and pericarp. Brunoniaceae differs from Goodeniaceae in the presence of a multinucleate suspensor haustorium of the embryo.

On comparative embryological data it is concluded that Goodeniaceae should be placed in a separate order Goodeniales very close to the Campanulales.

MELVILLE (1969) on the morphological and floral anatomical characters of *Emblingia calceoliflora* indicated a close affinity with the Goodeniaceae and in particular with *Scaevola*. This has been further supported on anatomical grounds by METCALFE (1969). LEINS (1969), however, pointed out that the presence of bitegmic and crassinucellate ovules in *Emblingia* does not favour relationship between this genus and Goodeniaceae, since the latter have genera with unitegmic and tenuinucellate ovules. ERDTMAN (1969) also stressed the point that the large three- or four-colporate pollen grains of *Emblingia* show no resemblance to *Scaevola*. METCALFE (1969) wisely remarked "In dealing with problems of this kind, however, it would be wise to treat our conclusions as provisional until our picture of the anatomy of dicotyledons as a whole is more complete." The real affinities of *Emblingia* must await a detailed embryological investigation of this taxon.

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Favargera and Gentianodes, Two New Genera of Alpine Gentianaceae

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ABSTRACT

LÖVE, Á. & LÖVE, D. 1972. Favargera and Gentianodes, two new genera of alpine Gentianaceae. — Bot. Notiser 125: 255—258.

The two new genera *Favargera* and *Gentianodes* are validated to accomodate the alpine representatives of the section *Frigida* KUSNETZOV of the collective genus *Gentiana*. They are typified by the species *G. froelichii* JAN and *G. frigida* HAENKE respectively. In addition to morphological characteristics, these new genera are clearly distinguished by their basic chromosome numbers x=7 and 6. *Favargera* is a monotypic genus endemic to the eastern Alps, whereas forty-one species are transferred to the genus *Gentianodes*. These taxa are mainly from the Himalayas and mountains of eastern Asia, although a few reach westward to the European mountains or eastward to alpine regions of western North America.

When studying the cytotaxonomy of the Slovenian flora in general and that of the endemics of the eastern Alps in particular, we observed a rare *Gentiana,* which traditionally has been placed within the section *Frigida.* It was originally collected by the Slovenian botanist HLADNIK (cf. RECHFELD 1849), on the summit of Planjava in the Kamnian Alps (Steinalpen) and given the name *Gentiana angustifolia* VILL. by REICHENBACH (1830—32), who was unaware of the real identity of the species described by VILLARS (1779). Later in the same manual it was described as *Gentiana Froelichii* JAN. Some authors proposed other names which were either homonyms or synonyms or both, but all agreed that the species is related to *G. frigida,* to which it is superficially similar, although it differs distinctly in having the anthers united into a pipe surrounding the almost one centimeter long style, and in having 3-nerved basal leaves and polypterous seeds, whereas *G. frigida* and its relatives have free anthers, very short or no style, 1-nerved basal leaves and seeds without wings. Only a single Himalayan species of the *Frigida* section of KUSNETZOV (1898) has polypterous seeds, as will be mentioned below.

Although the monographer KUSNETZOV (1898) included this Alpique species in his section *Frigida,* he placed it in a tribe of its own because of the morphological distinctions of the seeds and style. PAWLOWSKI (1970) found it to be so distinct as to warrant its separation as the subsection *Froelichiella* PAWL. Further evidence for its distinction has recently been presented by FAVARGER & HUYNH (in LÖVE & SOLBRIG 1964), FAVARGER (1965), and LOVKA, SUŠNIK, LÖVE & LÖVE (in LÖVE 1971, 1972), who showed it to be a hexaploid with 2n=42 chromosomes and the basic number x=7, whereas all other representatives of the section *Frigida* are characterized by the basic number x=6. In the Gentianaceae differences in basic chromosome numbers are a strong indication of generic status (D. LÖVE 1953;

LÖVE & LÖVE 1956, 1961; TOYOKUNI 1961, 1963, 1965). Since even the restricted remaining section *Frigida* differs in this respect from *Gentiana* s. str. and from other genera recently accepted as distinct from it, it is our opinion that there is a need to recognize two new genera for what has previously been regarded as the section *Frigida* of the collective genus *Gentiana*. Therefore, we propose for the subsection *Froelichiella* of PAWLOWSKI (1970) the new generic name *Favargera* LÖVE & LÖVE, gen. nov., based on *Gentiana* sectio *Frigida* group or tribe *G. Froelichii* KUSNETZOV, in Acta Horti Petrop. 15, 2 (1898), p. 289.

Planta perennis, 5—10 cm alta. *Caulis* humilis. *Folia* rosularia canaliculata, lanceolata, obtusa, trinervia, nervo medio crassiore. *Flores* solitarii (rarius 2). *Calyx* campanulatus, viridis, membranaceus laciniis lineari-filiformibus vel lanceolatis, crispulis recurvis. *Corolla* campanulata vel campanulato-infundibuliformis, caelestina concolor impunctata. *Antherae* connatae. *Stigmata* distincta, linearia, demum revoluta. *Testa* longitudinaliter lamellis crispis alaeformibus obtecta. *Chromosomata* x=7.

The new genus is named after Professor Dr. CLAUDE FAVARGER of Neuchâtel, an ardent student of the Alpique flora. Its type species and only species is *Favargera froelichii* (JAN) LÖVE & LÖVE, comb. nov., based on *Gentiana froelichii* JAN in REICHENBACH, Fl. Germ. excurs., Add. (1832), p. 865. It is an endemic of the Karavanken and the Kamnian Alps of Austria and Slovenia and of the Venetian Alps of Italy (cf. DERGANG 1903; PAWLOWSKI 1970; Fig. 1).

As mentioned above, only one other species of the *Frigida* group, the Himalayan *Gentiana phyllocalyx* C. B. CLARKE, has polypterous seeds, and KUSNETZOW (l.c.) included it in another monotypic group or tribe. Although this characteristic may indicate that this species could belong to the new genus, we hesitate to draw that conclusion and to propose its transfer because we have been unable to study it in detail and do not know its chromosome number. We therefore think it is wiser to leave it, at least for the time being, with the other *Frigidae* in the genus to be proposed below, without a formal transfer.

The remaining species of the *Frigida* section form a morphologically and cytologically well defined group for which we propose the new generic name *Gentianodes* LÖVE & LÖVE, gen. nov., based on *Gentiana* sectio *Frigida* KUSNETZOV, in Acta Horti Petrop. 13, 4 (1893), p. 61, excl. *G. froelichii*.

Planta perennis vel annua. *Caules* plerumque caespitosi, procumbentes vel adscendentes, rarius erecti. *Folia* saepius margine cartilaginea, ima rosulata vel fasciculata, rarius radicalia desunt, lanceolata vel ovato-lanceolata, obtusa, utrimque attenuata, uninervia. *Flores* plerumque speciosi plures vel solitarii. *Calyx* campanulatus, viridis, membranaceus laciniis ovato-lanceolatis. *Corolla* plica aucta, fimbriis destituta, clavata, obconica, vel campanulata, cyanea vel alba vel lactea striis dorsalibus quinque dilute caeruleis. *Antherae* liberae. *Stigmata* distincta, oblonga vel apice aucta vel orbiculata horizontalia. *Testa* lamelloso-rugosa, rarius utriculato-alveolata, lamellis albis areolas hexagonas formantibus. *Chromosomata* x=6.

The type species of this almost circumboreal alpine genus is *Gentianodes frigida* (HAENKE) LÖVE & LÖVE, comb. nov., based on *Gentiana frigida* (HAENKE, in JACQ. Coll. 2 (1788), p. 13.

Although the diversity of this genus still remains insufficiently known, especially in the mountains of southern and eastern Asia, we feel certain that at least the following species belong to it:

Gentianodes algida (PALLAS) LÖVE & LÖVE, comb. nov., based on *Gentiana algida* PALLAS, Fl. Ross. II (1788), p. 107.

Gentianodes amplicrater (BURKILL) LÖVE & LÖVE, comb. nov., based on *Gentiana amplicrater* BURKILL, in Journ. As. Soc. Beng. N. S. II (1906), p. 314.

Gentianodes cephalantha (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana cephalantha* FRANCH. ex HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 125.

