Vivi Täckholm

DEDICATED TO

VIVI TÄCKHOLM

ON HER 75th BIRTHDAY
JANUARY 7th, 1973

BY THE LUND BOTANICAL SOCIETY

Vivi Täckholm 75 Years Old

When Vivi Täckholm came to Egypt for the first time in 1926, her husband Professor Gunnar Täckholm (1891—1933) had already spent one year in the country. He had been invited by the authorities at the Egyptian University to establish a Botany department in the newly founded Faculty of Science. The couple started to explore the country and actively collected plants from different localities in order to build up a herbarium that might serve as a base for preparing a flora of Egypt. Several expeditions were made and, as a result, extensive material was deposited in the new herbarium.

From 1929 Vivi Täckholm spent some years in Europe studying the Egyptian plants in the herbaria specializing in oriental floras. In Geneva she worked in the "Conservatoire Botanique" for about 18 months, where the rich collections of Edmond Boissier from the Orient and Alfred Kaiser from Sinai are deposited. In Berlin-Dahlem she studied the important collections of Georg Schweinfurth from Egypt and the neighbouring regions. She also worked at Kew Gardens and British Museum on their rich collections of Egyptian plants. Besides these herbaria, she spent a considerable time studying the collections of Heinrich Haussknecht and Joseph Bornmüller in Weimar, as well as in the Natural History Museum of Stockholm, where ample material from the East Mediterranean is represented. As a result of these studies, she was able to determine her Egyptian collections and to prepare a manuscript on the flora of Egypt with descriptions, local names, uses, etc., as well as keys for their identification.

In 1933 her husband passed away, but the young wife, despite all difficulties, bravely decided to stay in Egypt and carry on the work already planned and started with him.

When the Second World War broke out in 1939, Vivi Täckholm was in Sweden and stayed there, keeping contact with her colleagues in Egypt, until the advent of peace. In 1941 the first volume of the "Flora of Egypt" appeared, carrying the names of Vivi and Gunnar Täckholm in collaboration with Mohammed Drar, as authors. She returned to Egypt in 1946 and again joined the staff of the Botany Department, Faculty of Science, Cairo University. During the years 1947—1948 she was attached to the University of Alexandria. From 1948 until the present day, she has been Professor of Botany in the Faculty of Science, Cairo University. Since her return to Egypt she has hardly ever spent any long periods outside the country. During her short occasional travels abroad, she has always longed to be back in her second home, Egypt. During these years she was engaged in research on Egyptian plants whilst continuing to collect plants, at the same time, with her numerous Egyptian students. Consequently the Herbarium (CAI), established in 1925, now contains some 200,000 specimens, mainly Egyptian plants.

The following volumes of her encyclopedic "Flora of Egypt", with Mohammed Drar, were published: vol. 2, 1950; vol. 3, 1954 and vol. 4, 1969, covering the Monocotyledons and the beginning of the Dicotyledons. This well-known flora deals with both wild and cultivated plants from Pharaonic to modern times. A comprehensive literature is listed in connection with every chapter. For some plants like Wheat, Barley, Date Palm, Papyrus, etc., having a special interest in relation to the ancient history of Egypt, full information is also given on their cultivation, economy, etc., in addition to the botanical details.

In 1951, her book "Faraos Blomster" came out, richly illustrated and containing the most valuable information on the plants of Ancient Egypt. Her "Students' Flora of Egypt", 1956, was a very welcome work containing in one volume all the Egyptian wild and naturalized plants hitherto known. A second edition will soon be published with many additions, numerous illustrations and colour plates.

In 1968 she initiated a new annual series, Publications of the Cairo University Herbarium, of which four numbers have appeared: 1. Street Trees in Egypt by M. NABIL EL-HADIDI and LOUTFY BOULOS, 1968 (reprinted 1970); 2. Alfred Kaiser's Sinai-Herbarium by VIVI TÄCKHOLM, 1969; 3. A Botanic Expedition to the Sudan in 1938 by MOHAMMED DRAR, edited after the author's death with introductory notes by VIVI TÄCKHOLM, 1970; 4. Results of a Botanic Expedition to Arabia in 1944—1945 by AHMED KHATTAB and M. NABIL EL-HADIDI, 1971.

In addition to her research, she has been actively engaged in teaching Plant Taxonomy and Flora of Egypt to undergraduate students at the Egyptian universities up to the present day. She has supervised two Master of Science Theses in Cytotaxonomy: one on the genus *Launaea* (Compositae) submitted by AMAL AMIN in 1957 and the other on the genus *Sonchus* (Compositae) submitted by LOUTFY BOULOS in 1960.

Almost daily, research workers bring their plant material for identification, or seek some item in the rich Herbarium Library which she established and enriched almost entirely through her own interest. This Library was generously offered to Cairo University. There is hardly any botanist in Egypt who is not a student of VIVI TÄCKHOLM's, or any amateur botanist who has not taken part in her happy excursions.

During recent years, she has published a series of books on Egypt, not particularly botanical but most useful, and now becoming indispensable, especially for the visitors interested in that subject, drawing upon her long and unique experience of the flora of Egypt and Egyptian civilization, past and present. These are: Egypten i Närbild, 1964; Faraos Barn, 1965; Egyptisk Vardag, 1966; Levande Forntid, 1967; Öknen Blommar, 1969; Sagans Minareter, 1971.

VIVI TÄCKHOLM represents a supreme example of the way in which cooperation between different countries possessing different cultures, climates and habits can be achieved through a single individual. For her Egyptian students, Sweden is symbolized by VIVI TÄCKHOLM and for her compatriots passing through, visiting or working in Egypt, their visits are incomplete if they fail to pay a visit, or rather a pilgrimage, to VIVI TÄCKHOLM.

On the occasion of her seventy-fifth birthday may I, as one of her younger students and most attached disciples, who has known and followed her for the last twenty years, wish her, for many years to come, a felicitous continuation of the unique work to which she has given such love and devotion.

LOUTFY BOULOS

Drawings of Scandinavian Plants 81–82

Chenopodium L.

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Sect. **Eublitum** Moq.

Glabrous species, with inflorescences composed of more or less orbicular, dense cymes, at fruiting stage similar to strawberry, due to the fleshy, juicy and reddish perianths. Stamen 1. Seeds vertical, in terminal flowers rarely horizontal. Testa almost smooth, lustrous. Embryo horseshoe-shaped. Section *Eublitum* comprises two or three species previously cultivated as a leaf vegetable. The succulent glomeruli are sweet and have been used as a delicacy. They also contain a red pigment used to improve the colour of wine. The seeds contain saponin.

81. **Chenopodium capitatum** (L.) Ascherson 1864

Annual, 15—60 cm high, erect or ascending, more or less branched. Stem angular. Foliage green. Leaves alternate, the lower ones long-petiolate, petiole equal to or longer than the leaf, triangular to hastate, with a hastate to somewhat cuneate base, acute, up to 8 cm long, length usually greater than breadth. Margins entire to dentate or with unevenly distributed, large teeth, and with generally prominent, outward-pointing basal lobes. Upper leaves triangular to rhomboid, entire or dentate, with or without basal lobes. Inflorescence of orbicular, sessile, glabrous cymes, the lower cymes distinctly separated, bracteate, the terminal ones clustered, ebracteate. A single cyme up to 1.5 cm in diameter, compact, consisting of a variable number of hermaphrodite and female flowers, at fruiting stage reddish, juicy and berry-like. Perianth united to a length of 1/3, 3—5-merous. Lobes ovate, broad to narrow, acute to obtuse, rounded, not keeled. Midvein indistinct. Stamen 1. Stigmas 2, papillate to the base, filiform, style short. Seeds vertical, at maturity detached from the perianth, brown to black, orbicular to elliptical, 0.6—1 mm in diameter, with a rather narrow, elliptical ridge, thus appearing keeled in transection. Pericarp white to brownish, thin, closely attached to the testa. Testa almost smooth, except for small, insignificant pits, lustrous. Radicula situated opposite the vestiges of the style, short, thick and with the apex attached to the seed. Embryo horseshoe-shaped.

Flowering time: June to August.

Chromosome number: 2n = 16, 18.

Habitat and distribution: *Ch. capitatum* occurs as a weed in biotopes influenced by man, as in gardens, on road-sides and waste places. Its origin is uncertain and it has been proposed that *Ch. capitatum* is only a cultivated form of *Ch. foliosum*. However, some of the differences between the species are so marked that this seems unlikely. *Ch. capitatum* is scattered throughout most of Europe, the southern and European parts of USSR and of North America. It is relatively rare and occa-

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[1] Engstrand is responsible for the drawings and Gustafsson for the text.

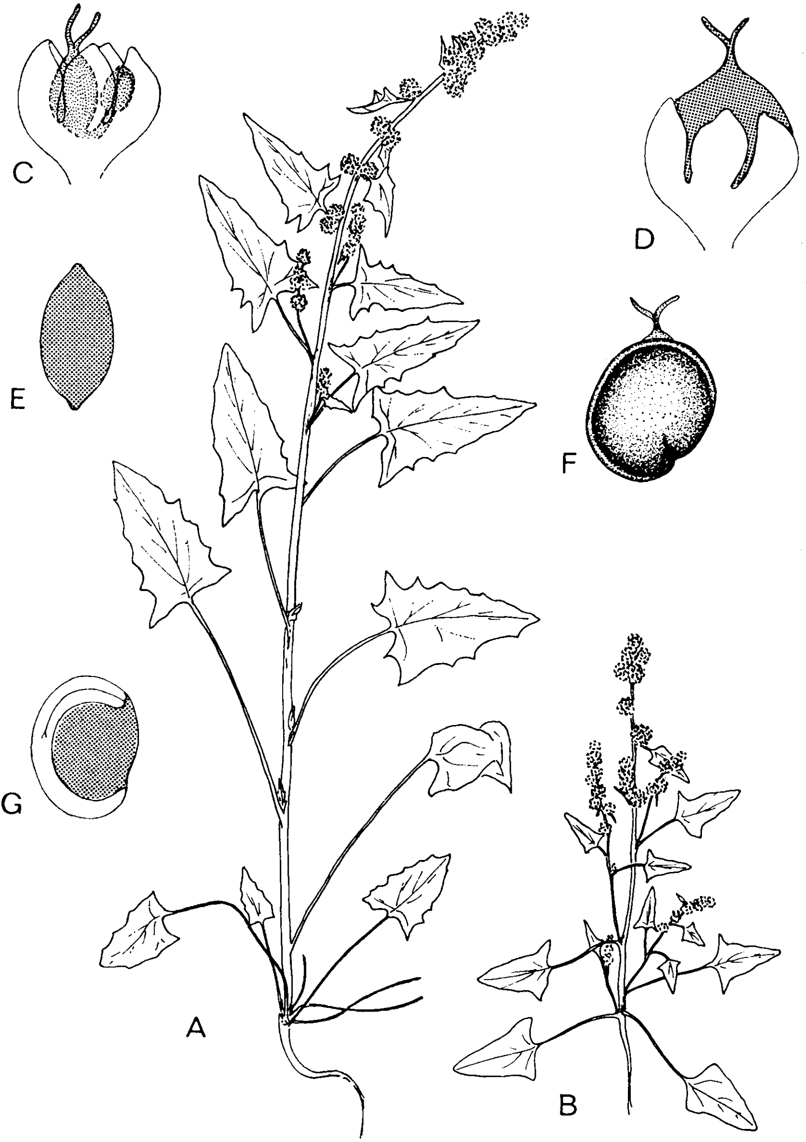

Fig. 81. *Chenopodium capitatum* (L.) ASCHERSON. — A: Habit, normal form. — B: Habit, extremely small plant. — C: Hermaphrodite flower. — D: Fruit enclosed in the perianth. — E: Seed in transection. — F: Fruit with pericarp, showing the position of the radicula in relation to the vestiges of the style. — G: Section through a seed, showing the embryo. — A—B: ×0.5. — C—G: ×20.

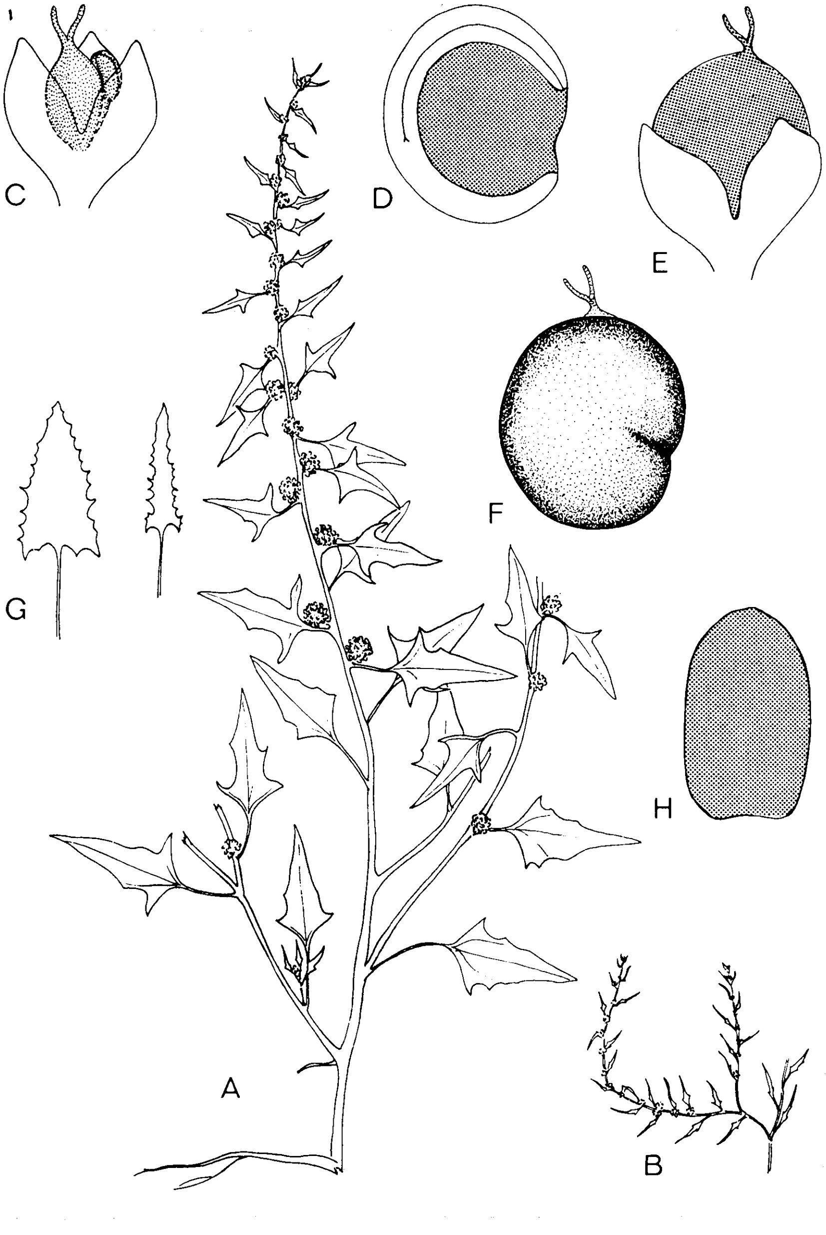

Fig. 82. *Chenopodium foliosum* (MOENCH) ASCHERSON. — A: Habit, normal form. — B: Habit, var. *minus* (VAHL) AELLEN. — C: Hermaphrodite flower. — D: Section through a seed, showing the embryo. — E: Fruit enclosed in the perianth. — F: Fruit with pericarp, showing the position of the radicula in relation to the vestiges of the style. — G: Shape of lower leaves. — H: Seed in transection. — A, B and G: ×0.5. — C—F and H: ×20.

sional in Scandinavia. According to HANSEN & PEDERSEN (1968) only a few reliable records are known from Denmark, mainly from the provinces of Sjælland, Fyn and Jylland. In Sweden it occurs in isolated localities from Skåne to Dalarna and in Norway mainly in the southernmost part, north to Sör-Tröndelag. Very few localities are reported from Finland.

Comments: *Ch. capitatum* has been confused with *Ch. foliosum,* but they can be separated on many characters. *Ch. capitatum* has no bracts in the upper part of the inflorescences, the cymes are larger and partly clustered and it has smaller seeds with conspicuously keeled margins.

82. **Chenopodium foliosum** (MOENCH) ASCHERSON 1864

Annual or sometimes biennial, usually 20—80 cm high, erect or ascending, branched. Stem rounded or angular, green striated. Glabrous or with few glandular hairs. Leaves alternate, the lower ones more or less long-petiolate, triangular to hastate, with a truncate to somewhat cuneate base, up to 7 cm long, often much less, 1—3 times as long as broad. Leaf margins variable, usually serrate to dentate. Upper leaves rhomboid to lanceolate, dentate to entire, generally with prominent basal lobes. Inflorescence conspicuously bracteate and consisting of many sessile or shortly stalked, orbicular, distinctly separated cymes, distributed along the main stem and the branches. A single cyme up to 1 cm in diameter, composed of a variable number of hermaphrodite and female flowers. Perianth of the central flowers in the cymes 4- or 5-merous, that of terminal ones usually 3-merous, glabrous, at anthesis green, at fruiting stage reddish and fleshy, united to a length of 1/3 or 1/4. The lobes broadly ovate, obtuse to somewhat acute, rounded, not keeled. Midvein indistinct to apparent. Stamen 1. Stigmas 2, papillate to the base. Seeds predominantly vertical, at maturity detached from the perianth, reddish-brown to black, orbicular to broadly ovoid, broadest in the upper part, 0.9—1.5 mm in diameter. Margins obtuse. Pericarp thin, white to brownish, closely and firmly attached to the testa. Testa lustrous, almost smooth, except for small pits and furrows. Radicula short, thick, mostly lateral, pointing downwards, apex attached to the seed. Embryo horseshoe-shaped.

Flowering time: June to August.

Chromosome number: 2n=18.

Variation: Most vegetative characters are variable, especially height, and size and shape of upper and lower leaves. One of the most deviating forms is f. *minus* (VAHL) AELLEN (=var. *chenopodioides* (L.) HARTM.), which grows in extremely dry biotopes and is characterized by greatly reduced height and green perianth not fleshy even at fruiting stage.

Habitat and distribution: *Ch. foliosum* occurs sporadically in many biotopes influenced by human activities, particularly in habitats rich in nitrogen, as in gardens, in court-yards, road-sides etc. It is probably only native to mountain regions, in Europe in the Iberian Peninsula and the Alps, further the mountains of Asia to Pamir and Himalaya and in northwest Africa. It occurs as a weed in most countries of Europe, the southern part of Asia, the Middle East, South Africa and North America. In Scandinavia *Ch. foliosum* is recorded from most provinces of Denmark and Sweden northwards to Jämtland and Ångermanland, from Oppland, Buskerud, Telemark and Oslo in Norway, and in the western to southwestern parts of Finland, from Österbotten to Nyland and on Åland.

LITERATURE CITED

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

Révision Systématique du Genre Sonchus L. s.l.

I. Introduction et Classification

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ABSTRACT

Boulos, L. 1972. Révision systématique du genre Sonchus L. s.l. I. Introduction et classification. — Bot. Notiser 125: 287—305.

An account of the history of the work from 1957 till 1972 is given. A historical review of the use of the name *Sonchus* and its systematic position follows. The concepts of taxa used in the revision are discussed in detail. Four genera are recognized within *Sonchus* L. s.l.: *Sonchus* L. including 3 subgenera, 54 species, 5 subspecies and 4 varieties; *Embergeria* Boulos including 2 subgenera and 2 species; *Babcockia* Boulos, monotypic; and *Taeckholmia* Boulos including 2 subgenera and 7 species. Within *Sonchus* L. s.l. 3 genera, 10 species and one subspecies are described and 15 new combinations are made. Detailed descriptions of the 4 genera are given, as well as a key to them. Keys to the subgenera, sections, species, subspecies and varieties are provided.

INTRODUCTION

Dans la famille des Composées, la tribu des Cichorieae renferme quelques genres tels que *Hieracium, Taraxacum, Prenanthes, Lactuca, Crepis, Launaea, Sonchus,* etc. intéressants à divers titres et notamment du point de vue caryosystématique.

Une mesure du champ de recherches ouvert dans ce domaine, peut être donnée par le travail de Babcock (1947), dont le mémoire monumental sur le genre *Crepis,* résume 25 années d'études caryologiques, génétiques, morphologiques, géographiques, paléobotaniques, etc. Notre collègue, Mme Amin, s'est d'ailleurs inspirée de cette monographie pour son travail sur le genre *Launaea* (1957). Notre étude du genre *Sonchus* voudrait contribuer de la même façon à la connaissance de ce groupe. Nous l'avons commencée en 1957 à l'Université du Caire, où nous avons étudié les espèces égyptiennes du genre *Sonchus* du point de vue morphologique, écologique et caryologique. Ces recherches nous ont montré le polymorphisme de quelques espèces comme *S. oleraceus* et *S. asper,* et en 1958, nous avons eu la chance de découvrir une nouvelle espèce tetraploïde, *S. macrocarpus* (cf. Boulos 1959; Boulos & Jeffrey 1969), dans le delta du Nil.

Pendant les trois mois de l'été 1958, et grâce à la bourse que nous devons à Monsieur B. Eng, ancien Ambassadeur de Suède au Caire, nous avons étudié un grand nombre d'échantillons d'herbier appartenant à l'herbier du Naturhistoriska Riksmuseet de Stockholm. D'autres échantillons nous ont été prêtés, soit à Stockholm (été 1958), soit au Caire (1959—1960) par les herbiers de C, G, LE, O et W (abbreviés d'après l'Index Herbariorum).

En 1959—1960 nous avons préparé au Caire une étude préliminaire sur les caractéristiques générales du genre, ainsi qu'une classification préliminaire en trois sous-genres (BOULOS 1960 a, 1960 b). Les espèces rangées dans chaque sous-genre correspondaient seulement aux échantillons que nous avions pu examiner, la liste des espèces n'étant pas complète. Le nombre d'espèces du genre *Sonchus,* citées en bibliographie et restant à analyser, démontrait la nécessité d'une étude plus détaillée et plus complète.

En automne 1960, nous avons eu la chance d'avoir une bourse de l'UNESCO, pour une période de deux ans, à l'institut de Botanique de l'Université de Montpellier. Monsieur le Professeur L. EMBERGER, Directeur de l'Institut de Botanique, Correspondant de l'Institut, a bien voulu accepter de surveiller notre travail. Nous tenons à rendre à sa mémoire un hommage particulierement reconnaissant.

En 1961, nous avons visité l'archipel des Canaries pendant un mois (mai—juin) et effectué un court voyage de deux jours au Maroc. Durant ce voyage, nous avons récolté des échantillons d'espèces endémiques du genre *Sonchus* de toutes les îles, sauf Gomera et Hierro. Au Maroc, nous avons récolté *S. pinnatifidus* qui est un élément canarien. Malgré notre court passage aux Îles Canaries, nous avons pu nous faire une idée générale sur quelques espèces, leur répartition, leur morphologie, leur polymorphisme et leur habitat.

Une étude dans les herbiers importants était nécessaire pour examiner l'ensemble du matériel, ce qui nous a amené à visiter les herbiers de BM, BR, CGE, G, K et P.

Plusieurs échantillons du genre *Sonchus* nous ont été prêtés et expédiés à Montpellier en 1961—1962; ils provenaient des herbiers de AD, B, BM, BR, CGE, G, K, L, LD, MA, O, P, UPS.

En 1962, nous avons de nouveau fait un séjour de deux semaines (avril—mai) au Maroc pendant lequel nous avons trouvé *S. pinnatifidus* en fleurs et en fruits, ainsi que *S. bourgeaui,* un autre élément canarien, nouveau pour la flore du Maroc.

Après avoir classé ces échantillons, nous avons remarqué que la moitié environ des espèces du genre *Sonchus* qui sont des espèces endémiques des Îles Canaries, sont peu abondantes dans ces collections. En outre, la plupart de ces espèces endémiques sont représentées par un petit nombre d'échantillons, lequel s'est révélé insuffisant pour nous permettre d'avoir une idée précise sur les caractères morphologiques, et spécialement sur la répartition géographique des espèces. Un autre voyage aux Îles Canaries était donc indispensable.

Durant deux mois (juin—août 1962), nous avons récolté de nouveau des spécimens d'espèces canariennes, surtout dans les îles peu fréquentées et, de ce fait, moins connues: Gomera, Hierro et La Palma. Nous avons aussi consacré une semaine à une visite de l'île de Madère où sont réunies trois espèces endémiques, que nous avons trouvées pendant leur période de floraison et de fructification. Nous avons récolté non seulement des échantillons d'herbier, mais aussi de jeune capitules, des akènes et des grains de pollen pour les études caryologiques et palynologiques.

Au cours de notre séjour en France (octobre 1960—janvier 1963) nous avons preparé quelques études préliminaires (BOULOS 1961, 1962 a, 1962 b).

En janvier 1963 nous avons presenté une thèse pour obtenir le grade de Docteur ès Sciences Naturelles d'État à l'Université de Montpellier.

Pendant la période 1963—1972 nous avons essayé de corriger et de compléter la monographie. Quelques brochures ont été publiées surtout pour des raisons de priorité (BOULOS 1965 a, 1965 b, 1967 a, 1967 b, 1967 c, 1968 et en 1969 avec C. JEFFREY). Entre-temps, nous avons effectué plusieurs voyages en Europe pour mettre au point le manuscript pour la publication. Nous avons visité B, BM, BR, CGE, E, FI, G, L, LD, M, MANCH, O, P, RNG, S, UPS et Z. La monographie est publiée dans "Botaniska Notiser" de l'ans 1972 et 1973.

Durant la réalisation de ce travail, plusiers amis et collègues n'ont cessé de nous aider par tous les moyens. Sans les mentionner, nous les prions, tous, de trouver ici l'expression de notre gratitude et notre reconnaissance.

Nous voudrions exprimer tout particulièrement notre sincère reconnaissance a notre maître, Mme le Professeur VIVI TÄCKHOLM, de l'Université du Caire, qui n'a jamais hésité à nous aider par tous les moyens, et à laquelle nous devons notre formation de botaniste.

HISTORIQUE

Le nom grec "σόγχος" (Sonchos), latin "Sonchus", est probablement dérivé de "σομφος", qui signifie spongieux ou creux, en raison de la nature délicate des tiges des premières plantes connues de ce groupe.

Ce nom fut utilisé par THÉOPHRASTE (370—285 A.J.) dans son "Étude des Plantes" (vi: 4, 3, 8), par PLINE L'ANCIEN (77 A.D.) dans son "Histoire Naturelle" (Historia Naturalis XXI, 88) et par DIOSCORIDE (d.c. 78 A.D.) dans son "Materia Medica Libri Quinque" (II, 131).

Dans l'Herbier de DIOSCORIDE, illustré par un Byzantin en 512 A.D. (cf. GUNTHER 1934), nous trouvons deux illustrations de *Sonchus oleraceus* et *Sonchus asper.*

"Codex Aniciae Julianae", le plus ancien herbier illustré (cf. STEARN 1954), renferme une illustration de *Sonchus asper* qui portait le nom de "*Sonchos trachus*".

Pendant le Moyen-Âge, le nom *Sonchus* fut employé dans l'herbier de LEONARD FUCHS (1542).

TOURNEFORT (1700) donna la description suivante: "Sonchus est plantae genus, flore A semiflosculose, plurimis scilicet semiflosculis B constante, embryoni C insidentibus et calyce crasso D comprehensis, qui per maturitatem conicus E ferè evadit. Embryo autem abit deinde in semen G pappis instructum H, thalamoque F affixum".

VAILLANT (1718—1721) distingua *Sonchus* de *Crepis*: "Sonchi: Semina glabra. — Crepis: Semina aculèolata".

LINNAEUS (1735) conserva le nom *Sonchus* et le classa sous la rubrique "Syngenesia, Monogamia, B semiflosculosi, T. *Sonchus*".

La description de *Sonchus,* LINNAEUS (1737 a) fut plus détaillée: "*Sonchus.* Tournef. 268. Vaill. A.G. 1721—22. *Crepis* Vaill. A.G. 1721. 55. 23.

Cal: Communis ventricosus: squamis plurimis, linearibus, inaequalibus.
Cor: Composita imbricata, uniformis: corollulis hermaphroditis numerosis, aequalibus, propria monopetala, ligulata, linearis, truncata, quinquedentata.
Stam: Filamenta quinque, capillaria, brevissima. Anthera cylindracea, tubulata.
Pist: Germen infra corollam propriam. Stylus filiformis, longitudine staminum. Stigmata duo, reflexa.
Per: Nullum. Calyx connivens in globum depressum, acuminatum.
Sem: Solitaria, oblongiuscula, coronata pappo simplici.
Rec: Nudum.
Obs: Sonchi V. Semina glabra.
(Crepis V. Semina aculeolata)."

LINNAEUS (1737 b) divisa le genre *Sonchus* en groupes sans donner leurs caractéristiques générales. Il décrivit (1753) les espèces suivantes:

1. *Sonchus canadensis*
2. *S. palustris*
3. *S. arvensis*
4. *S. oleraceus* (avec les variétées α, β, γ et δ)
5. *S. tenerrimus*
6. *S. alpinus*
7. *S. floridanus*
8. *S. sibiricus*

Les espèces 2, 3, 4 et 5 sont des vrais *Sonchus*; 1, 7 et 8 appartiennent au genre *Lactuca* et 6 est un *Cicerbita.*

Une grande confusion continua à régner

après l'époque de LINNAEUS, du fait du manque de précision dans la conception du genre et de l'ignorance des travaux publiés. Le résultat en fut l'accumulation, dans la bibliographie, d'un grand nombre de synonymes et d'espèces appartenant à d'autres genres.

LES CONCEPTIONS DES TAXONS DANS CE TRAVAIL

Depuis l'époque linnéenne, les biologistes essaient d'établir des principes pour définir les différents taxons. On trouve dans leurs nombreux ouvrages des conceptions également nombreuses et souvent très différentes et contradictoires. Aussi, au cours de l'examen d'un groupe de plantes du point de vue systématique, trouve-t-on rarement des lignes de démarcation claires séparant les taxons, surtout pour les unités infraspécifiques. Il est inutile de rappeler que la definition de l'espèce reste jusqu'à nos jours un des problèmes les plus importants et les plus délicate de la biologie moderne.

Les conceptions modernes sur lesquelles sont basées les catégories taxonomiques font appel aux disciplines les plus diverses, morphologie au sens le plus large, donc incluant l'anatomie, la palynologie et les caractères des chromosomes, écologie, répartition géographique, caractères chimiques et physiologiques, etc. La systématique, pour déceler les liens de parenté entre les taxons, demande le concours de toutes les disciplines; elle est une science de synthèse.

Dans ce mémoire, nous avons donc pris en considération, pour délimiter les différents taxons, le plus grand nombre de caractères possibles, notamment les caractères morphologiques, écologiques, biogéographiques, caryologiques et palynologiques.

Avant de rappeler les conceptions générales qui ont été appliquées à un grand nombre de groupes systématiques, et peut-être à toutes les Phanérogames, les espèces apomictiques exceptées, nous voudrions attirer l'attention sur le fait suivant:

Dans le genre *Sonchus,* toutes les espèces du sous-genre *Dendrosonchus* et la plupart des espèces des autres deux sous-genres, *Origosonchus* et *Sonchus,* possèdent le même nombre chromosomique, c.-à-d. 2n=18. L'aide que le nombre chromosomique peut apporter à la séparation des taxons de ces sous-genres, lorsqu'ils possèdent le même nombre de chromosomes, est donc très faible.

Il est probable que la différence entre la structure de leurs chromosomes soit à l'origine des barrières de stérilité entre les espèces et, partant, la cause de la différentiation taxonomique. Autrement dit, et comme RUNEMARK (1961) l'a constaté: Entre deux espèces qui possèdent le même nombre de chromosomes, mais ayant des structures chromosomiques dissemblables, la dissemblance des gènes, même d'un seul, peut déterminer une barrière génétique des hybrides stériles. Cet auteur admet que les écotypes, les races géographiques et biologiques morphologiquement bien distinctes, ainsi que les types morphologiquement différents, et plus ou moins génétiquement isolés, sont des sous-espèces.

VALENTINE & LÖVE (1958) ont énoncé le principe suivant: Quand les différences morphologiques et écologiques entre deux populations sont peu importantes, et que l'expérimentation démontre l'interfertilité complète, les populations en question ne doivent pas être traitées comme espèces. Mais si ces différences sus-indiquées sont considérables, et s'il existe des barrières génétiques s'apposant à l'échange des gènes, il faut considérer ces taxons comme espèces.

LÖVE (1960 a) a constaté que le critère de l'isolement sexuel, c.-à-d. la barrière, cause de stérilité, n'est pas toujours facile à déterminer; ce critère n'est donc pas facile à utiliser pour séparer deux espèces. Cet auteur ajoute que: "Morphological differences are essential to those who deal with classification, but they are usually of minor significance for the plant itself." Pour lui les chromosomes sont les caractères fondamentaux d'une espèce, car ils détermineraient tous les caractères visibles et invisibles de la plante.

Beaucoup d'auteurs ont traité le problème de la définition des catégories taxonomiques, mais il est hors de notre travail de les résumer tous ici. Nous renvoyons le lecteur aux travaux de quelques-uns seulement, en raison de la place qu'ils occupent dans l'histoire de la systématique.

Les principaux travaux classiques sont ceux de RAY (1686), LINNAEUS (1751), JUSSIEU (1789), LAMARCK (1809), DE CANDOLLE (1813) et DARWIN (1859). De la bibliographie moderne, nous citons les ouvrages suivants: MATTHEW (1915), TURESSON (1922 a, b), WODEHOUSE (1928), DU RIETZ (1930), CUÉNOT (1932, 1936), DOBZHANSKY (1935, 1951), DARLINGTON (1939, 1956), HUXLEY (1940, 1942), CLAUSEN (1941), MAYR (1942, 1957, 1958), VALENTINE (1949), STEBBINS (1950), LÖVE (1954, 1960 b, c, 1962), GOOD (1956), VAN STEENIS (1957), HEDBERG (1958), MANN (1959), EMBERGER (1960), BEAUDRY (1960), etc. (Les ouvrages édités par HUXLEY (1940), MAYR (1957) et de HEDBERG (1958) contiennent de nombreux articles communiqués par plusieurs auteurs sur le même sujet.)

Le but de ce chapitre n'est pas la définition des différentes unités systématiques en général, mais seulement la délimitation des taxons traités dans ce travail; nous pensons que la définition d'un rang systématique doit être conçue après une étude détaillée des taxons. Il est probable que cette définition, au moins du point de vue de la morphologie, doit être adaptée pour chaque genre, et peut-être à l'intérieur d'un même genre.

Nous exposons ci-dessous la définition des différents taxons retenus pour cette étude. Il nous paraît utile de répéter encore que ces définitions ne sont valables que pour le groupe de plantes que nous avons étudié; pour les autres, elles peuvent naturellement être différentes.

LA FORME

Le terme "forme", latin *forma,* ne sera pas utilisé dans notre mémoire au sens taxonomique.

La conception de la *forme* varie suivant les auteurs. Pour les uns, elle a une valeur taxonomique réelle, basée sur un seul caractère héréditaire de faible importance dans l'ensemble, mais stable. Pour les autres, la *forme* est le résultat de l'action temporaire du milieu, donc se modifiant avec celui-ci.

Quand à nous, nous comprenons sous ce nom les individus qui diffèrent de la forme-type de l'espèce par des caractères, surtout morphologiques, peu significatifs, dus à l'influence du milieu. Exemple: *Sonchus oleraceus* est une espèce polymorphe, c.-à-d. qu'elle comprend, à notre sens, plusieurs *formes,* représentées par les individus ayant des feuilles de formes différentes. Si les feuilles étaient considérées, dans cette espèce, comme un caractère ayant une valeur taxonomique réelle, toutes ces *formes* devraient être considérées comme taxons différents; le résultat serait l'impossibilité de reconnaître ou de redéterminer ces multiples *formes* à l'intérieur de cette espèce.

Cet exemple nous montre que l'utilisation du terme *forma* (au sens taxonomique) compliquerait la taxonomie du genre *Sonchus,* à l'intérieur de cette espèce et des espèces polymorphes en général. C'est la raison pour laquelle nous n'utiliserons pas, dans ce travail, le terme *forma*; le taxon le plus inférieur sera la variété.

LA VARIÉTÉ

Le terme "variété", latin *varietas,* délimite les taxons qui diffèrent de la variété-type de l'espèce par un caractère ou un petit nombre de caractères stables, et sont interfertiles, quel que soit l'isolement géographique. Autrement dit, deux variétés appartenant à la même espèce doivent être interfertiles, qu'elles se trouvent dans la même population ou dans deux populations géographiquement éloignées. En outre, cette interfertilité doit pouvoir être réalisée artificiellement, en donnant le même résultat que dans la nature. Une variété doit, bien entendu, être égalemant interfertile avec la variété-type de l'espèce.

Les variétés sont souvent mélangées avec la variété-type de l'espèce, dans l'aire géographique de celle-ci.

LA SOUS-ESPÈCE

Le terme "sous-espèce", latin *subspecies,* délimite les taxons immédiatement inférieurs à l'espèce et qui diffèrent de la sous-espèce-type de l'espèce par un caractère ou quelques caractères morphologiques stables et assez saillants, et dont les individus sont en partie interfertiles aussi bien entre eux qu'avec la sous-espèce-type de l'espèce.

Une sous-espèce peut être une race géographique, ou quelquefois, un écotype de l'espèce. Les écotypes et les races géographiques et biologiques morphologiquement bien distincts, ainsi que les types morphologiquement différentes et plus ou moins génétiquement isolés, peuvent avoir le rang de sous-espèces (RUNEMARK 1961).

Une sous-espèce, selon nous, ne doit pas obligatoirement présenter des différences morphologiques avec la sous-espèce-type de l'espèce plus importantes que la variété, car nous croyons que la distinction entre sous-espèce et variété d'une même espèce doit être basée, avant tout, sur les différences d'ordre génétique et géographique mentionnées ci-dessus.

En l'attente de données expérimentales, surtout génétiques, et comme les caractères morphologiques seuls ne suffisent pas pour délimiter la sous-espèce et la variété, on pourra souvent résoudre les problèmes en ayant recours à la répartition géographique.

Donc, selon nous, et c'est ainsi que nous avons employé ce terme, une sous-espèce est, en principe, géographiquement isolée de la sous-espèce-type de l'espèce, alors qu'une variété est pratiquement mélangée avec l'espèce à l'intérieur de l'aire géographique de celle-ci.

L'ESPÈCE

Le terme "espèce", latin *species,* constitute un problème impossible à exposer en quelques phrases, non seulement dans le genre

Sonchus que nous avons étudié, mais dans tout le règne végétale.

En principe, une espèce représente une ou plusieurs populations d'individus possédant une certaine homogénéité morphologique et faciles à distinguer des individus d'autres populations avec lesquelles elles présentent des barrières de stérilité.

Toutefois, il existe des espèces qui sont morphologiquement voisines, mais complètement isolées du point de vue génétique. En contre-partie, il en existe d'autres qui sont morphologiquement bien distinctes, mais chez lesquelles l'isolement génétique n'existe pas, comme l'ont montré les expériences de croisement.

Pour nous limiter au genre *Sonchus*, indiquons, à titre d'exemple, que *Sonchus oleraceus* L., 2n=32, forme avec *S. asper* (L.) HILL, 2n=18, un hybride stérile, *S. asper*× *oleraceus*, 2n=25 (BARBER 1941).

Sonchus arvensis L., 2n=54, forme avec *S. uliginosus* M. BIEB., 2n=36 un hybride fertile possédant 2n=45. Les individus de cet hybride se croisent facilement entre eux, ainsi qu'avec les parents (SHUMOVICH & MONTGOMERY 1955).

Comment faut-il classer ces plantes, et quel rang taxonomique doit-on donner à chacune d'elles?

La stérilité du premier hybride, *S. asper*× *oleraceus*, confirme l'existence de barrières génétiques entre ses parents, donc *S. asper* et *S. oleraceus* doivent être considérés comme deux espèces distinctes.

Dans la deuxième cas, il faut considérer *S. arvensis* comme une espèce, et *S. uliginosus* comme une sous-espèce de *S. arvensis* pour les raisons suivantes: a) *Sonchus arvensis* L. est une espèce décrite en 1753, avant *S. uliginosus* BIEB. 1808 (point de vue nomenclature). b) La fertilité de l'hybride confirme l'absence de barrières de stérilité entre les deux taxons (point de vue génétique). c) Les deux taxons existent en mélange dans une partie limitée de leurs aires de répartition (point de vue phytogéographique). d) On peut distinguer les deux taxons d'après quelques différences morphologiques stables (point de vue morphologique).

Dans ce travail, nous ne considérons pas *S. uliginosus* BIEB. ni comme une espèce (SHUMOVICH & MONTGOMERY 1955) ni comme une variété (plusieurs auteurs), ni comme une forme (KIRPICZNIKOV 1964), ni un synonyme de *S. arvensis* (BOULOS 1961), parce que les nombres chromosomiques sont différents chez les deux taxons.

Quelle est la valeur taxonomique des deux hybrides dont il a été question ci-dessus? Faut-il les considérer comme des taxons? Et de quel rang?

La réponse n'est pas la même pour les deux cas envisagés: *S. asper*×*oleraceus* est un hybride stérile, qui est incapable de se reproduire et ne peut pas exister sans ses parents. Une population isolée et constituée uniquement de cet hybride disparaîtra, car il est incapable de se reproduire par voie végétative. Cet hybride ne mérite donc aucun rang taxonomique, parce qu'il ne présente pas une étape dans l'évolution du genre.

Quant à l'autre hybride, *Sonchus arvensis*× *S. uliginosus*, que nous avons pris comme exemple, il est impossible de le séparer morphologiquement de l'espèce *S. arvensis* (SHUMOVICH & MONTGOMERY 1955). Mais, malgré sa fertilité et malgré la différence entre les nombres chromosomiques, il faut classer les hybrides comme des races chromosomiques de la même espèce.

Alors, à partir de quel moment un hybride peut-il être considéré comme espèce?

A notre avis, un hybride-espèce est un hybride fertile qu'il est facile à distinguer morphologiquement de ses parents, et qui a réussi à s'insérer dans la chaine évolutive de son genre. Souvent, la plante issue d'une hybridation couronnée de succès remplace ses parents dans leurs aires géographiques. Un exemple: l'espèce hybride *Sonchus*×*pitardii* BOULOS, endémique de l'île d'Hierro (Canaries), a presque complètement remplacé ses parents dans leurs aires géographiques. Nous avons constaté sur place l'abondance nettement plus grande de l'espèce hybride par rapport à celle des parents, *S. gandogeri* PITARD et *S. lidii* BOULOS.

En résumé, la définition des espèces dans ce travail est faite d'après les principes mentionnés plus haut. Mais, dans le cas où les données caryologiques et expérimentales font défaut, l'espèce continue à être définie uniquement par les critères classiques, en se référant naturellement, quand c'est possible, aux espèces définies avec le concours des méthodes cytogénétiques et expérimentales.

LE SOUS-GENRE

Un "sous-genre", latin *subgenus*, comprend les espèces qui représentent, dans leur ensemble, un stade déterminé dans l'évolution du genre.

Les membres d'un sous-genre doivent être reliés les uns aux autres par l'histoire du genre, au cours de son évolution; ils ne sont pas obligatoirement très voisins du point de vue morphologique.

LE GENRE

Un "genre", latin *genus*, comprend un groupe de taxons qui forment dans leurs ensemble une unité bien définie génétiquement et morphologiquement. En d'autres termes, une discontinuité morphologique et génétique doit exister entre les membres de deux genres voisins.

Il arrive quelquefois que certaines espèces appartenant à deux genres voisins soient semblables par leur aspect extérieur, mais l'étude détaillée permet toujours de déceler des différences morphologiques et génétiques importantes. C'est ainsi que certaines espèces du genre *Launaea* ont été décrites comme *Sonchus, Lactuca, Dianthoseris, Rhabdotheca, Lomatolepis, Microrhynchus,* etc. (cf. Boulos 1962 a, Jeffrey 1966) alors qu'elles sont typiquement des *Launaea.*

CLASSIFICATION

La révision du genre *Sonchus* L. sens. lat. (Cichorieae, Liguliflorae, Compositae) nous permet de distinguer les quatre genres suivants: *Sonchus* L. 1754, *Embergeria* Boulos 1965, *Babcockia* Boulos 1965 et *Taeckholmia* Boulos 1967.

CLEF POUR LES GENRES

1\. Akène non comprimé (± cylindrique) .... 3. *Babcockia* (p. 302)
1\. Akène comprimé
  2. Akène pourvu au sommet d'un disque blanc à protubérance centrale .... 4. *Taeckholmia* (p. 302)
  2. Akène sans disque blanc au sommet
    3. Akène 0,5—1,75 mm de large .... 1. *Sonchus* (p. 293)
    3. Akène 2—3 mm de large .... 2. *Embergeria* (p. 301)

1. Genre **Sonchus** L.

Linnaeus, Gen. Pl. (ed. 5): 347, 1754.
Trachodes D. Don in Trans. Linn. Soc. 16: 182, 1830.
Sonchoseris Fourr. in Ann. Soc. Linn. Lyon, N.S. 17: 102, 1869.
Sonchidium Pomel, Nouv. Mat. Fl. Atl. 6, 1874.
Sonchos St. Lag. in Ann. Soc. Bot. Lyon 8: 171, 1881.
Espèce-type: *Sonchus oleraceus* L. emend. Gouan

Plantes annuelles, bisannuelles ou vivaces, dressées, herbacées, suffrutescentes ou plus rarement arbustives, à latex blanc, de 3 à 300 cm de haut. *Organes souterrains*: racines pivotantes (rarement tubéreuses) ou rhizomes rampants portant des racines fibreuses. *Collet* simple ou ramifié, herbacé ou ligneux. *Tige* herbacée ou ligneuse, creuse ou pleine, cylindrique ou légèrement anguleuse, glabre, légèrement tomenteuse ou à poils glanduleux surtout vers le sommet. *Feuilles* en rosette ou caulinaires, non divisées, pinnatifides, pennipartites ou pinnatiséquées, généralement auriculées; marges généralement denticulées. *Pédoncule* de 0,2—16 cm de long, cylindrique, creux, glabre, tomenteux ou à poils glanduleux au sommet, portant 1—12 bractées triangulaires. *Capitules* généralement nombreux, rarement solitaires, généralement cylindriques avant et coniques après l'anthèse, à 36—480 fleurs bisexuées. *Écailles de l'involucre* au nombre de 18—70 par capitule, typiquement imbriquées en 3 séries: les externes généralement triangulaires à base épaisse; les intermédiaires plus longues, plus étroites et plus minces, à marges scarieuses; les internes minces et transparentes. *Corolle* jaune, plus rarement bleue sur la face inférieure chez les fleurs extérieures du capitule, de 10—32 mm de long. *Ligule* généralement linéaire, pourvue au sommet de 4—5 dents courtes. *Tube de la corolle* poilu au niveau de la ligule, glabre et atténué vers la base; ligule et tube de la corolle de même longueur ou l'un plus long que l'autre. *Anthères* 5, formant un tube staminal de 2—5 mm de long et 0,4—0,8 mm de diam., orangé à brunâtre. *Style* à 2 branches de 1—2,5 mm de long, densement poilues et généralement brunâtres. *Akènes* de 2—6,5 mm de long et 0,5—1,75 mm de large, généralement atténués vers les deux extrémités, souvent elliptiques, comprimés et pourvus de 1—4 côtes principales sur chaque face, lisses ou rugueux. *Aigrette* sessile, de 4—14 mm de long, composée de soies dimorphes, les unes solitaires, très caduques, à base épaisse et à aspérités latérales bien developpées; les autres réunies en groupes, cotonneuses et ± persistantes. L'abondance relative de l'un ou l'autre de ces types de soies détermine le caractère caduc ou persistant de l'aigrette. x=7, 8 et 9.

CLEF POUR LES SOUS-GENRES

1. Plantes généralement à tiges ligneuses, aigrette de l'akène caduque. Espèces endémiques des Îles Canaries, Madère et Cap Vert (une espèce aussi au sud-ouest du Maroc) .... II. *Dendrosonchus* (p. 297)
1. Plantes généralement à tiges herbacées; aigrette persistante, moins souvent caduque
    2. Espèces vivaces, endémiques de l'Afrique au sud du Sahara, Madagascar et des Comores; aigrette généralement persistante (trois espèces à aigrette caduque possèdent une taille importante jusqu'à 2—3 mètres) ...... III. *Origosonchus* (p. 299)
    2. Espèces annuelles, bisannuelles ou vivaces, cosmopolites ou d'une distribution non limitée aux régions des autres deux sous-genres .... I. *Sonchus* (p. 294)

I. Sous-genre **Sonchus**

Sonchi genuini W. KOCH, Syn. Fl. Germ.: 433, 1837.

Sonchus Sect. *Eusonchus* DC., Prodr. 7, 1838.

Sonchus Ser. *Oleracei* KIRP. in Nov. Syst. Plant. Vasc. 1964: 342, 1964.

Espèce-type: *Sonchus oleraceus* L. emend. GOUAN

Plantes annuelles, bisannuelles ou vivaces, herbacées ou suffrutescentes, 10—250 cm de haut, à racines pivotantes (rarement tubéreuses) ou rhizomes rampants. *Tige* herbacée, creuse, cylindrique ou légèrement anguleuse, glabre ou à poils glanduleux vers le sommet. *Feuilles* de forme variable, généralement divisées. *Pédoncule* 0,2—10 cm de long, glabre, tomenteux ou à poils glanduleux au sommet et portant 1—8 bractées. *Capitules* généralement nombreux, à 40—300 fleurs. *Écailles de l'involucre* 20—56. *Corolle* 10—24 mm de long. *Ligule* 4—14 mm de long. *Tube de la corolle* 4—14 mm de long. *Akènes* 2—2,5×0,5—1,75 mm. *Aigrette* 4,5—14 mm de long, caduque à persistante. x=7, 8 et 9.

CLEF POUR LES SECTIONS ET LES ESPÈCES DU SOUS-GENRE SONCHUS

1. Akènes fortement comprimés, ailés, à 3 côtes principales sur chaque face, ± lisses; tube de la corolle plus long que la ligule .... section 2. *Asperi*
    2. Plantes à rhizomes rampants ou à racines pivotantes et renflées vers le collet; feuilles principalement en rosette
        3. Plantes à rhizomes .... 6. *S. mauritanicus*
        3. Plantes à racines renflées vers le collet .... 5. *S. littoralis*
    2. Plantes à racines pivotantes et non renflées; feuilles principalement caulinaires (souvent en rosette chez les plantes jeunes de *S. asper* subsp. *glaucescens*)
        4. Akènes 4—5,5 mm long .... 7. *S. macrocarpus*
        4. Akènes 2—3,75 mm long
            5. Akènes typiquement lisses .... 8. *S. gigas*
            5. Akènes ciliés sur les marges et souvent sur les côtes surtout vers les deux extrémités
                6. Plantes annuelles, herbacées .... 4. *S. asper* ssp. *asper*
                6. Plantes bisannuelles ou probablement vivaces, suffrutescentes
                    7. Plantes des milieux subhumides (champs cultivés, jardins, etc.); feuilles pennipartites ou pinnatiséquées; akènes à marges et côtes densement ciliées et recourbées; pollen 30—32 μ de diamètre .... 4 a. *S. asper* ssp. *glaucescens*

7. Plantes des milieux très humides; feuilles non divisées ou pinnatifides; akènes à marges et côtes légèrement ciliées; pollen 45—49 μ de diamètre .... 9. *S. hydrophilus*

1. Akènes faiblement comprimés, non ailés, à nombre variable de côtes principales sur chaque face, ± rugueux ou ridés; tube de la corolle aussi long ou plus court que la ligule

8. Plantes à racines tubéreuses; pédoncule à 3—8 bractées; capitule ± 40-flores .... (section 6. *Tuberiferi*) 21. *S. tuberifer*

8. Plantes à racines pivotantes ou rhizomes rampants; pédoncule à 1—3 bractées; capitules 55—300-flores

9. Plantes naines, 10—30 cm de haut; akènes souvent courbés .... section 5. *Pustulati*

10. Plantes ± 10 cm de haut; capitules ± 55-flores .... 18. *S. fragilis*

10. Plantes 15—30 cm de haut; capitules 100—200-flores

11. Capitules poilus-glanduleux .... 20. *S. masguindalii*

11. Capitules glabres

12. Feuilles coriaces, à lobes imbriqués; ligule plus courte que le tube de la corolle .... 19. *S. briquetianus*

12. Feuilles non coriaces, à lobes non imbriqués; ligule deux fois aussi longue que le tube de la corolle .... 17. *S. pustulatus*

9. Plantes jusqu'à 250 cm de haut; akènes non courbés

13. Plantes annuelles, bisannuelles ou plus rarement vivaces, à racines pivotantes; akènes atténués surtout vers la base .... section 1. *Sonchus*

14. Ligule et tube de la corolle ± de la même longueur .... 1. *S. oleraceus*

14. Ligule plus longue que le tube de la corolle

15. Capitules glabres; fleurs ± 11 mm long .... 3 a. *S. bourgeaui* var. *imbricatus*

15. Capitules poilus-glanduleux ou blancs-tomenteux; fleurs 14—20 mm long

16. Feuilles à lobes resserrès vers la nervure médiane; akènes rugueux-tuberculeux sur les côtes .... 2. *S. tenerrimus*

16. Feuilles à lobes triangulaires; akènes très rugueux transversalement .... 3. *S. bourgeaui* var. *bourgeaui*

13. Plantes vivaces, à rhizomes rampants (sauf chez *S. malaianus* à racines pivotantes); akènes atténués vers les deux extrémités

17. Plantes des marécages et des terrains salés humides; akènes ± quadrangulaires, finement ridés; aigrette ± caduque .... section 3. *Maritimi*

18. Inflorescence densement poilue-glanduleuse, à capitules nombreux .... 11. *S. palustris* ssp. *palustris*

18. Inflorescence non poilue-glanduleuse, à capitules peu nombreux

19. Capitules axillaires et terminaux; pédoncule 0,2—1,2 cm long; feuilles à marges très piquantes .... 12. *S. crassifolius*

19. Capitules terminaux; pédoncule jusqu'à 7 cm long; feuilles à marges non piquantes

20. Feuilles peu ou non disséquées; akènes étroitement ellipsoïdes; aigrette ± 3 fois plus longue que l'akène .... 10. *S. maritimus*

20. Feuilles disséquées, à lobe terminal large et triangulaire; akène oblong-ovoïde; aigrette ± 2 fois plus longue que l'akène .... 11 a. *S. palustris* ssp. *sosnowskyi*

17. Plantes des terrains cultivés subhumides et des hautes montagnes asiatiques; akènes ellipsoïdes ou étroitement ellipsoïdes, rugueux ou fortement ridés; aigrette ± persistante .... section 4. *Arvenses*

21. Plantes à racines pivotantes; feuilles ± coriaces .. 16. *S. malaianus*

21. Plantes à rhizomes rampants; feuilles non coriaces

22. Capitules poilus-glanduleux

23. Capitules blancs-tomenteux; akènes étroitement ellipsoïdes, ridés .... 15. *S. wightianus* ssp. *wightianus*

23. Capitules non blancs-tomenteux; akènes ellipsoïdes, rugueux .... 13. *S. arvensis* ssp. *arvensis*

22. Capitules non poilus-glanduleux

24. Capitules glabres; akènes rugueux .... 13 a. *S. arvensis* ssp. *uliginosus*
24. Capitules blancs-tomenteux à la base; akènes ridés
    25. Capitules légèrement tomenteux; involucre à écailles externes larges (1,5—3 mm); fleurs 16—24 mm long; aigrette brillante, ± 11 mm long .... 14. *S. brachyotus*
    25. Capitules densement tomenteux; involucre à écailles externes étroites (± 1,5 mm); fleurs 12—14 mm long; aigrette non brillante, ± 8 mm long .... 15 a. *S. wightianus* ssp. *wallichianus*

Section 1. **Sonchus**

Sonchus Ser. *Oleracei* Kirp. in Nov. Syst. Plant. Vasc. 1964: 342, 1964; excl. *Sonchus asper* (L.) Hill

Espèce-type: *Sonchus oleraceus* L. emend. Gouan

Plantes annuelles, bisannuelles ou vivaces, herbacées ou suffrutescentes, 10—140 cm de haut, à racine pivotante; capitules 80—230-flores; écailles de l'involucre 20—35; corolle 10—20 mm long; tube de la corolle aussi long ou plus court que la ligule; akènes 2,5—3,75×0,5—1,25 mm, étroitement obovales, non ailés, rugueux; aigrette 5—8 mm long, ± persistante; x=7, 8 et 9.

1. *Sonchus oleraceus* L. emend. Gouan
2. *S. tenerrimus* L.
3. *S. bourgeaui* Sch. Bip.
    3 a. *S. bourgeaui* Sch. Bip. var. *imbricatus* (Svent.) Boulos

Section 2. **Asperi** Boulos, sect. nov.

Espèce-type: *Sonchus asper* (L.) Hill

Plantae annuae, biennes vel perennes, herbaceae vel suffruticosae, 10—130 cm altae, radice palari rarius rhizomate repente; calathia 80—300-flora; phylla involucri 25—45; corollae 10—16 mm longae, tubo limbum superante; achaenia 2—5,5×1—1,75 mm metientia, valde compressa, alata, sublaevia, costis principalibus in utroque latere ternis cum marginibus saepe ciliolatis; pappus 6—8 mm longus, plus minusve deciduus; x=9.

Plantes annuelles, bisannuelles ou vivaces, herbacées ou suffrutescentes, 10—130 cm de haut, à racine pivotante ou rarement à rhizome rampant; capitules 80—300-flores; écailles de l'involucre 25—45; corolle 10—16 mm long, tube de la corolle plus long que la ligule; akènes 2—5,5×1—1,75 mm, fortement comprimés, ailés, ± lisses, à 3 côtes principales sur chaque face, à marges et côtes souvent ciliées; aigrette 6—8 mm long, ± caduque; x=9.

4. *Sonchus asper* (L.) Hill
    4 a. *S. asper* (L.) Hill subsp. *glaucescens* (Jordan) Ball
5. *S. littoralis* (T. Kirk) Allan
6. *S. mauritanicus* Boiss. & Reut.
7. *S. macrocarpus* Boulos & C. Jeffrey
8. *S. gigas* Boulos ex Humbert
9. *S. hydrophilus* Boulos

Section 3. **Maritimi** (Kirp.) Boulos, stat. nov.

Basionym: *Sonchus* Ser. *Maritimi* Kirp. in Nov. Syst. Plant. Vasc. 1964: 343, 1964.

Sonchus Ser. *Palustres* Schchian ex Kirp. in Nov. Syst. Plant. Vasc. 1964: 343, 1964.

Espèce-type: *Sonchus maritimus* L.

Plantes vivaces, herbacées ou suffrutescentes, 10—250 mm de haut, à rhizomes rampants; collet généralement non ramifié; capitules 80—150-flores; écailles de l'involucre 25—42; corolle 11—18 mm de long; akènes 2—3,75×1—1,6 mm, finement ridés transversalement, à marges épaisses; aigrette 6—10 mm de long, ± caduque; x=9.

10. *Sonchus maritimus* L.
11. *S. palustris* L.
    11 a. *S. palustris* L. subsp. *sosnowskyi* (Schchian) Boulos, comb. et stat. nov. Basionym: *Sonchus sosnowskyi* Schchian in Not. Syst. Geogr. Inst. Bot. Tphilis 15: 72, 1949.
12. *S. crassifolius* Pourr.

Section 4. **Arvenses** (KIRP.) BOULOS, stat. nov.

Basionym: *Sonchus* Ser. *Arvenses* SCHCHIAN ex KIRP. in Nov. Syst. Plant. Vasc. 1964: 343, 1964.

Espèce-type: *Sonchus arvensis* L.

Plantes vivaces, herbacées ou suffrutescentes, 25—180 cm de haut, à rhizomes rampants ou rarement à racines pivotantes; capitules 100—300-flores; écailles de l'involucre 35—56; corolle 12—26 mm de long; tube de la corolle aussi long ou un peu plus long que la ligule; akènes 2,2—4,5×1—1,2 mm, ± elliptiques, rugueux ou ridés; aigrette 8—14 mm de long, ± persistante; x=9.

13. *Sonchus arvensis* L.
    13 a. *S. arvensis* L. subsp. *uliginosus* (M. BIEB.) BÉGUINOT
14. *S. brachyotus* DC.
15. *S. wightianus* DC.
    15 a. *S. wightianus* DC. subsp. *wallichianus* (DC.) BOULOS, comb. et stat. nov. Basionym: *Sonchus wallichianus* DC. Prodr. 7: 185, 1838.
16. *S. malaianus* MIQ.

Section 5. **Pustulati** BOULOS, sect. nov.

Espèce-type: *Sonchus pustulatus* WILLK.

Plantae perennes suffruticosae, 10—30 cm altae; calathia 55—200-flora; phylla involucri 23—40; corollae 11—21 mm longae; achaenia 2,25—5×0,6—1,5 mm metientia, saepe incurva; pappus 6—9 mm longus, plus minusve deciduus; x=9.

Plantes vivaces, suffrutescentes, 10—30 cm de haut; capitules 55—200-flores; écailles de l'involucre 23—40; corolle 11—21 mm de long; akènes 2,25—5×0,6—1,5 mm, souvent courbés; aigrette 6—9 mm de long, ± caduque; x=9.

17. *Sonchus pustulatus* WILLK.
18. *S. fragilis* BALL
19. *S. briquetianus* GANDOGER
20. *S. masguindalii* PAU & FONT QUER

Section 6. **Tuberiferi** BOULOS, sect. nov.

Espèce-type: *Sonchus tuberifer* SVENT.

Plantae perennes herbaceae, 20—40 cm altae, radicibus tuberosis; pedunculi 0,8—4 cm longi, 3—8-bracteati; calathia c. 40-flora; phylla involucri c. 20; corollae 10—15 mm longae, limbo tubum superante; achaenia 2,5×1 mm metientia, rugosa; pappus c. 4,5 mm longus, deciduus; x=9.

Plantes vivaces, herbacées, de 20—40 cm de haut, à racines tubéreuses; pédoncules 0,8—4 cm de long, à 3—8 bractées; capitules ± 40-flores; écailles de l'involucre ± 20; corolle 10—15 mm de long; ligule plus longue que le tube de la corolle; akènes 2,5×1 mm, rugueux; aigrette ± 4,5 mm de long, caduque; x=9.

21. *Sonchus tuberifer* SVENT.

II. Sous-genre **Dendrosonchus** SCH. BIP. ex BOULOS, subgen. nov.[1]

Espèce-type: *Sonchus congestus* WILLD.

Plantes vivaces, suffrutescentes ou arbustives, 20—250 cm de haut, à racines pivotantes, rarement à rhizomes ligneux. *Collet* ligneux. *Tige* cylindrique, ligneuse, creuse ou pleine. *Feuilles* divisées. *Pédoncule* 0,2—10 cm de long, glabre ou blanc tomenteux au sommet et portant 1—12 bractées. *Capitules* à 36—480 fleurs. *Écailles de l'involucre* 24—70. *Corolle* 11—32 mm de long. *Ligule* 5,5—16 mm de long. *Tube de la corolle* 4,5—16 mm de long. *Akènes* 2—4,5×0,6—1,5 mm. *Aigrette* 4—14 mm de long, généralement caduque. x=9.

Plantes endémiques de Macaronésie et du Maroc occidental.

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[1] Le nom de *Sonchus* subgen. *Dendrosonchus* SCH. BIP. in WEBB, P. B. & BERTHELOT, S., Hist. Nat. Îles Canar. 3(2): 425, 1849—1850 qui est invalide en raison de l'article 33, note 2 du Code (sous-genre subdivisé en divisions) est ici validé.

CLEF POUR LES SECTIONS ET LES ESPÈCES DU SOUS-GENRE DENDROSONCHUS

1. Plantes suffrutescentes
   2. Plantes à rhizome ligneux, feuilles avec 3 à 4 paires de lobes, écailles de l'involucre ± 27, capitules ± 60-flores .... section 2. *Brachylobi*
      3. Feuilles à lobe terminal large et à lobes lateraux mal développés .... 33. *S. brachylobus* var. *brachylobus*
      3. Feuilles à lobe terminal étroit et à lobes latéraux bien développés .... 33 a. *S. brachylobus* var. *canariae*
   2. Plantes à racine pivotante, feuilles avec plus de 4 lobes, écailles de l'involucre 30—70, capitules 80—480-flores .... section 1. *Dendrosonchus*
      4. Capitules tomenteux
         5. Feuilles glabres .... 22. *S. congestus*
         5. Feuilles tomenteuses
            6. Plantes 50—80 cm de haut, feuilles en rosette
               7. Lobes lateraux des feuilles à sommet arrondi et à marges spinuleuses, capitules 1,5×2,5 cm .... 26. *S. bornmuelleri*
               7. Lobes lateraux des feuilles à sommet pointu et à marges non spinuleuses, capitules 2,5×4,5 cm .... 23. *S. acaulis*
            6. Plantes 60—220 cm de haut, feuilles en majorité caulinaires .... 24. *S. hierrensis*
      4. Capitules glabres ou rarement légèrement tomenteux
         7. Feuilles en majorité caulinaires, pédoncule renflé vers le sommet et portant 6—12 bractées au-dessous de l'involucre
            8. Pédoncule à ± 12 bractées, proportion entre la longueur de la ligule et celle du tube de la corolle 4:5 .... 31. *S. fauces-orci*
            8. Pédoncule à ± 6 bractées, proportion entre la longueur de la ligule et celle du tube de la corolle 2:1 .... 32. *S. pinnatifidus*
         7. Majorité des feuilles en rosette, pédoncule non renflé
            9. Tige très courte (1—5 cm), ramifications florifères presque nues
               10. Feuilles lyrées, akène 2—2,5×0,6—0,8 mm, aigrette très caduque .... 27. *S. radicatus*
               10. Feuilles pinnatifides à pinnatiséquées, akène 2,5—3,2×1—1,25 mm, aigrette moins caduque
                   11. Nombre de fleurs par capitule ± 100, akènes lisses ou faiblement rugueux (plantes de l'île de Madère) .... 30. *S. ustulatus*
                   11. Nombre de fleurs par capitule 265—480, akènes rugueux (plantes des îles du Cap Vert et Gomera des îles Canaries)
                       12. Écailles externes de l'involucre larges (5—8,5 mm) (plantes des îles du Cap Vert) .... 25. *S. daltonii*
                       12. Écailles externes de l'involucre étroites (2,5—4 mm) (plantes de l'île de Gomera des îles Canaries) ...... 28. *S. gomerensis*
            9. Tige plus longue (5—20 cm), ramifications florifères portant de petites feuilles écartées à lobes ± égaux .... 29. *S. gummifer*
1. Plantes arbustives .... section 3. *Pinnati*
   13. Capitules ± 400-flores, fleurs 20—27 mm de long, ligule plus longue que le tube de la corolle .... 37. *S. fruticosus*
   13. Capitules 36—200-flores, fleurs 11—18,5 mm de long, ligule et tube de la corolle de longueur ± égale
       14. Capitules 36—48-flores .... 35. *S. palmensis*
       14. Capitules 50—200-flores
           15. Akènes 3—3,5 mm de long, écailles de l'involucre 40—57
               16. Fleurs 16—18,5 mm de long, aigrette 8—10 mm de long .. 38. *S. lidii*
               16. Fleurs ± 14 mm de long, aigrette 6—7 mm de long
                   17. Lobes des feuilles larges (3—12 mm), capitules 1,2—1,5 cm de long .... 36. *S. canariensis* ssp. *canariensis*
                   17. Lobes des feuilles étroits (2—5 mm), capitules plus petits .... 36 a. *S. canariensis* ssp. *orotavensis*
           15. Akènes 2,25—2,75 mm de long, écailles de l'involucre 24—37
               18. Capitules ± 60-flores, pédoncule 0,5—3 cm de long 39. *S. gandogeri*

18. Capitules 100—150-flores, pédoncule 1—9 cm de long
    19. Pédoncule à 2—5 bractées, akène elliptique (plantes de l'île de Madère) .... 34. *S. pinnatus*
    19. Pédoncule à 1 bractée, akène oblanceolé (plantes de l'île de Hierro des îles Canaries) .... 40. *S. pitardii*

Section 1. **Dendrosonchus**

Espèce-type: *Sonchus congestus* WILLD.

Plantes suffrutescentes, 20—220 cm de haut, à racine pivotante; capitule 80—480-flores; écailles de l'involucre 30—70; corolle 11—32 mm de long; akènes 2—3,75×0,6—1,5 mm; aigrette 4,5—12 mm de long.

22. *Sonchus congestus* WILLD.
23. *S. acaulis* DUM.-COURS.
24. *S. hierrensis* (PITARD) BOULOS
25. *S. daltonii* WEBB
26. *S. bornmuelleri* PITARD
27. *S. radicatus* AIT.
28. *S. gomerensis* BOULOS
29. *S. gummifer* LINK
30. *S. ustulatus* LOWE
31. *S. fauces-orci* KNOCHE
32. *S. pinnatifidus* CAV.

Section 2. **Brachylobi** BOULOS, sect. nov.

Espèce-type: *Sonchus brachylobus* WEBB & BERTH.

Suffrutices, 20—70 cm alti, rhizomate lignescente; folia lyrata, glabra, coriacea; calathia c. 60-flora; phylla involucri c. 27; corollae 11—13 mm longae; achaenia 2.4—3×0.8—1 mm metientia; pappus c. 6 mm longus.