Gentianodes chinensis (KUSNETZOV) LÖVE & LÖVE, comb. nov., based on *Gentiana chinensis* KUSNETZOV, in Bull. Acad. Sci. St. Pétersb. XXXV (1894), p. 250.

Gentianodes crassa (KURZ) LÖVE & LÖVE, comb. nov., based on *Gentiana crassa* KURZ, in Journ. As. Soc. Beng. XLII (1873), p. 235.

Gentianodes davidii (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana Davidii* FRANCH., Pl. Davidiana I (1884), p. 211.

Gentianodes delavayi (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana Delavayi* FRANCH., in Bull. Soc. Bot. France XXXI (1884), p. 377.

Gentianodes depressa (D. DON) LÖVE & LÖVE, comb. nov., based on *Gentiana depressa* D. DON, Prod. Fl. Nep. (1825), p. 125.

Gentianodes duclouxii (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana Duclouxii* FRANCH., in Bull. Soc. Bot. France XLVI (1899), p. 305.

Gentianodes elwesii (C. B. CLARKE) LÖVE & LÖVE, comb. nov., based on *Gentiana Elwesii* C. B. CLARKE, in HOOK. FIL., Fl. Brit. India IV (1883—1885), p. 115.

Gentianodes emodii (MARQUAND) LÖVE & LÖVE, comb. nov., based on *Gentiana Emodii* MARQUAND ex SEALY, in CURTIS's Bot. Mag. CLXX (1954), t. 230.

Gentianodes farreri (BALF. FIL.) LÖVE & LÖVE, comb. nov., based on *Gentiana Farreri* BALF. FIL., in Trans. Bot. Soc. Edinb. XXVII (1918), p. 248.

Gentianodes filistyla (BALF. FIL.) LÖVE & LÖVE, comb. nov., based on *Gentiana filistyla* BALF. FIL., in Kew Bull. 1928, p. 60.

Gentianodes glauca (PALLAS) LÖVE & LÖVE, comb. nov., based on *Gentiana glauca* PALLAS, Fl. Ross. II (1788), p. 104.

Gentianodes hexaphylla (MAXIM.) LÖVE & LÖVE, comb. nov., based on *Gentiana hexaphylla* MAXIMOVICZ, in KUSNETZOV, in Bull. Acad. Sci. St. Pétersb. XXXV (1894), p. 126.

Gentianodes jamesii (HEMSLEY) LÖVE & LÖVE, comb. nov., based on *Gentiana Jamesii* HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 128.

Gentianodes lineolata (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana lineolata* FRANCH., in Bull. Soc. Bot. France XXXI (1884), p. 375.

Gentianodes longipetiolata (KUSNETZOV) LÖVE & LÖVE, comb. nov., based on *Gentiana longipetiolata* KUSNETZOV, in Acta Horti Petrop. XIII (1894), p. 361.

Gentianodes melandrifolia (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana melandrifolia* FRANCH. ex HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 129.

Gentianodes microdonta (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana microdonta* FRANCH. ex HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 130.

Gentianodes ornata (WALLICH) LÖVE & LÖVE, comb. nov., based on *Gentiana ornata* WALLICH, Cat. no. 4386.

Gentianodes picta (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana picta* FRANCH. ex HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 131.

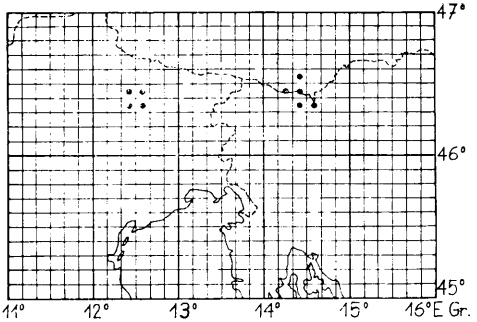

Fig. 1. The total distribution area of *Favargera* LÖVE & LÖVE. — The base map is that of the mapping scheme of Central Europe, grid units 10' long.×6' lat.

Gentianodes praeclara (MARQUAND) LÖVE & LÖVE, comb. nov., based on *Gentiana praeclara* MARQUAND, in Kew Bull. 1928, p. 54.

Gentianodes rigescens (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana rigescens* FRANCH. ex HEMSLEY, in Journ. Linn. Soc. XXVI (1890), p. 134.

Gentianodes sikkimensis (C. B. CLARKE) LÖVE & LÖVE, comb. nov., based on *Gentiana sikkimensis* C. B. CLARKE, in HOOK. FIL., Fl. Brit. India IV (1883—1885), p. 114.

Gentianodes sino-ornata (BALF. FIL.) LÖVE & LÖVE, comb. nov., based on *Gentiana sino-ornata* BALF. FIL., in Trans. Bot. Soc. Edinb. XXVII (1918), p. 253.

Gentianodes stipitata (EDGEWORTH) LÖVE & LÖVE, comb. nov., based on *Gentiana stipitata* EDGEWORTH, in Trans. Linn. Soc. XX (1846), p. 84.

Gentianodes stragulata (BALF. FIL. & FORREST) LÖVE & LÖVE, comb. nov.. based on *Gentiana stragulata* BALF. FIL. & FORREST, in Kew Bull. 1928, p. 61.

Gentianodes subocculta (MARQUAND) LÖVE & LÖVE, comb. nov., based on *Gentiana subocculta* MARQUAND, in Kew Bull. 1931, p. 81.

Gentianodes szechenyii (KANITZ) LÖVE & LÖVE, comb. nov., based on *Gentiana Szechenyii* KANITZ, Pl. exped. Szechenyi in As. centr. coll. (1891), p. 40.

Gentianodes tetraphylla (KUSNETZOV) LÖVE & LÖVE, comb. nov., based on *Gentiana tetraphylla* KUSNETZOV, in Bull. Acad. Sci. St. Pétersb. XXXV (1894), p. 350.

Gentianodes tizuensis (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana tizuen-*

sis FRANCH., in Bull. Soc. Bot. France XLIII (1896), p. 489.

Gentianodes tongolensis (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana tongolensis* FRANCH., in Bull. Soc. Bot. France XLIII (1896), p. 490.

Gentianodes trichotoma (KUSNETZOV) LÖVE & LÖVE, comb. nov., based on *Gentiana trichotoma* KUSNETZOV, in Acta Horti Petrop. XIII (1893), p. 61.

Gentianodes tubiflora (WALLICH) LÖVE & LÖVE, comb. nov., based on *Gentiana tubiflora* WALLICH, Catal. no. 4388.

Gentianodes urnula (H. SMITH) LÖVE & LÖVE, comb. nov., based on *Gentiana urnula* H. SMITH, in Kew Bull. XV (1961), p. 51.

Gentianodes vaniotii (LÉVEILLÉ) LÖVE & LÖVE, comb. nov., based on *Gentiana Vaniotii* LÉVEILLÉ, in Feddes Repert. XII (1913), p. 182.

Gentianodes veitchiorum (HEMSLEY) LÖVE & LÖVE, comb. nov., based on *Gentiana Veitchiorum* HEMSLEY, in Gard. Chron. XLVI (1909), p. 178.

Gentianodes venusta (WALLICH) LÖVE & LÖVE, comb. nov., based on *Gentiana venusta* WALLICH, Catal. no. 4389.

Gentianodes yunnanensis (FRANCH.) LÖVE & LÖVE, comb. nov., based on *Gentiana yunnanensis* FRANCH., in Bull. Soc. Bot. France XXXI (1884), p. 376.

ACKNOWLEDGEMENTS

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A New Species of Iris Subgenus Oncocyclus[1]

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ABSTRACT

Chaudhary, S. A. 1972. A new species of Iris subgenus Oncocyclus. — Bot. Notiser 125: 259—260.

Iris yebrudii Dinsmore ex Chaudhary sp. nov., is described. It is known from only one locality, Yebrud in Syria.

Two specimens of *Iris* from Yebrud, Syria — one in the Post Herbarium (BEI) and the other in the Blanche Herbarium of the St. Joseph University in Beirut — as also reported by P. Mouterde (1966), bear the labels with *Iris yebrudi* written on them by J. E. Dinsmore. While P. Mouterde, too, considered these as constituting a distinct species, it remained undescribed. It was possible to collect some material from the above locality in the spring of 1971. A study of the fresh material confirmed that it really was a distinct species. It is now described for the first time.