Plantes suffrutescentes, 20—70 cm de haut, à rhizome ligneux; feuilles lyrées, glabres et coriaces; capitules ± 60-flores; écailles de l'involucre ± 27; corolle 11—13 mm de long; akènes 2,4—3×0,8—1 mm; aigrette ± 6 mm de long.

33. *Sonchus brachylobus* WEBB & BERTH.
    33 a. *S. brachylobus* WEBB & BERTH. var. *canariae* (PITARD) BOULOS

Section 3. **Pinnati** BOULOS, sect. nov.

Espèce-type: *Sonchus pinnatus* AIT.

Frutices, 50—250 cm alti, radice palari; calathia 36—400-flora; phylla involucri 24—60; corollae 11—27 mm longae, ligula tubum longitudine subaequante; achaenia 2.25—4.5×0.75—1.2 mm metientia; pappus 4—14 mm longus.

Plantes arbustives, 50—250 cm de haut, à racine pivotante; capitule 36—400-flores; écailles de l'involucre 24—60; corolle 11—27 mm de long, ligule et tube de la corolle ± de la même longueur; akènes 2,25—4,5×0,75—1,2 mm; aigrette 4—14 mm de long.

34. *Sonchus pinnatus* AIT.
35. *S. palmensis* (SCH. BIP.) BOULOS
36. *S. canariensis* (SCH. BIP.) BOULOS
    36 a. *S. canariensis* (SCH. BIP.) BOULOS subsp. *orotavensis* BOULOS
37. *S. fruticosus* L. FIL.
38. *S. lidii* BOULOS
39. *S. gandogeri* PITARD
40. *S. pitardii* BOULOS

III. Sous-genre **Origosonchus** BOULOS, subgen. nov.[1]

Espèce-type: *Sonchus schweinfurthii* OLIV. & HIERN

Plantes vivaces, herbacées ou suffrutescents à la base, 3—300 cm de haut, à rhizome rampant. *Tige* herbacée, creuse, cylindrique. *Feuilles* généralement divisées. *Pédoncule* 0,2—16 cm de long, souvent tomenteux, rarement à poils glanduleux au sommet. *Capitules* à 40—220 fleurs. *Écailles de l'involucre* 18—40. *Corolle* 10—20 mm de long, tube de la corolle plus long que la ligule. *Akènes* 2,5—6,5×0,8—1,35 mm. *Aigrette* 3—13 mm de long, persistante ou rarement caduque. x=9.

Plantes endémiques de l'Afrique au sud du Sahara et de Madagascar.

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[1] Le nom de *Sonchus* subgen. *Origosonchus* BOULOS in Bot. Notiser 113: 413, 1960, qui est invalide en raison de l'article 37 du Code (type non designé) est ici validé.

CLEF POUR LES SECTIONS ET LES ESPÈCES DU SOUS-GENRE ORIGOSONCHUS

1. Akènes 4—6,5 mm de long, aigrette 12—13 mm de long .... section 2. *Dregeani*
   2. Capitules glabres .... 51. *S. integrifolius*
   2. Capitules blancs-tomenteux à la base
      3. Plantes richement ramifiées à la base, feuilles en rosette ...... 50. *S. dregeanus*
      3. Plantes rarement ramifiées à la base, feuilles en majorité caulinaires
         4. Feuilles pennipartites à pinnatiséquées, capitules ± 20×12 mm .... 53. *S. wilmsii*
         4. Feuilles entières à pennipartites, capitules ± 15×8 mm .... 52. *S. friesii*
1. Akènes 2,5—4(—4,5) mm de long, aigrette 3—11 mm de long
   5. Plantes naines (3—12 cm de haut), akènes 4×1,35 mm .... (section 3. *Nani*) 54. *S. nanus*
   5. Plantes plus élevées (12—300 cm de haut), akènes 2,5—3,5×0,8—1 mm .... section 1. *Origosonchus*
      6. Écailles externes de l'involucre à pilosité dense
         7. Plantes de 15—30 cm de haut; feuilles en rosette, 3—6 cm de long; capitules peu nombreux .... 49. *S. obtusilobus*
         7. Plantes de 80—300 cm de haut; feuilles en majorité caulinaires, 5—25 cm de long; capitules nombreux .... 42. *S. angustissimus*
      6. Écailles externes de l'involucre sans poils glanduleux ou légèrement poilues
         8. Feuilles non divisées, 2—20 mm de large
            9. Capitules et pédoncules à poils glanduleux .... 46 a. *S. bipontini* var. *glanduligerus*
            9. Capitules et pédoncules sans poils glanduleux
               10. Feuilles étroites (2—5 mm) .... 43. *S. stenophyllus*
               10. Feuilles plus larges (jusqu'à 20 mm)
                   11. Feuilles à marges serrées .... 46 b. *S. bipontini* var. *louisii*
                   11. Feuilles à marges entières .... 46. *S. bipontini* var. *bipontini*
         8. Feuilles divisées ou plus larges
            12. Akène ± 4,5 mm de long .... 44. *S. camporum*
            12. Akène 2,8—3,8 mm de long
                13. Écailles externes de l'involucre à nervure médiane noirâtre .... 45. *S. afromontanus*
                13. Écailles externes de l'involucre sans nervure médiane noirâtre
                    14. Plantes de 15—40 cm de haut; capitules peu nombreux, petits (± 10×5 mm) .... 48. *S. melanolepis*
                    14. Plantes de 60—200 cm de haut; capitules nombreux, plus grands
                        15. Capitules à tomentum blanc .... 47. *S. luxurians*
                        15. Capitules à tomentum brunâtre ...... 41. *S. schweinfurthii*

Section 1. **Origosonchus**

Espèce-type: *Sonchus schweinfurthii* OLIV. & HIERN

Plantes vivaces, herbacées ou suffrutescentes à la base, 12—300 cm de haut; capitules 40—220-flores; écailles de l'involucre 18—35; corolle 10—18 mm de long; akènes 2,5—4,5×0,8—1 mm; aigrette 3—10 mm de long, persistante ou caduque.

41. *Sonchus schweinfurthii* OLIV. & HIERN
42. *S. angustissimus* HOOK. FIL.
43. *S. stenophyllus* R. E. FRIES
44. *S. camporum* (R. E. FRIES) BOULOS ex C. JEFFREY
45. *S. afromontanus* R. E. FRIES
46. *S. bipontini* ASCHERS.
    - 46 a. *S. bipontini* ASCHERS. var. *glanduligerus* (R. E. FRIES) ROBYNS
    - 46 b. *S. bipontini* ASCHERS. var. *louisii* ROBYNS
47. *S. luxurians* (R. E. FRIES) C. JEFFREY
48. *S. melanolepis* FRESEN.
49. *S. obtusilobus* R. E. FRIES

Section 2. **Dregeani** BOULOS, sect. nov.

Espèce-type: *Sonchus dregeanus* DC.

Plantae perennes herbaceae, 12—90 cm altae; folia plerumque parce divisa; calathia 55—200-flora; phylla involucri 25—40; corollae 12—20 mm longae; achaenia 4—6.5 mm longa; pappus 12—13 mm longus, persistens.

Plantes vivaces, herbacées, 12—90 cm de haut; feuilles généralement peu divisées; capitules 55—200-flores; écailles de l'involucre 25—40; corolle 12—20 mm de long; akènes 4—6,5 mm de long; aigrette 12—13 mm de long, persistante.

50. *Sonchus dregeanus* DC.
51. *S. integrifolius* Harv.
52. *S. friesii* Boulos
53. *S. wilmsii* R. E. Fries

Section 3. **Nani** Boulos, sect. nov.

Espèce-type: *Sonchus nanus* Sond. ex Harv. & Sond.

Plantae perennes herbaceae nanae, 3—12 cm altae; folia in rosulam congesta; calathia c. 80-flora; phylla involucri c. 27; corollae 14—17 mm longae; achaenia 4×1,35 mm metientia; pappus 8—11 mm longus, persistens.

Plantes vivaces, herbacées, naines, 3—12 cm de haut; feuilles en rosette; capitules ± 80-flores; écailles de l'involucre 27 environ; corolle 14—17 mm de long; akènes 4×1,35 mm; aigrette 8—11 mm de long, persistante.

54. *Sonchus nanus* Sond. ex Harv. & Sond.

2. Genre **Embergeria** Boulos

Boulos in Eichler, Suppl. Black's Fl. S. Australia 332, 1965.
Espèce-type: *Embergeria grandifolia* (T. Kirk) Boulos

Plantes vivaces, dressées, 15—150 cm de haut. *Organes souterrains:* rhizome rampant, jusqu'à 5 cm de diam. *Collet* généralement non ramifié. *Tige* ligneuse à la base, glabre, ± cylindrique, creuse, à cannelures étroites. *Feuilles* coriaces, glabres; feuilles du collet 5—60×1,5—18 cm, sessiles ou longuement-pétiolées, entières ou pinnatiséquées, à 2—3 pairs de lobes, marges à dents piquantes irrégulières; feuilles caulinaires de 8—30 cm de long (celles au-dessous de l'inflorescence plus courtes), entières à pennipartites, marges à dents piquantes. *Pédoncule* 0,2—10 cm de long sur 1—3 mm de diam., glabre ou à tomentum blanc et dense, à 1—3 bractées triangulaires. *Capitules* ouverts de 1—2 cm de long sur 2—4 cm de diam., nombre de fleurs 80—220 par capitule. *Écailles de l'involucre* au nombre de 25—36, imbriquées, 5—17 mm de long sur 2—6 mm de large. *Corolle* jaune, quelquefois pourpre clair chez les fleurs extérieures, 17—22 mm de long. *Ligule* 7—9 mm de long. *Tube de la corolle* poilu au niveau de la ligule, 10—14 mm de long. *Anthères* 5, formant un tube staminal de ± 3 mm long sur ± 0,5 mm de diam. *Style* à 2 branches de 1,5—2 mm de long. *Akènes* de 5—7 mm de long sur 2—3 mm de large, de couleur crème jaunâtre à brunâtre, ± elliptiques, comprimés, atténués surtout vers le sommet, lisses, à ailes larges et à 2—6 côtes. *Aigrette* sessile, 10—15 mm de long, persistante, composée de soies dimorphes, les unes à base épaisse, les autres à base mince; chaque type uni en groupes par la base; apex pointu ou glochidé. 2n=36.

CLEF POUR LES SOUS-GENRES

1. Feuilles du collet longuement-pétiolées, 30—60 cm de long; pédoncule blanc-tomenteux .... I. *Embergeria*
1. Feuilles du collet sessiles, 5—15 cm de long, pédoncule glabre ...... II. *Megalocarpa*

I. Sous-genre **Embergeria**

Espèce-type: *Embergeria grandifolia* (T. Kirk) Boulos

Plantes vivaces, 60—150 cm de haut; feuilles du collet longuement-pétiolées, 30—60 cm de long; feuilles caulinaires généralement non divisées; pédoncule 0,5—2,5 cm de long, blanc-tomenteux; capitules ± 100-flores; écailles de l'involucre ± 26; corolle 18—22 mm de long;

akènes 5—5,5×2,5—3 mm; aigrette 12—15 mm de long.

1. *Embergeria grandifolia* (T. KIRK) BOULOS

II. Sous-genre **Megalocarpa** BOULOS

BOULOS in EICHLER, Suppl. Black's Fl. S. Australia 333, 1965.
Espèce-type: *Embergeria megalocarpa* (HOOK. FIL.) BOULOS

Plantes vivaces, 15—70 cm de haut; feuilles du collet sessiles, 5—15 cm de long; feuilles caulinaires divisées; pédoncule 1—10 cm de long, glabre; capitules 80—220-flores; écailles de l'involucre ± 36; corolle 17—19 mm de long; akènes 5—7×2—3 mm; aigrette ± 10 mm de long.

2. *Embergeria megalocarpa* (HOOK. FIL.) BOULOS

3. Genre **Babcockia** BOULOS

BOULOS in Bull. Jard. Bot. État Bruxelles 35: 64, 1965.
Espèce-type: *Babcockia platylepis* (WEBB) BOULOS

Plantes vivaces, dressées, de 30—80 cm de haut. *Organes souterrains*: racine pivotante, renflée à la partie supérieure. *Tige* non ou peu ramifiée dès la base, 5—15 cm de long. *Feuilles du collet* ovales ou elliptiques, 4—12×2—5 cm, à lobes ± triangulaires, aigus, irrégulièrement dentés, les juvéniles à tomentum blanc. *Feuilles caulinaires*: la plupart groupées à la base de la tige florifère, ± elliptiques, 10—30 cm de long, pinnatifides à pennipartites, à lobes triangulaires, entières, rarement dentés, acuminés et à lobe terminal nettement plus long que les latéraux. *Pédoncule* 4—18 cm de long, portant, surtout au sommet, 5—15 bractées ± triangulaires, de 0,5—3 cm de long. *Capitules* peu nombreux, 2,5—3×3—6 cm, nombre de fleurs par capitule ± 550. *Écailles de l'involucre* au nombre de 98 environ, imbriquées, en 4 séries: les externes ± 21, légèrement ondulées, denticulées, 8—18×6—9 mm, triangulaires ou allongées, à base épaissie; les intermédiares inférieures ± 19, 16—22×4,5—8 mm, étroitement oblongues, entières, légérement atténuées vers la base, à marges scarieuses et apex denticulé; les intermédiaires supérieures ± 28, 22—25×3—4 mm, étroitement oblongues à ± linéaires, scarieuses, à apex pointu, obtus ou arrondi; les internes ± 30, 18—23×1,5—3 mm, ± linéaires, minces, ± transparantes, scarieuses. *Corolle* jaune orangé, 20—28 mm de long. *Tube de la corolle* 8,5—13 mm de long, poilu au sommet, atténué vers la base. *Ligule* 11,5—15 mm de long. *Anthères* 5, formant un tube staminal de 5 mm de long et 0,5 mm de diam. *Style* à 2 branches de 2 mm de long, brunâtres. *Akènes* de 5,5 mm de long sur 1 mm de diam., légèrement atténués aux extrémités, souvent légèrement courbés, ± oblongs ou étroitement elliptiques, ± cylindriques, à 4 cannelures et dépourvus de côtes, dimorphes sur un même capitule; les externes brunâtres, rugueux; les internes crème jaunâtre, lisses. *Aigrette* de 9—12 mm de long, à soies les unes longues, nombreuses, caduques, multicellulaires à la base, à épines latérales bien développées, à apex souvent multicellulaire avec quelques cellules réfléchies vers la base; les autres d'environ 4 mm de long, persistantes, minces, cotonneuses, à épines latérales presque absentes, à apex multicellulaire, semblable à celui des autres soies mais à cellules plus développées. x=9, 2n=18.

1. *Babcockia platylepis* (WEBB) BOULOS

4. Genre **Taeckholmia** BOULOS

BOULOS in Bot. Notiser 120: 97, 1967.
Espèce-type: *Taeckholmia pinnata* (L. FIL.) BOULOS

Plantes arbustives, 50—200 cm de haut. *Organes souterrains*: racines pivotantes. *Collet* ligneux, épais, généralement ramifié. *Tige* ligneuse, pleine chez les plantes agées. *Feuilles* ± densément groupées au sommet des tiges végétatives ou au-dessous de l'inflorescence, non auriculées, glabres ou les jeunes pubescentes à la base, pinnatiséquées, de 2—20 cm de long, à lobes du 1—2 mm (rarement jusqu'à 6 mm) de large. *Pédoncule* 0,3—3 cm de long, ± 1 mm de diam., cylindrique, creux, à ± 4 bractées. *Capitules* généralement nombreux, 3—7 mm de long (rarement plus longs), 2—4 mm de diam. avant l'anthèse, à 12—29 fleurs jaunes. *Écailles de l'involucre* 10—30, non ou légèrement imbriquées; les externes de 1—4 mm de long, ± triangulaires, à base épaisse; les internes de 5—9 mm de long, étroitement rectangulaires, minces (rarement à ± 4 écailles intermédiaires chez les espèces possédant des écailles imbriquées). *Corolle* 6,5—12 mm de long; ligule plus longue que le tube de la corolle. *Akènes* 1,7—2,5 × ± 0,6 mm, attenués vers les deux extrémités, comprimés, rugueux, étroitement oblancéolés, étroitement elliptiques ou ± étroitement rectangulaires, souvent courbés, à ± 4 côtes sur chaque face, pourvus au sommet d'un disque blanc à protubérance centrale. *Aigrette* 3,5—6 mm de long, caduque. x=9, 2n=18.

CLEF POUR LES SOUS-GENRES ET LES ESPÈCES

1\. Feuilles à lobes de 0,2—1 mm de large, ligule d'au moins deux fois la longueur du tube de la corolle .... sous-genre I. *Taeckholmia*

  2\. Feuilles à lobes de 0,5—1 mm de large, capitule plus de 4 mm de long

    3\. Fleurs 7,5—9 mm de long, aigrette 3,5—5,75 mm de long .... 1. *T. pinnata*

    3\. Fleurs 7 mm de long, aigrette 2,5—3 mm de long .... 3. *T. canariensis*

  2\. Feuilles à lobes ± capillaires, moins de 0,5 mm de large; capitules 3—4 mm de long

    4\. Pédoncule jusqu'à 3 cm de long, akène 2—2,2 mm de long ...... 2. *T. capillaris*

    4\. Pédoncule jusqu'à 1,5 cm de long, akène 1,7—1,8 mm de long .... 4. *T. microcarpa*

1\. Feuilles à lobes de 1—6 mm de large, ligule moins de deux fois aussi longue que le tube de la corolle .... sous-genre II. *Pseudodendrosonchus*

  5\. Nombre de fleurs inférieur à 20 par capitule, feuilles de formes diverses sur la même plante .... 5. *T. heterophylla*

  5\. Nombre de fleurs supérieur à 20 par capitule, feuilles ± de la même forme

    6\. Feuilles à lobes largement espacés, 1,5—2 mm de large ...... 6. *T. regis-jubae*

    6\. Feuilles à lobes étroitement espacés, jusqu'à 4 mm de large ...... 7. *T. arborea*

I. Sous-genre **Taeckholmia**

Espèce-type: *Taeckholmia pinnata* (L. fil.) Boulos

Arbustes, feuilles à lobes de 0,2—1 mm de large; capitules 3—7×1,2—3 mm, à 12—19 fleurs; écailles de l'involucre 10—15, en deux séries; ligule au moins deux fois aussi longue que le tube de la corolle; akènes 1,7—2,5 mm de long; aigrette 2,5—2,75 mm de long.

1. *Taeckholmia pinnata* (L. fil.) Boulos
2. *T. capillaris* (Svent.) Boulos
3. *T. canariensis* Boulos
4. *T. microcarpa* Boulos

II. Sous-genre **Pseudodendrosonchus** Boulos

Boulos in Bot. Notiser 120: 98, 1967.
Espèce-type: *Taeckholmia heterophylla* Boulos

Arbustes, feuilles à lobes de 1—6 mm de large; capitules 6—12×3—4 mm, à 15—29 fleurs; écailles de l'involucre 19—30, en trois séries; ligule plus longue que le tube de la corolle (mais moins du double); akènes ± 2,5 mm de long; aigrette 4—6 mm de long.

5. *Taeckholmia heterophylla* Boulos
6. *T. regis-jubae* (Pitard) Boulos
7. *T. arborea* (DC.) Boulos

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Révision Systématique du Genre Sonchus L. s.l.

II. Étude Caryologique

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ABSTRACT

ROUX, J. & BOULOS, L. 1972. Révision systématique du genre Sonchus L. s.l. II. Étude caryologique. — Bot. Notiser 125: 306—309.

The basic chromosome numbers of the four genera are: *Sonchus* (x=7, 8, 9); *Embergeria* (x=?18); *Babcockia* (x=9) and *Taeckholmia* (x=9). Within the genus *Sonchus* 32 species, 2 subspecies and 2 hybrids are studied: 14 species, 2 subspecies and 2 hybrids belong to subgenus *Sonchus,* 15 species to subgenus *Dendrosonchus* and 3 species to subgenus *Origosonchus.* The highest chromosome number is 2n=54 and the lowest 2n=14. Polyploids are known in subgenus *Sonchus* only, while the other 2 subgenera comprise diploids only. The 2 species of *Embergeria* have the same somatic chromosome number 2n=36, and the monotypic genus *Babcockia* has 2n=18. In the genus *Taeckholmia* 2n=18 is valid for the 3 species studied.

Nous mentionnons dans le Tableau 1 les nombres chromosomiques des espèces étudiées; elles appartiennent au genres *Sonchus, Embergeria, Babcockia* et *Taeckholmia* (cf. BOULOS 1972).

Dans le genre *Sonchus,* les nombres de base des chromosomes sont: x=7, 8 et 9; le nombre x=9 étant le plus fréquent. Toutes les espèces du sous-genre *Dendrosonchus* étudiées (15 espèces sur les 19 connues) ont le même nombre somatique 2n=18. Les trois espèces du sous-genre *Origosonchus,* ainsi que sept espèces du sous-genre *Sonchus,* possèdent également le nombre 2n=18.

Les nombres de base x=7 et 8 sont chacun représenté par une espèce. Parmi les espèces du genre *Sonchus* étudiées, quatre sont des polyploïdes, avec le nombre de base x=9. Une seule espèce, *S. oleraceus,* représente, probablement, un amphidiploïde (STEBBINS & al. 1953).

Deux hybrides de *Sonchus,* ont l'un 2n=25 (16+9), l'autre 2n=45 (27+18).

Les trois espèces étudiées sur les sept connues du genre *Taeckholmia,* possèdent le nombre 2n=18. Le nombre de base x=9 est confirmé par une espèce, *T. pinnata.*

Les deux espèces du genre *Embergeria* possèdent le nombre chromosomique 2n=36. Le nombre de base x n'est pas connu, mais il nous semble que ce sont deux espèces tetraploïdes avec un nombre de base x=9.

Dans le genre monotypique *Babcockia* le nombre de base est x=9, le nombre somatique 2n=18.

Les données mentionnées ci-dessous,

nous montrent que le sous-genre *Dendrosonchus* renferme une série d'espèces ayant le nombre 2n = 18. Malheureusement, trois espèces seulement du sous-genre *Origosonchus* sont caryologiquement étudiées; elles possèdent le nombre 2n = 18. Les caractères morphologiques, assez voisins, des espèces du sous-genre *Origosonchus* et leur répartition géographique limitée en Afrique, nous amènent admettre la possibilité que ce sous-genre renferme également une série d'espèces avec le nombre chromosomique 2n = 18.

L'absence, très probable, d'espèces polyploïdes dans le sous-genre *Origosonchus,* et certainement dans le sous-genre *Dendrosonchus,* ainsi que l'homogénité des nombres chromosomiques, et de la morphologie des chromosomes de ces espèces, nous laissent prévoir leur origine primitive.

C'est dans le sous-genre *Sonchus,* qu'on trouve des espèces ayant des nombres chromosomiques de base variables: x = 7, 8 et 9, et qu'on rencontre des espèces polyploïdes. Ces critères importants montrent clairement l'origine récente du sous-genre *Sonchus* comparée à celle des autres sous-genres.

Tableau 1. Nombres chromosomiques des espèces étudiées des genres *Sonchus, Embergeria, Babcockia* et *Taeckholmia.* Pour les références des divers auteurs marqués [1], voir «caractères caryologiques» sous l'espèce en question dans les parties suivantes.

Espèce	n	2n	Références
GENRE SONCHUS L., x = 7, 8, 9			
Sous-genre *Sonchus,* x = 7, 8, 9			
Sonchus oleraceus L.	16	32	plusieurs auteurs [1] cf. LÖVE & LÖVE 1961; ROUX & BOULOS (Kafr-El-Dawar, Égypte, BOULOS s.n.).
S. tenerrimus L.	—	14	STEBBINS & al. 1953; LARSEN 1956; ROUX & BOULOS (Montpellier, France, BOULOS s n.; Banyuls-sur-Mer, Pyrénées-orientales, France, BOULOS s.n.; Valverde, Hierro, Iles Canaries, BOULOS s.n.).
S. bourgeaui SCH. BIP.	8	—	HENIN in BOULOS 1960, erron. cité 2n = 16.
S. asper (L) HILL	—	18	plusieurs auteurs [1] (cf. LÖVE & LÖVE 1961).
S. asper (L.) HILL ssp. *glaucescens* (JORD.) BALL	—	18	HENIN (sennoris, Égypte, BOULOS s.n.).
S. macrocarpus BOULOS & C. JEFFREY	—	36	HENIN in BOULOS 1959, sous *S. gigas* BOULOS.
S. gigas BOULOS ex HUMB.	—	36	MARCHANT 1970 (Jebel Marra, Sudan, WICKENS 1703).
S. maritimus L.	—	18	BOULOS 1960; HENIN in BOULOS 1960; ROUX & BOULOS (Wadi Natroun, Égypte, BOULOS s.n.); DELAY 1968.
S. palustris L.	—	18	cf. LÖVE & LÖVE 1961; HENIN in BOULOS 1960.
S. arvensis L.	—	54	cf. LÖVE & LÖVE 1961.
S. arvensis L. ssp. *uliginosus* (M. BIEB.) BÉGUINOT	—	36	cf. LÖVE & LÖVE 1961.
S. brachyotus DC.	—	18	ROUX & BOULOS 1970 (Chöjiagasaka, Miura Peninsula, near Tokyo, Japan, FUJIWARA s.n.).
S. wightianus DC.	9	—	MITRA & DATTA 1967, erron. cité pour *S. brachyotus* DC.
S. malaianus MIQ.	—	54	STEBBINS & al. 1953 sous *S. javanicus* SPRENG.

Espèce	n	2n	Références
S. pustulatus Willk.	—	18	Stebbins & al. 1953.
S. tuberifer Svent.	—	18	Roux & Boulos (Masca, Tenerife, Iles Canaries, Sventenius s.n.).
Hybrides			
S. arvensis×*S. uliginosus*	—	45	(=27+18) Shumovich & Montgomery 1955.
S. oleraceus×*S. asper*	—	25	(=16+9) Barber 1941.
Sous-genre *Dendrosonchus* Sch. Bip. ex Boulos, x=9			
Sonchus congestus Willd.	—	18	Larsen 1960, sous *S. jacquini* DC.; Roux & Boulos in Boulos 1967 b (Orotava, Tenerife, Iles Canaries, Boulos s.n.); Bramwell & al. 1972, sous *S. abbreviatus* Link.
S. acaulis Dum.-Cours.	—	18	Henin (Jardin Botanique, Orotava, Tenerife, Iles Canaries); Roux & Boulos in Boulos 1967 b (Tejeda, Gran Canaria, Iles Canaries, Boulos s.n.).
S. hierrensis (Pitard) Boulos	—	18	Roux & Boulos in Boulos 1967 b (Breña Alta, La Palma, Iles Canaries, Boulos s.n.).
S. bornmuelleri Pitard	—	18	Bramwell & al. 1972.
S. radicatus Ait.	—	18	Larsen 1960; Roux & Boulos (Las Canteras, N La Laguna, Tenerife, Iles Canaries, Boulos s.n.).
S. gomerensis Boulos	—	18	Roux & Boulos in Boulos 1967 b (Gomera, Iles Canaries, Boulos s.n.).
S. gummifer Link	—	18	Roux & Boulos (3 km S Güimar, Tenerife, Iles Canaries, Boulos s.n.); Bramwell & al. 1972.
S. pinnatifidus Cav.	—	18	Roux & Boulos (Jardin Botanique, Tafira, Gran Canaria, Iles Canaries, Boulos s.n.).
S. brachylobus Webb & Berth.	—	18	Roux & Boulos in Boulos 1967 b (entre Guia et El Pagador, Gran Canaria, Iles Canaries, Boulos s.n.).
S. pinnatus Ait.	—	18	Stebbins & al. 1953.
S. palmensis (Sch. Bip.) Boulos	—	18	Roux & Boulos in Boulos 1967 b (Breña Alta, La Palma, Iles Canaries, Boulos s.n.).
S. fruticosus L. fil.	—	18	Stebbins & al. 1953; Roux & Boulos (Entre Funchal et Camacha, Ile de Madère, Boulos s.n.).
S. lidii Boulos	—	18	Roux & Boulos in Boulos 1967 b (Los Llanillos, Hierro, Iles Canaries, Boulos s.n.).
S. gandogeri Pitard	—	18	Roux & Boulos (Las Lapas, Hierro, Iles Canaries, Boulos s.n.).
S. pitardii Boulos	—	18	Roux & Boulos in Boulos 1967 b (Los Llanillos, Hierro, Iles Canaries, Boulos s.n.).
Sous-genre *Origosonchus* Boulos, x=9			
Sonchus bipontini Aschers.	—	18	Stebbins & al. 1953.
S. dregeanus DC.	—	18	Marchant 1970 (Gordon-Gray 6255, 6256, Foxhill, Pietermaritzburg, Natal, S Africa).
S. wilmsii R. E. Fries	—	18	Marchant 1970 (Gordon-Gray 6257, Foxhill, Pietermaritzburg, Natal; Hilliard 4889, Princetown Distr., Everton, Natal, S Africa).
GENRE EMBERGERIA Boulos, x=?18			
Embergeria grandifolia (T. Kirk) Boulos	—	36	Stebbins & al. 1953, sous *Sonchus grandifolius* T. Kirk.

Espèce	n	2n	Références
E. megalocarpa (Hook. fil.) Boulos	—	36	Roux & Boulos (près Beachport, entre le marge SW du lac George et la mer, S Australie, Wilson s.n.).
GENRE BABCOCKIA Boulos, x=9			
Babcockia platylepis (Webb) Boulos	9	18	Larsen 1958, 1960, sous *Sonchus platylepis* Webb.
	—	18	Roux & Boulos in Boulos 1965.
GENRE TAECKHOLMIA Boulos, x=9			
Taeckholmia pinnata (L. fil.) Boulos	9	18	Roux & Boulos in Boulos 1967 a (Monte et Tafira Alta, Gran Canaria, Iles Canaries, Boulos s.n.).
T. microcarpa Boulos	—	18	Roux & Boulos in Boulos 1967 a (Güimar, Tenerife, Iles Canaries, Boulos s.n.).
T. heterophylla Boulos	—	18	Roux & Boulos in Boulos 1967 a (Agulo, Gomera, Iles Canaries, Boulos s.n.).

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Révision Systématique du Genre Sonchus L. s.l.

III. Étude Palynologique

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ABSTRACT

Pons, A. & Boulos, L. 1972. Révision systématique du genre Sonchus L. s.l. III. Étude palynologique. — Bot. Notiser 125: 310—319.

Pollen grains of all but one species of *Sonchus* L. s.l. (63) are studied. Measurements and descriptions of pollen grains are given. Pollen grains are either tricolporate or tetracolporate: both types occur together in subgenus *Sonchus,* while in the other two subgenera *Dendrosonchus* and *Origosonchus,* as well as in the other three genera *Embergeria, Babcockia* and *Taeckholmia* pollen grains are tricolporate. For each of the three genera segregated from *Sonchus* L. there is a special pollen type which is described, thus confirming the new taxonomic classification. The phylogenetical relationships between different taxonomic groups within *Sonchus* s.l. are discussed on a palynological basis.

INTRODUCTION

La morphologie pollinique du genre *Sonchus* L. a été précisée dans le travail de Saad (1961). Cependant, ayant observé un plus grand nombre d'espèces (63 au lieu de 39), nous croyons, tout en confirmant l'essentiel des résultats de Saad, pouvoir apporter quelques éléments nouveaux concernant les caractères polliniques et leur signification sur le plan de la taxonomie, de l'origine et de l'évolution du genre.

Ainsi que l'a fort justement observé Saad, les variations que présente la calotte polaire constituent un caractère majeur dans l'étude palynologique de ce genre. Les pollens de presque toutes les espèces sont, en effet, batis sur le même type qui correspond à un pollen tricolporé pourvu de quinze lacunes. Ces dernières, dont l'exine est relativement mince et de structure simple, sont séparées par des crêtes épaisses et échinuleuses dont la structure complexe a été parfaitement décrite et figurée par Saad (1961 p. 250 et fig. 6). On distingue trois *lacunes porales* qui entourent les endoapertures, chacune d'elles communiquant, par deux brèches (qui figurent l'ectoaperture) de la crête qui l'entoure, avec deux *lacunes abporales*; enfin deux *lacunes paraporales* occupent l'espace interapertural et sont séparées par une crête équatoriale (Fig. 1 et 2). De part et d'autre de la ceinture équatoriale formée par les lacunes, un épaississement, supportant des échinules identiques à celles des crêtes, constitue la calotte polaire. Celle-çi, selon Saad (1961 p. 250

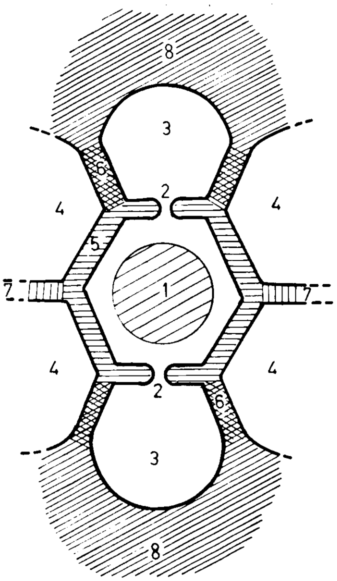

Fig. 1. Grain de pollen de *Sonchus*. Schéma d'une vue méridienne d'une aperture et du système lacunaire qui l'entoure. — 1: endoaperture et lacune porale, — 2: brèche (ectoaperture), — 3: lacune abporale, — 4: lacune paraporale, — 5: crête paraporale, — 6: crête abporale, — 7: crête équatoriale, — 8: calotte polaire.

et 252) présente quatre types chez les *Sonchus:*

type 1: la calotte polaire est entièrement occupée par un épaississement sans «lacune polaire» ou avec des lacunes mal définies;

type 2: l'épaississement polaire est moins développé du fait de l'existence de trois «lacunes polaires» (Fig. 2, a) situées sur le méridien des lacunes paraporales;

type 3: l'épaississement polaire est un petit triangle limité par trois grandes lacunes polaires (Fig. 2, b);

type 4: l'épaississement polaire est plus réduit encore, représenté seulement par la confluence des bords de trois très grandes lacunes polaires (alors du type schématisé en Fig. 2, c).

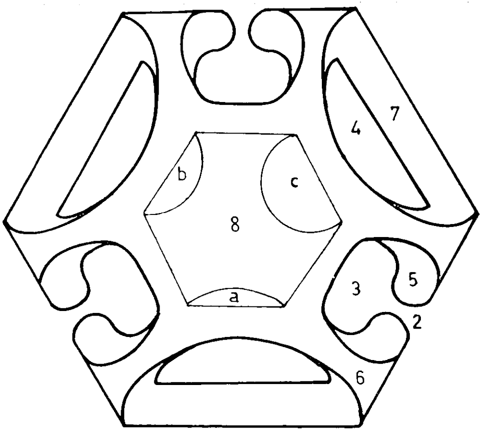

Fig. 2. Schéma d'une vue polaire d'un grain de pollen de *Sonchus*. Les chiffres correspondent à ceux de la Fig. 1. — a: «lacune polaire» d'une calotte du type 2 de Saad, — b: «lacune polaire» d'une calotte du type 3 de Saad, — c: «lacune polaire» d'une calotte du type 4 de Saad.

Ayant montré qu'à partir des espèces du sous-genre *Origosonchus* à travers le sous-genre *Dendrosonchus* pour aboutir au sous-genre *Sonchus* on voit se manifester une évolution générale du type 1 (de règle dans le genre *Launaea*) vers le type 4, Saad pense que les *Sonchus* représentent une partie de la lignée qui, à partir du genre *Launaea* aurait conduit aux genres *Crepis* et *Lactuca* chez lesquels la calotte polaire est presque inexistante.

Avant de passer en revue les résultats de notre étude il nous semble nécessaire de faire quelques remarques préliminaires concernant les «lacunes polaires» sensu Saad. En effet, ces lacunes présentent des particularités par rapport aux autres lacunes. Tout d'abord, si elles ont un contour net dans certains cas (*Sonchus asper, S. fragilis, S. masguindalii* et *S. radicatus*) leur dessin est le plus souvent imprécis et même extrêmement flou (*S. tenerrimus, S. palustris, S. brachyotus, S. gomerensis, Taeckholmia arborea*). Chez *Sonchus integrifolius, S. luxurians,* et d'autres, ces lacunes serpentent même entre les épines de la calotte. Enfin, leur position n'est pas absolument fixe puisqu'elles peuvent se trouver sur le méridien des lacunes abporales (*S. bourgeaui*) ou constituer une couronne plus ou moins régulière au tour de la calotte (*S. pinnatifidus, S. brachylobus* et l'ensemble des *Taeckholmia* sensu BOULOS 1967).

D'autre part, il existe une relation assez fixe entre le type de calotte polaire et le nombre d'épines polaires (si l'on excepte celles bordant les lacunes abporales et paraporales qui demeurent fixes):

chez les espèces du sous-genre *Origosonchus* on observe de 10 à 18 épines polaires (à l'exception de *S. luxurians* à 25 épines) sur une calotte du type 1;

chez les *Dendrosonchus,* où domine le type 3, on compte de 8 à 18 épines polaires;

chez les *Sonchus* et les *Taeckholmia,* où le type 4 est plus ou moins réalisé, on dénombre 6 (et même 4 seulement chez *S. palustris* et *S. mauritanicus*) à 10 épines polaires.

Cette relation semble indiquer que les «lacunes polaires» correspondent seulement à l'absence d'une ou plusieures épines (partie effilée plus base renflée d'ectexine). Chez plusieurs espèces nous avons observé sur les lacunes polaires une ornementation en très fin réseau toujours absolument absente dans les autres lacunes: ceci confirme la différence de nature existant entre les «lacunes polaires» décrites par SAAD chez les *Sonchus* et les lacunes qui sont caractéristique de l'immense majorité des *Cichorieae.* Dans l'ignorance où nous sommes de la structure de l'exine des deux types de lacunes nous ne pouvons préciser cette différence: seules des coupes ultraminces permettraient de le faire. De telles coupes sont en voie de réalisation. Dès à présent, cependant, nous pourrons tirer profit de nos premières observations concernant les «lacunes polaires» dans la discussion des enseignement phylogéniques que peut comporter l'étude du pollen des *Sonchus.*

MÉTHODE

Les données quantitatives concernant ce matériel peuvent se résumer dans le tableau 1 (nomenclature et disposition des espèces en conformité avec les conclusions de BOULOS 1972).

Toutes nos mesures ont été effectuées sur des grains très fraîchement acétolysés et chlorés (ERDTMAN 1960) montés dans la glycérine pure.

Nous donnons les chiffres extrêmes mesurés sur 30 grains environ et, pour certaines mesures de petites dimensions nous ne donnons que la valeur moyenne lorsque les écarts sont de même ordre de grandeur que les erreurs de mesures.

Nos chiffres sont en général très inférieures, de 20 à 30 %, à ceux donnés par SAAD mais le décalage est à peu près constant. Il y a donc tout lieu de penser que la différence provient de l'influence du milieu de montage. En effet, il a été démontré que sur certains grains au moins (FAEGRI & DEUSE 1960) un long séjour dans la glycérine gelatinée — milieux utilisé par SAAD — peut entraîner un gonflement de l'ordre de 10 % en diamètre. En fait la structure lacunaire des pollens de *Sonchus* semble propre à permettre un gonflement beaucoup plus important. D'ailleurs, des mesures effectuées un mois après le montage nous ont donné — même en glycérine — sur les grains de dix espèces prises au hasard des chiffres supérieurs de 8 à 9 % à ceux indiqués ci-dessus. Il eut été souhaitable d'attendre la fin de ce gonflement qui peut s'étaler sur quatre mois, pour effectuer les mesures, mais cela n'était pas possible dans les conditions imposées par le travail en commun.

OBSERVATIONS

Sonchus sous-genre **Origosonchus**

Les tailles minimales vont de 24,7 µ à 29 µ et les tailles maximales de 28,5 µ à 36,5 µ. L'épaississement polaire est le plus fréquemment du type 1, le nombre d'épines polaires est important (8 à 20).

La section *Dregeani* est très homogène à tous égards et, en adoptant le schéma évolutif dégagé par SAAD, la morphologie pollinique confirme l'ordre des espèces suggéré par l'ensemble des données morphologiques; de même elle correspond à l'ensemble le plus primitif dans le genre.

La section *Origosonchus* est palynologiquement plus évoluée. Il faut cependant noter que *Sonchus luxurians* et *S. bipontini* bien que placés dans la section supposée la plus évoluée, possèdent une brèche paraporale très ouverte semblable à celle des *Launaea* qui, dans le schéma de SAAD, est proposé comme archétype. Au contraire, du point de vue de la calotte polaire, ces deux espèces, malgré la place que la morphologie leur assigne dans la section, sont fort proches de *S. schweinfurthii,* et constituent avec lui la jonction avec le sous-genre *Dendrosonchus.*

Sonchus sous-genre **Dendrosonchus**

Même si l'on exclue *Soncus hierrensis,* dont le pollen est particulier à tous points de vue, les tailles minimales (24,7 à 29 μ) et surtout maximales (28,6 à 39 μ) montrent un accroissement de volume par rapport aux pollens de sous-genre précedent.

L'épaississement polaire est le plus souvent du type 3 avec 8 à 18 épines polaires. Les épines atteignant une hauteur relativement plus importante (5,2 μ) que dans les deux autres sous-genres.

L'étude palynologique n'apporte aucun élément substantiel à l'appui de la division en sections proposés: toutes les sections paraissent aussi hétérogènes que le sous-genre en son ensemble.

Il faut cependant noter que chez *Sonchus pinnatifidus* et *S. brachylobus,* voisins bien que dans deux sections différentes, les lacunes polaires ont tendance à former un anneau autour de la calotte comme il est presque de règle dans le genre *Taeckholmia.*

Sonchus hierrensis possède une calotte polaire qui rapproche cette espèce du sous-genre *Origosonchus* (type 1 et 19—25 épines) bien que son grand diamètre (39—45 μ) l'en éloigne.

Chez *Sonchus acaulis* et *S. canariensis* on observe une calotte du type 1 et 2 et, particulièrement chez le second, un grand nombre d'épines polaires: la palynologie tendrait donc à placer ces deux espèces à la base du sous-genre ce qui va à l'encontre des conclusions du taxonomiste, surtout pour *S. acaulis.*

Il faut enfin noter que l'étude du pollen de *Sonchus pitardii* suggère qu'il s'agit là d'un hybride: la calotte polaire est tout à fait anarchique et la taille des grains montre une marge de variation assez exceptionnelle.

Sonchus sous-genre **Sonchus**

On y observe des grains dont la taille minimale varie de 32,5 à 45 μ et la taille maximale de 33 à 49 μ: l'accroissement de taille par rapport aux deux autres sous-genres est net.

Le type 4 d'épaississement polaire est le plus général et le nombre d'épines polaires va de 4 à 12, exception faite du *Sonchus macrocarpus* où il est plus élévé (16—19).

Parmi les sections proposées celle dont le type est *Sonchus asper* présente une remarquable individualité du fait de la réduction de la calotte polaire, résultant du développement des lacunes abporales et paraporales, et de leur grande taille. De plus, toutes les espèces qui la composent offrent un mélange, en proportions variables, de grains tétracolporés et de grains tricolporés. Ce caractère semblerait lié au fait que tous les taxons de cette section constituent vraisemblablement des polyploïdes de *S. asper.* Cependant on trouve aussi chez ce dernier — quoique en proportion moindre — des grains tétracolporés: la véritable origine de ce mélange reste donc obscure.

L'état tétracolporé de *Sonchus asper* explique, par contre, fort bien les rares pollens tétracolporés de *Sonchus oleraceus* qui est supposé être un amphidiploïde de *S. asper* et *S. tenerrimus.*

A coté de ce groupe très homogène il est difficile de retrouver dans l'étude du pollen la justification des section pro-

Tableau 1. Palynologie du genre *Sonchus* s.l. Données quantitatives.

Taxon	Nombre de pores	Diamètre total	Hauteur des crêtes	Hauteur des épines	Diamètre sans crêtes	Type de calotte	Nombre d'épines polaires	Nombre d'épines paraporales
GENRE SONCHUS L.								
Sous-genre *Sonchus*								
Section 1. *Sonchus*								
1. *Sonchus oleraceus* L. emend. Gouan	3—4	33,5—35,9	5,2	3,2	23 —25,3	4	6— 8	6—7
2. *S. tenerrimus* L.	3	31,5—33	3,2	2,6	24 —26,5	4	7— 8	6—9
3. *S. bourgeaui* Sch. Bip.	3	26 —31,2	3,2—3,9	2	18,8—24	4	8—10	7
Section 2. *Asperi* Boulos								
4. *Sonchus asper* (L.) Hill ssp. *asper*	3—4	35 —42	4,2—5	3,2	28 —32	4	6— 9	7
4 a. *S. asper* (L.) Hill ssp. *glaucescens* (Jordan) Ball	3—4	30 —35,5	3,9—4,2	1,6	23,5—27	4	6— 7	7—8
5. *S. littoralis* (T. Kirk) Allan	—	—	—	—	—	—	—	—
6. *S. mauritanicus* Boiss. & Reut.	3	29,2—31,5	3,2	2,6	23 —25,5	4	9	7—8
7. *S. macrocarpus* Boulos & C. Jeffrey	3—4	42,5—44	4	2,6	35 —37	3—4	16—19	6—8
8. *S. gigas* Boulos ex Humbert	3—4	35,7—40	3,2—3,9	2,6	29 —34,5	3—4	9	6—8
9. *S. hydrophilus* Boulos	3—4	45 —49	5,2	2,6	35 —39	2—3	9—14	?
Section 3. *Maritimi* (Kirp.) Boulos								
10. *Sonchus maritimus* L.	3	27,9—30	3,2	1,9	22,4—22,7	4	7	7
11. *S. palustris* L.	3	32,5—38	4,8	3,2	25 —30	4	5— 9	7
12. *S. crassifolius* Pourr.	3	36,4—38	4,6	3,2	27,3—29	3	15	7
Section 4. *Arvenses* (Kirp.) Boulos								
13. *Sonchus arvensis* L. ssp. *arvensis*	3	36,4—40	4,55	2,6—3	29 —32	4	10	7
14. *S. brachyotus* DC.	3	29,2—35	2,6	2	24 —31	4	4	6
15. *S. wightianus* DC. ssp. *wightianus*	3	36,4—40	3,9	2	28,5—31	3—4	11	7
16. *S. malaianus* Miq.	3—4	32,5—36	3,9	2,6	26 —31	(4)	6— 7 (3)	7
Section 5. *Pustulati* Boulos								
17. *Sonchus pustulatus* Willk.	3	35 —37	5,2	2,5	27 —28,5	3—4	6— 7	7
18. *S. fragilis* Ball	3	32,5—38	4	2	24 —30	4	7	7

19. *S. briquetianus* GANDOGER	3	33,4—34,5	4,6	2 —2,6	24 —25,4	3—4	11	7
20. *S. masguindalii* PAU & FONT QUER	3	32,5—37,5	4,6	2	22 —28	3	7— 9	7—8
Section 6. *Tuberiferi* BOULOS								
21. *Sonchus tuberifer* SVENT.	3	30 —32	3,3	3,3	23,5—26	3—4	7	7
Sous-genre *Dendrosonchus* SCH. BIP. ex BOULOS								
Section 1. *Dendrosonchus*								
22. *Sonchus congestus* WILLD.	3	33,8—35,5	3,2	2,6	27,2—29	2—3	9	7
23. *S. acaulis* DUM.-COURS.	3	35 —37,7	4,5—5	3,9	23,4—27,3	2	16—18	7
24. *S. hierrensis* (PITARD) BOULOS	3	39 —42	3,9	2,6	33,8—36,5	1	19—25	6—7
25. *S. daltoni* WEBB	3	35 —38,5	3,9	2,6	26 —30	3	10—14	7
26. *S. bornmuelleri* PITARD	3	31,2—36,5	3,9	2,6	23,4—28	3	13	7
27. *S. radicatus* AIT.	3	32,5—35,5	3,9—4,3	4,5—5,2	24 —27	3—4	8—11	7
28. *S. gomerensis* BOULOS	3	31,5—35,5	3,2	2,6	24 —28,5	4	8	6—7
29. *S. gummifer* LINK	3	31,2—36	2,6	2,6	25,4—30,7	3—4	10	7
30. *S. ustulatus* LOWE	3	26 —32,5	2,6	2 —2,5	24,7—27,3	2—3	9	6—7
31. *S. fauces-orci* KNOCHE	3	35,2—36,5	4,4—5,2	2,6	26 —27,3	3—4	11—13	7
32. *S. pinnatifidus* CAV.	3	28,6—30	3,2—3,9	1,9	21,4—25,5	3	8	7
Section 2. *Brachylobi* BOULOS								
33. *Sonchus brachylobus* WEBB & BERTH.	3	30 —32,5	3,2—5,2	2,6	22,1—22,7	4	8	7
Section 3. *Pinnati* BOULOS								
34. *Sonchus pinnatus* AIT.	3	29,5—32	3,2	3,2	22,8—24	2—3	13	6
35. *S. palmensis* (SCH. BIP.) BOULOS	3	29,5—35,4	2,6—3,9	2,6—3,9	24,7—26,5	3—4	7—12	7
36 *S. canariensis* (SCH. BIP.) BOULOS	3	31,8—33,8	3,2—3,9	2,6	24 —26	1	11—12	6—7
37. *S. fruticosus* L. FIL.	3	34 —37	3,9—4,5	3,8	26 —28,6	2—3	8—10	7
38. *S. lidii* BOULOS	3	28,6—30,5	3,2	3 —3,2	22,1—23,4	2—3	7—12	7
39. *S. gandogeri* PITARD	3	32,5—35,2	3,9	3,2	23,4—25	3	12—14	7
40. *S. pitardii* BOULOS	3	36,4—42	5,2—5,8	2,5—3,2	27,3—32	1—2—3—4	8—14	7
Sous-genre *Origosonchus* BOULOS								
Section 1. *Origosonchus*								
41. *Sonchus schweinfurthii* OLIV. & HIERN	3	29,5—33	3,2	3,2	22,7—24	3—4	10	7—8
42. *S. angustissimus* HOOK. FIL.	3	27,3—30	3,2	2,6—3	22,5—23	1	14—20	7
43. *S. stenophyllus* R. E. FRIES	3	30 —32,5	4 —4,5	2 —2,5	20,8—24,5	1	12—14	7
44. *S. camporum* (R. E. FRIES) BOULOS ex C. JEFFREY	3	33,8—39	4	2,6—3	24,7—29,2	1	10—19	6—7
45. *S. afromontanus* R. E. FRIES	3	31,2—33,8	4	2,6	23 —25,8	1	15—17	7

Taxon	Nombre de pores	Diamètre total	Hauteur des crêtes	Hauteur des épines	Diamètre sans crêtes	Type de calotte	Nombre d'épines polaires	Nombre d'ép.nes paraporales
46. *S. bipontini* Aschers.	3	35,1—36,4	4,5—5,2	2,6	26 —27,5	2—3	8—10	7
47. *S. luxurians* (R. E. Fries) C. Jeffrey	3	31,2—34,5	4	2,6	24 —27,5	2—3	10	7
48. *S. melanolepis* Fresen.	3	26,5—29	3,2	2,6	20,8—22,7	3	9	7
49. *S. obtusilobus* R. E. Fries	3	24,7—28,6	3,2	2,3	19 —22,7	3—4	10	7
Section 2. *Dregeani* Boulos								
50. *Sonchus dregeanus* DC.	3	32,5—34	4,9	2,6	22,2—23,5	1	14	7
51. *S. integrifolius* Harv.	3	32,5—34	3,2	2,6	26 —28	1	14—16	7
52. *S. friesii* Boulos	3	28,6—35,7	3,2	2,6	22,1—28	1	13—18	5
53. *S. wilmsii* R. E. Fries	3	29,2—32,5	3,2	2,6	22,7—26	1—2	12—14	7—8
Section 3. *Nani* Boulos								
54. *Sonchus nanus* Sond. ex Harv. & Sond.	3	27,3—29,9	3,9	2,6	20,8—22,1	1	12—14	6
GENRE EMBERGERIA Boulos								
Sous-genre *Embergeria*								
1. *Embergeria grandifolia* (T. Kirk) Boulos	3	37,7—40	3,6	7,2	30,2—33	—	—	—
Sous-genre *Megalocarpa* Boulos								
2. *Embergeria megalocarpa* (Hook. fil.) Boulos	3	41 —45	3,8	2,6	33 —37,5	3—4	7—11	7
GENRE BABCOCKIA Boulos								
1. *Babcockia platylepis* (Webb) Boulos	3	38,9—42	6 —6,5	3,2	28 —31	2—3	18—22	7
GENRE TAECKHOLMIA Boulos								
Sous-genre *Taeckholmia*								
1. *Taeckholmia pinnata* (L. fil.) Boulos	3	35,2—36,5	3,2—3,9	3,5	28,8—29,5	4	8—14	7
2. *T. capillaris* (Svent.) Boulos	3	33,8—35,3	3,9	3	26 —28	4	6	6—7
3. *T. canariensis* Boulos	3	24,7—35,1	2,5	2,6	20,1—31,2	3—4	9—14	7
4. *T. microcarpa* Boulos	3	31,2—32,5	3	2,8	26 —27,3	2	8	7
Sous-genre *Pseudodendrosonchus* Boulos								
5. *Taeckholmia heterophylla* Boulos	3	26 —28,5	2,3	2,5	21,6—23	3	11	7
6. *T. regis-jubae* (Pitard) Boulos	3	30,8—32	3,9	2,6	23 —24,7	2—3	11—13	6—7
7. *T. arborea* (DC.) Boulos	3	29,2—30,5	3,2	3,9	22,7—28,5	2—3	4—10	7

posées. Seul le développement des lacunes paraporales et abporales chez *Sonchus mauritanicus* et *S. bourgeaui* confirme la proximité des sections *Sonchus* et *Asperi*. Cependant ces deux espèces sont remarquables aussi par une certaine confluence des lacunes polaires propre au genre *Taeckholmia*.

Enfin, il est intéressant de trouver un certain pourcentage de pollens tétracolporés chez *Sonchus malaianus* connu pour son importante garniture chromosomique ($2n = 54$).

Taeckholmia

Les grains de pollen des espèces réunies dans ce genre nouveau ont un diamètre minimal de 26 à 35 μ et maximal de 28 à 36,5 μ. Ils sont surtout caractérisés par le fait que les lacunes polaires tendent à se joindre sur les méridiens des lacunes abporales pour former une sorte d'anneau autour de la calotte (chez *T. canariensis* cet anneau est même plus large dans le méridien des lacunes abporales).

De ce fait il est extrêmement difficile de classer les calottes polaires dans un des types de SAAD; de plus le nombre d'épines polaires (de 6 à 14) semble assez indépendant du type auquel on peut parvenir à les rattacher.

Par ailleurs les épines des crêtes sont en général très évasées: on voit mal le dessin en escalier qui caractérise la base des épines des *Sonchus:* à cet égard *Taeckholmia regis-jubae* et *T. canariensis* sont très typiques.

Palynologiquement les deux sous-genres proposés sont indiscernables.

Embergeria

Les deux sous-genres sont içi très différents. *Embergeria megalocarpa* est palynologiquement très proche des *Sonchus* de la section *Asperi:* la taille et l'importance des lacunes abporales et paraporales, avec la réduction corrélative de la calotte polaire, évoquent en effet *S. asper* et ses proches.

Le pollen d'*Embergeria grandifolia* est extrêmement different du pollen de toutes les espèces du genre *Sonchus* s.l.: les lacunes paraporales n'existent pas, les lacunes porales sont pratiquement réduites à l'endoaperture et l'extrémité de l'ectoaperture seule s'entoure d'une lacune abporale très réduite; l'exine est mince, de structure simple, et les épines, réparties uniformément sur tout le grain, sont très hautes (7,2 μ). Ce type de pollen semble très proche du type *Catananche* L. (WODEHOUSE 1959, Pl. XI, 3 et fig. 114).

La palynologie étaie donc la création du genre *Embergeria* en ce qui concerne *Embergeria grandifolia* mais conduirait à en exclure *E. megalocarpa* dont elle ferait un *Sonchus* proche de *S. asper*.

Babcockia

La grande taille des grains de *Babcockia platylepis,* l'épaisseur des crêtes (6 à 6,5 μ) et le fait que malgré des lacunes polaires consitantes (type 2—3) on trouve un grand nombre d'épines polaires constituent un ensemble de caractères, relativement ténus, suffisamment particulier pour justifier la création de ce nouveau genre.

DISCUSSION

Notons en terminant cette revue que le nombre d'épines paraporales, relativement beaucoup plus fixe que ne semble l'indiquer SAAD, constitue un élément négligeable de la morphologie pollinique.

En conclusion nous devons d'abord examiner la validité des tendances évolutives qui ont été dégagées soit dans le groupe voisin des *Ambrosiae* (WODEHOUSE 1928) soit au sein même de l'ensemble des *Cichorieae* (PAUSINGER 1951 in SAAD, 1960).

Nos résultats confirment qu'un accroissement de taille a marqué l'évolution du pollen, ainsi que le pensait WODEHOUSE. Cependant cette tendance est à peine sensible à travers des moyennes qui se recouvrent toutes et, hormis le cas des trois sous-genres de *Sonchus,* il est difficile de lui assigner un tracé net.

Les raccourcissement des sillons, valable chez les *Ambrosiae,* ne semble pas pouvoir être retenu pour notre matérial: tous les pollens des espèces de la section *Asperi* auxquelles la taxonomie et la palynologie accordent une place parmi les taxons les plus avancés, possèdent des lacunes abporales, donc des sillons, très importantes.

La réduction du nombre d'épines signalée par WODEHOUSE ainsi que la disparition de l'épaississement polaire et la multiplication des lacunes constatées par PAUSINGER sont parfaitement visibles chez les pollens des *Sonchus* et consorts: notre théorie sur la nature des «lacunes polaires» rend compte exactement de la concommittance de cas trois phénomènes qui ne seraient, en fait, que trois manifestations d'une unique tendance à l'allègement de la calotte polaire.

Du point de vue taxonomique nos observations confirment les coupures majeures proposées mais, sauf dans le cas du sous-genre *Origosonchus,* elles ne parviennent pas à s'insérer dans le détail de l'élaboration des sections. A tous les échelons, des complications interviennent du fait qu'il est difficile de faire le partage entre les enchainements au sein d'un même phylum et les convergences entre paliers équivalents de lignées distinctes: il est ainsi difficile de percer la nature véritable des ressemblances entre *Embergeria megalocarpa* et les *Sonchus* de groupe *Asperi,* entre *S. fragilis* et *S. bipontini* ou *S. luxurians,* entre *S. bourgeaui* et la majorité des *Taeckholmia,* etc. D'autre part certains caractères polliniques montrent une grande indépendance et des espèces peuvent ainsi paraître palynologiquement à la fois primitives et évoluées: *S. fragilis* (lacunes polaires nettes et brèche paraporales très ouverte), *S. hierrensis* (grande taille et calotte polaire du type 1 avec de nombreuses épines) etc. La prise en compte de la morphologie pollinique est donc importante pour le taxonomiste mais il ne s'agit que d'un élément complémentaire qui ne saurait suffire à lever toutes les indéterminations demeurées sans solution avec l'ensemble des autres données.

Contrairement à l'opinion de SAAD, la morphologie ne semble pas prouver que l'origine des *Sonchus* soit à rechercher parmi des *Launaea.* Certes le pollen de ces derniers a une calotte du type 1, comme les *Sonchus* jugés les plus primitifs, mais elle s'accompagne d'un nombre d'épines polaires plus faible (6 à 8). On peut donc seulement affirmer que *Sonchus* et *Launaea* ont un ancêtre commun sans qu'une filiation directe, dans un sens ou l'autre, puisse être tracée entre eux.

De même, il est impossible d'admettre, comme le fait SAAD, une relation directe entre les pollens de *Sonchus* à calotte du type 4 et les pollens du type *Lactuca* ou *Crepis*: chez les premiers la réduction de la calotte est liée aux «lacunes polaires» — elle demeure donc superficielle — tandis que dans le second cas cette réduction, beaucoup plus profonde au regard de l'exine, provient du développement des lacunes abporales et paraporales.

Le coexistence des deux phénomènes chez certains *Sonchus* (section *Asperi*), ainsi que la manifestation de tendances dont l'aboutissement a conduit à des types de pollens d'autres genres (*Catananche*) impose donc une conclusion qui s'éloigne un peu du schéma évolutif proposé par SAAD: *Sonchus, Taeckholmia, Embergeria, Babcockia,* ainsi que *Lactuca* et *Crepis* sont vraisemblablement issu d'un tronc commun qui nous est encore inconnu et dont aucune espèce actuelle du groupe ne semble pouvoir donner une idée exacte.

La palynologie est donc, malgré sa précision, incapable de reconstituer l'histoire, vraisemblablement fort ancienne, de ce groupe de taxons et, a fortiori, mal armée pour évaluer les hypothèses avancées à ce propos (STEBBINS & al. 1953, BOULOS 1960) sur la base des résultats de méthodes d'investigation beaucoup plus complètes.

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Studies in Galápagos Plants XIII

Three New Floristic Records and Two Supplementary Remarks

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ABSTRACT

ELIASSON, U. 1972. Studies in Galápagos plants. XIII. Three new floristic records and two supplementary remarks. — Bot. Notiser 125: 320—322.

Alternanthera lehmannii HIERON., *Callitriche deflexa* A. BR. ex HEGELM. and *Rumex crispus* L. are reported as new to the Galápagos. The differences between *Chrysanthellum fagerlindii* ELIASS. and *Ch. pusillum* HOOK. FIL. are pointed out. A recent record of *Lecocarpus lecocarpoides* (ROBINS. & GREENM.) CRONQ. & STUESSY from San Cristóbal is discussed.

Alternanthera lehmannii HIERON.

A. lehmannii is new to the Galápagos. It might be a recent introduction to the archipelago. The collection studied agrees well with *A. lehmannii* as circumscribed by STANDLEY (1937 p. 501), except that the sepals in the Galápagos material vary from straw-coloured to pale violet red.

This taxon is very close to *A. lanceolata* (BENTH.) SCHINZ, and differs from the latter mainly in the pilose sepals, the sepals of the latter taxon being glabrous. It is possible that these taxa will be found to fall within the range of variation of one species, as pointed out by STANDLEY (1937 p. 501). *A. lehmannii* and *A. lanceolata* are plants of the South American mainland, ranging from Peru and Bolivia in the south to Colombia and Venezuela in the north (STANDLEY 1937 p. 501).

COLLECTION STUDIED. Isabela. GORDILLO 1032, Volcán Santo Tomás, south part of the rim of the caldera, alt. ca. 1000 m, 17 April 1971 (GB).

Callitriche deflexa A. BR. ex HEGELM.

This is the first definite record of the genus in the Galápagos. I have collected *C. deflexa* on three islands, viz. Isabela, San Salvador and Santa Cruz. It was found on wet soil in disturbed localities, such as paths, cultivated ground and areas ruined by wild goats and pigs. Very probably it is of recent introduction in the archipelago. On the American continents it ranges from Mexico to Argentina (FASSETT 1951).

FASSETT (1951) recognizes a var. *subsessilis* FASSETT with smaller and more short-pedicelled fruits than in var. *deflexa*. The Galápagos material has fruit the same size as var. *deflexa* but approaches var. *subsessilis* in the short pedicels.

An old report (WOLF 1879 p. 284) of a *Callitriche* on Floreana in the Galápagos is very doubtful and was probably based on a misidentification:

"Auf dem Weg zur Hacienda kommen wir über einen kleinen Bach, der links an den Bergen entspringt, sich aber bald in einem Sumpf verliert; er ist von Binsen und Ried-

Table 1. Comparison between *Chrysanthellum fagerlindii* and *Ch. pusillum.*

Ch. fagerlindii	*Ch. pusillum*
Leaf segments generally 0.2—0.4(—0.5) mm wide.	Leaf segments generally 0.5—0.7(—0.8) mm wide.
Flower heads ca. 2 mm wide.	Flower heads ca. 4 mm wide.
Phyllaries narrowly triangular.	Phyllaries ovate-lanceolate.
Ray-flowers minute, hidden by the phyllaries.	Ray-flowers well developed with long ligulate corollas.
Corollas of disk-flowers deeply cleft to a half or more of their length.	Corollas of disk-flowers shallowly cleft to about a fifth of their length.
Paleae ca. 0.05 mm wide, 1-striate.	Paleae ca. 0.1 mm wide, 2-striate.

gräsern eingefasst und von Wasserpflanzen (Myriophyllum, Callitriche, Salvinia, Lemna) bedeckt. Dieselben Gewächse treffen wir an den kleinen Lagunen des Hochplateaus, welche nur austrocknen, wenn es mehrere Jahre hintereinander sehr wenig regnet."

Whether WOLF did see a *Callitriche* on Floreana is far from certain and has been doubted by recent workers on the Galápagos flora. Many of WOLF's records are doubtful (e.g., neither *Myriophyllum* nor *Salvinia* have been seen in the archipelago by subsequent collectors). If WOLF did see a *Callitriche,* it was probably not *C. deflexa,* since this is a terrestrial rather than an aquatic species.

COLLECTIONS STUDIED. Isabela. ELIASSON 1240, Volcán Alcedo, on the south part of the rim of the caldera, alt. ca. 1000 m, 11 Feb. 1967 (S). — San Salvador. ELIASSON 1332, the highest part of the island, alt. ca. 900 m, 21 Feb. 1967 (S). — Santa Cruz. ELIASSON 402, south side of the island, on cultivated ground, alt. ca. 220 m, 21 Oct. 1966 (S).

Rumex crispus L.

The first record of this introduced weed in the Galápagos was made on the rim of Volcán Santo Tomás in an open grassy area strongly influenced by free-ranging horses and cattle. The first record of another introduced weed, *Stellaria media* (L.) VILL., was made in the vicinity.

R. crispus is a polymorphic species of European origin having been introduced into many parts of the world. The genus is new to the Galápagos.

COLLECTION STUDIED. Isabela. ELIASSON 1473, Volcán Santo Tomás, the east part of the rim of the caldera, alt. ca. 1000 m, 3 March 1967 (S).

Chrysanthellum fagerlindii ELIASS.

Without having seen material of *Ch. fagerlindii,* CRONQUIST (1971 p. 322) relegated it to synonymy under *Ch. pusillum* HOOK. FIL. The morphological differences between these two taxa are, however, so important that they have to be regarded as different species. CRONQUIST's supposition that the first-named taxon is nothing but a minor form of *Ch. pusillum* is quite wrong. *Ch. fagerlindii* is habitually different, being more slender with smaller flower heads and narrower leaf segments. The two species are morphologically distinct in the characters given in Table 1 (cf. ELIASSON 1967).

In my brief description (ELIASSON 1967) of the generic characters in *Chrysanthellum,* the limb of the disk-flowers was erroneously described as 5-fid. In fact both 4-fid and 5-fid disk-corollas occur in the genus and are often found in the same flower head in several species. In the two endemic Galápagos species, however, only 4-fid corollas have been seen.

Lecocarpus lecocarpoides (ROBINS. & GREENM.) CRONQ. & STUESSY

In my recent treatment of this genus I briefly described (ELIASSON 1971 p. 263) a collection made by DARWIN on San Cristóbal which did not fit satisfactorily any of the species recognized. Recently CRONQUIST (1971 p. 342) has reported *L.*

lecocarpoides from San Cristóbal. His report was based on the following collection, the existence of which I was unfortunately not aware of when I wrote my paper on the genus: CASTRO s.n., north side of the island, 2 km from the beach, alt. 100 m, 21 Dec. 1965 (DS). The three small branches on this sheet agree well with the specimens in DARWIN's collection. The numerous diaspores of the recent collection, however, show a wide range of variation. Many diaspores completely lack spines, whereas others have narrowly triangular spine-like wings. The whole scale of transition forms between these two types occur. In the DARWIN collection mentioned, the relatively few diaspores completely lack spines and wings.

Having studied the CASTRO collection from San Cristóbal I refer this as well as the DARWIN collection, described in my previous paper, to *L. lecocarpoides*. Thus this species can no longer be regarded as endemic to Española and the adjacent Gardner Island, as I previously thought it to be. It could be interesting to note, however, that the two known collections from San Cristóbal differ from the specimens of *L. lecocarpoides* hitherto found on Española and Gardner in having larger involucral bracts, 10—13 mm long, and longer ray-flower corollas, 9—11 mm long. The corresponding figures for the Española-Gardner specimens are 8—10 mm and 6—7.5 mm, respectively. The specimens available are, however, too few to permit any conclusions concerning possible recognizable subspecific taxa.

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Scorzonera scyria, a New Chasmophytic Species from Greece

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ABSTRACT

GUSTAFSSON, M. & SNOGERUP, S. 1972. Scorzonera scyria, a new chasmophytic species from Greece. — Bot. Notiser 125: 323—328.

The new locally endemic species *Scorzonera scyria* M. GUST. & SNOG. is described from the island of Skiros, Greece. It is a perennial, obligate chasmophyte belonging to subgen. *Scorzonera* sect. *Foliosae* (BOISS.) LIPSCHITZ. The chromosome number is 2n = 14. A schematic karyotype is given.

INTRODUCTION

The flora of the island of Skiros is being investigated in detail by a team including the present authors, Prof. D. PHITOS, Patras, and R. V. BOTHMER, Lund. Several new taxa have been discovered during the field work and will be published separately as soon as they have been sufficiently investigated.