The financial assistance provided by the Aril Society International, Tujunga, Calif., USA for studies on the subgenus in the region is gratefully acknowledged. The Latin diagnosis of the species was possible only through the kindness of Dr. O. Almborn.

Iris yebrudii Dinsmore ex Chaudhary sp. nov.

Rhizoma breve, spissum. Caulis 15—25 cm., uniflorus. Folia falcata, 5 vel 6, ca. tertiam ad dimidiam partem longitudinis caulis obtegentia. Folia majora 14—16 cm. longa, a carina ad marginem ca. 1 cm. lata; folium caulinum 1, foliis basalibus propin-

Fig. 1. *Iris yebrudii* Dinsmore ex Chaudhary, sp. nov. — ×0.4.

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[1] Faculty of Agricultural Sciences, AUB, Scientific Series Publication No. 184.

quum vel paulo remotum. Bracteae 2, carinatae, superne fusco-purpureae, inferne pullae. Ovarium ca. 2.5 cm. longum, sulcatum. Tubus perianthii ca. 1.5 cm. longus. Flores solitarii plusminusve globosi, ca 8 cm. diametro. Tepala externa orbiculata, arcuata, ca. 6.5 cm. diametro, dense et subtiliter maculosa vel venulis et maculis purpureis vel fusco-purpureis supra fundum album vel subflavum instructa, venulae mediae distincte flavae; macula media ca. 0.7×1.3 cm., rhombea, purpureo-obscura. Tepala interna orbiculata, breviter unguiculata, ca. 7 cm. longa, 6 cm. lata, ad marginem venulis purpureis instructa, venae et venulae apicem et medium versus distincte flavae; fundus ad marginem candidus, in partibus mediis et inferioribus flavus; tepala interna in partibus inferioribus maculosa purpurea vel purpureo-obscura, in partibus mediis interioribus et inferioribus capillis paulis longis flavis instructa. Rami styli ca. 3.5 cm. longi, 2 cm. lati, acute carinati, purpurei vel purpureo-obscuri, apices bifidi; lobi sursum versi, maculosi et striati ut tepala externa.

HOLOTYPE: Syria, Yebrud, May 1971. Coll. S. A. CHAUDHARY no. 786. In Post Herbarium (BEI).

OTHER COLLECTION: Syria, Yebrud, May 1935. Coll. J. E. DINSMORE no. 25515. In Post Herbarium (BEI) and Blanche Herbarium of St. Joseph University of Beirut.

Rhizomes small, compact. Stem 15—25 cm tall. Leaves falcate, 5 or 6, covering about 1/3—1/2 of stem; larger leaves 14—21 cm long, about 1 cm wide from the keel to the margin; stem-leaf (spathe) one, close to or a little removed from the basal leaves. Bracts two, keeled, the upper halves brownish purple and the lower halves dark-brown. Ovary about 2.5 cm long, grooved; the perianth tube about 1.5 cm long. Flowers solitary, rather globular in outline, about 8 cm long and wide. Falls orbicular, recurved, about 6.5 cm long and wide, closely finely dotted or veined with purple or brown-purple spots on a clear white to yellowish-white ground, the middle veins distinctly yellow; signal patch about 0.7×1.3 cm, more or less diamond-shaped, dark purple. Standards with short claw, orbiculate, about 7 cm tall and 6 cm wide with fine purple veins towards the periphery, the major veins and those in the central top end distinctly yellow; the ground clear white towards the periphery, yellow in the middle and basal parts; standards dotted with purple or dark-purple spots towards the base and with a few long, yellow hairs on the median inner basal areas. Style branches to about 3.5 cm long, 2 cm wide, sharply keeled, purple to dark-purple; apices bilobed, the lobes turned upwards and spotted and streaked like the falls.

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Studies on Bipolar Disjunct Species II

Plantago maritima L.

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ABSTRACT

MOORE, D. M., WILLIAMS, C. A. & YATES, B. 1972. Studies on bipolar disjunct species II. Plantago maritima L. — Bot. Notiser 125: 261—272.

An analysis of 22 morphological characters showed that *Plantago maritima* L. from South America tends to differ modally from the usually more variable material from the Northern Hemisphere, but the distinction is not sufficient to be recognized taxonomically. The 14 flavonoids found in the species show a rather uniform pattern, the only major amphitropical discontinuity being in the occurrence of 6-hydroxyluteolin 7-glucoside. The South American plants show closest affinities with those from North America, which are also self-compatible and invariably diploid, and show a tendency to be more similar to material from eastern than western North America, although in the absence of annulate pollen-pores they resemble lowland European and facies of the western American populations. The Atlantic coast is considered to have been the route by which long-distance amphitropical dispersal was effected to the south and birds seem the most likely vectors. Artificial hybrids between South American and European plants are fertile and have normal chromosome pairing. This, together with earlier studies, shows that the South American, North American and diploid European populations of *P. maritima* constitute an interfertile complex spanning considerable oceanic and climatic barriers.

INTRODUCTION

The sea plantains allied to *Plantago maritima* L. occur widely through the North Temperate zone and in southern South America (Fig. 1). In the New World they are largely coastal, but in Eurasia they also occur in other lowland as well as in alpine and subalpine habitats. There have been various attempts to subdivide the complex. For example, the South American populations were separated as *P. juncoides* LAM., a name applied to most of the plants from North America and Greenland by FERNALD (1925), who, however, referred the salt-marsh plants from the eastern United States to *P. oliganthos* ROEM. & SCHULT. In Europe, the populations from high elevations in the Alps have been variously described as *P. alpina* L., *P. serpentina* ALL. and *P. carinata* SCHRAD.

The variation within and between populations of sea plantains from many habitats and localities in the Northern Hemisphere was intensively studied in the experimental garden by GREGOR and his associates (GREGOR 1930, 1938, 1939; GREGOR & LANG 1949; GREGOR, DAVEY & LANG 1936; DAVEY & LANG 1939), who showed that a great deal of ecotypic differentiation had taken place and that interpopulational variability in characters used taxonomically reduced confidence in the taxa recognized formally. Furthermore, most populations were shown to be diploid (2n=12) and hybrids between them were fully fertile, as were those between the few tetraploid populations found in

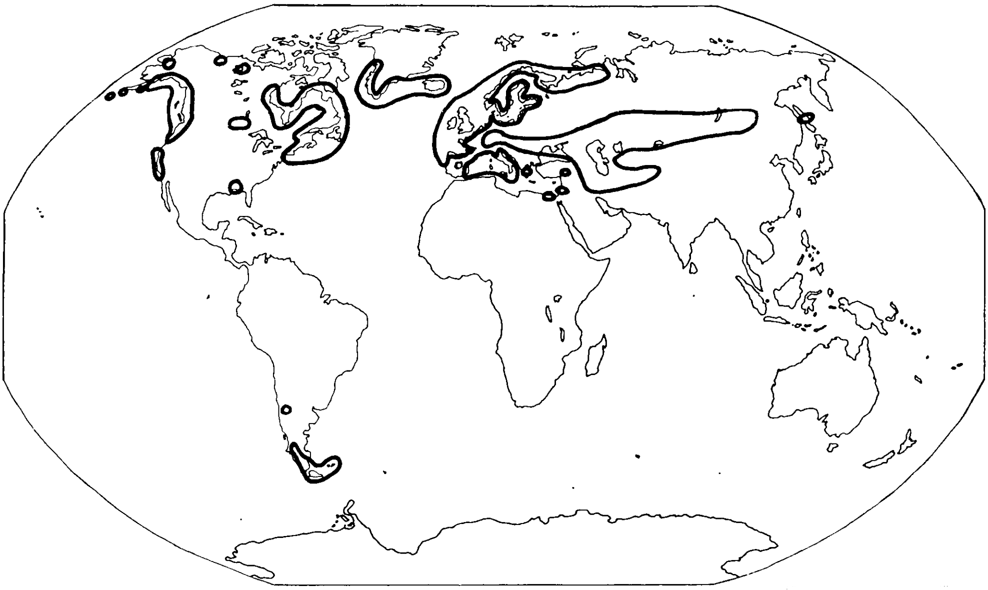

Fig. 1. Distribution of *Plantago maritima.* Northern Hemisphere data derived from HULTÉN (1971).

the Alps, which were said to be morphologically indistinguishable.