The specimens of *Scorzonera scyria* transplanted into a greenhouse in the Botanical Garden, Lund, became much modified, e.g. in having longer stems, more capitula and longer leaves. Thus, the description below is entirely based on material collected in field, with only some remarks on the cultivated material.

Scorzonera scyria M. GUSTAFSSON & SNOGERUP, sp. nov. (Figs. 1, 2)

Typus: SNOGERUP & GUSTAFSSON 42666 (LD holotypus, W, G, K, PATRAS).

Planta perennis, e basi lignosa, ramosa, caules floriferos et rosulas vegetativas plures emittens. Folia basalia et caulina pluria, alterna, basalia et caulina inferiora e basi vaginata petiolata, elliptica usque lanceolata, caulina superiora semiamplexicaulia, cordiformia, superne sensim acuminata. Capitula florentia 4—6 cm lata, flores dilute lutei. Involucri squamae ovatae vel inferiores suboblongae, obtusae vel acutae, apice floccosae. Pappi setae 5 longiores apice simplices, scabridae, et c. 30 breviores, tota longitudine pennatiramosae, scabridae.

Perennial, with a branched, woody basal part each year producing 1—10 herbaceous flowering shoots and a variable number of non-flowering rosettes. Basal woody branches short, 1—2 cm thick, dark, covered with remnants of former leaves, annual rings inconspicuous, only the outer ones recognizable. Flowering stems 20—35 cm high, usually 4—5 mm thick in the basal part, striate, or in dried material sulcate, with 4—10 basal and 6—15 cauline leaves, 1—5-headed (or in cultivated specimens up to 10-headed). Basal leaves petiolated, petiole short or up to 3(—6) cm long, from a sheathy basal part flat, 2—7 mm broad, lamina lanceolate to elliptic, acute, entire, 4—8 cm long, 1.5—2.5(—3) cm broad, curve-ribbed with anastomosing veinlets forming an irregular reticulum. Lower cauline leaves up to 11 cm long, and 3 cm broad,

Fig. 1. *Scorzonera scyria.* — Part of flowering specimen, ×0.6. Type collection.

lanceolate to narrowly ovate, short-petiolated or all with a broad, semiamplexicaul base, upper leaves gradually smaller, semiamplexicaul, ovate with a prolonged tip. Floccose hair-covering of multiradiate hairs, densely developed on ventral leaf surface, basal part of the stem and basal part of the dorsal surface of some upper

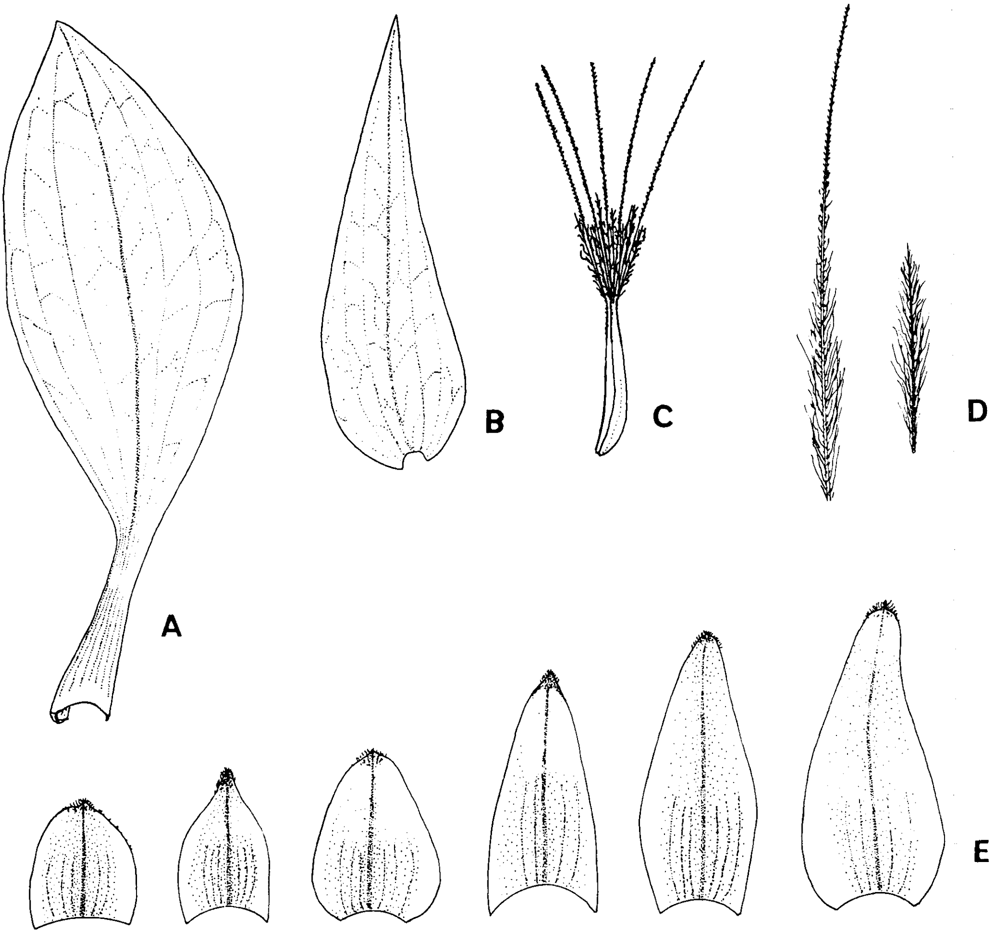

Fig. 2. *Scorzonera scyria.* — A: Basal leaf, ×1.2. — B: Middle cauline leaf, ×1.2. — C: Achene, ×1.5. — D: Pappus bristles, ×3. — E: Involucral scales, ×2. — A, B and E: Type collection. C and D: S & G 44329.

leaves, sparse or lacking on other parts of dorsal leaf surfaces and stem.

Capitulum usually 50—60-flowered, (3—)4—6 cm broad at anthesis. Involucrum cylindrical, 20—30 mm long and 8—15 mm thick. Involucral bracts 12—18, overlapping, of varying sizes, lower ones broad, ovate to oblong, obtuse, mucronate or rarely acute, upper ones gradually longer and more narrowly ovate, some of them with an elongated, oblong tip, obtuse to acute. Involucral bracts green all over or with a darker, ± purplish apex, with narrow scarious margins and a marked tuft of flocculose hairs at the apex, at the margin also some simple hairs. Receptacle hairy with predominantly simple hairs.

Florets pale yellow, tube 8—12 mm long, lamina 14—20 mm long and 2—5 mm broad, varying in form from oblong to narrowly lanceolate, apically markedly 5-fid, with 2—4(—8) striae, quite glabrous or with a sparse covering of predominantly simple hairs on the ventral side. Anthers

4.5—6.5 mm, greenish yellow to light brown, filaments c. 1.5 mm. Ripe stigmata 6—7 mm, light brown.

Achene 12—14 mm, c. 1.5 mm broad, glabrous, 4-costate but costae often inconspicuous especially in the symmetric inner achenes, those of the slightly curved marginal achenes sometimes irregularly rugulose, in their apical part setose. Pappus bristles of two discrete types. Long bristles normally 5, 15—18 mm long, densely covered with 0.1—0.2 mm long setae and in their basal part with lateral, crispulate hairs. Short bristles c. 30, 5—10 mm long, densely covered with lateral, crispulate hairs along their entire length and with some setae like those of the long bristles.

Pollen yellow, of Helianthus-type (ERDTMAN et al. 1961), with verrucae or broad spinulae on the ridges. Chromosome number 2n=14.

The name is formed from the name of the island of Skiros, to indicate the local distribution.

COLLECTIONS: Skiros, 2.5—3 km N—NW of the top of Mt. Kochilas, 100—200 m, cliffs of hard limestone. SNOGERUP & GUSTAFSSON 42666. (LD holotypus, W, G, K, PATRAS). — Skiros, cliffs of predominantly N—NE exposure at Akr. Korakias and up to 1 km S of Akr. Korakias, 10—200 m, hard limestone. SNOGERUP & GUSTAFSSON 44329. (LD, PATRAS).

DISTRIBUTION AND ECOLOGY

In 1971 *Scorzonera scyria* was found on the lower, N-facing cliffs of Mt. Kochilas, 2.5—3 km to the N of the top. The following year it was also observed growing along the cliffs at Akr. Korakias, situated in the E part of the same mountain. Thus, both collections originate from the same cliff system, which extends for 10—12 kms with cliffs of varying altitudes from sea level up to 700 m. *S. scyria* has only been observed within a distance of one km from the sea and preferably at altitudes of 50 to 200 m. Both the higher parts of the same cliff system as well as several other cliffs of Skiros, the neighbouring island of Skiropoula and all the islets around Skiros have been investigated too, but unsuccessfully. It seems most probable that *S. scyria* is restricted to the maritime cliffs on the northern and eastern sides of Mt. Kochilas. In particular the southern populations visited in 1972 comprised many specimens, at the least more than 500 and probably thousands of individuals, particularly if the adjacent cliffs, which have not yet been closely investigated, also are included. *S. scyria* must be considered as being locally well established and its existence secure for the nearest future. Further, it is restricted to small crevices containing very little earth or none, in the open, very steep, sometimes vertical cliff surfaces. The influence of grazing or other agricultural practices is insignificant or nonexistent and it has probably remained wholly undisturbed by human activity. The species has only been observed growing on cliffs composed of hard limestone.

The cliff system to which *Scorzonera scyria* is endemic, contains a very rich cliff flora. From the cliff surfaces have been noted: *Senecio bicolor* (WILLD.) TOD., *Centaurea rechingeri* PHITOS, *Ptilostemon chamaepeuce* (L.) LESS., *Inula* cf. *sophiae* BEAUV., *Campanula merxmülleri* PHITOS, *Galium reiseri* HAL., *Scrophularia heterophylla* WILLD., *Athamantha macedonica* (L.) SPR., *Hedera helix* L., *Erysimum senoneri* (HELDR. & SART.) WETTST. ssp. *senoneri*, *Aethionema* sp. nov. (PHITOS et al. in manuscr.), *Malcolmia scyria* RECH. FIL., *Brassica oleracea* L. s.l. (=*B. cretica* LAM.), *Aubrieta scyria* HAL., *Silene italica* (L.) PERS., *Silene fabaria* SIBTH. & SM., *Minuartia verna* (L.) HIERN s.l., *Polypodium australe* FEE, and *Ceterach officinarum* DC.

The island of Skiros has at least four locally endemic species of chasmophytic plants. Two of them, *Campanula merxmülleri* and *Aethionema* sp., it shares with the small neighbouring island of Skiropoula, like most of the cliff flora. The other two species, *Scorzonera scyria* and

Aubrieta scyria, are however, endemic to the main island of Skiros and both are only known from Mt. Kochilas. Most other chasmophytes are in common with the Northern Sporades, to which the cliff flora of Skiros shows the closest affinities.

POSSIBLE TAXONOMIC RELATIONSHIPS

Scorzonera scyria belongs to subgen. *Scorzonera,* sect. *Foliosae* (BOISS.) LIPSCHITZ (1964). In our opinion it shows close affinity to the widespread *S. hispanica,* but can be distinguished from that species by several characters. Thus *S. hispanica* has a more or less herbaceous and usually unbranched basal part, *S. scyria* a branching woody base. The lower leaves of *S. hispanica* have long, tapering tips, in *S. scyria* they are acute to obtuse. The upper cauline leaves of *S. hispanica* are narrow, in *S. scyria* they have a broad, heart-shaped base. The scales of the involucre have a long, sharp point in *S. hispanica* and its pappus hairs are not as clearly separated into two types as in *S. scyria.* The pollen of *S. hispanica* has high spinulae on the ridges, not verrucae to broad spinulae as in *S. scyria. S. scyria* is not closely related to the chasmophytic *S. araneosa* S. & S. group, occurring in the southern part of the Aegean area. *S. araneosa* has linear leaves with unbranched, parallel veins, villose achenes and only one type of pappus bristles.

CYTOLOGY

METHODS. The chromosome number was determined from material originating from the type locality and cultivated in the Botanical Garden, Lund. Mitotic chromosomes were studied in root tip squashes. The root tips were kept in a solution of 2 mM 8-hydroxiquinoline over a night at a temperature of 5°C and then fixed in Carnoy (3: 1). The tips were squashed in a solution of 2 % orcein. The squash technique used was similar to that

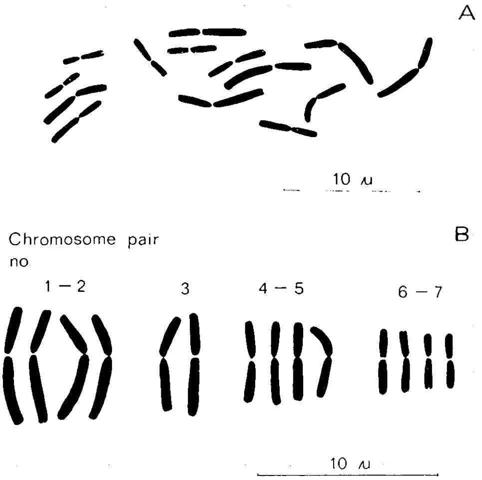

Fig. 3. *Scorzonera scyria.* Chromosomes from root tip mitosis. — A: Metaphase plate. — B: Schematic karyotype. — Further explanation in text.

described by ÖSTERGREN and HENEEN (1962).

RESULTS. The chromosome number of *Scorzonera scyria* was found to be $2n=14$ (Fig. 3 A). All the chromosomes are metacentric or submetacentric and the length varies between 6.5 and 3.0 μ. The karyotype is illustrated in Fig. 3 B. Four different groups of chromosomes are distinguishable. Chromosome pairs 1—2 are submetacentric with a length of about 6.5 μ. Pair no. 3 is somewhat smaller, about 5.5 μ and distinguishable from 1 and 2 at least in those cells seen by the authors. Chromosome pairs 4—5 and 6—7 have a length of 4.5 μ and 3.0—3.5 μ respectively. No chromosomes with satellites have been observed in the material studied. In some cells, chromosomes with minor constrictions have been noticed but as they are weak or absent in other cells they have been excluded.

The most common basic chromosome number in the genus is $x=7$, but species with $x=6$ are also represented. Like *Scorzonera scyria* all investigated species of sect. *Foliosae,* i.e. *S. hispanica* L., *S. in-*

conspicua Lipsch. and *S. stricta* Hornem., have x=7 and are diploids with 2n=14. In addition tetraploid forms of *S. hispanica* have been reported by Sosnowec (1960). The karyotypes of *S. hispanica* and *S. scyria* seem to be very similar.

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The Chromosomes of Leopoldia bicolor (Boiss.) Eig & Feinbr. (Liliaceae)

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ABSTRACT

Bentzer, B. 1972. The chromosomes of Leopoldia bicolor (Boiss.) Eig & Feinbr. (Liliaceae). — Bot. Notiser 125: 329—330.

The karyotype for *Leopoldia bicolor*, 2n = 18, is given.

INTRODUCTION

L. bicolor has a yellow perianth with blackish teeth. It is endemic to Egypt and appears mainly in sandy biotopes (Täckholm & Drar 1954). It is most similar to *L. eburnea* Eig & Feinbr. but differs from the latter mainly in having more than one leaf (Eig & Feinbrun 1947). It also shows great similarities with *L. gussonei* Parl. which is endemic to Sicily (Garbari & Martino 1972).

L. bicolor was placed in *Muscari* sect. *Leopoldia* by Boissier (1884). The taxonomy in *Muscari* s.l. is confused but according to the taxonomy proposed by Garbari & Greuter (1970) *L. bicolor* is most appropriately placed in *Leopoldia* sect. *Leopoldia*.

MATERIAL AND RESULTS

10 specimens from 2 localities in Egypt were investigated. The localities are: 1) 111 km W of Mersa Matruh, 1 km south of the road near an old air field. Leg. Björkqvist et al. 10.3. 1969. Coll. no. 612. — 2) Agiba Bay, NW of Mersa Matruh. Leg. Björkqvist et al. 11.3. 1969. Coll. no. 770.

Preparations were made according to Bentzer (1972). The chromosome nomenclature follows Levan et al. (1965).

The diploid somatic chromosome set, 2n = 18, is bimodal. It comprises one group of 10 long chromosomes and one group of 8 short ones. The long chromosomes comprise 2 markedly st SAT chromosomes with the satellites on the short arms, 2 weakly st, 4 sm and 2 m chromosomes. The group of small chromosomes comprises sm to m ones. The satellites were found to be of different sizes (Fig. 1 A).

In the meiosis the diakinesis was normal and 9 bivalents were regularly formed (Fig. 1 B).

The chromosome complement shows similarities with that of *L. gussonei* (Garbari & Martino 1972 and e.g. *Muscari kerneri* March. (Garbari 1966, 1968) and can be characterized as 10L+8S. A typical chromosome complement of other members of *Leopoldia* can be characterized as n(4L+6M+8S) (Garbari 1968, Bentzer 1969).

The general habit of *L. bicolor* is in agreement with that of other members of the genus *Leopoldia* Parl., while the chromosome morphology shows similarities to members of the genus *Muscari* Mill. The same quality is valid for *L. gussonei* (Garbari & Martino 1972).

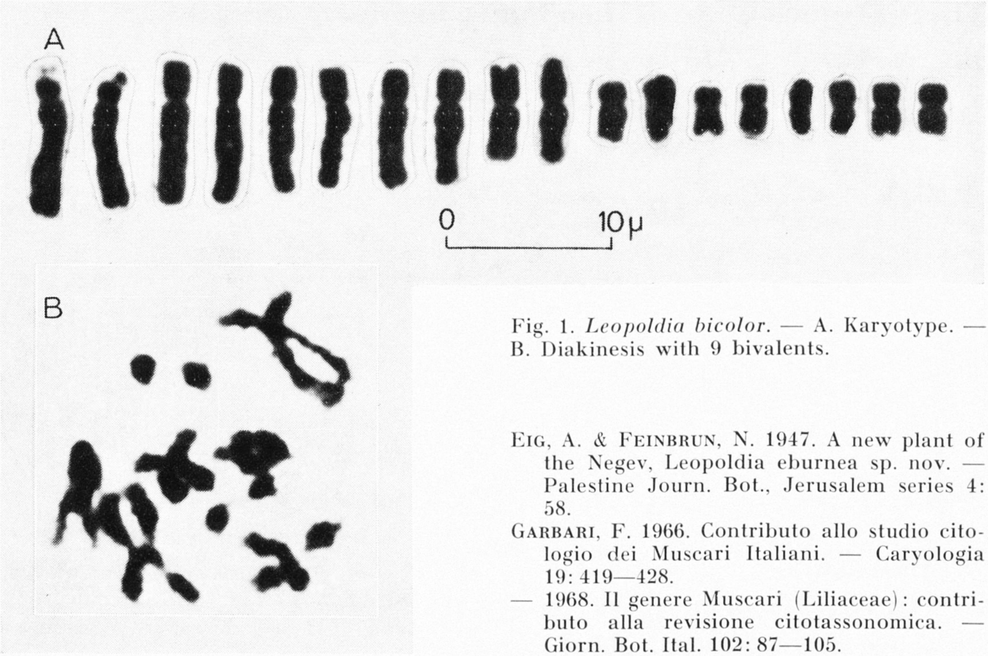

Fig. 1. *Leopoldia bicolor.* — A. Karyotype. — B. Diakinesis with 9 bivalents.

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Studies in African Cyperaceae VII

Panicle Morphology and Possible Relationships in Sclerieae and Cariceae

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ABSTRACT

HAINES, R. W. & LYE, K. A. 1972. Studies in African Cyperaceae VII. Panicle morphology and possible relationships in Sclerieae and Cariceae. — Bot. Notiser 125: 331—343.

The panicle and spikelet structure are similar in Sclerieae (*Scleria poaeoides* RIDL., *S. clathrata* A. RICH., *S. hildebrandtii* BOECK., and *S. pergracilis* (NEES) KUNTH illustrated) and Cariceae (*Schoenoxiphium lehmannii* (NEES) STEUD. and *S. caricoides* C. B. CL. illustrated). Both tribes may have male spikelets at the tips of the rachis and branches and bisexual spikelets below, the bisexual with a single female flower set below several males. Cariceae could have been derived from Sclerieae by loss of the glumes below the female flower and conversion of the prophyll at the base of the rachilla into a utricle.

In *Carex* subgenus *Indocarex* (*C. echinochloe* KUNZE illustrated) the male flowers of the bisexual spikelets have been lost. The many-flowered terminal spikelets are no longer set off by pedicels from the single-flowered female spikelets, both being associated in spikes. In *Carex* subgenus *Carex* (*C. mannii* E. A. BRUCE illustrated) the female flowers may lie above, below or between the males. So the flowers are no longer arranged strictly in spikelets and the genus *Carex* must be defined using other concepts.

In the tropics *Scleria, Schoenoxiphium, Carex* subgenera *Indocarex, Carex,* and *Primocarex* occupy successive height zones from the lowland forests to mountain-swamps. Possibly the *Carex* species of temperate regions were derived from those of tropical mountains.

INTRODUCTION

Cariceae are usually considered to be directly descended from Rhynchosporeae (KUKKONEN 1967). But in Sclerieae the flowers are already unisexual, and the arrangement of the inflorescence may parallel that of some Cariceae very closely. It seemed then worth considering the possibility that Sclerieae, not Rhynchosporeae, were the direct progenitors of Cariceae. Again the inflorescence and spikelet arrangements in Cariceae have been much disputed, for they are difficult to understand in terms of branch order

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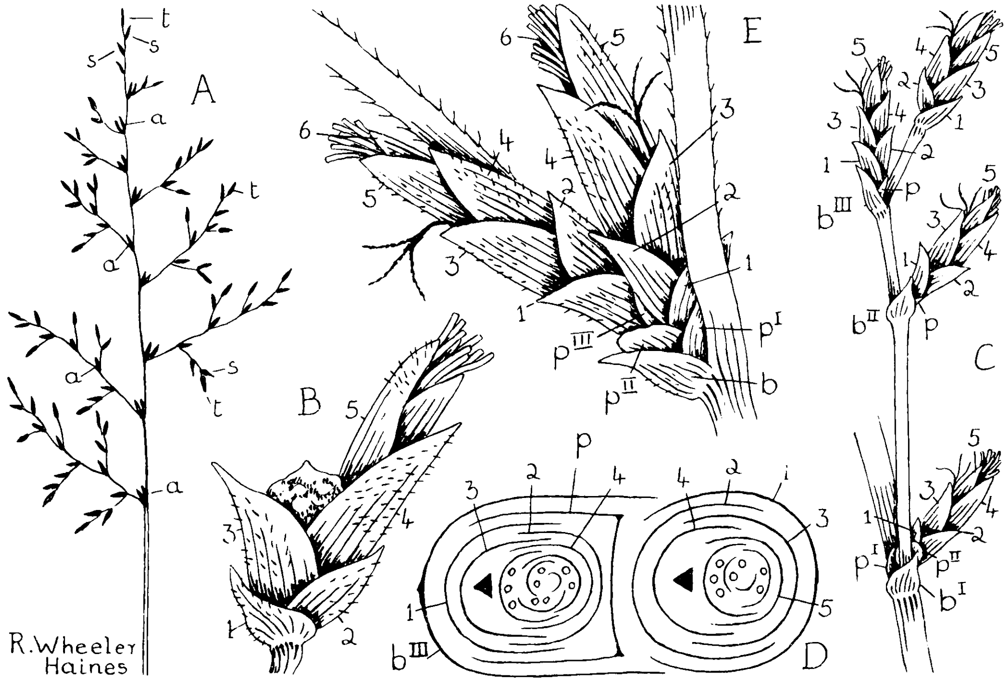


Fig. 1. *Scleria poaeoides* RIDL. — A: Inflorescence with terminal *t,* subterminal *s* and axillary *a* spikelets. — B: Spikelet in fruit, the glumes numbered. — C: A branch with 4 spikelets subtended by a bract b^{I} and itself carrying 2 bracts, b^{II} and b^{III}. The branch has a prophyll p^{I} at its base subtending an axillary spikelet with prophyll p^{II}. Each of the subterminal spikelets has its own prophyll *p* but the terminal spikelet has no prophyll. — D: Plan of the upper 2 spikelets of C. — E: A bract *b* subtends a branch with its prophyll p^{I} subtending an axillary spikelet with p^{II} and this a second axillary spikelet with p^{III}. — Drawn from ROBINSON 4362 (Mungai, Kasama, Zambia).

and spikelet structure applicable to most Cyperaceae. Here the morphology of a few African species of *Scleria, Schoenoxiphium* and *Carex* is discussed and a possible evolutionary sequence proposed.

THE INFLORESCENCE OF SCLERIA

Scleria poaeoides RIDL. has a loose expanded panicle with a main axis and a number of branches, each ending in a terminal spikelet (Fig. 1 A, t and B). Below the terminal spikelet are sessile subterminal spikelets (A, s) of a similar structure to the terminal but each subtended by an inflorescence bract (C and D, b^{III} and b^{II}) and bearing a prophyll (p) at its base. Below these again the main axis bears branches carrying 2 or more spikelets, and these branches may carry secondary branches. The branches are subtended by bracts (E, b) and provided with basal prophylls (p^{I}). Springing from the axil of the basal prophyll is a sessile axillary spikelet with a prophyll p^{II}, and a second sessile spikelet with its own prophyll p^{III} usually springs from the axil of p^{II}.

Since each shoot has a prophyll at its base and a spikelet at its tip the numbers of prophylls and spikelets over the plant as a whole are, in principle, equal, as in Scirpeae. But whereas the sessile spikelets are close to the prophylls of the shoots that carry them, the terminal spikelets of the branches are separated from their prophylls by the lengths of the branches, and the terminal spikelet of the whole inflorescence from its prophyll by the length of the culm (HAINES 1966, RAYNAL 1971).

The spikelets are bisexual, with the glumes distichous below the solitary female flower but spiralled above in the male part of the spikelet. Apart from minor variations in the numbers of glumes the spikelets are of uniform structure.

In Fig. 1 B and in the subterminal spikelet subtended by the bract b^{III} in C and D the glumes 1 and 2 are empty while 3 subtends a female flower which is partly enwrapped in the margins of the empty glume 4. Several glumes above subtend male flowers. In the terminal spikelet of C, shown in plan on the right of fig. D, there are 3 empty glumes at the base of the spikelet and 4 subtends the female flower. Young spikelets are straight but as the fruit ripens the upper male part with the flowers now spent is pushed to one side, as in B. This account of spikelet structure follows the views of NELMES (1955, "primitive androgynaeceous spikelets") and many others, but alternative views will be discussed later.

The peculiar grass-like inflorescence of *Scleria poaeoides* with its reduced bracts and prophylls is quite atypical of *Scleria* and indeed of Cyperaceae as a whole and must be a specialised feature. The uniformity again is atypical of *Scleria*. NELMES (1955) stated that all sections had 2 kinds of spikelet, one purely male, the other bisexual or female, but KERN (1961) found "all spikelets alike, bisexual" in *S. motleyi* C. B. CL. It is possible then that uniformity was an early character of the Sclerieae and that it has been retained or regained in these species.

In *Scleria clathrata* A. RICH. of the section *Scleria* (Fig. 2 A—D) the spikelets are male or female, the male (B) many-flowered and the female (C and D) 1-flowered. The terminal spikelets are all male, the axillary all female. Thus the terminal males are separated from their prophylls by at least one well developed internode forming a pedicel, whereas the females, having only short pedicels, are set nearer their prophylls. In *S. naumanniana* BOECK., analysed by HAINES (1966), there are numerous axillary spikelets arising from prophylls in the axils of the bracts to give a crowded group, and some are male though sessile. But at least the terminal spikelets of the main branches are male and long-pedicelled, while the females are short-pedicelled or sessile.

In *S. chinensis* (KOYAMA 1961) and *S. hildebrandtii* BOECK. (Fig. 2 E), as in many other species of the section, the female spikelet may be continued by a few delicate empty glumes representing a remnant of an upper male part (m). In *S. corymbosa* (CLARKE 1909) and *S. naumanniana* some of the sessile spikelets may be fully bisexual, with functional stamens.

In the section *Ophyroscleria, Scleria racemosa* POIR. (CLARKE 1909) and *S. verrucosa* WILLD. (HAINES 1966), and in section *Acriulis, S. greigiifolia* RIDL. have panicles with terminal male and axillary female spikelets similar to those in the section *Scleria*. In the section *Hypoporum* there appears to be a combination of advanced and primitive characters (NELMES 1955). The spicules are gathered together in glomerules spaced along an axis without leafy bracts. Purely male spikelets are plentiful but the fruiting spikelets all have well-developed male extensions. *Scleria pergracilis* (NEES) KUNTH has the parts well spread out and clearly defined (Fig. 3 A). The spikelets are male (B) or bisexual (C and D). The terminal spikelet of the inflorescence is usually male (E), but CLARKE (1909) shows a terminal bisexual spikelet in his figure of this species, and each glomerule usually has both male and bisexual spikelets closely packed together.

The formation of the glomerules de-

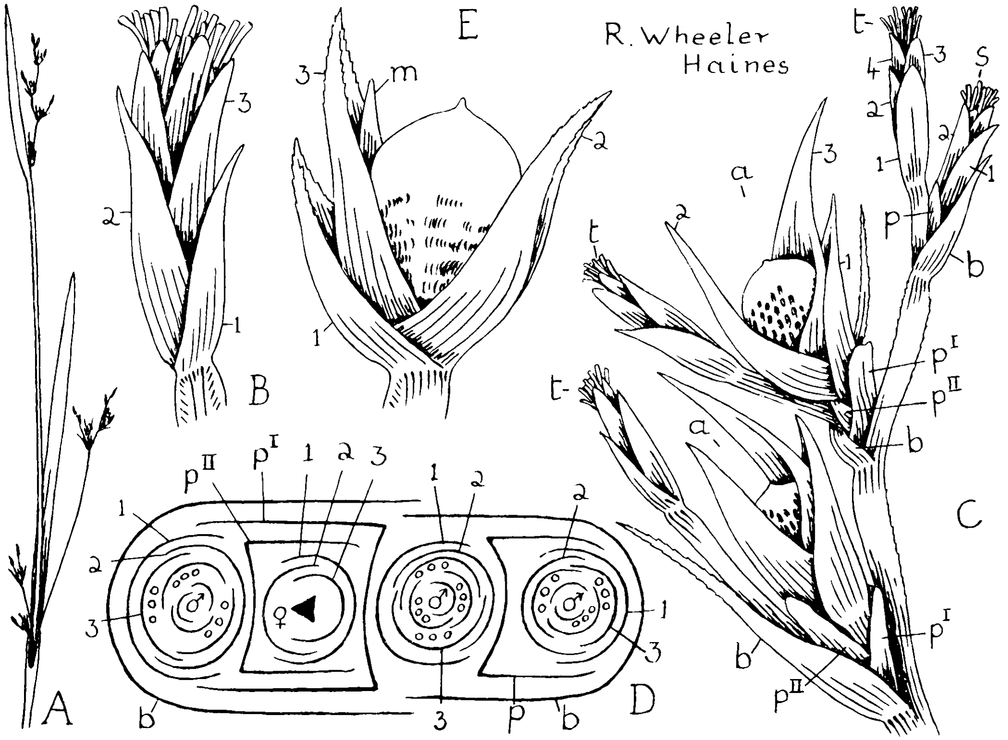


Fig. 2. A—D: *Scleria clathrata* A. RICH. — A: Terminal part of inflorescence. — B: Male spikelet. — C and D: Fragment of inflorescence and plan; *t* terminal, *s* subterminal and *a* axillary spikelets, *b* bracts, *p* prophylls, 1—4 glumes. — E: *Scleria hildebrandtii* BOECK., female spikelet with *m*, male remnant. — A—D drawn from ROBINSON 5211 (Abercorn, Zambia), E from HAINES 4186 (Dar es Salaam, Tanzania).

pends on "prophyll branching" (HAINES 1966), the primary, longest pedicelled, usually male spikelet having a prophyll (Fig. 3 F and G, p^{I}) which bears the succeeding shorter pedicelled spikelet with its prophyll (p^{II}) and so on. BLASER (1944) gives an excellent section through a set of imbricated prophylls in *Scleria triglomerata,* the largest with 2 keels and several vascular bundles, others without keels and with only 2 bundles and a small prophyll without either keels or bundles. In section *Hypoporum* the only bracts, as opposed to prophylls and glumes, in the whole inflorescence are those that subtend the glomerules as a whole.

Apart from *Scleria* the genera of Sclerieae are small and geographically restricted. Most have unisexual spikelets and where the spikelets are bisexual they are arranged as in *Scleria* (RAYNAL 1963, e.g. *Afrotrilepis* and *Coleochloa*). KERN (1962) believed an arborescent or subarborescent habit to be more primitive than a herbaceous type, as it certainly is in some dicotyledonous families. So he derived Lagenocarpeae, a group including, besides *Afrotrilepis, Trilepis* and *Coleochloa,* the shrubby *Microdrachoides* and *Cephalocarpus,* directly from *Prionium,* a shrubby member of the Juncaceae. But Lagenocarpeae are usually placed near to or are included in Sclerieae (SCHULTZE-MOTEL 1959), and it seems likely that the very

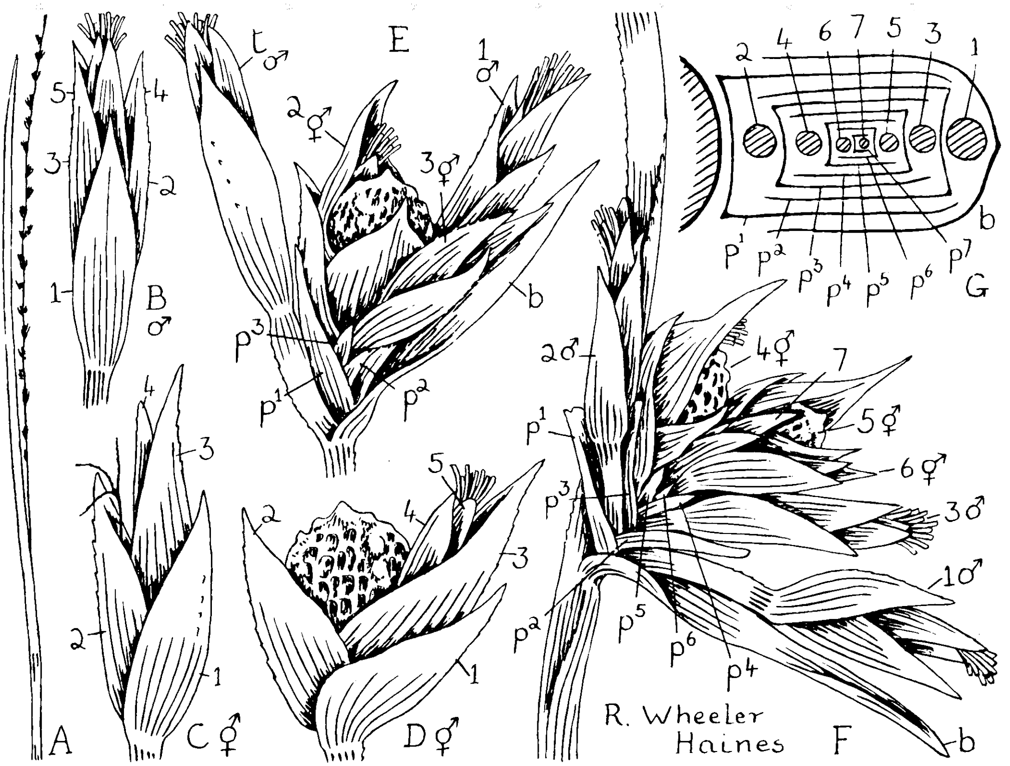


Fig. 3. *Scleria pergracilis* (NEES) KUNTH. — A: Inflorescence. — B and C: Male and bisexual spikelets. — D: Fruiting spikelet. — E: Terminal group of spikelets. — F and G: Spikelet cluster and plan; 1—7 shoots, p^1—p^7 their prophylls. — Drawn from HAINES 217 (Igboora, Nigeria).

large, widespread and varied genus *Scleria* is not far removed from the fore-runners of the tribe. Many of its features reappear in Cariceae, particularly the paniculate inflorescence, the unisexual flowers, the terminal male spikelets and the subterminal bisexual spikelets with several male flowers set above the female.

THE INFLORESCENCE OF CARICEAE

In *Schoenoxiphium lehmannii* (NEES) STEUD. (Fig. 4 A—E), as in other species of the genus, the habit is slender. The terminal spikelet (B, t) is entirely male, set off by a distinct internode from the female spikelets below. The glumes (1, 2) are closely imbricate and shorter than the bracts subtending the female spikelets, and the lowest glume is empty. Taken alone, the terminal spikelet could not be distinguished from that of a *Scleria*. LEVYNS (1945) gave a diagram of this species showing the male flowers above the female but not set off from them, though KUNTH's (1835) diagram of a *Schoenoxiphium* showed the terminal "männliche Aehre" set off on a well-developed pedicel and he described it as a "spicula . . . terminalis, mascula pluriflora".

The bracts subtending the female spikelets are set in continuous series with the glumes of the terminal spikelet (C, b^{I}—b^{IV}, 1—6). The female spikelet has a

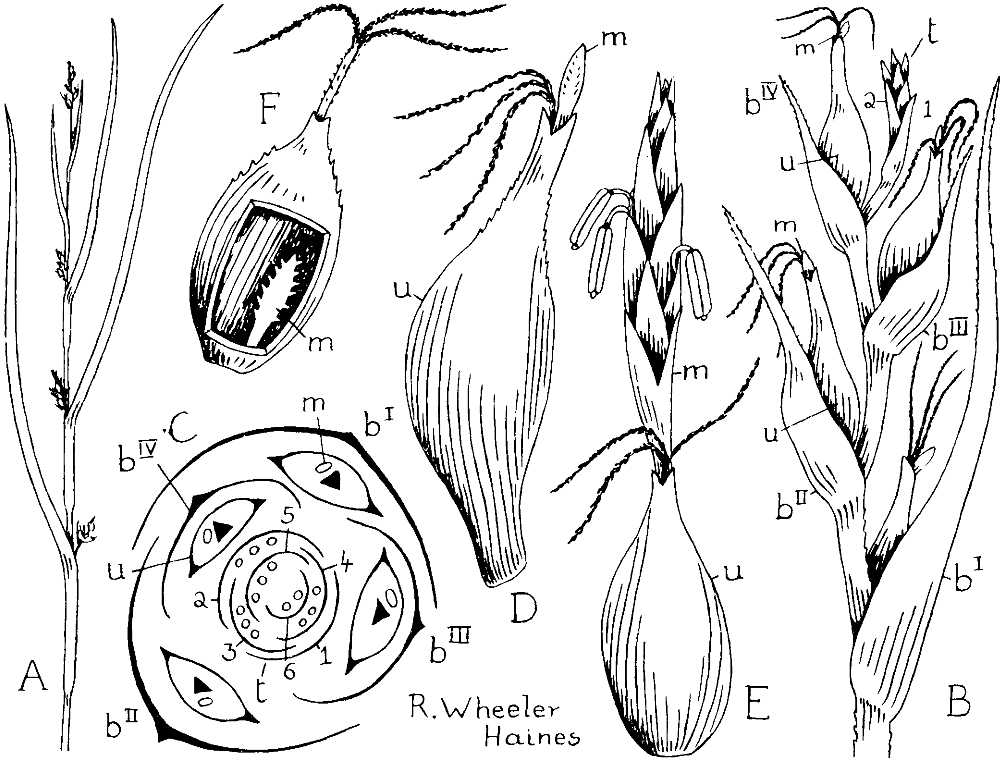


Fig. 4. *Schoenoxiphium.* — A—E: *S. lehmannii* (NEES) STEUD. — A: Inflorescence. — B: Male terminal *t* and female spikelets with male remnants *m* protruding from the utricles *u*. — C: Plan. — D: Female spikelet. — E: Bisexual spikelet with male flowers *m* springing from the utricle. — F: *S. caricoides* C. B. CL., the male remnant *m* enclosed in the utricle. — A—D drawn from LYE 4888 (Mt. Meru, Tanzania), E from WILSON 1153 B (Mt. Moroto, Uganda), and F from TALLANTIRE 64/52 (Mt. Moroto, Uganda).

solitary pistil enclosed in a utricle with a narrow neck from which the style branches protrude. The rachilla of the spikelet is continued as a slender process whose expanded end also protrudes (D, m). In certain plants of *Schoenoxiphium lehmannii* the rachilla sometimes carries a series of glumes subtending male flowers (E, m), leaving no doubt that it is in fact a rachilla, while in *S. caricoides* C. B. CL. (F) it is too short to protrude from the utricle.

Other *Schoenoxiphium* species are similar. *S. ecklonii* is a relatively small plant with short compact panicles and open *Kobresia*-like utricles. As drawn in KÜKENTHAL (1909), it has a many-flowered terminal male spikelet set off from the bisexual spikelets by a well-developed pedicel. LEVYNS (1945), however, does not show this pedicel in her detailed diagram of the species. The presence of male flowers protruding from the utricle in *Schoenoxiphium* is highly variable, and fruiting spikelets with and without male flowers can be found in the same panicle (KERN 1958, NAPPER 1963).

The genus *Kobresia* differs from *Schoenoxiphium* in having an open (or sometimes partly closed) utricle, and a less conspicuous and not flattened rachilla inside the utricle. *Elyna* is another genus

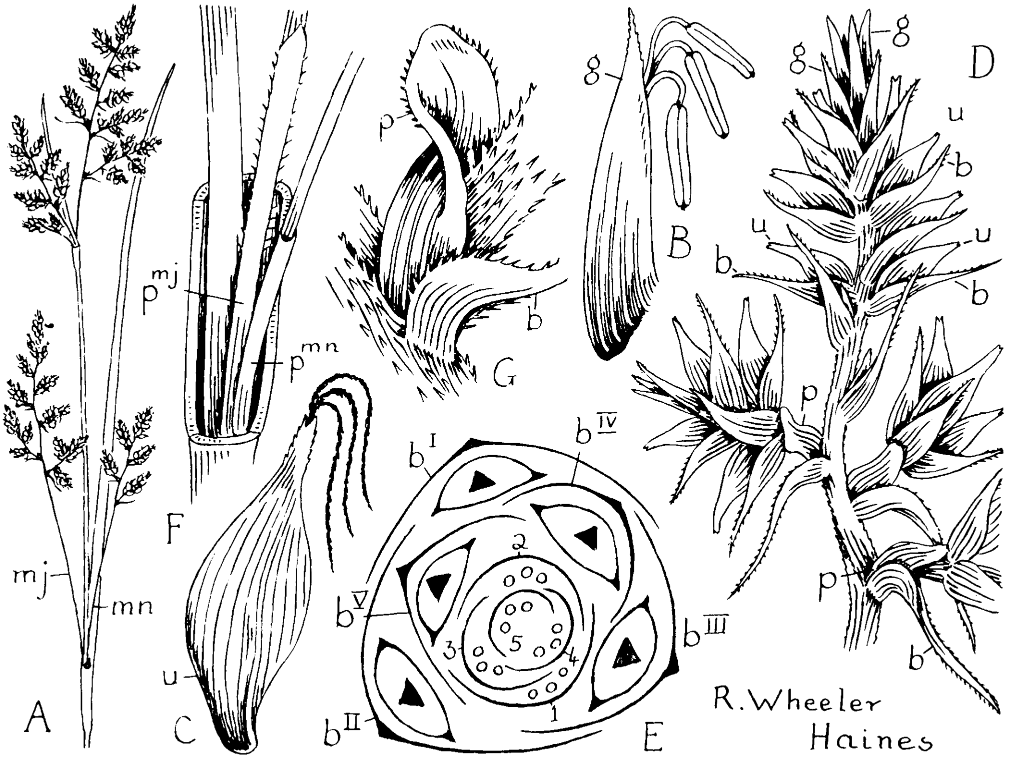


Fig. 5. *Carex echinochloe* KUNZE. — A: Inflorescence with major *mj* and minor *mn* branches. — B: Male flower and subtending glume *g*. — C: Female spikelet with its utricle *u*. — D and E: Inflorescence fragment and plan, b^{I}—b^{V} bracts, 1—5 glumes. — F: Origins of branches with prophylls p^{mj} and p^{mn}. — G: Bract *b* and prophyll *p* of an inflorescence branch. — Drawn from HAINES 4593 (Ibanda, Ruwenzori, Uganda).

sometimes separated from *Kobresia* on account of its spike-like inflorescence consisting of androgynaceous spikelets with a basal female flower and a superposed male one. However, many intermediate species are known and all these three genera are ill defined. *Kobresia kobresioidea* (KÜK.) KERN, previously named *Schoenoxiphium kobresioideum* KÜK., has the open prophyll of *Kobresia,* but a flattened rachilla with a vestigial male flower on top. In *Kobresia* the bisexual spikelet, if present, has usually one male flower, but occasionally two as in the spikelets of *Kobresia nitens* figured by CLARKE (1883) and *K. myosuroides* (VILL.) FIORI & PAOL., syn. *Kobresia scirpina* WILLD., figured by SCHUMANN (1890) and SCHULTZE-MOTEL (1959). The genera *Schoenoxiphium* and *Kobresia* have been distinguished by geographical rather than morphological criteria (KERN 1958), and KOYAMA (1961) therefore included *Schoenoxiphium* in *Kobresia.* However, *Kobresia* sensu KOYAMA is probably of mixed origin, and we have therefore accepted *Schoenoxiphium* as a genus distinct from *Kobresia,* especially since the East African species of *Schoenoxiphium* are more closely related to *Carex* subgenus *Indocarex* than they are to the type-species of *Kobresia,* viz. *K. simpliciuscula* (WG.) MACK.

The tropical subgenus *Indocarex* is

considered relatively primitive in the genus *Carex* on account of its expanded panicle of numerous, mostly stalked, bisexual spikes (NELMES 1951, HAMLIN 1959). *Carex echinochloe* (Fig. 5) has such a panicle with two branches, a major and a minor (Fig. 5 A, mj and mn), arising at each node. They are set one before the other, each with its own prophyll, in the axil of a bract (F). Such an arrangement is relatively common in dicotyledons but rare in monocotyledons, being known in Cyperaceae in *Cladium* (HAINES 1966, "tandem branching") and some species of *Scleria, Schoenoxiphium* and *Carex.*

The male and female flowers (B and C) are arranged spirally on an axis (D) to form a terminal spike and below, subtended by bracts and provided with prophylls, are similar spikes. As in most species of *Carex* there are no male flowers or continuation of the rachilla within the utricle. The plan (E) resembles that of *Schoenoxiphium,* but does not show the essential difference, the separation of male flowers in a terminal spikelet in *Schoenoxiphium* and their incorporation, with no marked internode and no sterile basal glume, in the spike of *Carex echinochloe.* KÜKENTHAL's (1909) fine drawing of *C. spicato-paniculata* C. B. CL. shows a similar panicle.

SPIKELET STRUCTURE

KUNTH's (1835) very clear diagram of *Schoenoxiphium* supported his account of the three forms of spikelet, male, female and bisexual. All these were simple spikelets, comparable to those of a *Scirpus* or *Fuirena* with the flowers arranged in racemose or spike-like manner along an unbranched axis, the rachilla. In the bisexual spikelet the female flower lay in the axil of the utricle with the male flowers above as in Fig. 4 E. CLARKE (1883) agreed with KUNTH: "In *Carex* . . . we consider the terminal male flowers as forming one spikelet, each of the female utricles we consider a spikelet". KUNTH showed further that the utricle was a modified prophyll placed at the base of the spikelet, similar to the "adossierte Vorblatt" at the base of the branches of many monocotyledons.

But though KUNTH's view of the utricle has been almost universally accepted (SCHUMANN 1890, review) his account of the spikelet has been under repeated attack. PAX (1886 and 1887) separated "Caricoideen", which included both Sclerieae and Cariceae, from other Cyperaceae as having cymose pseudospikelets in which the apparently simple rachilla was in fact a compound structure built up of branches of more than one order. Thus in the spikelet figured in Fig. 1 B the female flower, represented by its fruit would be terminal to the main axis bearing glumes 1—4 and the male part of the spikelet would represent a branch springing from the axil of 4, the empty glume 5 being its prophyll.

In Cariceae on the other hand PAX believed the male part of the spikelet (Fig. 4 B, D and E, m) to be carried on the main axis and the female flower on a side branch. His concept was based on *Kobresia* (*Elyna*) *myosuroides* which usually has only two flowers, one female and one male in each spikelet. So by the loss of one or other of these flowers the spikelets became unisexual in *Carex.* The modern generic description "Flowers unisexual, borne in 1-flowered spikelets each subtended by a glume" (TUTIN 1952) comes from PAX's work. Since he considered the spikelet arrangements so different in Sclerieae and Cariceae he made no attempt to derive one from the other. Indeed the only direct association between the two groups was made by BENTHAM (1877) who put *Kobresia* in Sclerieae, but excluded *Carex* as having a different spikelet structure.

ČELAKOVSKÝ (1889) criticised PAX's theory of the pseudospikelet, supporting the simple spikelet of KUNTH (1835) and CLARKE (1883). He rejected PAX's suggestion that each male flower of *Carex* was derived from a bisexual spikelet by the loss of the female flower and returned to KUNTH's view that each group of male flowers represented a terminal male spikelet comparable to that of *Schoenoxiphium.* Thus whereas PAX would have given the number of spikelets as 10 in Fig. 5 E, 5 female and 5 male, ČELAKOVSKÝ would have given 6 only as the number, 5 one-flowered female and 1 many-flowered male. Since ČELAKOVSKÝ's count agrees with the number of prophylls we believe it correct, though it is supported by only one recent author, viz. RAYNAL (1971): "chez *Carex,* si l'épillet mâle est bien constitué par l'epi mâle entier, l'épillet femelle, par contre, semble reduit à la fleur ♀ contenue dans l'utricle."

KÜKENTHAL (1909) again derived the male flowers of *Carex* from a supposed terminal bisexual partial inflorescence of *Schoenoxiphium* by suppression of the female flowers, seemingly forgetting that the terminal spikelet in *Schoenoxiphium* was already male. MORA's (1960) diagram of *Scleria* showed the cymose structure suggested by PAX but with no new evidence. KERN (1962) described a "prophyll" as "sometimes still present" in the bisexual spikelet and KOYAMA (1971) reported "a much reduced prophyll . . . present at the base of the staminate branch", shown in his diagram as of normal bidentate monocotyledonous type. Such a prophyll would give strong evidence for a cymose arrangement, but we have not found it, nor is it seen in CLARKE's (1909) figures or in KOYAMA's (1961) own excellent dissections. So we accept KUNTH's (1835) account of Cariceae and RAYNAL's (1963) of Sclerieae as having simple racemose spikelets, and draw attention to the similarity of these spikelets (Figs. 1 B and 4 E) in the two tribes.

MORE SPECIALIZED SUBGENERA OF CAREX

In *Scleria* and *Schoenoxiphium* the spikelets are distinct but in *Carex* subgenus *Indocarex* the male spikelet is not clearly set off from the female spikelets below. So the unit has become a complex bisexual spike. Fig. 5 D shows 4 such spikes, one terminal and 3 lateral, each lateral spike with its bract b and its prophyll p, shown in detail in G.

In *Carex mannii* E. A. BRUCE of the subgenus *Carex* the spikes are, as usual in this subgenus, fewer and larger (Fig. 6 A). The branches arise as pairs, set in tandem, at the nodes (B, mj and mn). The individual flowers with their utricles and subtending bracts and glumes resemble those of an *Indocarex* but are set differently in the spikes (C and D). Thus in the terminal spike the lowest flower is female and most of the flowers male with a further band of females below the tip (E, F and G). A lateral spike (Fig. 7 K) again has male flowers above and below the female while a spike of *C. thomasii* NELMES (Fig. 7 J) has all the male flowers below the females.

It seems reasonable to assume that, as in *Indocarex,* the female flowers with their utricles represent reduced spikelets and are subtended by bracts while all the males taken together represent a single spikelet with the flowers subtended by glumes. If this is so the glumes and bracts have become able to replace each other in the composite spike and the strict arrangement of the flowers in spikelets has been lost in this subgenus. A correct description for *Carex* would be: Flowers unisexual, set in the axils of bracts to form one or more spikes, each female flower enclosed in a utricle, the male naked.

The subgenus *Vignea* (Fig. 7 L) has the short and uniformly bisexual spikes of *Indocarex* but they are crowded and the lateral spikes have lost their basal prophylls. Subgenus *Primocarex* has been a puzzle, for it combines a relatively primitive well-developed rachilla sometimes ending in reduced glumes (Fig. 7 G, m) with the specialized feature of having but one spike. PAX (1887) made it the first of his subgenera and SCHULZ (1887) elabo-

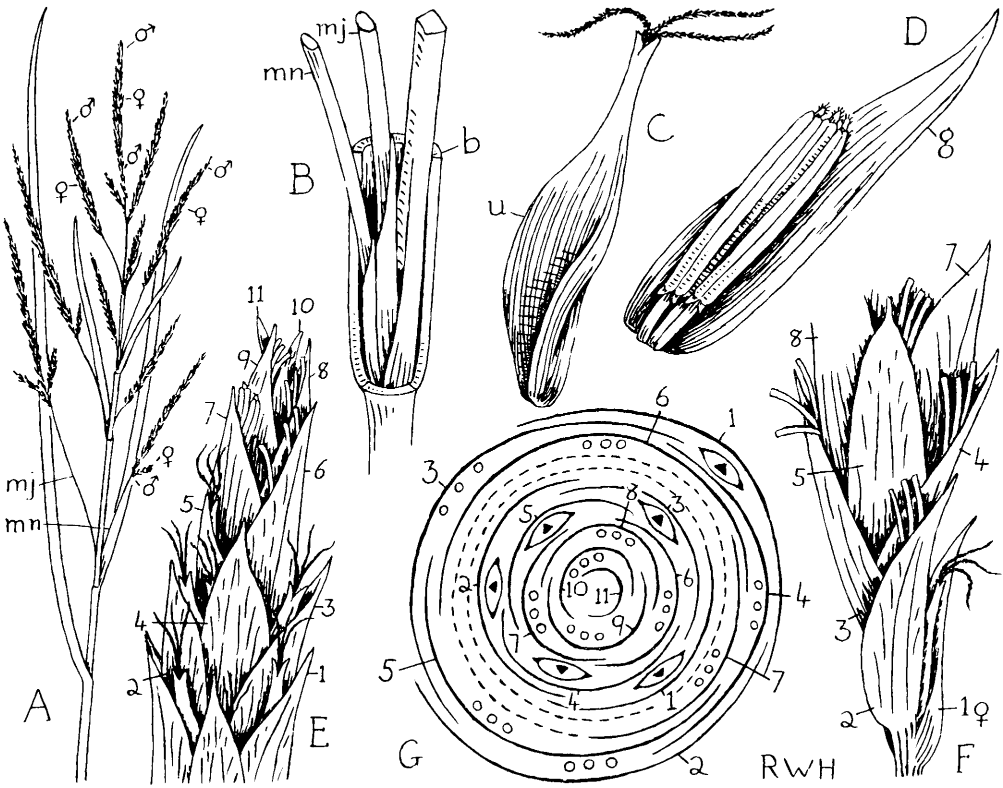


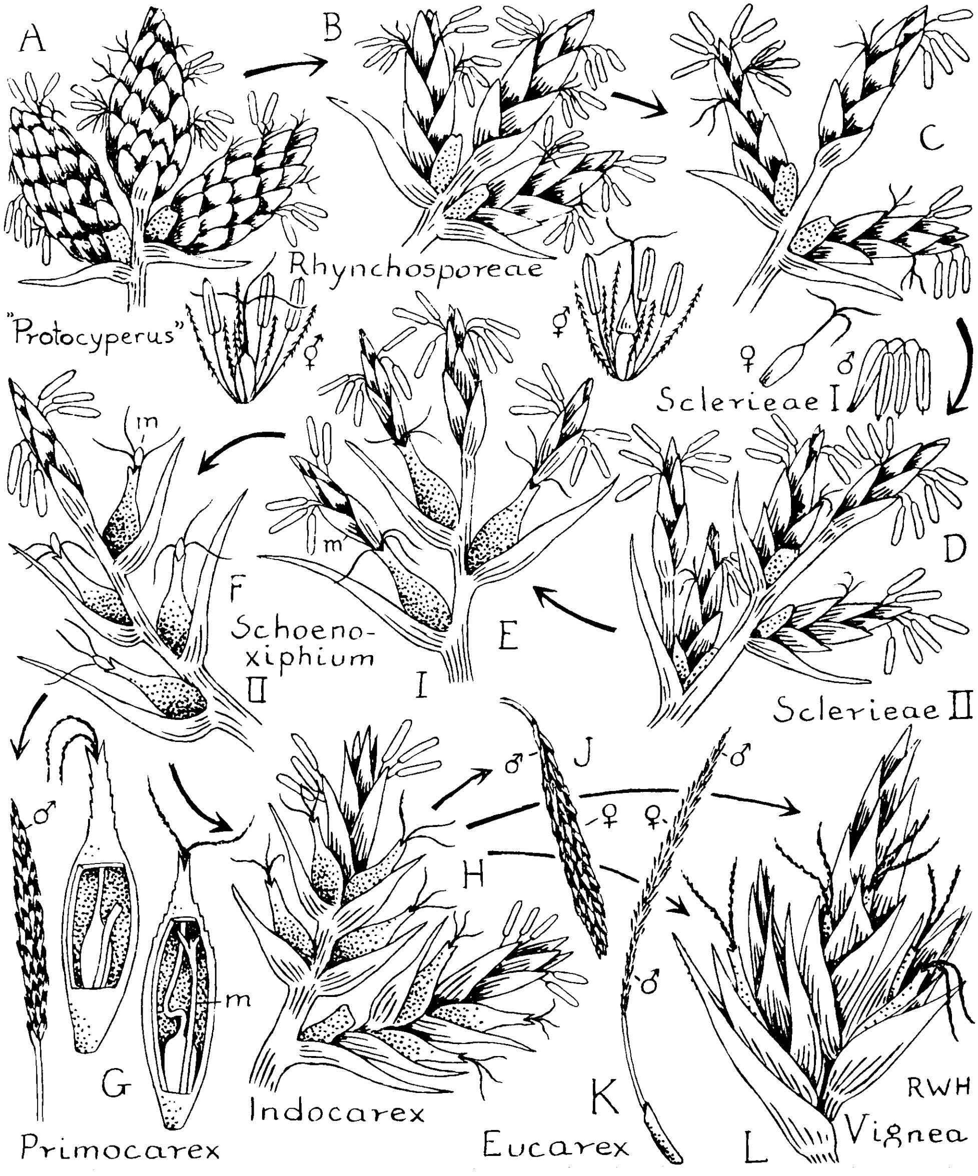
Fig. 6. *Carex mannii* E. A. BRUCE. — A: Inflorescence. — B: Origins of major *mj* and minor *mn* branches. — C: Female spikelet. — D: Male flower and subtending glume. — E, F and G: Apex, base and plan of a spike, 1—11 scales of the spike. — Drawn from HAINES 4597 (Aberdares, Kenya).

rated the improbable suggestion that the complex panicles of *Schoenoxiphium* and *Indocarex* had developed from a single spike. HAMLIN's (1959) suggestion, based on NELMES (1952) and others, that *Primocarex* is a group of mixed origin only partly derived from other groups of *Carex* and highly specialized, seems more acceptable.

THE POSITION OF THE FEMALE FLOWER

In Sclerieae as in most Cyperaceae the female flowers, like the males, are subtended by ordinary glumes, glumes 3 or 4 in Fig. 1, glumes 2 in Figs. 2 and 3. In Cariceae the female flowers lie in the axils of the utricles and no one has suggested how they got there. They appear

Fig. 7. Possible relationships of genera and changes leading to *Carex*. Prophylls stippled. — A: Spikelets and flower of an unspecialized species of Cyperaceae (based on *Scirpus* and *Fuirena*). — B: Species of Rhynchosporeae with few bisexual flowers and male flowers above (based on *Rhynchospora*). — C: Species of Sclerieae with all the flowers unisexual but the spikelets uniformly bisexual (based on *Scleria poaeoides* but with bracts and prophylls well developed as in other species of the genus). — D: More advanced species of Sclerieae with two kinds of spikelets, male and bisexual (based on *Scleria naumanniana*). — E: Relatively primitive species of *Schoenoxiphium* with style



branches and male flowers protruding from the utricle (based on *S. lehmannii*). — F: More advanced *Schoenoxiphium*-spikelets with male flowers confined to the terminal spikelet (based on *S. lehmannii*). — G: Solitary spike and 2 female spikelets of a *Primocarex* with remnants of the male parts of the spikelet *m* beside the female flower (based on *C. runsoroensis* K. SCHUM.). — H: Relatively primitive species of *Carex* subgenus *Indocarex,* the spikes few-flowered with the males above the females (based on *C. echinochloe* as fig. 5). — J: *Carex* subgenus *Carex.* Spike of *C. thomasii* NELMES, male flowers below the female (based on THOMAS 1794 from Mt. Imatong, Sudan). — K: *Carex* subgenus *Carex.* Spike of *C. mannii* E. A. BRUCE, female flowers between the male, as fig. 6. — L: *Carex* subgenus *Vignea.*

to be subtended by the utricles but utricles usually subtend branches, not solitary flowers. Possibly in passing from a *Scleria*-like to a *Carex*-like spikelet the glumes below the female flower, 1 and 2 in the lateral spikelet of Fig. 1 D, have been lost, leaving the female flower just above the prophyll p. In *Scleria* the number of glumes below the flower is variable and variation in the number of lost glumes in *Carex* may account for the variations of achene position, with sometimes a face and sometimes a margin facing the rachis as noted by CARUEL (1867). The biological significance of the enclosure of the female flower in a utricle is not known. That there is some significance is evidenced by the close similarity of the disseminule of *Coleochloa* to that of *Carex,* though the actual wall in *Coleochloa* is built of ovarian, not prophyllar, tissue, a clear example of convergent evolution starting from different bases (NELMES 1953, RAYNAL 1963).

A POSSIBLE PHYLOGENY

A scheme of evolution may be suggested. A hypothetical ancestor (Fig. 7 A, "*Protocyperus*"), with the flowers bisexual, provided with a perianth and arranged in many-flowered spikelets set in a panicle, may have resembled the modern *Fuirena* in appearance. It gave rise, with some reduction of spikelet complexity to Rhynchosporeae (B). The flowers became unisexual, with a single female below and several males above. All flowers lost the perianth to give Sclerieae with uniform spikelets resembling those of *Scleria poaeoides* (C). Loss of the female flowers in the spikelets at the tips of the panicle axis and its main branches gave more advanced Sclerieae with two kinds of spikelets, viz. male and bisexual, resembling *Scleria clathrata,* but with the male parts of the bisexual spikelets better developed (D).

Sinking of the female flower toward the base of the bisexual spikelet, possibly by loss of the glumes below it, and its enclosure by the prophyll at the base of the spikelet, now modified to a utricle, gave primitive Cariceae resembling some forms of *Schoenoxiphium lehmannii* (E, prophyll stippled). Reduction of the male parts of the bisexual spikelets to a tongue gave more advanced types resembling the typical form of *Schoenoxiphium lehmannii* (F). Compaction of the spikelets by shortening of the internodes between them, particularly the internode at the base of the terminal male spikelet, gave an *Indocarex* resembling *Carex echinochloe* (H). Other subgenera of *Carex* were derived from *Indocarex* or directly from *Schoenoxiphium*-like types (G, J, K and L).

The largest gap is that separating Sclerieae and Cariceae (D and E), for no transitional types have survived. Probably *Scleria* itself, mostly with fruits having polished thick walls set on a gynophore, is too specialised to lie on the direct line to *Carex,* though *S. guineensis* has thin-walled fruits (RAYNAL 1964). The scheme indicated here is, of course, provisional.

TROPICAL CARICEAE

NELMES (1951) suggested that *Carex* originated in Malaysia, where subgenus *Indocarex* "as befits its more primitive and warm-age origin, still retains a foothold in the lowlands of its ancestors but it ascends to nearly 3000 m." In Uganda there are only two species of *Indocarex, C. echinochloe* and *C. chlorosaccus,* and neither grows in the lowland forests, but they are found below the species of subgenus *Carex* from the montane forests and far below the *Primocarex* of the alpine swamps.

NAPPER (1963) has noted that "in tropical Africa" the species of *Carex* "are restricted to the damp grasslands, forest and montane vegetation of the higher altitudes (mostly over 7,000 ft.)" while "the similar, but more slender, representatives of *Schoenoxiphium* in East Africa normally occur at lower altitudes". *Scleria* species are abundant in swamps and forest margins of the forests and savannas of the lowlands but do not ascend the mountains. It is possible that Sclerieae have been a tropical group since their inception but have been unable to grow on mountains without the specializations leading to Cariceae, though once these were attained they spread over the grasslands, marshes, sands, and woodland and stream margins in temperate zones. An origin of Cariceae from Sclerieae would tally well with NELMES' proposals.

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Leaf Anatomy in Sporobolus rigens (Tr.) Desv. (Gramineae)

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ABSTRACT

Böcher, T. W. 1972. Leaf anatomy in Sporobolus rigens (Tr.) Desv. (Gramineae). — Bot. Notiser 125: 344—360.

Sporobolus rigens, a South American xerophytic grass from dry, sandy and saline habitats, has been studied anatomically. The long leaf blades which in the terminal part are cylindrical exhibit a number of deviating structural features. The photosynthetic tissues are arranged very regularly with green arm cell areas inside sunken stomata alternating with larger green bundle sheath cells. This structure suggests that the species belongs to the group of plants which utilize the C-4 dicarboxylic acid pathway in photosynthesis.

Other characteristics of particular interest which are described and discussed are the epidermal short cells which are interpreted as salt glands, and some large inner bundle sheath cells which may function as transfer cells. The development and degeneration of the arm cell tissue and the green sheath cells raise many cytological problems to be solved in the future.

INTRODUCTION, MATERIAL AND METHODS

Sporobolus rigens is a coarse and densely tufted grass species occurring in dry, often sandy and saline soils in the arid areas of Western Argentina. Details of its choice of habitat can be found in Böcher, Hjerting & Rahn (1972). Leaves of *Sporobolus rigens* were preserved in alcohol during a stay in 1955 at Estancia El Sosneado south of Mendoza. This material has now been studied anatomically using light microscopy and various staining procedures. The most important stains were Fast green-safranin, Sudan IV, Johansen's quadruple stain, Aniline blue-black (cp. Fisher 1968), Toluidine blue (Feder & O'Brien 1968) and Periodicacid-Schiff. Slides were produced by using a freezing microtome or a normal microtome and the Glycol methacrylate method according to Feder & O'Brien (1968). By the latter method the thickness of the sections was about 2 μ.

In the present paper the main anatomical features are described. The many deviating and problematic characters found in the species make further studies highly desirable. New material has now been made available thanks to Dr. Fidel Antonio Roig, Mendoza, who very kindly sent me seeds of *Sporobolus rigens* from Dorrego, Prov. Buenos Aires. The new material, to which a few references are made in the text, will, I hope, make it possible to carry out studies on the fine structure and the differentiation of the tissues as well as ecophysiological experiments.

The author is indebted to Dr. Ole Mattsson for valuable discussion and to Mr. Ole B. Lyshede for technical assistance.

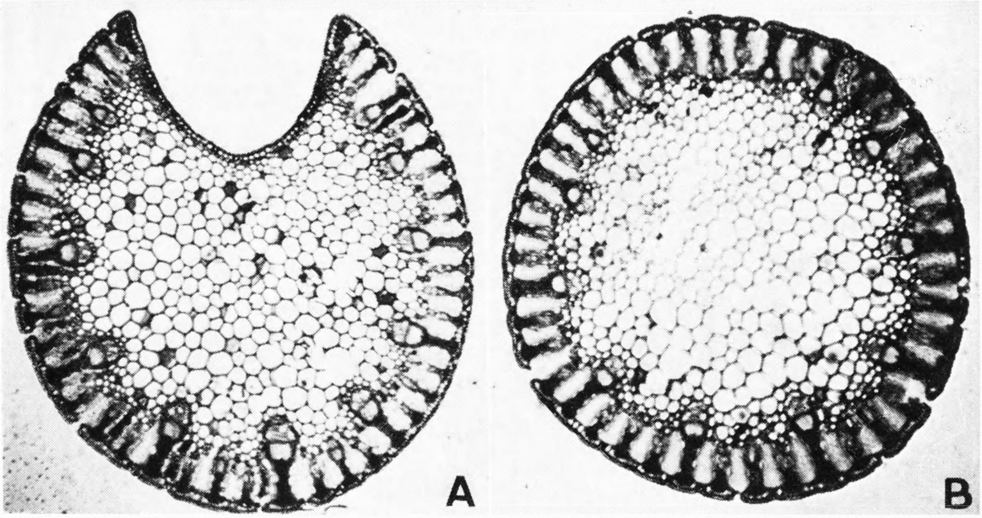


Fig. 1. *Sporobolus rigens.* — A: Cross section of base of blade with adaxial groove. — B: Cross section of cylindrical distal part. — Xylem and fibre plates darkly stained. ×33.

MORPHOLOGY OF THE LEAVES

The overlapping leaf sheaths are broad and the ligules are replaced by long hairs. At the base the adaxial side of the leaf blade is concave and cross sections are crescent-shaped (Fig. 1 A). The concave upper side gradually narrows, first to a shallow groove, later to a narrow split. The adaxial side finally disappears and the blade becomes cylindrical.

The development of the abaxial side of the blade is strongly promoted and results in a complete suppression of the adaxial side at some distance from the base. The distal part thereby becomes unifacial.