GREGOR (1939) found that in North America and Greenland the plants were self-compatible and usually had 4 seeds per capsule, while from Iceland eastwards they were self-incompatible and with about 2 seeds per capsule. This was suggested by HULTÉN (1949, 1958) as a basis for recognizing a western ssp. *juncoides* (LAM.) HULTÉN and an eastern ssp. *maritima* in the Northern Hemisphere. However, MOORE (1968) pointed out that at least some Falkland Islands and Patagonian plants, although self-compatible, had 2 seeds per capsule, whilst DOWLING (1936) showed that British and North American plants contain 3 and 4 ovules respectively which, by abortion, frequently give 1 and 2—3 seeds in the mature capsule.

Regional differences have also been shown in the structure of the pollen grain (ANDERSON 1961; BASSETT & CROMPTON 1968). The pores have a raised marginal annulus in plants from the east coast of North America and Greenland, while from Iceland eastwards the annulus is lacking in lowland populations. In the Alps annulate pores are present in material referable to both diploid and tetraploid forms of *P. alpina* but not in *P. serpentina* (CARTIER 1971). Both types of pollen-pore were found on the west coast of North America.

In summarizing the current taxonomic opinion it appears that most authors follow GREGOR's results in referring the American and lowland Eurasiatic populations to *P. maritima* L. This species is generally diploid ($2n=12$), although tetraploid and triploid plants are known (EARNSHAW 1942; GORENFLOT & MARCOTTE 1970). HULTÉN (1971) recognizes three subspecies within *P. maritima*: (i) ssp. *juncoides* (LAM.) HULTÉN (incl. depauperate plants sometimes referred to ssp. *borealis* (LANGE) BLYTT & DAHL) with wide bracts and an ovoid to globose capsule, which occurs throughout the Ameri-

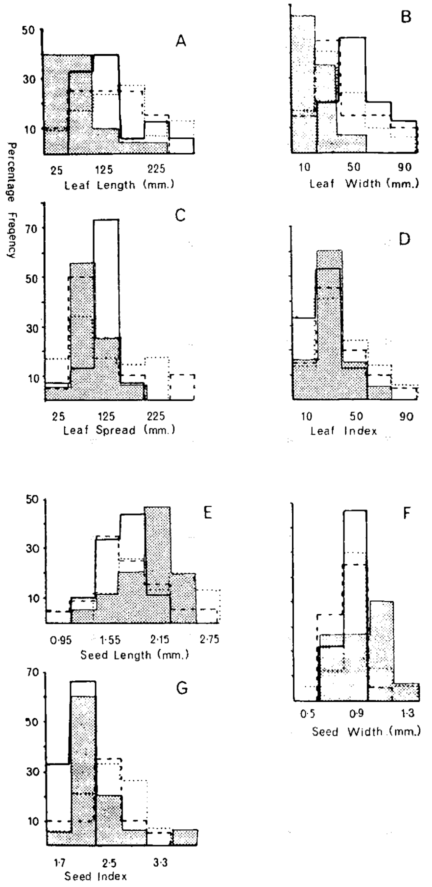

Fig. 2. Morphological characteristics of Northern and Southern Hemisphere plants of *Plantago maritima*. — A: Leaf-length. — B: Leaf-width. — C: Leaf-spread. — D: Leaf-length/width. — E: Seed-length. — F: Seed-width. — G: Seed-length/width. (Stippling: South America; dotted line: Europe; solid line: W. North America; broken line: E. North America and Greenland).

cas and Greenland, and extends via Iceland to northern Scandinavia and Arctic Russia (long. 69°E.); (ii) ssp. *maritima*, with wide bracts, a long-conical capsule and eciliate petals, which occurs in coastal Europe, overlapping with ssp. *juncoides* in Iceland and Scandinavia, and intergrades through inland Europe with (iii) ssp. *salsa* (PALLAS) HULTÉN, which has narrow bracts, long-conical capsule and usually ciliate petals, and occurs throughout the inland areas of Asia as far east as long. c. 122°E.

There has been much study in recent years of the plants occurring in the Alps (eg. CARTIER 1965, 1970; CARTIER & LENOIR 1968) and, although their taxonomic status is still not completely clear, *P. carinata* (2n=12) and *P. alpina* (2n=12, 24) are currently recognized as distinct species while *P. serpentina* (2n=12, 24) is considered a variant of *P. maritima* (CARTIER 1970; pers. comm.). Fertile hybrids are possible between all these species at the diploid and tetraploid levels (CARTIER 1970) but the most successful crosses having *P. maritima* as a parent were those with *P. serpentina*. Inter- and intraspecific crosses between the different ploidy levels were abortive.

In contrast with the considerable amount of morphological and experimental information on Northern Hemisphere material referable to *P. maritima*, there are relatively few data on the species in southern South America. The purpose of this paper is to provide such information on the Southern Hemisphere populations and to use it, together with phytochemical and cytogenetical studies, to examine their affinities with the Northern Hemisphere material. The various types of data will be described and discussed separately, after which their combined relevance to the general problem of bipolar disjunct distributions will be discussed.

MORPHOLOGY

MATERIAL AND METHODS

In addition to herbarium material collected in the field, 15 population-samples, mostly South American, were raised from seed and cultivated in the greenhouse for some five years. These samples, usually comprising 10—15 plants, were used to assess performance under relatively uniform environmental conditions in pot culture and also to prepare voucher herbarium specimens. Material for analysis was chosen to represent as wide a

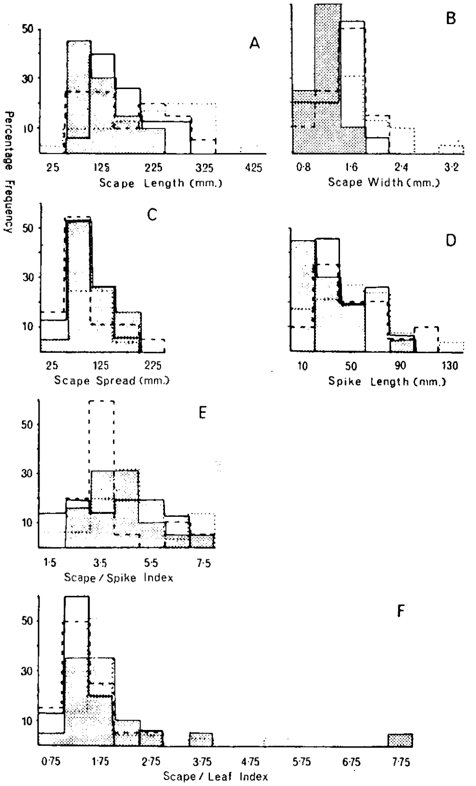

Fig. 3. Morphological characteristics of Northern and Southern Hemisphere plants of *Plantago maritima*. — A: Scape-length. — B: Scape-width. — C: Scape-spread. — D: Spike-length. — E: Scape-length/spike-length. — F: Scape-length/leaf-length. (Stippling: South America; dotted line: Europe; solid line: W. North America; broken line: E. North America and Greenland).

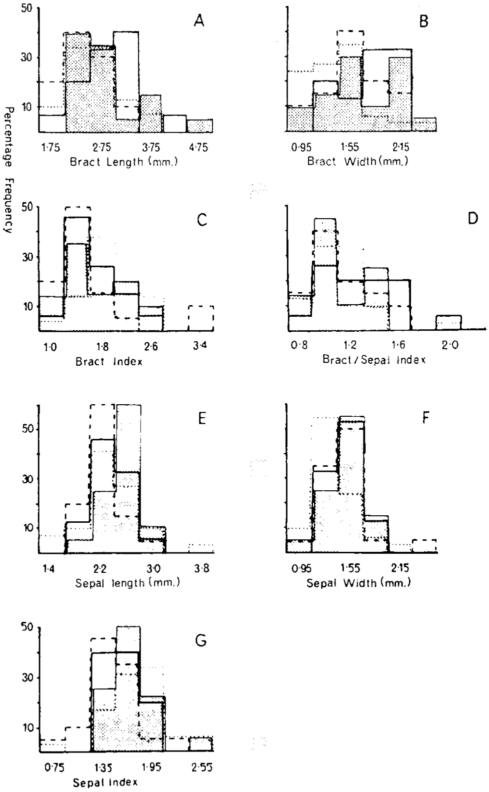

Fig. 4. Morphological characteristics of Northern and Southern Hemisphere plants of *Plantago maritima*. — A: Bract-length. — B: Bract-width. — C: Bract-length/width. — D: Bract-length/sepal-length. — E: Sepal-length. — F: Sepal-width. — G: Sepal-length/width. (Stippling: South America; dotted line: Europe; solid line: W. North America; broken line: E. North America and Greenland).

geographical and morphological range as possible.

Characters scored were those which have been shown to vary by various workers, particularly those used by GREGOR (1938 et seq.) in his studies of ecotypic variation. In a preliminary survey 33 characters were analysed, of which 22 were selected for further study. They may be divided into vegetative and floral characters as follows: **Vegetative:** 1. Leaf-length; 2. Leaf-width; 3. Leaf-spread, (i.e. greatest diameter spanned by leaf-apices); 4. Leaf-length/width index; 5. Scape-length; 6. Scape-diameter; 7. Scape-spread (i.e. greatest diameter spanned by scapes); 8. Scape-length/leaf-length index; 9. Spike-length; 10. Scape-length/spike-length index. **Floral:** 11. Bract-length; 12. Bract-width; 13. Bract-length/width index; 14. Sepal-length; 15. Sepal-width; 16. Sepal-length/width index; 17. Bract-length/sepal-length index; 18. Seed number; 19. Seed-length; 20. Seed-width; 21. Seed-length/width index; 22. Pollen-pore with/without annulus.

RESULTS AND DISCUSSION

The data on characters 1—17 and 19—21 for material from various major geographical regions are plotted as frequency histograms in Figs. 2—4, while the results for character 18 are summarized in Table 1.

It can be seen that in some characters, such as scape-length/leaf-length index (Fig. 3 F), bract-width (Fig. 4 B) and seed-length/width index (Fig. 2 G), the South American material is as variable as that derived from major regions in the Northern Hemisphere. Some of this undoubtedly reflects the presence of ecotypic differentiation, since populations derived from various habitats and sites showed differences in habit, stature and pigmentation which persisted in cultivation and were obviously genotypically determined. Nevertheless, South American *P. maritima* is generally restricted to coastal habitats in a rather circumscribed geographical area and consequently the total variation is less than in the Northern Hemisphere for most other characters studied.

Although the Southern and Northern Hemisphere plants show a generally continuous pattern of variation (cf. Figs. 2, 3 and 4), thus confirming their inclusion in a single species, the former tend to be smaller than the latter in a number of characters, all of them vegetative — scape-length and width (Fig. 3 A, B), leaf-length and width (Fig. 2 A, B) and spike-length (Fig. 3 D). In contrast, the Southern Hemisphere material tends to have higher values in some floral characters, viz. sepal-length (Fig. 4 E), seed-length and width (Fig. 2 E, F). In none of these characters is the Southern Hemisphere material sufficiently different from that of the Northern Hemisphere to warrant any formal taxonomic recognition within the species.

The histograms (Figs. 2—4) show that, in general, the morphological affinities of the South American plants are closer to those from North America than to those from Europe. This is also true for the number of seeds per capsule (Table 1) which, furthermore, show differences between the American and European populations that agree more with the earlier reports of DOWLING (1936) than of GREGOR and others (see p. 262). A few characters suggest a further trend, in which the South American material is more similar to that from eastern than western North America. This is indicated by the histograms for leaf-spread (Fig. 2 C), scape-spread (Fig. 3 C), bract-length (Fig. 4 A) and bract-length/sepal-length index (Fig. 4 D).

Table 1. Number of seeds per capsule in *Plantago maritima* from different geographical areas.

South America	(1—)2(—4)
W. North America	(1—)2
E. North America	2—3
Europe	1(—2)

The remaining character to be considered, for which data are not given in the histograms, is the occurrence of a marginal annulus round the pores of the pollen grains. This proved to be consistently absent from all plants examined from South America, which consequently resemble those from lowland Europe and some from western North America.

In summary then, the morphological data support the view that Northern and Southern Hemisphere populations belong to a single species and show that the latter more closely resemble North American than European material, which is not unexpected in view of the geographical distribution. Although modal differences exist between North and South American material they are not sufficiently clear to permit formal taxonomic recognition. The similarity in a few characters between South American plants and those from eastern North America might simply result from comparable environmental selection pressures in the two regions but it may indicate a closer affinity reflecting past migrations. Interestingly, the occurrence of annulate pollen-pores does not accord with this. The regional differences may result from independent events, but if similarities in this character reflect affinities then the resemblance between the South American, European and some western North American populations is somewhat unexpected. Possibly an early polymorphism for the presence or absence of the annuli has been maintained in the latter region, as well as in the Alps (CARTIER 1971), but lost elsewhere as a consequence of selection or, more likely, by the operation of the 'founder principle' during the colonisation phases.

PHYTOCHEMISTRY

MATERIAL AND METHODS

Forty four samples of *Plantago maritima* were examined for their flavonoid constituents, 35 from the Northern and 9 from the Southern Hemisphere. Both herbarium and living material were utilized, no differences being detectable between them when at a comparable stage of growth (i.e. with flowering spikes). Bulk collections of fresh material from the field and greenhouse were used for the identification and characterization of the various constituents. Leaf-samples were extracted with 70 % EtOH and the extracts were concentrated and chromatographed two-dimensionally on Whatman no. 1 paper, first in *n*-butanol: acetic-acid: water (4:1:5) (BAW) and then in 15 % HOAc. Flavonoid glycosides and other phenolics were detected by examination of the dried papers in ultraviolet light alone and in the presence of ammonia. The major constituents were separated and purified by paper chromatography using standard procedures (see HARBORNE 1967 a). Known glycosides were identified on the basis of Rf, UV spectral analysis, acid hydrolysis to aglycone and sugar and, where possible, by direct comparison with authentic samples. Authentic 6-hydroxyluteolin 7-glucoside was isolated from leaf-material of *Catalpa bignonioides* (HARBORNE 1967 b). 6-Hydroxyluteolin 7-glucuronide is reported here for the first time. Its Rf values (together with the 7-glucoside for comparison) are as follows: 20 (24) in n-butanol-acetic acid-water 4:1:5, 10 (31) in n-butanol-ethanol-water, 11 (44) in phenol, 02 (01) in water and 08 (08) in 15 % acetic acid. Spectral data for the two glycosides are very similar: $\lambda^{\text{EtOH}}_{\text{max}}$ 286, 349; $\lambda^{\text{NaOAc}}_{\text{max}}$ 285, 350; $\lambda^{\text{alk}}_{\text{max}}$ 402; $\lambda^{H_3BO_3}_{\text{max}}$ 362.

RESULTS AND DISCUSSION

Fourteen flavonoids were found on the two-dimensional chromatograms (Fig. 5; Table 2), of which five (viz. 6-hydroxyluteolin 7-glucoside, luteolin 7-glucuronide, chrysoeriol 7-glucuronide, luteolin 7-glucoside and 6-hydroxyluteolin 7-glucuronide) were identified.

The most unusual flavonoid found was the comparatively uncommon 6-hydroxyluteolin, already shown to be a useful phyletic marker at family level by HARBORNE & WILLIAMS (1971). They report its presence in 8 out of 26 species of *Plantago* and also in the related families Globulariaceae, Labiatae, Buddleiaceae and Valerianaceae. Three flavonoids, luteolin 7-glucoside (F4), chrysoeriol 7-glucuronide (F3) and, to a lesser extent, luteolin 7-glucuronide (F2) appear to be characteristic for *Plantago maritima,* occurring in all Southern Hemisphere and most Northern Hemisphere samples. 6-Hydroxyluteolin 7-glucoside (F1) is absent from the Southern Hemisphere material but occurs in virtually all the Northern Hemisphere samples. However, 6-hydroxyluteolin 7-glucuronide (F8) is present in 30 % of the Southern samples as compared with 45 % of the Northern. None of the other compounds shows any significant pattern of distribution, although it is worth nothing that the American samples are poorer in flavonoids than those from Europe, perhaps a reflection of the larger number of samples from the latter region.