The development does not result in a tubular blade as in many species of *Allium,* but in a cylindrical stem-like blade which has a central colourless parenchyma very much resembling the ground tissue in piths. The unifacial structure is probably due to an inhibition of or the absence of marginal growth (cp. TROLL 1955, ROTH 1957). The cylindrical distal part in *Sporobolus rigens* may be compared to that found in *Ornithogalum caudatum* which was interpreted by TROLL (1939 p. 1179) as an elongated apex ("Vorläuferspitze").

Sporobolus rigens may represent a final stage in a series of leaf margin reductions which can be seen in desert grasses and which can presumably be interpreted as an adaptional, evolutionary series arising out of xeric conditions. VOLKENS (1887 p. 148) mentions *Andropogon hirtus* and *Elionurus hirsutus* in which the lamina of the blade is reduced to a narrow ribbon on both sides of the central keel region which includes the midvein. In the keel regions in these species the adaxial sides are without ribs and green cells. Beneath the epidermis follows a layer of fibres which covers a large area of parenchyma. The cells in this parenchyma are wide and colourless and are assumed to have a water-storing function. The blade structure in the two species described by VOLKENS presumably represents a stage which precedes that found in the blades of *Sporobolus rigens.* The lamina is here absent or when present is reduced to two narrow involute margins covering the basal groove on the adaxial side. The colourless parenchyma which occupies the upper portion in the basal part and the central portion of the distal part may also have a water-storing function. The long blades of *Sporobolus rigens* consist exclusively of the keel regions. In nature they tend to be spirally curved, which gives the plant a striking appearance.

LEAF BLADE ANATOMY IN SPOROBOLUS

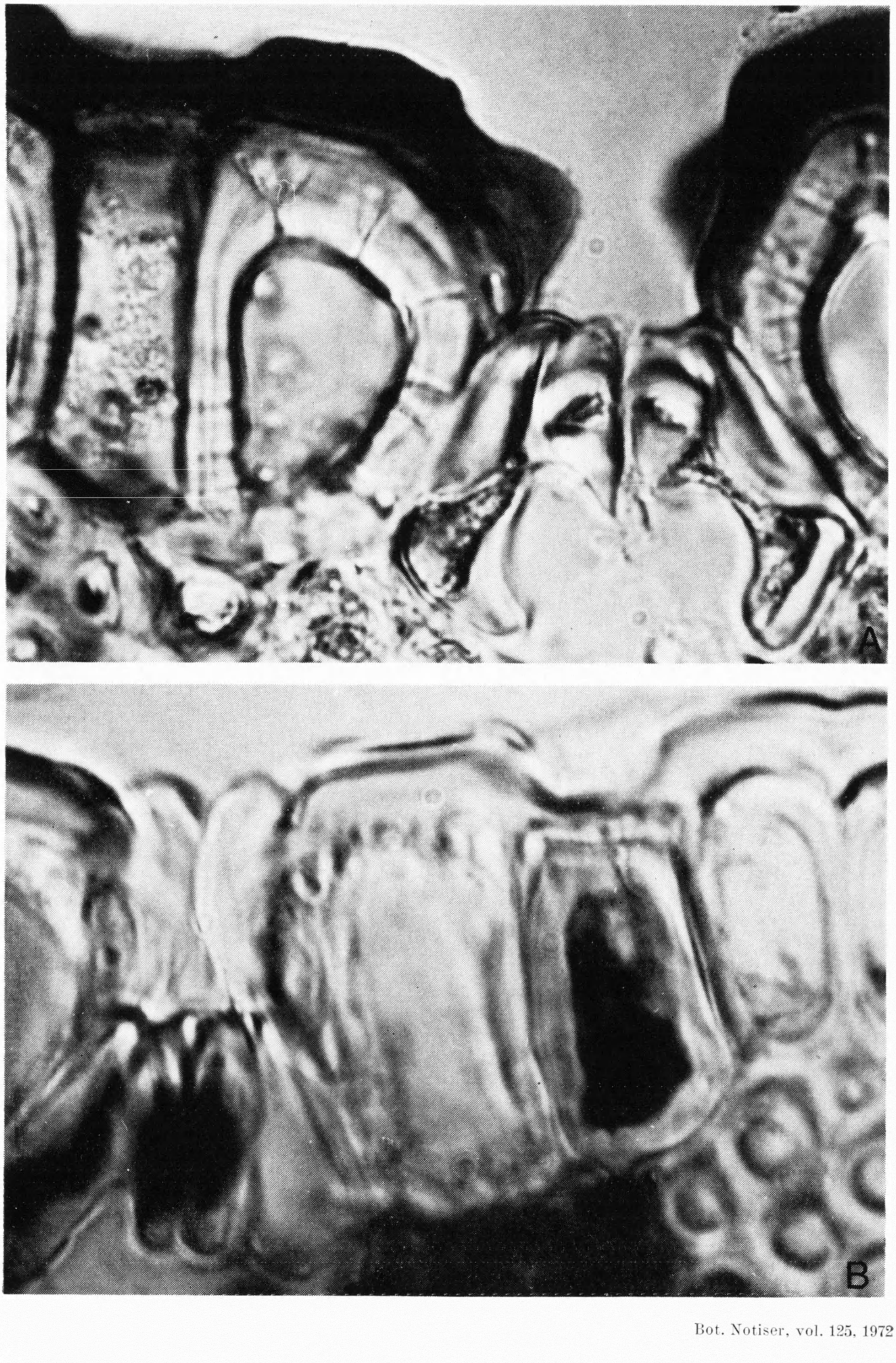
The leaf anatomy in the genus *Sporobolus* is summarized by METCALFE (1950 pp. 462—476). A great number of species has been thoroughly studied by VOLKENS (1887), HOLM (1902), GOOSSENS (1938), ZEMKE (1939), SCHWABE (1949 a, b) and SHIELDS (1951). In the paper by SCHWABE (1949 b) one finds comparisons of the leaf anatomy of several Argentinian species including *S. rigens* which, together with two other species is described as being a member of a very advanced and specialized xerophytic group characterized by the lack of bulliform cells and the occurrence of a colourless parenchyma which occupies the major part of the blade.

In most other species of *Sporobolus* the blade is flat or involute, and the many parallel veins are provided with green bundle sheaths and supported by fibre plates on both sides. The mesophyll is found between the bundle areas and consists of chlorenchyma and colourless, frequently larger cells. In the case of *S. rigens* these colourless cells between the veins are absent and the green cells, which in most other species are palisades radiating from the veins, are replaced by arm cells.

In *S. rigens* there are up to 40—50 veins of which a quarter are larger than the rest and are nearer the central axis (Fig. 1). They are here usually surrounded by the central parenchyma except on their out-turned sides, where the accompanying fibre plates are found. Of the larger veins one is the middle vein and occurs opposite the bottom of the groove in the basal part (Fig. 1 A). In the cylindrical part larger veins are absent from the areas which represent the margin of the keel region (Fig. 1 B).

The parenchyma which in *S. rigens* occupies the central part of the blade may have a water-storing function. It has the same position as the adaxial parenchyma in the ribs in *Sporobolus airoides* studied by SHIELDS (1951 Fig. 7 and p. 233). In that species protecting fibres are absent from the upper portions of the ribs. Natural wilting implies that the large mesophyll cells above the veins collapse, while the bulliform cells show varying degrees of buckling. The parenchyma in the basal part of the blade in *S. rigens* is protected against water loss by the epidermis which has thick outer cell walls with thick cuticular layers and by a hypodermal cell layer of small colourless cells. In the cylindrical distal part the colourless parenchyma has a central position almost the same as in the majority of succulent leaves. *S. rigens* is, however, by no means a succulent plant, but we must not forget that it prefers saline soils and therefore may approach the succulent halophytes in some of its anatomical characters. In several of the South African species of *Sporobolus*, e.g. *S. argutus, S. pyramidalis, S. robustus* and *S. fimbriatus,* the keel region is rather wide and thick. According to GOOSSENS (1938) a parenchyma of large, thin-walled cells is prominent in the

Fig. 2. *Sporobolus rigens*. Cross sections of epidermis. — A: Sunken stomatal opening surrounded by two normal epidermal cells with thick stratified walls traversed by microchannels, some of which are branched; one short-cell with cutinized wall lamella. Sudan IV staining, interference contrast. — B: Similar epidermal area as in A but Fast green-safranin staining emphasizing dense cytoplasm in short-cell and guard cells. Delicate strands leading to surface and connection towards arm cells below visible. — A—B ×2000.


A
B

keel regions on the adaxial side. As in *S. rigens* this parenchyma is protected by 1—2 layers of small, thick-walled cells ("stereome") situated beneath the epidermis. Bulliform cells ("motor cells") are usually absent from the keel regions in the South African species, and the width of this region varies greatly among the species. In no case, however, are the blades reduced to the keel region as in *S. rigens*.

The system of assimilatory tissues in the genus, viewed in the light of the recent discovery of the C-4 dicarboxylic acid pathway of photosynthesis connected with bundle sheath chloroplasts, is of particular interest. By comparing the many pictures of cross sections of leaf blades which are found in the literature, it appears that the mesophyll in most species consists of green cells that radiate from the centre of the bundles and which frequently are elongate palisade cells. Furthermore, it appears that the bundles are provided with chloroplasts in the larger outer bundle sheath cells. This structure is characteristic of the Panicoideae and the Chloridoid-Eragrostoid group (STEBBINS 1956 p. 898, BROWN 1958) and it occurs in several C-4 plants such as maize and sugar cane (LAETCH 1968) and among non-graminoid plants in for example *Atriplex rosea* (BOYNTON et al. 1971). However, it is not common to all species of *Sporobolus*. A few species although possessing bundle sheaths have normal chlorenchyma between the veins (e.g. *S. panicoides*, GOOSSENS 1938 Fig. 27), while *S. rigens* belongs to a third type which is characterized by the presence of large green bundle sheath cells, and the absence of the radiating green palisade cells. Instead, *S. rigens* has developed a tissue of green arm cells which evidently co-operate with the large bundle sheath cells. Utilizing leaves from plants of the new material which had been exposed to sunlight for several hours, it was possible to demonstrate an accumulation of starch in the sheath cells. There was no starch in the arm cell tissues. When stained with iodine solution, however, the products of photosynthesis did not attain a dark blue colour but became dark brownish and were therefore considered to be composed partly of waxy starch.

EPIDERMIS IN THE LEAF BLADES OF SPOROBOLUS RIGENS

According to SCHWABE (1949 b p. 260) *S. rigens* stands out from the other Argentinian species of the genus in having sunken stomata. This character, shown in Fig. 2 A, is clearly xeromorphic. The same is true of the great thickness of the cuticular layer of the outer epidermal cell walls. The cuticular layer is distinctly separated from the inner wall layers which, like the thick guard cell walls, are ± lignified. The inner walls which are mostly thick are composed of several separate layers which can be distinguished by their different reactions to PAS. As a rule, the latest-formed innermost layer is deeply stained, probably because it has not yet undergone lignification. The cuticular layer is either not stained in PAS or parts of it have a reddish-violet colour indicating traces of carbohydrates together with lipids. In Sudan IV the whole cuticular layer stains deeply. The staining is probably mostly due to the presence of cutin, but in polarized light and using the red I plate the inner part of the cuticular layer shows a birefringence of the opposite sign to that of the cellulose walls thus indicating the presence of wax.

The thick stratified more or less lignified interior epidermal cell walls are traversed by many micro-channels which often branch (Fig. 2 A). Those which traverse the thick anticlinal or interior walls separating epidermal cells or epidermal cells from fibre cells are canal-like pit cavities while those in the outer walls with the same dimensions behave as a kind of ectodesmata. They also sometimes branch and they often widen distally be-

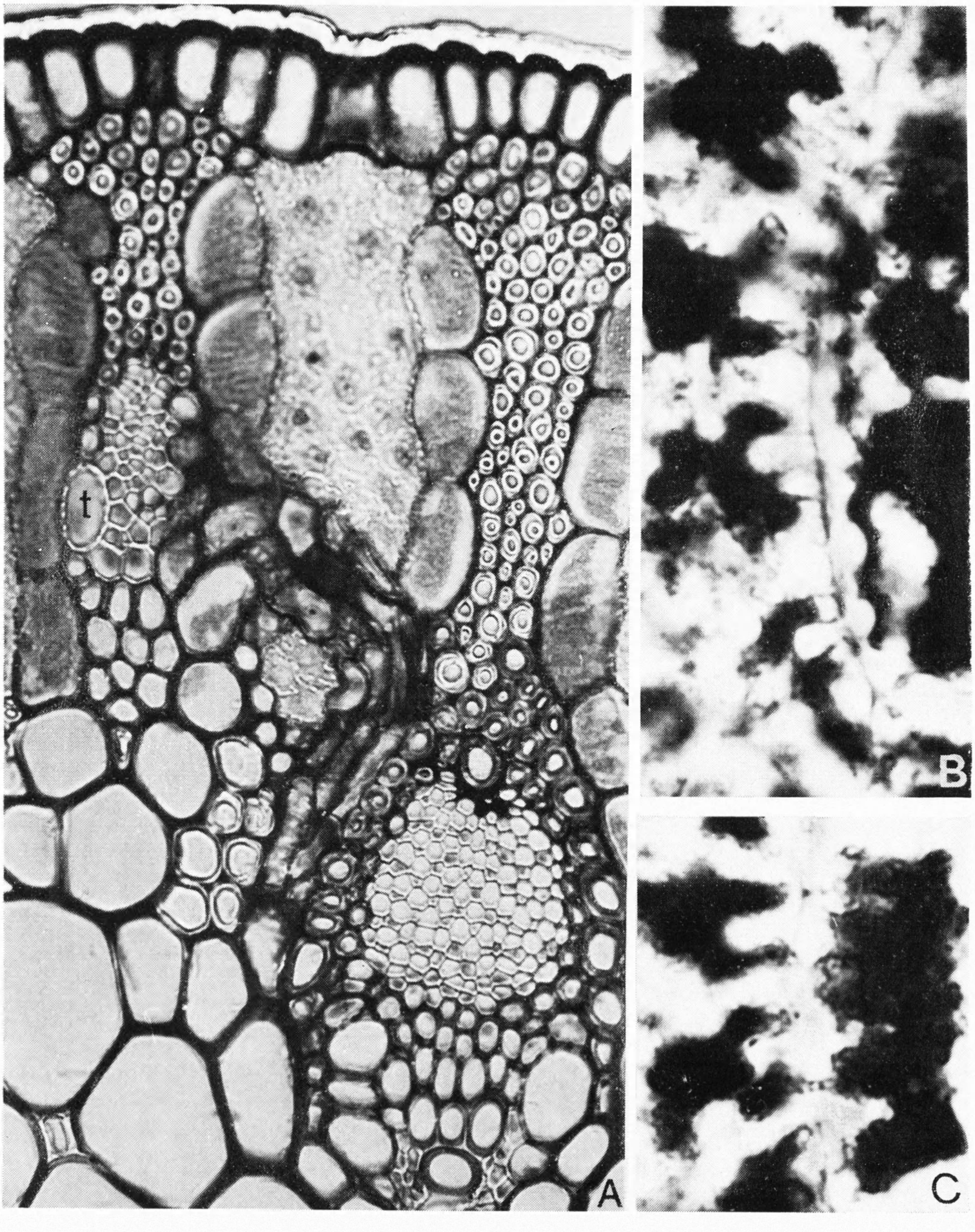


Fig. 3. *Sporobolus rigens.* — A: Cross section of small and large vein which are connected by commissural strand crossing inter-rib arm cell area. Pits in walls separating arm cells and green outer sheath cells and in walls of single transfer cell (t) stand out as a result of interference contrast. Outer sheath cells with chloroplasts arranged in lamellae. Fast green-safranin staining. ×500. — B—C: Plasmatic connections between arm cells (on the left) and large outer sheath cells. Staining with Aniline blue-black. ×2000.

fore stopping where the cuticular layer begins.

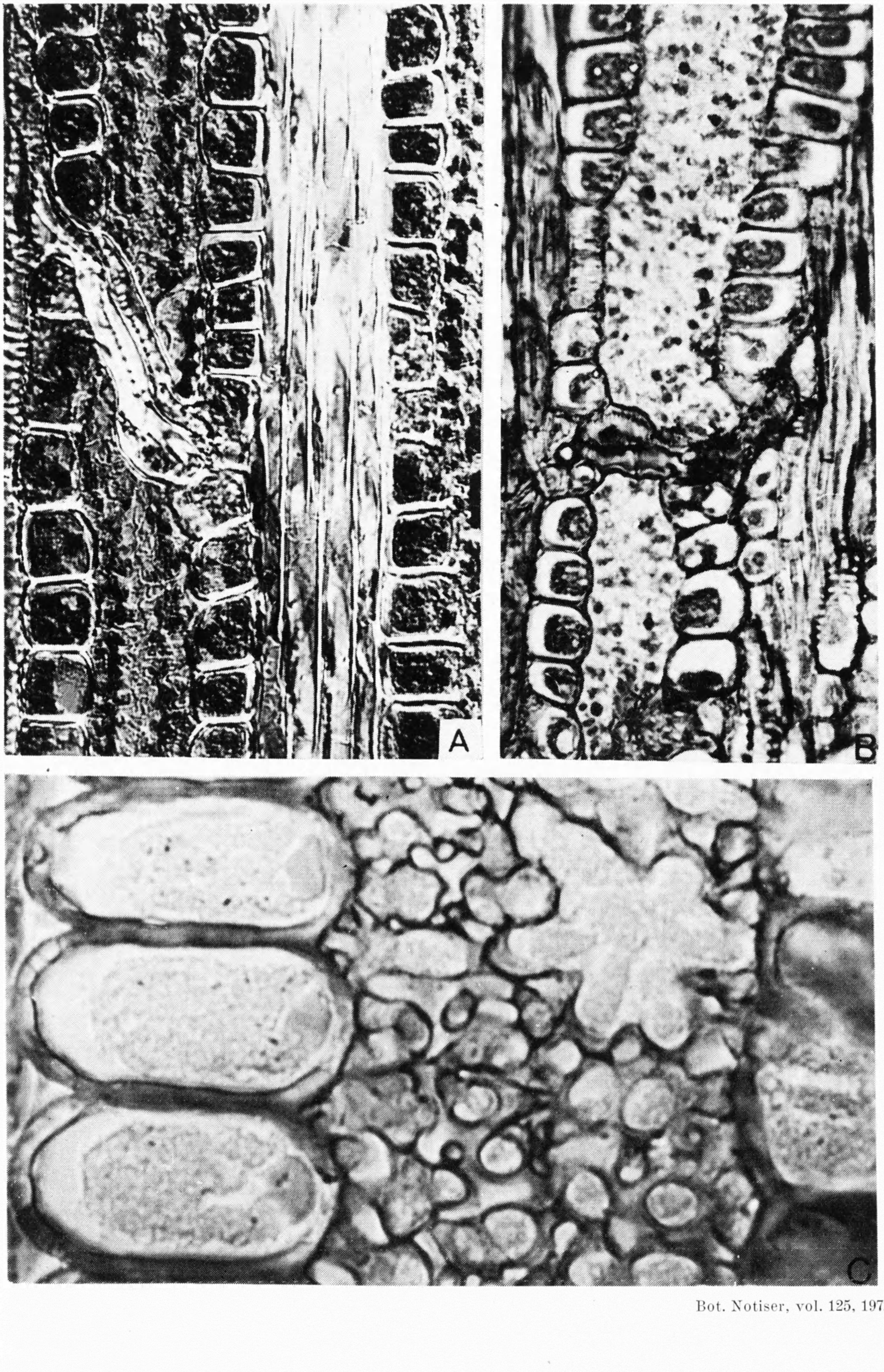
In *S. rigens* several epidermal short-cells have a deviating wall structure which merits discussion. The outer wall has often two cutinized layers separated by a non-cutinized one. The inner layer continues as a cutinized lamella lining the anticlinal walls and sometimes also parts of the inner wall. The cutinized parts stain deeply in Sudan IV (Fig. 2 A), but in Toluidine blue all parts of the innermost lamella stain deep blue while the remaining parts are unstained. In polarized light the walls of the short-cells do not show up, apart from the inner walls which behave like the cellulose parts of the outer epidermal walls which show up brightly. Another important feature is that the short-cells always have a relatively thin outer wall (Fig. 2 B) which is sometimes traversed by a delicate channel or contains a centrally placed inversely conical depression. The large nuclei are located in the middle of the cells which are usually richer in cytoplasm than the normal epidermal cells. The structure of these cells thus indicates some kind of metabolic activity. One possibility would be that they act as glands which discharge water together with soluble salts. ZEMKE (1939 p. 397) says that *Sporobolus pungens* which occurs near brackish water in South Africa is a non-succulent "absalzender Halophyt". The species possesses glands ("Salzdrüsen") described as slightly cutinized epidermal cells resting upon single large cells half embedded in the assimilatory tissue. In *S. rigens* a theory of a similar salt-excretion is supported by the fact that because of the cutinized interior lamellae in the anticlinal walls the cells are isolated from the surrounding cells. In this respect they resemble large salt glands e.g. in *Tamarix* where the secretory cells are almost enclosed by cutinized walls, cp. THOMSON & LING LING LIU (1967). Another point is that they always occur near the outer bundle sheath. Although often bordering fibre cells they have connections with the bundle sheath cells or with some of the small mesophyll arm cells which are wedged in between the epidermis and the large bundle sheath cells (Fig. 5). They occur as if they were bundle sheath extensions. A final point to be considered is the fact that *S. rigens,* as mentioned in the introduction, occurs on dry salt steppes, and even on the shores of salt lakes.

The epidermal cells vary considerably in size. Not only do we have short-cells inserted between the long normal cells, but the height of the cells as it appears from cross sections also varies. The cells covering the fibre plates that are associated with the bundles are narrow and low. The height and size usually increases from the fibre plate areas towards the stomatal depressions (Fig. 3 A). The short-cells mentioned above occur mainly adjacent to large bundle sheath cells but separated from them by one or a few smaller cells. Very often they occur next to the cell which adjoins the stomatal apparatus (Fig. 2).

INTERFASCICULAR ARM CELL AREAS IN SPOROBOLUS RIGENS

The inter-rib mesophyll consists of so-called arm cells. The *Sporobolus* cells of this type were described by VOLKENS (1887 p. 147) who says that in *S. spicatus* a

Fig. 4. *Sporobolus rigens.* Longitudinal sections of blades, in A and B with commissural strands crossing inter-rib arm cell areas. — A, B: In A on the left, a small vein which is cut through in the xylem, the vein on the right is cut through the outer fibre plate. In B the plane of sectioning is slightly oblique, the commissural vein on the right is connected with three inner sheath parenchyma cells, probably transfer cells. Quadruple staining, interference contrast. ×500. — C: Sheath cells and arm cells stained with PAS. One arm cell cut through middle part, the other arm cells are cut through the peripheral branched parts. ×2000.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tissue of this kind occurs just below the stomata. It has the same type of intercellular spaces as those found in *Cynodon dactylon*. In both species, however, the arm cells are colourless and have been interpreted as water-cells. In *S. rigens* the water-storing function seems to have been taken over by the central pith-like parenchyma, whereas part of the photosynthetic function, probably the CO_2 uptake, though not the CO_2 fixation, has been transferred to a tissue composed of arm cells which here contain chloroplasts.

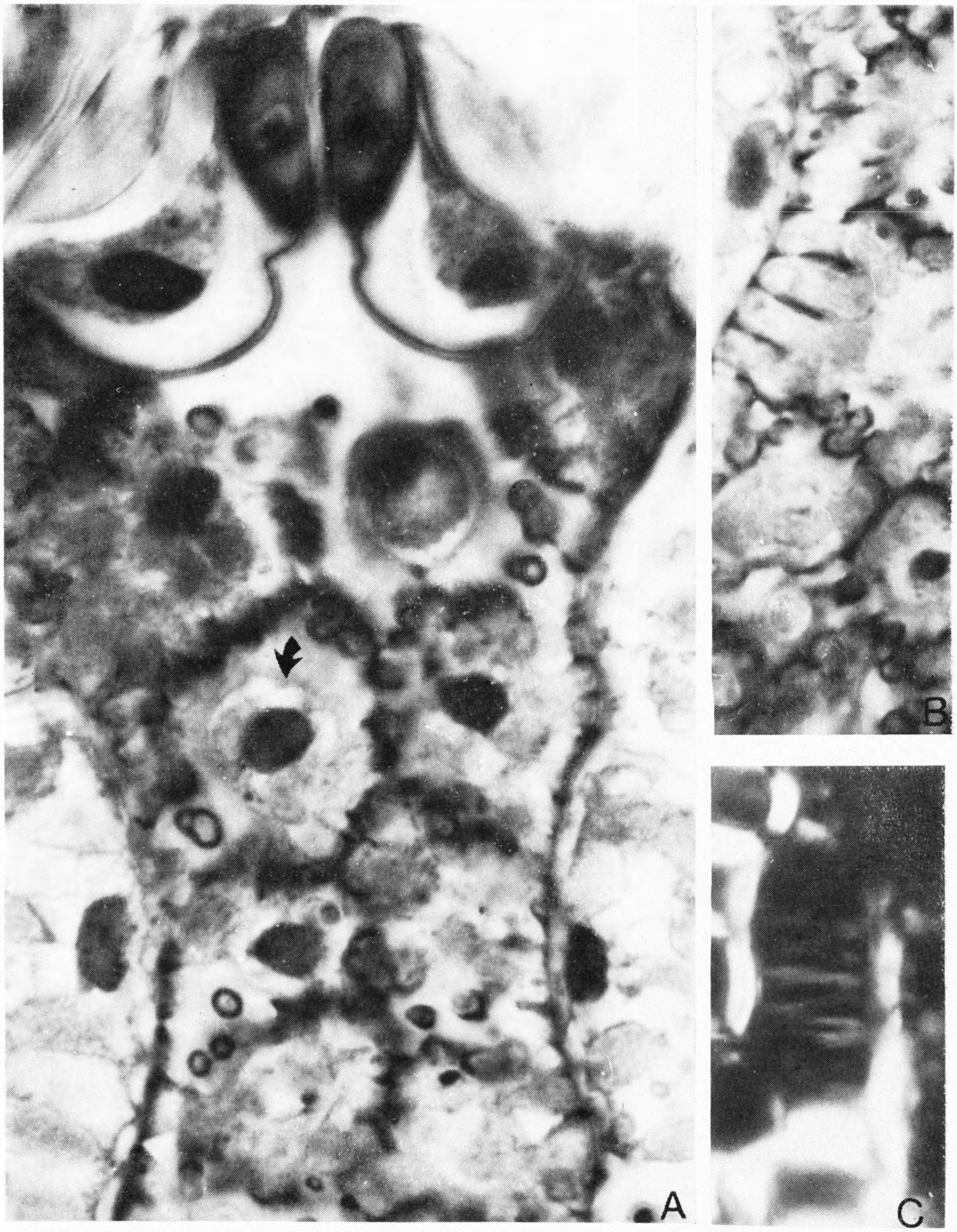
According to VOLKENS (1887) the radiating green palisades around each bundle in *Sporobolus spicatus* are separated by colourless mesophyll arm cells the intercellular spaces of which are connected with the substomatal chambers on the adaxial side. According to the drawings in GOOSSENS (1938) a similar separation by colourless cells occurs in *S. acrinifolius, S. ludwigii, S. bechuanicus* and a few other species. *S. rigens* probably represents a more advanced stage where the radiating palisades have disappeared, whereas the arm cells have developed into a photosynthetic parenchyma with numerous narrow tubular and winding intercellular spaces.

Green arm cells are known from several genera of grasses, e.g. in species of *Arundinaria, Calamagrostis* and *Elymus* (cp. MEYER 1962 pp. 39 and 43), but do not normally seem to have a particularly complicated structure. In *Sporobolus rigens*, on the other hand, they resemble the plicate mesophyll occurring in gymnosperm leaves, where the wall folds sometimes contain loops or eyes (MEYER l.c. Fig. 59 b, c).

The arm cells in *Sporobolus rigens* are difficult to interpret, but after staining very thin sections with Toluidine blue or PAS it is possible to see the cell structure as these stains make the walls stand out whereas the chloroplasts remain unstained. Concerning the cell structure, METCALFE (1960 p. XXVI) says that it is not certain how the projections arise. They could result from folds of the walls but in some grasses their appearance suggests that they arise as partitions that at first traverse the cells but that subsequently become broken as the cells enlarge during development.

Fig. 6 shows arm cells in *Sporobolus rigens* in a thin longitudinal section stained in PAS. In one cell on the right, the knife has removed the wall parallel to the plane of the section; the cell is otherwise entire with two terminal walls that separate it from neighbouring cells in the same row. These walls contain several "eyes" but the folded wall sections also form "eyes" which develop into air-filled spaces. The projections are just broad enough to contain single chloroplasts. The cells in Fig. 6 above illustrate what the walls look like seen from above. The many air-filled folds are light, and surrounded by wall material which is stained. However, where the projections or arms have been cut by the knife the wall has been removed and so the areas in question are light. Below, near the arching walls of the adjacent sheath cells, the cell lumen appears to be subdivided by means of interior walls running parallel to the wall towards the sheath cells. But what we see here are wall sections of some of the invaginations which expand towards the interior of the cell so that a partition of the cell appears to have taken place. The arm cells may thus be characterized as being highly modified stellate cells. This also appears from observations of those sections that were stained in Aniline blue-black which stained the protoplasm (proteins) leaving vacuoles and wall material unstained (Figs. 3 B and 8 B). Chloroplasts are present in the central part and in the broad arms

Fig. 5. *Sporobolus rigens.* — A: Cross section of inter-rib arm cell area with surrounding large outer sheath cells. Subsidiary cells of stomatal apparatus bordering arm tissue extensions. The plasmatic lamellation in the sheath cells obvious. In two of the arm cells



the demarcation of the central part of the cytoplasm has commenced. — B: Detail of border between arm cells and sheath cell showing parallel orientation of arms near border. — A—B: Toluidine-blue staining of nuclei and last-formed walls. ×2000. — C: Scalariform wall thickenings in transfer cell showing weak birefringence. Polarized light. ×2000.

but not in the narrow ones. The cells are connected by many narrow plasmatic projections which resemble pit canals. The cytoplasm in the connecting projections seems to be alveolate.

With increasing age some of the interfascicular arm cell areas undergo considerable changes. The walls lignify and increase in thickness, whilst the nuclei also die and the cells become empty. Such empty arm cell areas may act as a kind of lenticel that enables oxygen to penetrate into the central parenchyma. The empty arm cell areas are not randomly distributed. They are more frequent in the areas adjacent to large veins and more numerous in the basal parts of the blades. The stomatal openings adjacent to the empty arm cell areas are maintained.

The development of the arm cell areas into a system of cells with circular central holes takes place in several stages. One of the first signs is a demarcation of a spherical cytoplasmatic area around the nucleus (Fig. 5 A, arrow). Next, the cell wall increases considerably in thickness and continues to grow until it reaches the line of demarcation of the central area. At the same time, the wall becomes lignified. Cellulose may be present during wall formation. It is possible to demonstrate that cellulose is very probably formed in the latest formed wall by using polarized light. A weak birefringence is observed in a ring-shaped area outside the demarcation. The nucleus is present during this stage (Fig. 7 D), whereas the chloroplasts disappear. Finally the nucleus dies and the central area becomes empty (Fig. 7 B).

At the same time as the changes are taking place in the arm cells, a degeneration sets in in the large adjacent bundle sheath cells. Here too the chloroplasts disappear but the cells remain alive and the nuclei persist.

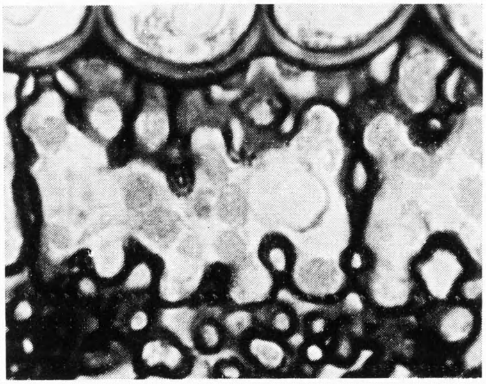
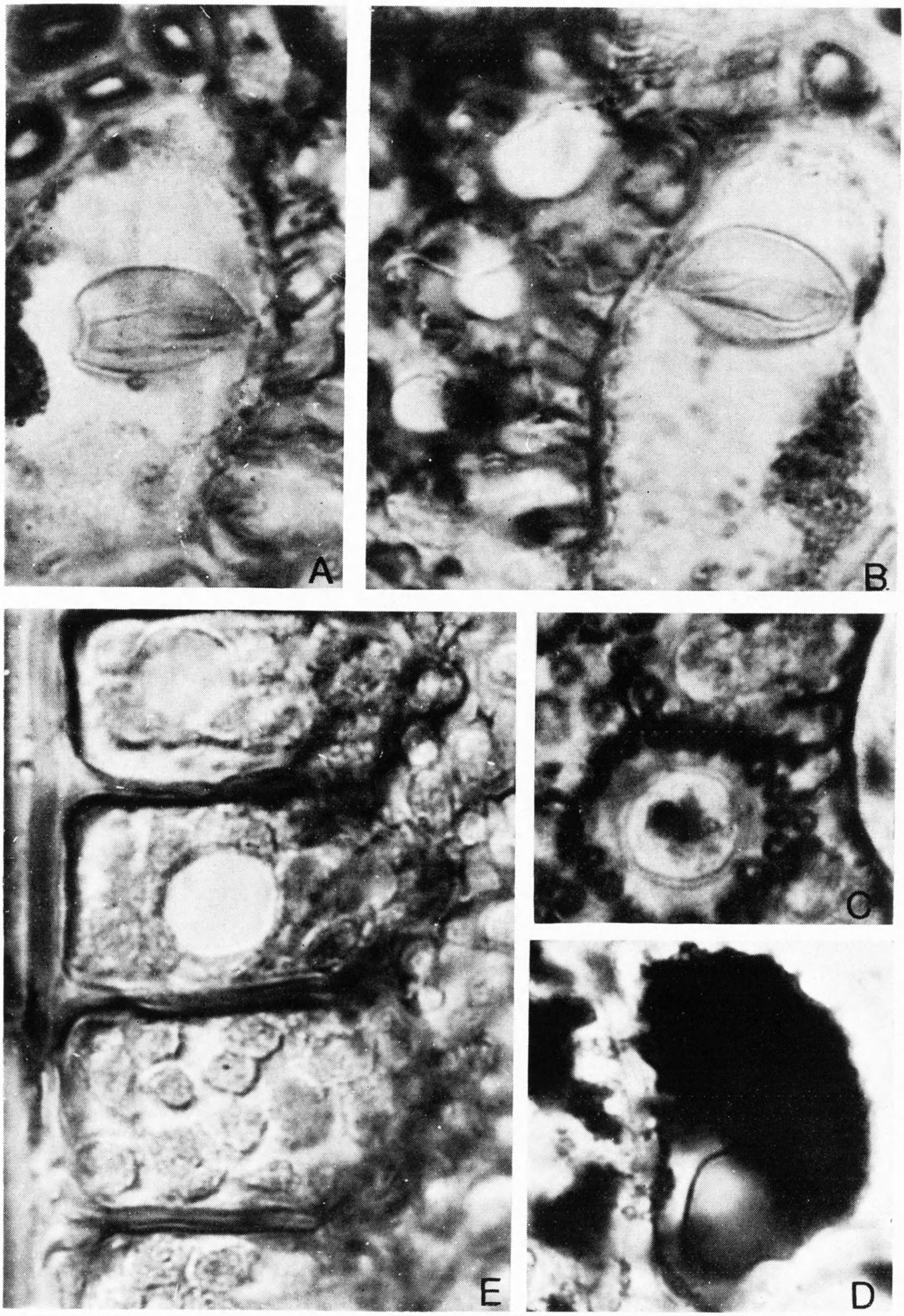


Fig. 6. *Sporobolus rigens.* Arm cell tissue stained with PAS showing folded-in wall sections which form "eyes"; chloroplasts probably with grana. Further explanation in the text. ×1020.