Here, then, is an example of a cosmopolitan species with a rather uniform flavonoid pattern. Most of the variation which does occur cannot be correlated with obvious phytogeographical or evolutionary factors. The only major discontinuity is the complete absence of 6-hydroxyluteolin 7-glucoside from all the Southern Hemisphere samples but as the glucuronide of the same aglycone is present in some of these samples perhaps this is not so significant. Interestingly, the hybrid between South American and European material (10) resembles the female parent in lacking this compound, whilst containing 6-hydroxyluteolin 7-glucuronide present in the male parent.

Table 2. Occurrence of chromatographically separable flavonoids in samples of *Plantago maritima* throughout its range. — F1: 6-hydroxyluteolin 7-glucoside; F2: luteolin 7-glucuronide; F3: chrysoeriol 7-glucuronide; F4: luteolin 7-glucoside; F8: 6-hydroxyluteolin 7-glucuronide. The Rf's of the unidentified compounds in BAW and 15 % HOAc are as follows: F6: 46/27; F7: 56/21; F9: 12/37; F10: 18/30; F11: 10/21; F12: 32/12; F13: 22/40; F14: 16/18; F15: 23/13. The colours of the unknown flavonoids in UV without and with NH$_3$ are as follows: F6, F7, F9, F10, F11, F14: dark to yellow; F12, F13, F15: dark to dark. Relative positions on chromatogram are shown in Fig. 5.

Origin of the material	F1	F2	F3	F4	F6	F7	F8	F9	F10	F11	F12	F13	F14	F15
South America														
1. Chile: Tierra del Fuego; Isla Navarino	—	+	+	+	—	—	—	—	—	—	—	—	—	—
2. Chile: Tierra del Fuego; Isla 3 Mogotes	—	+	+	+	—	—	—	—	—	—	—	—	—	—
3. Chile: Tierra del Fuego; Estancia Cameron	—	+	+	+	—	—	—	—	—	—	—	—	—	—
4. Chile: Magallanes; Fuerte Bulnes	—	+	+	+	—	—	—	—	—	—	—	—	—	—
5. Argentina: Tierra del Fuego; Estancia Harberton	—	+	+	+	+	+	—	—	—	—	—	+	+	—
6. Argentina: Tierra del Fuego; Estancia Harberton	—	+	+	+	+	+	+	—	—	—	—	—	+	—
7. Argentina: Tierra del Fuego; Cabo San Pablo	—	+	+	+	—	—	—	—	—	—	—	—	—	—
8. Argentina: Tierra del Fuego; Cabo San Pablo	—	+	+	+	—	—	—	—	—	—	—	—	—	—
9. Argentina: Mendoza; Atuel Valley	—	+	+	+	+	+	+	—	—	—	—	+	+	—
South America×Europe														
10. Tierra del Fuego; Cabo San Pablo×England: E. Norfolk	—	+	+	+	+	—	—	—	—	—	—	—	—	—
North America														
11. U.S.A.: California; Sonoma Co.	+	+	+	+	+	+	+	—	—	—	—	—	+	—
12. U.S.A.: Alaska; Kenai Peninsula	—	+	+	+	—	—	—	—	—	—	—	—	—	—
13. U.S.A.: Alaska; Kodiak Island	+	+	+	+	+	+	+	—	—	—	—	—	+	—
14. Canada: Cape Breton; North Sydney	+	+	—	—	+	—	—	—	—	—	—	—	+	+
15. Canada: Newfoundland; Bay of Isles	+	+	+	+	+	—	—	—	—	—	—	—	—	+
16. Greenland: Sarajugnitak v. Sulatsivik	+	+	+	+	+	+	—	—	—	—	—	—	—	+
Europe and Asia														
17. Iceland	+	+	+	+	—	—	—	—	—	—	—	—	—	—
18. Norway: Akershus; Asker	+	+	+	+	—	—	—	—	—	—	—	—	—	—
19. Norway: s.loc.	+	—	+	+	+	—	+	—	—	—	—	—	—	—
20. Norway: Tromsö	+	—	+	+	+	—	—	—	—	—	—	—	—	—
21. Finland: Ostrobothnia media	+	—	+	+	+	—	+	—	—	—	+	—	—	—
22. Wales: Cardigan	+	—	+	+	+	—	—	—	—	—	—	—	—	—
23. Wales: Merioneth	+	—	+	+	+	—	—	—	—	—	—	—	—	—
24. England: Cornwall; Newquay	+	+	+	+	—	—	—	+	—	—	—	—	—	—
25. England: Cornwall; Coverack	+	+	+	+	+	+	—	—	—	—	—	—	—	—
26. England: Gloucester	+	—	+	+	—	—	—	—	—	—	—	—	—	—
27. England: Sussex	+	—	+	+	—	—	—	—	—	—	+	—	—	—
28. England: E. Norfolk, Scolt	+	—	+	+	—	—	—	—	—	—	—	—	—	—
29. England: W. Norfolk, Wolferton	—	—	+	+	+	—	+	—	—	—	—	—	+	—
30. England: Isle of Man	+	+	+	+	+	—	+	+	+	+	—	—	—	—
31. England: Cheshire	+	+	+	+	—	—	—	—	—	—	—	—	—	—
32. England: Cumberland	+	+	+	+	+	+	+	+	—	—	—	—	—	—
33. England: Durham; Teesdale	+	+	+	+	—	—	—	—	—	—	—	—	—	—
34. Scotland: Argyll	+	+	+	+	+	+	—	—	—	—	—	—	—	+
35. France: Puy de Dôme	+	+	+	+	+	+	—	—	—	—	—	—	—	—
36. Spain: Santander	+	+	+	+	+	+	—	—	—	—	—	—	—	—
37. Spain: Albacete	+	+	+	+	+	—	—	—	—	—	—	+	—	—
38. Austria: Burgenland	+	+	+	+	+	+	—	+	—	—	—	—	—	—
39. Romania: Constante	+	+	+	+	+	—	—	+	—	—	—	—	+	+
40. U.S.S.R.: Domu Zkvskaja	—	+	+	+	+	—	+	—	+	+	—	—	—	—
41. U.S.S.R.: Urals	+	+	+	+	+	—	—	—	—	—	—	—	—	—
42. U.S.S.R.: C. Asia; Kurgan	—	+	+	+	+	+	—	—	—	—	—	—	—	—
43. Turkey: Van.	—	+	+	+	—	—	—	+	—	—	—	—	—	—

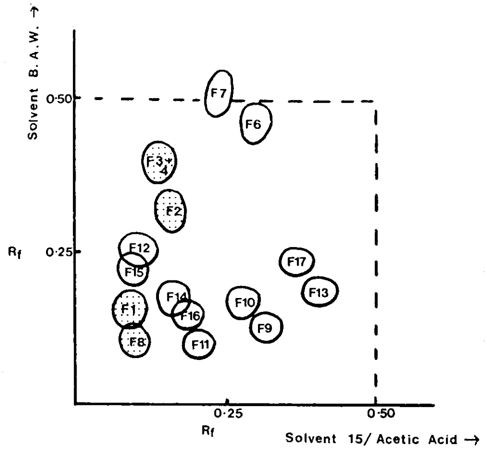

Fig. 5. Part of a two-dimensional chromatogram showing the approximate locations of all the major flavonoid constituents occurring in leaf-extracts from samples of *Plantago maritima.* Identified compounds are stippled (for key see Table 2).

CYTOLOGY AND BREEDING SYSTEM

Northern Hemisphere Populations

As noted earlier (p. 262) *Plantago maritima* is generally diploid (2n=12) throughout Europe (many refs., see e.g. Bolkhovskikh et al. 1969) and entirely so in Greenland and North America (e.g. Jørgensen et al. 1958; Bassett & Crompton 1968; Taylor & Mulligan 1968). No meiotic irregularities have been recorded. Gorenflot & Marcotte (1970) have shown that unreduced gametes are sometimes present in the species and these may be responsible for the formation of the tetraploids (2n=24) reported in Arctic Europe (Earnshaw 1942), Portugal (Rodriguez 1954) and Finland (Sorsa 1962). Naturally occurring triploids have been reported from Poland (Czapska 1961).

The observation by Gregor (1939) that European plants are self-incompatible, while North American and Greenland plants are self-compatible (see p. 262), has not been refuted by subsequent workers. Our observations on cultivated European material are in agreement with this.

Southern Hemisphere Populations

All material examined from South America has been shown to be diploid. Chromosome counts are available for 9 populations representing the morphological and geographical range of the species[1] in the Southern Hemisphere and no variation could be detected, either in somatic karyotype or in the regular formation of 6 bivalents at meiotic metaphase.

Subsequent observations on field and cultivated material have confirmed the earlier observation (Moore 1968) that the South American plants are self-compatible and capable of self-pollination. The seed shows a consistently high germination with values of over 75 per cent being usual.

INTERPOPULATIONAL HYBRIDS

MATERIAL AND METHODS

Artificial hybrids were produced by crossing plants held in pot culture in the greenhouse. Since the species is protandrous, the anthers appearing in sequence from the base of the spike, emasculation was carried out as soon as the anthers were exserted but before their dehiscence, and was continued for several days until about 10 flowers had thus been treated; the remainder of the spike was then removed. Pollinators were excluded by means of a clear polythene tube, stoppered with cotton wool at both ends, which enclosed the spike after emasculation was commenced.

RESULTS AND DISCUSSION

In view of the information already available (Gregor 1939; Cartier 1970) on crosses between Northern Hemisphere populations, only hybrids involving the

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[1] The following collections show 2n=12. Argentina: Mendoza; Atuel Valley (Rahn, in Böcher et al. 1963); Tierra del Fuego; Estancia Cullen, Moore 1470; Cabo Domingo, Moore 1490; Cabo San Pablo, Moore 1514; Estancia Policarpo, Goodall 2269 (Moore unpub.). Chile: Magallanes, Fuerte Bulnes; Tierra del Fuego; Bahía Inutil, Estancia Cameron (Moore 1967); Isla 3 Mogotes, Moore s.n.; Isla Navarino, Caleta Wulaia, Barrett 50—34 B (Moore, unpub.).

Table 3. Chromosome configuration at first meiotic metaphase and percentage pollen fertility of F_1 interpopulational hybrids involving South American *Plantago maritima*. (Voucher collection numbers of D. M. MOORE unless otherwise shown.)

♀ parent	♂ parent	Meiotic configuration	Pollen fertility percentage
Tierra del Fuego; Ea. Cullen (1470)	Chile; Magallanes, Fte. Bulnes (2318)	6II	98
Tierra del Fuego; Ea. Cameron (2320)	Chile; Magallanes, Fte. Bulnes (2318)	6II	95
Tierra del Fuego; Isla 3 Mogotes (2319)	Chile; Magallanes, Fte. Bulnes (2318)	6II	55
Tierra del Fuego; Ea. Cameron (2320)	Tierra del Fuego; Isla 3 Mogotes (2319)	6II	51
Tierra del Fuego; Cabo San Pablo (1514)	Tierra del Fuego; Ea. Cullen (1470)	6II	99
Tierra del Fuego; Cabo San Pablo (1514)	England: Norfolk; Scolt Head (WOODELL, s.n.)	6II	70

Southern Hemisphere populations were studied. The results are given in Table 3.

It can be seen that hybrids between Southern Hemisphere populations consistently showed regular chromosome pairing at meiotic metaphase, as did the hybrid between Northern and Southern Hemisphere plants. In most cases the pollen fertility of the hybrids was as high as in the parents but lower values were shown by the Southern Hemisphere hybrids involving the population from Isla 3 Mogotes. This indicates a moderate genic sterility barrier which is not evident elsewhere. The slightly lowered pollen fertility of the hybrid between Northern and Southern Hemisphere plants is probably not significant, falling as it does at the lower end of the range of values encountered in the parental populations.

In view of the general lack of internal barriers to gene exchange between Northern Hemisphere populations demonstrated by GREGOR (1939) and CARTIER (1970) it is clear that there seems to be little or no cytogenetic differentiation of the diploid populations of *P. maritima,* which constitute an interfertile complex throughout its range. The only significant internal barriers to gene flow being in Europe, where the diploids and tetraploids form sterile hybrids; this is not relevant to the bipolar disjunction shown by the species.

GENERAL DISCUSSION

Plantago maritima is basically a diploid species which apparently originated in Eurasia, where its closest allies are to be found, where it exhibits the greatest morphological diversity and the widest ecological and geographical distribution, and where it is self-incompatible. Here also tetraploid populations have arisen. It spread to the New World, where it is self-compatible, within a circumboreal pattern exhibited by many species and extended down both coasts of North America to about lat. 30°N. As in Eurasia, considerable ecotypic differentiation has taken place in North America (GREGOR 1939), although it is ecologically and probably geographically more restricted.

There is a gap (Fig. 1) of some 9000 km. between the southernmost North American occurrence of *P. maritima* and its most northerly populations in South America. The austral populations are entirely self-compatible like those in North America with which they show the closest morphological affinities. In South America *P. maritima* almost always occurs in coastal habitats, but it is known from an inland saline area at c. 2800 m. at its northern limit in the province of Mendoza, Argentina (BÖCHER et al. 1963). It shows less morphological and perhaps chemical variation than in the Northern Hemisphere, although a significant amount of ecotypic variation can still be demonstrated.

Within the pattern of morphological and chemical variation demonstrated for *P. maritima* the South American populations show a tendency to be distinct, but this is insufficient to warrant formal taxonomic recognition. The austral populations seem to consist of a somewhat restricted series of segregates derived from those in the Northern Hemisphere, particularly North America, within which autogamy and local ecotypic differentiation have emphasized certain features. Thus, the universal absence of 6-hydroxyluteolin 7-glucoside in South American plants points to their affinities with the very few Northern Hemisphere populations lacking this flavonoid. There is no constant pattern in the trend shown by the morphological variation, for some characters values are higher and for others they are lower in Southern than in Northern Hemisphere material. This contrasts with bipolar *Carex* species (MOORE & CHATER 1971) in six of which the southern populations tended to give higher values for most measurable characters. The morphological affinities of the South American populations appear to be somewhat closer to those from eastern than western North America but in their lack of annulate-pored pollen they resemble material from the other Northern Hemisphere regions, particularly from lowland Europe.

Both geographical considerations and morphological affinities clearly indicate that *P. maritima* migrated from North to South America after its arrival in the New World. The occurrence of self-compatibility, associated with the extension from Eurasia, would be an important factor in its migration to the Southern Hemisphere, particularly since long-distance dispersal was certainly involved. There is nothing in the present American distribution of *P. maritima* to suggest that it might have migrated from north to south along the cordilleran system in the west, as have the majority of bipolar species (MOORE 1972; MOORE & CHATER 1971; RAVEN 1963) and the disjunction between suitable temperate coastal habitats in the Northern and Southern Hemispheres must always have involved a larger gap to be crossed than that for the cordilleran migrants.

The modest suggestion of closer morphological affinities with eastern than western North American material, together with its present austral distribution, suggests that *P. maritima* was dispersed to South America along the Atlantic coast. The currents in the Atlantic Ocean do not appear favourable for such amphitropical transport and the seeds are scarcely suited for wind dispersal. Human agency cannot be completely ruled out but the species is not obviously associated with man's voyages elsewhere in the world so that its bipolar distribution most probably results, therefore, from birds migrating between the North and South Atlantic Oceans. It is possible that the seeds could be carried internally, but they are glutinous when moist and could readily travel attached to the plumage or body of the frequent birds which traverse the tropics and feed in habitats where the species grows. It was suggested earlier (p. 266) that the pollen affinities might indicate that migration from North America had occurred when there was perhaps still some polymorphism in the occurrence of the annulate pollen-pore in populations from the east. This would be likely to be a time of climatic change when ecological conditions were in a state of flux and could well have been at the time of the Plio-cene-Pleistocene glaciations or immediately afterwards. All our observations would agree with this general period or more recently.

Although it is impossible, of course, to be completely certain about the sequence of events outlined above, there must be few species for which all the data point more strikingly to its arrival into the

Southern Hemisphere by long-distance dispersal. The close morphological similarity to North American populations, the restricted morphological and chemical variation, the narrow ecological and geographical distribution, the self-compatibility, high germination rates and preference for open habitats all combine to indicate that this species is an ideal long-distance migrant which could well have reached South America during or subsequent to the Pleistocene. A possible dispersal mechanism has been suggested but, as in other instances, there is as yet no direct evidence of its operation.

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Botanical Literature

AINSWORTH, C. G. (ed.): Ainsworth & Bisby's Dictionary of the Fungi. Ed. 6. — Commonwealth Mycological Institute, Kew, 1971. 663 pp.+16 pp. illustrations (drawings). Price £ 5.00 (cloth).

Since 1943 "AINSWORTH & BISBY" has been a standard work on the bookshelves of all serious mycologists. Ed. 5 (1961) has been reprinted three times without changes, and the need for a revised edition has been urgent. The present volume is much enlarged (by more than 100 pages) as compared to Ed. 5. The increase is due to a considerable extent to the incorporation of lichens. These were not included in the previous issues.

The skeleton of the Dictionary is a list of all the generic names of fungi and lichens. For each accepted genus a systematic position is given, together with its distribution and number of species, sometimes with short references to literature. The higher taxa have also been recorded concisely. Under "Fungi" we find a survey of the six "Classes of Fungi" accepted by AINSWORTH and a comparison with other recent mycological systems viz., BESSEY, GÄUMANN, ALEXOPOULOS and KREISEL. The Myxomycetes and some related groups are classified as Division Myxomycota vs. Division Eumycota comprising what is normally known as Fungi. The Phycomycetes have been divided into Mastigomycotina and Zygomycotina. The Imperfect Fungi are recorded as Subdivision Deuteromycotina at the same level as Ascomycotina and Basidiomycotina.

A remarkable feature of the work is the acceptance of the Fungi as a special "kingdom" parallel with Plantae and Animalia, instead of being, as previously, a subdivision of the Thallophyta. No doubt these ideas, which have gradually received support during the last few decades, will soon be accepted also in elementary textbooks.

The taxonomic framework has been mingled with numerous entries covering most fields of pure and applied mycology, e.g., air pollution, edible fungi, ergot, genetics of fungi, geographical distribution, metabolic products, numerical taxonomy, sex, wood-attacking fungi. We also find condensed biographies, often with references to bibliographies, of certain prominent mycologists and lichenologists.

As mentioned above, the lichens have been included in this work for the first time. This has been made possible by the collaboration of Mr. P. W. JAMES and Dr. D. L. HAWKSWORTH. In the reviewer's opinion, this incorporation has not been wholly successful. One would not have expected to find the old-fashioned group "Lichenes" recognized as a taxonomic unit in a mycological handbook. Though the complex nature of the lichens is discussed and it is admitted that "lichens are polyphyletic in origin" no effort has been made to integrate them in a mycological system. It is well known that the concepts Ascoloculares and Ascohymeniales introduced by NANNFELDT (1932) have proved to be useful for the classification of lichens. HALE (1967, cf. review in Bot. Notiser 1968 p. 136), following LUTTRELL (1951) and SANTESSON (1952), has proposed a system for the integration of the lichens with the fungi. The ascolocular lichenized fungi form a minor group (included in the orders Pleosporales and Hysteriales), whereas the ascohymenial groups are referred to Sphaeriales (comprising the major part of the "pyrenocarpous lichens"), Lecanorales (± equalling the "gymnocarps") and Caliciales (± equalling the "coniocarps"). It is surprising that the last-mentioned three orders have no entries in the Dictionary.

Some minor remarks. The Swedish lichenologist ACHARIUS is said to have lived at Wadstena, Lake Mälar (should be Lake Vetter). The American lichenologist TUCKERMAN was professor at Amherst (not at Farlow); ALEXANDER ZAHLBRUCKNER died in 1938 (not in 1933). "Steiner's stable PD solution" is said to contain Na_2SO_4 (instead of Na_2SO_3). The lichen genus *Lecanephebe* is recorded as described by FREY (1929). It should have been added that its only species was identified as *Zahlbrucknerella calcarea* by HENSSEN (1963).

The critical reader will find several similar corrigenda. He will appreciate, however, the treasure of useful information to be found in this condensed volume. Undoubtedly the rapid progress in mycology and the equally increasing number of mycologists will make a new edition necessary in the near future.

OVE ALMBORN

NORDIN, I.: Caloplaca, sect. Gasparrinia i Nordeuropa. Taxonomiska och ekologiska studier. — Thesis for Ph.D. degree, Institute of Systematic Botany, Uppsala, 1972. X+184 pp. 16 photographs (black-and-white), 15 distribution maps. Price Sw. Cr. 30:— (paperback).

The lobate, orange-yellow species of the lichen genus *Caloplaca* have mostly been recorded as sect. *Gasparrinia,* exceptionally as a proper genus. They include some well-known species, often ecologically specialized, e.g. *C. marina,* which is restricted to a belt on marine rocks just above the *Verrucaria maura* belt, and *C. murorum,* a calciphilous apophytic lichen occurring fairly commonly on mortar. The present study is a monograph of the 14 species of *Gasparrinia* occurring in N.W. Europe, i.e., the four Scandinavian countries and adjacent territories. Somewhat surprisingly, from a taxonomist's point of view, we also find two other species treated, viz. *C. chrysodeta* (sect. *Leproplaca*) and *C. aractina* (sect. *Caloplaca*). The former has been mistaken for *C. citrina,* the latter often grows together with *C. verruculifera.*

The species in question are treated in detail, including synonymy, morphology, history of discovery in Scandinavia, ecology and distribution in N.W. Europe. Extra-Scandinavian distribution is briefly recorded. For most species all localities known are mentioned, and their distribution is illustrated by dot maps. Correlations with ecological and other factors, e.g., salinity and amount of limestone in the substrate, are discussed. In some cases, a comparison is made with the distributional areas of species recorded in HULTÉN's Atlas of the distribution of vascular plants in N.W. Europe.

NORDIN has added many new facts to our knowledge of these species. *C. microthallina,* unknown from N.W. Europe before 1966, has proved to be a fairly common lichen on marine rocks (up to Trondheim, Ångermanland and S.E. Finland). Following POELT, NORDIN has treated *C. verruculifera* (an ornithocoprophilous species common on marine rocks) as different from *C. granulosa* (known from calcareous rocks mainly in the Alps, not recorded from N.W. Europe). An interesting type of distribution is represented by *C. heppiana,* which, in the area under consideration, is known from calcareous rocks and mortar mainly in Öland, Gotland and southern Denmark but also, in isolated localities, in western Norway and central south Sweden (Alvastra). It should be looked for elsewhere. *C. citrina,* mostly recorded under sect. *Caloplaca,* is treated in a broad sense to include *C. phlogina* and collections reported as *C. microphyllina* from Sweden and Denmark. The latter is a lobate species mainly known from N. America. It is evident that its range of variation should be studied further.

Some species with very restricted distributional areas are particularly interesting, viz. *C. biatorina* (one station in Sweden: Visingsö in Lake Vetter), *C. proteus* (ditto: Härjedalen, Tännäs) and *C. tominii* (some localities in central Norway). The first two of these are published by NORDIN as new to Sweden.

The polymorphous lichen *C. murorum* (incl. *C. miniata, C. pusilla, C. steropea, C. tegularis* etc.) is recorded as *C. saxicola* (HOFFM.) NORDIN comb. nov. This procedure is, unfortunately, necessary from a nomenclatural point of view. It is surprising however, to find *Lecanora lobulata* FLOERKE listed as a synonym under this species. FLOERKE's taxon is not a nomen nudum, as NORDIN believes, but is validly described in the schedae of "Deutsche Lichenen Fasc. I" (1815). This is the basionym of the lichen known as *Xanthoria lobulata* (FLK.) B. DE LESD. The combination "*Caloplaca lobulata*" with varying authors' names has been attributed to different lichens. As stated by NORDIN, it was often used in the first two decades of this century for the lichen now known as *C. marina*. It may be added, though this is outside the scope of NORDIN's paper, that "*C. lobulata*" in the sense of North American lichenologists is another saxicolous lichen somewhat similar to *C. marina*, but growing at high altitudes. It seems to be fairly frequent in the Rocky Mountains. Dr. W. A. WEBER, Boulder, Colorado, has suggested (in litt.) that it may be identical to *C. squamosa* (B. DE LESD.) ZAHLBR. This complex is well worth a detailed study.

As is evident from the above remarks Dr. NORDIN's treatise is a stimulating and important work on this interesting group of lichens. The non-Scandinavian reader will regret that it is written in Swedish (with a brief summary in English). When defending his thesis at Uppsala (on May 15, 1972) the author promised, however, that a revised edition in English will be published later.

OVE ALMBORN