BUNDLE AREAS IN SPOROBOLUS RIGENS

The bundle sheaths are double being composed of an outer sheath of large cells that in the peripheral parts of the blade are green, and an inner sheath which is mainly built up of narrow, thick-walled, densely pitted cells and fibre cells. The outer sheath is interrupted by the bundle fibre plates which reach the epidermis (Fig. 3 A). The green cells in the outer sheath are towards the central axis of the blade replaced first by pitted cells with few chloroplasts, later by very

Fig. 7. *Sporobolus rigens.* — A—D: Cross sections. — A—B: Outermost opposite placed ageing outer sheath cells each with a large faintly stained collapsed body, probably mainly consisting of tonoplast material; nucleus and degenerating cytoplasm. The arm cell tissue has developed circular holes as well as wall thickenings in the former arms. Toluidine-blue staining, semi-polarized light. — C: Late stage in the formation of circular central holes in arm cells. Nucleus still present. Toluidine-blue staining. — D: Plasmatic connections between arm cells and outer sheath cell stained with Aniline blue-black showing coating of large vacuole. — E: Longitudinal section of outer sheath cells with chloroplasts and large vacuoles. In many of the chloroplasts grana may be visible and a minute, often centrally placed body. On the right, a network of arm cell extensions. Staining with PAS and interference contrast. — A—E: ×2000.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wide cells that cannot be distinguished from the colourless central parenchyma. Thus, it may be said that the outer sheath is interrupted on two sides. The inner sheath of the larger veins appears to be more continuous (Fig. 3 A) although also interrupted towards the axis.

The chloroplasts in the large outer bundle sheath cells are larger than those in the arm cells. The difference in size, is probably of almost the same magnitude as that found in *Saccharum* (LAETCH 1968, LAETCH & PRICE 1969). As the material was fixed in alcohol it was unfortunately unfit for electron microscopical (EM) techniques. Hence details of fine structure are not available and attempts at exact measurement of the size had to be abandoned because the cytoplasm which surrounded the chloroplasts was either alveolate or foamy and adherent.

The arrangement of the nuclei is interesting. In by far the most cases they are situated near the thick walls that separate the bundle sheath cells from the arm cells (Figs. 5 A, 8 A). Plasmolysis almost always involves a withdrawal of the cytoplasm from the walls facing the inner sheath (Fig. 4 B).

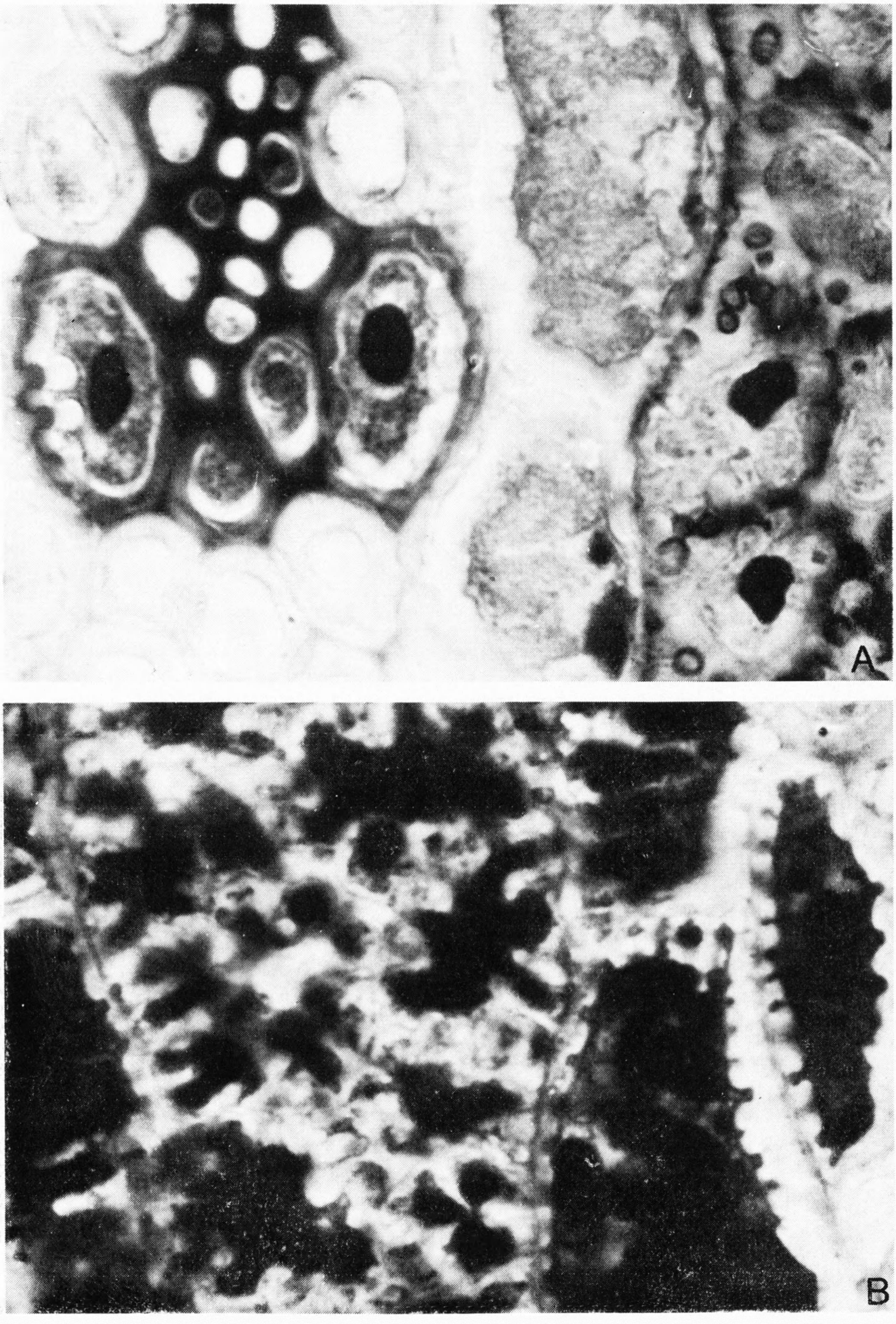
Another striking feature is the arrangement of the vacuoles. In transverse sections of the blades the outer bundle sheath cells are usually long and tend to appear to be more or less cross-striated. This appearance is due to a transverse arrangement of the larger vacuoles which divide the cell into transversely running tracks composed of cytoplasm and large chloroplasts (Figs. 3 A, C). Several arm cells are connected with a single outer sheath cell which again sometimes is connected with a large cell located in the inner sheath and possibly acting as a kind of passage cell or rather a transfer cell. In many cases it is evident that the transversely arranged cytoplasmic tracks begin on a level with the arms that border the sheath cells. Intimate contact between the two types of green cells is facilitated by the presence of numerous plasmodesmata which issue from the broad pit canals of the sheath cells and lead to the extensions from the arm cells. The plasmodesmata are easy to see when stained with aniline blue-black. They appear as delicate strands which, when they reach the area of the middle lamella, become distended to form small globular bodies (Fig. 3 C). These bodies may even fuse to form median nodules. The EM observations of KOLLMANN & SCHUMACHER (1963) on median nodules in sieve areas in *Metasequoia* show clearly that the nodules here are protoplasmic. In our case, the staining properties of the globular bodies point in the same direction. But it must be admitted that sometimes parts of the middle lamella apparently involved are too wide to be described as nodules. Another indication of intimate contact is the maintenance of the marginal cytoplasm just inside the pit canals during plasmolysis (Figs. 3 B and 7 D).

Similar median nodules also occur in the walls separating the outer sheath cells and the sheath-transfer cells, the phloem and the xylem. The intimate contact between a sheath-transfer cell and two outer sheath cells can be seen in Fig. 8 B.

The cytoplasmic tracks which transversely divide the sheath cells usually consist of rows of densely spaced chloroplasts in a cytoplasmic belt connected at regular intervals with the neighbouring belt by cytoplasmic strands bridging the area of separating vacuoles (Fig. 8 B).

Leaf blades of plants from the new material which were cut in the living

Fig. 8. *Sporobolus rigens*. Cross sections. — A: Small vein with two transfer cells and phloem with walls heavily stained by Toluidine-blue. Also the cytoplasm bordering tonoplasts and plasmalemma in the two large sheath cells and last-formed walls in transfer cells and arm cells stained. Incipient hole formation in two arm cells. — B: Aniline blue-black staining of one transfer cell (extreme right), sheath and arm cells. Several lamellae with large chloroplasts in the sheath cells. ×2000.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condition and mounted in iodine solution showed accumulations of starch in the chloroplasts in the outer sheath cells, but also occasionally in some inner sheath parenchyma cells of larger veins. The starch showed deviating staining qualities attaining a dark brown colour and hardly showing up in polarized light. In the material fixed in alcohol in 1955, the presence of starch could not be demonstrated. As already mentioned, no starch was found in the green arm cells, a fact which suggests that *Sporobolus rigens* resembles maize where the C-4 pathway and the carbon fixation seem to be confined to the bundle sheaths (Bednarz & Rasmussen 1972).

Tannin was present in the vacuoles in the old material and was found in great quantities in the green outer sheath cells as well as in the inner sheath transfer cells.

In the old material as well, many cells contained a number of more or less globular, or somewhat angular bodies of different sizes. These bodies were believed to be coated vacuoles. Some cytoplasmatic material was assumed to stick to the tonoplast and was stained by Aniline blue-black. The bodies were not stained by PAS nor by Sudan IV and were optically isotropic. That they were a kind of vacuole was supported by the fact that they were small in cells having well-developed chloroplasts, but large and spherical in aging cells where the chloroplasts had decomposed. In cells with dying cytoplasm they had collapsed and had attained a characteristic appearance resembling the shells of bivalves. In Toluidine blue they were stained faintly bluish (Fig. 7 A and B). It is assumed that at this stage the tonoplasts remain while the cell sap disappears. Thus the occurrence of the bodies is connected with the degeneration of the green bundle sheath cells and has undoubtedly nothing to do with the carbon metabolism of these cells.

The inner sheaths of small bundles deviate conspicuously from the large ones in having some very large living cells which occur on both sides of the bundle almost outside the interior part of the phloem. These cells have very large nuclei and are connected with the green outer sheath cells and with the bundle cells through many pit canals (Fig. 8 B). They may be compared to transfer cells as they seem to function in a similar way as those described by Gunning and co-workers (1968, 1970).

The cells have the same dense cytoplasm as other transfer cells and their surface/volume ratio is undoubtedly high owing to a system of wall ingrowths which surround the spindle-shaped thinner wall areas (Fig. 5 C). The inner part of the thick wall, and thus also the ingrowths, is stained bluish by Toluidine blue (Fig. 8 A) and shows a weak birefringence indicating the presence of cellulose. A large nucleus is situated in the centre.

Gunning et al. (1970 p. 164) referring i.a. to transfer cells in *Festuca* say that in this genus the form of ingrowth is rather bizarre, appearing as a straight-sided transverse flange across the cell, often forked midway along its length, the ingrowths together giving an appearance strongly resembling the scalariform thickings of certain tracheids and vessels (though the staining reactions are very different). The form of wall ingrowth in *Sporobolus rigens* seems to be similar, cp. Fig. 5 C.

The location of the sheath transfer cells is very characteristic. In the majority of cases they are found where two large outer bundle sheath cells meet (Fig. 8 B), on the bundle side bordering on the phloem on the one side and the xylem on the other. This position may indicate that they are able to collect substances produced during photosynthesis and transmit them to the phloem and are also able to provide the outer sheath cells with water.

A general feature is that all commissural veins issue from the transfer cells or from the area where such cells usually occur. This means that another sheath transfer cell is placed opposite to the place where the commissural small vein begins (Fig. 3 A). The commissural veins contain elongate cells which are pitted and have wall ingrowths as well as elongate cells with distinct nuclei and dense cytoplasm. While the former are connected with the xylem, the latter are clearly a continuation of the phloem parenchyma. In cross sections the sheath transfer cells occur singly or rarely two together, while in longitudinal sections they are seen as a single row of cells (Fig. 4 B). In most cases the commissural veins run obliquely from a small bundle towards a large one and cross on their way one of the inter-rib mesophyll areas (Fig. 4 A, B). In rare cases they could be traced for their entire course even in a cross section (Fig. 3 A). It appears that they substitute a part of the outer sheath and penetrate the inner sheath of the large bundle where the phloem and xylem meet.

DISCUSSION AND CONCLUSION

In many respects the cylindrical leaf blade in *Sporobolus rigens* has a structure reminiscent of a photosynthetic stem, in particular those stems in which the green cortex tissues are interrupted by fibre strands going out to the epidermis (cp. Böcher & Lyshede 1972). Considering that shrubs with photosynthetic stems constitute an important life-form in the arid zone of South America we may perhaps be allowed to regard the leaf structure in *S. rigens* and the stem structure in the apophyllous shrubs as an example of analogous convergence. Evidence obtained from comparative anatomical studies within the genus *Sporobolus* and related genera make it clear that the leaf structure in *S. rigens* is very different from the majority of the other species. In all probability *S. rigens* represents an advanced and specialized type adapted to extreme environmental conditions.

The most obvious deviations in the structure of the leaf blades in *Sporobolus rigens* are:

(1) the transformation of a flat blade to a cylindrical blade by an inhibition of marginal growth and a promotion of the keel region. The colourless parenchyma which in many other species is found on the adaxial side of the keel region has a central position thus resembling a pith;

(2) the bulliform cells have disappeared, as have the colourless cells separating the groups of green cells in other species of the genus. The radiating green palisades have also disappeared. They have been replaced by green arm cells.

Many of the anatomical or cytological characters that were demonstrated in *Sporobolus rigens* need to be studied further using EM observations and experiments. It would be of great interest to explore the nature of the epidermal short cells, which perhaps function as salt glands. Another interesting task would be to follow the development of the green arm cells in young blades and using EM to study their degeneration in connection with the very peculiar formation of wall thickenings and central circular holes. We may further point out that our physiological understanding of the transfer cells occurring in the minor veins is very meagre and we lack sufficient information on the large vacuoles with unknown contents which occur abundantly in the bundle sheath cells. They are clearly formed in active green cells and reach their maximum size in cells with degenerating chloroplasts. The coating of these vacuoles and the persistence of the tonoplasts raise other questions.

According to Krenzer & Moss (1969) and Downton (1971) *Sporobolus caroli, cryptandrus* and *spicatus* have low compensation points and are therefore listed as C-4 plants. Many structural features suggest that *S. rigens* has to be added to the list. While carbon fixation and starch accumulation seem to be confined to the bundle sheath cells, the role played by the mesophyll arm cells is obscure. The many cytoplasmatic connections between the arm cell extensions and the green sheath cells suggest that rapid translocations between these cells take place, but in view of the recent studies by BEDNARZ & RASMUSSEN (1972) which indicate that the primary site of carbon fixation, at any rate in maize, is the bundle sheath, we must be very cautious and await further evidence on the metabolism occurring in the arm cells and their connections.

However, the fact that stomata are confined to the epidermis adjacent to inter-rib mesophyll arm cell areas, makes it fairly evident that the CO_2 uptake in *Sporobolus rigens* is connected primarily with the arm cells.

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Biosystematic Studies in Hieracium pilosella L. and Some Related Species of the Subgenus Pilosella

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ABSTRACT

GADELLA, T. W. J. 1972. Biosystematic studies in Hieracium pilosella L. and some related species of the subgenus Pilosella. — Bot. Notiser 125: 361—369.

Cytogeographic investigations of *Hieracium pilosella* L. revealed the occurrence of four cytotypes: 2n=18, 36, 45, and 54. Both *Hieracium peleterianum* MÉRAT and *H. hoppeanum* SCHULT. turned out to be diploid (2n=18). Some notes on the morphology of the various cytotypes are given. Emasculation experiments revealed that diploid and tetraploid plants reproduce amphimictically, the higher polyploids apomictically. It seems likely that the apo-amphimictic mode of reproduction plays an important part in the formation of the higher polyploids. Special attention is paid to the remarkable distribution pattern of the cytotypes on the Dutch Wadden Islands.

INTRODUCTION

The genus *Hieracium* is divided into two subgenera, viz. *Archieracium* and *Pilosella*. In the former the diploid species are usually amphimictic, the polyploids apomictic, i.e. they display diplospory, followed by parthenogenesis. In the latter the diploid species are always amphimictic, whereas in the polyploids either obligate or facultative sexual reproduction occurs, or apomixis of the aposporic type followed by parthenogenesis.

The present study covers three species of the subgenus *Pilosella*, viz. *H. hoppeanum* SCHULT., *H. peleterianum* MÉRAT, and *H. pilosella* L. s.l. These species belong to the section *Pilosellina*, which is characterized by one-headed inflorescences. The group is extremely polymorphic. Many intraspecific taxa have been recognized (more than 600 in the collective species *Hieracium pilosella* L. by ZAHN 1923).

Cytological studies have been few. It is true that TURESSON and TURESSON (1960) studied more than 500 collections, but most of their plants originated from a limited area of the range of *H. pilosella*, i.e. from Sweden. SKALIŃSKA (1967) studied some plants from the Eastern Carpathian mountains, whereas GADELLA & KLIPHUIS (1968 a, b, 1970 a, b, 1972) studied plants from the Netherlands, the Alps and Yugoslavia, respectively. In older studies the exact place of origin of the material studied was not mentioned (CHRISTOFF & POPOFF 1933; CHRISTOFF & CHRISTOFF 1948; GENTSCHEFF 1937). Moreover, these authors made errors in the determination of the material. For these reasons their results have not been taken into account in this study.

In order to obtain a better insight into the distribution of the various cytotypes in Europe, the present author decided to study a large number of samples, collected in various parts of the distributional area not covered by the studies of TURES-

SON and TURESSON (1960). Most plants originated from the Dutch Wadden Islands. The data presented in this paper are the first results of these studies, which the present author carried out in close cooperation with his colleague Mr. E. KLIPHUIS, whose help is gratefully acknowledged. Some notes on the distribution patterns are given together with some preliminary notes on the mode of reproduction of the various cytotypes. The samples studied have been assigned to collective species, not to intraspecific taxa.[1] More extensive investigations on the mode of reproduction and on the distribution patterns are in progress.

MATERIAL AND METHODS

The plants studied were collected in their natural habitats. As a rule 3—5 plants from each population (or clone) were dug up and transferred to the experimental garden. Root tips were used in cytological studies. They were fixed in Karpechenko's fixative, embedded in paraffin wax, sectioned (15 μ) and stained according to Heidenhain's haematoxylin method. The method proved to be quite satisfactory and as a rule no difficulties in the counting of the chromosomes were met with. The emasculation experiments, described by TURESSON and TURESSON (1960 p. 718), were repeated by the present author.

Voucher material of all plants studied has been deposited in the Herbarium of the State University of Utrecht (U).

RESULTS

Morphology

Most of the diploid plants (2n=18) belong either to *H. peleterianum* MÉR., or *H. hoppeanum* SCHULT. These species appear to differ in well-correlated characters, despite considerable similarity in general appearance.

Fig. 1. *Hieracium pilosella* L. (2n=18). Material originating from the valley of Aosta (Italy).

Diploid plants were also found near Aosta, N. Italy. These plants show the following characters (see also Fig. 1):

Leaves lanceolate to oblong, obtuse at the apex, up to 10 cm long, with many stellate hairs below and long pilose hairs above. Stolons long and slender, the leaves gradually diminishing in size towards the apex. The scapes are undivided, never furcate, 25—30 cm long, provided with many greyish-white floccose stellate hairs and many dark brown or black glandular hairs. Scales of the involucre rather small (6—10 mm), provided with many glandular dark brown or black hairs and broad more or less glabrous margins. Pappus greyish white.

These characters are typical for *H. pilosella* L.; Prof. J. VAN SOEST (Leyden, Rijksherbarium) determined the plants

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[1] In the paper by B. TURESSON (1972) many strains, from various localities in Sweden, were carefully investigated taxonomically and assigned to different subspecies.

from Aosta and assigned them to the subspecies *subvirescenticeps* ZAHN.

The triploid plants ($2n=27$) are intermediate between *H. pilosella* and *H. peleterianum.* In general they resemble *H. peleterianum,* but their stolons are longer and more slender. They were found in association with *H. peleterianum,* and *H. pilosella* was found in the vicinity (150—300 m).

The tetraploid plants are very variable and belong to the group (grex) *eupilosella.* Their leaves are never greyish floccose on the upper surface.

The penta- and hexaploid plants from the Alps ($2n=45$ and $2n=54$, respectively), belong to the grex *incanum* (DC.) ZAHN. Their scapes are usually very tall, especially when the achenes are ripe. The stolons are very long. The leaves are characterized by greyish-white, short stellate hairs both on the upper and lower surfaces. In the experimental garden loosely branched inflorescences (with two or three heads) are sometimes (usually in autumn) produced by plants that formed one-headed inflorescences during the summer.

The penta- and hexaploid plants in localities outside the Alps belong to the grex *eupilosella.* The stolons are usually long and the mats are therefore less dense than in the tetraploids. The scapes are usually rather tall, especially when the achenes are ripe. In some populations, e.g. in the population from Winterswijk (the Netherlands), the inflorescences of the pentaploids are branched, i.e. very loosely furcate (see the figure in GADELLA & KLIPHUIS 1968 b).

Distribution

The results obtained are listed in Table 1 (the Dutch Wadden Islands) and the Appendix (all European samples studied). The distribution of the various cytotypes is shown on the maps (Figs. 2—5). The triploid plants were found in one locality on the Island of Terschelling (the Netherlands). The tetraploid cytotype is widespread in Denmark and W. Europe. All plants collected in Scotland proved to be pentaploid. The hexaploid cytotype seems to be rare, only some scattered populations (or clones) were found.

Table 1. The distribution of diploid, triploid, tetraploid, pentaploid and hexaploid *Hieracium* Subg. *Pilosella* plants in the Dutch Wadden Area. Numerals give the numbers of plants studied.

Taxon	2n	Texel	Vlieland	Terschelling	Ameland	Schiermonnikoog
Hieracium peleterianum MÉR.	18	—	—	92	—	—
Hybrid between *H. pilosella* L. and *H. peleterianum* MÉR.	27	—	—	12	—	—
H. pilosella L.	36	154	18	69	53	15
	45	6	20	15	—	25
	54	2	5	—	—	—

Emasculation experiments

In all cases diploid plants (belonging to the species *H. pilosella, H. hoppeanum* and *H. peleterianum*) proved to be amphimictic. The triploid plants are presumably sterile, as none of the achenes formed gave rise to seedlings. The higher polyploids ($2n=45$ and $2n=54$, both of the groups *eupilosella* and *incanum*) usually formed achenes after emasculation, which indicates that they reproduce apomictically. In some cases, however, only a few achenes were formed. Another observation is that all seedlings grown from pentaploid plants are also pentaploid. Neither tetraploid nor hexaploid plants could be obtained from achenes produced by pentaploid plants. This supports the view that pentaploids reproduce apomictically. The experiments, however, were carried out on a comparatively small scale.

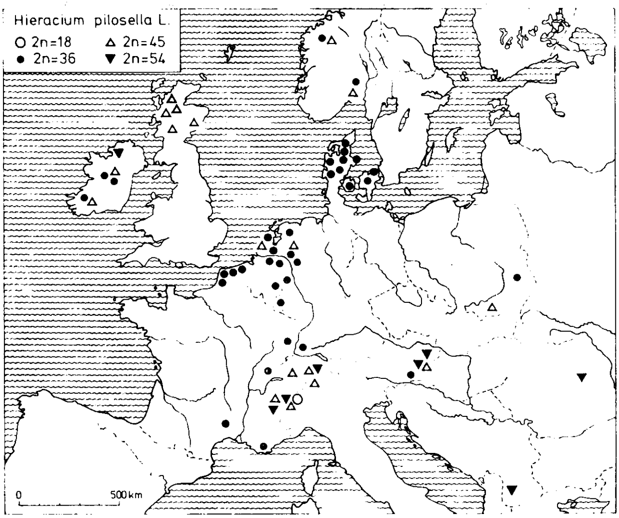


Fig. 2. *Hieracium pilosella* L. The known distribution of the cytotypes 2n=18, 36, 45 and 54 in Europe.

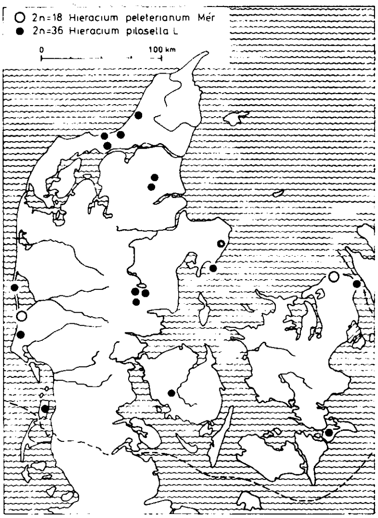


Fig. 3. Material studied of *Hieracium pilosella* L. and *H. peleterianum* MÉR. in Denmark.

DISCUSSION

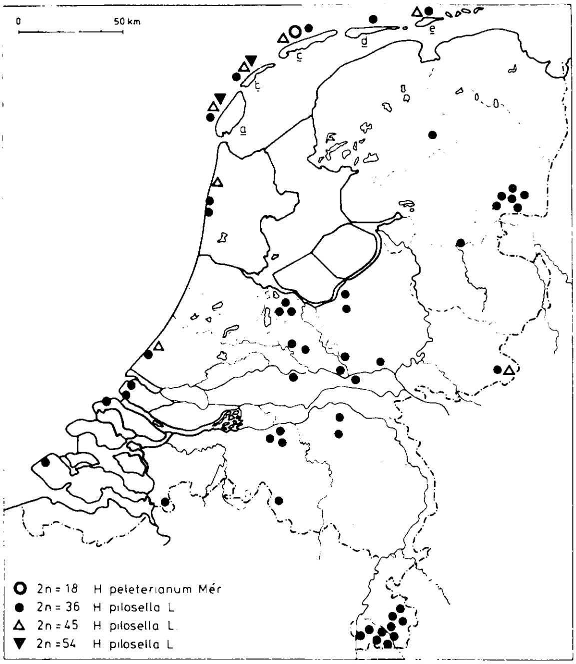
Most of the data obtained by TURESSON and TURESSON (1960) could be confirmed.

The diploid cytotype of *H. pilosella,* however, was not found by these authors. The distribution of the diploid plants of *H. pilosella* is possibly rather limited. This is not exceptional in polyploid apo-amphimictic complexes. *Crepis occidentalis,* which was studied by BABCOCK and STEBBINS (1938), is a diploid—polyploid apo-amphimictic complex in N. America. The 7 diploid species of this complex are all amphimictic. The range of only one of them is extensive, the other 6 species are restricted to very small areas. More extensive studies, especially in N. Italy and adjacent regions, are clearly necessary in order to obtain a better insight into the distribution pattern of the diploid cytotype of *H. pilosella.*

The fact that in the Netherlands *H. peleterianum* is restricted to the Island of Terschelling is remarkable. It seems likely that the achenes, which are clearly adapted to wind dissemination, have a wide radius of dispersal, especially in the Dutch Wadden area, where strong winds are of almost daily occurrence. Contrary to this expectation it appears that *H. peleterianum* is found in a very small area in the Dutch Wadden area.

The triploid plants mentioned by TURESSON and TURESSON (1960), are to a great extent sterile. The triploid plants from Terschelling proved to be entirely sterile. If the triploid plants are occasionally amphimictic, it would be of interest to study the chromosome numbers of the progeny. Crossing experiments between the triploid hybrids and of the hybrid with the diploid and tetraploid parents may shed some light on this problem. Only on the Island of Terschelling do diploid and tetraploid plants occur in close proximity to each other, which lends support to the supposed hybrid origin of the triploid plants.

The tetraploids studied by TURESSON and TURESSON are mainly restricted to



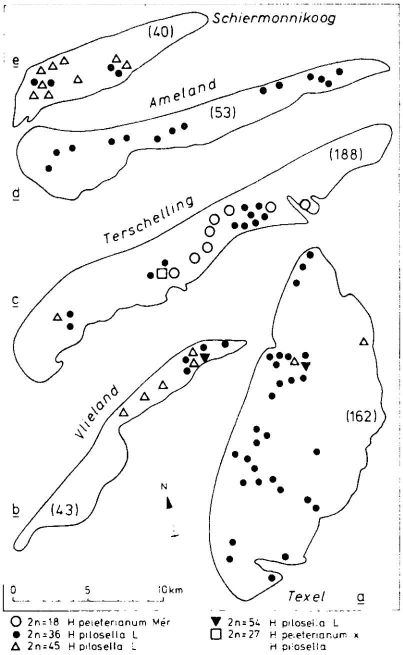


Fig. 4. The known distribution of *H. peleterianum* MÉR. and of the various cytotypes of *H. pilosella* L. in the Netherlands. The letters a, b, c, d, e correspond to the Dutch Wadden Islands Texel, Vlieland, Terschelling, Ameland and Schiermonnikoog, respectively. (For further details see Fig. 5).

Fig. 5. The known distribution of *Hieracium peleterianum* MÉR. and of the various cytotypes of *H. pilosella* L. on the Wadden Islands. The figures in parentheses refer to the number of plants that were cytologically studied. The letters a, b, c, d, e correspond to the same letters of the map of Fig. 4.

S. Sweden and Denmark. Our results obtained on Danish plants corroborate TURESSON's and TURESSON's results. Most Dutch plants and many Irish plants are also tetraploid. From these results the conclusion may be drawn that tetraploid plants are widely distributed in the lowlands of Europe. They are very scarce in northern parts of Europe, e.g. in the greater part of Sweden (except in Scania) and in Scotland. In the Tatra Mountains no tetraploids were found by SKALIŃSKA (1967). SKALIŃSKA et al. (1971), however, found tetraploid plants in Stronie Slaskie in the south-eastern part of the Sudetic Mountains. The fact that the tetraploid cytotype is also represented in Poland could be confirmed in plants from Opole.

The distribution of the tetraploid and pentaploid plants on the Wadden Islands shows some remarkable patterns: the amphimictic tetraploid cytotype is widespread and very common on the islands of Texel and Ameland, but less common on the islands of Vlieland and Schiermonnikoog, where the apomictic pentaploid cytotype is very common. On the island of Terschelling the pentaploids are far less common. The hexaploid plants are rare. They were found on the islands of Texel and Vlieland and proved to be associated with (at least at some distance) tetraploid and pentaploid plants. On the island of Vlieland a large mat of hexaploid plants was found at a distance of ca. 300 m from a clone of pentaploid plants, and

200 m from a population of tetraploid plants. On the island of Texel (near de "Slufter") two hexaploid and three pentaploid plants were found in a very large population consisting of tetraploid plants. This proved to be the only mixed population found in the Netherlands, all other topodemes studied consisted of either tetraploid or pentaploid plants. Mixed populations were also reported by SKALIŃSKA (1967) in Poland. In the latter case, however, the hexaploid cytotype always occurred in association with other *Hieracium* species, i.e. *H. pratense* and *H. auricula* and with the pentaploid cytotype (the tetraploid cytotype is lacking in the Tatra Mountains). According to SKALIŃSKA this suggests a putative hybrid origin for the hexaploids. In the Netherlands, on the other hand, the type with higher chromosome number was found in pure local populations of *H. pilosella,* in which also tetraploid and pentaploid plants occur at least within the vicinity. No other species of the subgenus *Pilosella* were found by the present author on the islands of Texel and Vlieland. For that reason it seems highly probable that the hexaploid plants from Texel and Vlieland were formed intraspecifically. A plausible explanation seems to be that an unreduced egg cell of the tetraploid is fertilized by a sperm cell of a pollen grain with the reduced chromosome number: $2n=36+n=18 \rightarrow 2n=54$. The tetraploids, however, are amphimictic and their gametes have the reduced chromosome number. It does not seem likely that the pentaploids are involved in the formation of hexaploids. If pentaploid plants are kept isolated, the progeny raised from the achenes formed is always characterized by having $2n=45$, which indicates that apomictic reproduction is involved in the formation of the embryos. In a related species, *Hieracium aurantiacum,* SKALIŃSKA (1971) was able to demonstrate that in pentaploids aposporic (unreduced) embryo sacs occasionally gave rise to derivatives with deviating, i.e. increased chromosome numbers. From these experiments it is clear that in *Hieracium aurantiacum* unreduced apomictic embryo sacs occasionally require fertilization. If this were the case in pentaploid *Hieracium pilosella,* pollination by pollen grains with the number $n=18$ (produced by amphimictic tetraploid plants) would be probable. In that case it would be expected that the hybrid was characterized by having $2n=63$, a number which has not yet been found in the Netherlands.

In order to demonstrate the occurrence of amphimictic reproduction in pentaploids, heteroploid intraspecific crosses followed by cytological studies of the hybrids formed will have to be performed. A detailed analysis of meiosis during both macro- and microsporogenesis may also contribute to a better understanding of the phenomena leading to the formation of the hexaploid cytotype. The way in which the pentaploid cytotype originated seems to constitute another interesting problem. Further studies to elucidate these problems are in progress. It seems highly probable that the apo-amphimictic mode of reproduction plays an important part in the formation of the higher polyploid cytotypes.

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APPENDIX. LIST OF MATERIAL CULTIVATED

Hieracium hoppeanum SCHULT. (2n=18)

SWITZERLAND. Julier Pass, 2600 m. (Graubünden), 10656; Waltenburg, 1450 m. (Graubünden), 10651.

YUGOSLAVIA. Between Dobri and Beloviste (Macedonia), 9062, 9063, 9065; near Mavrovo (Macedonia), 8933.

Hieracium peleterianum MÉRAT (2n=18)

DENMARK. Nymindegab (Jylland), 13240—13243; Rågeleje (Sjaelland), 13048—13051.

FRANCE. Entragues (Aveyron), 11544; Bonneval sur Arc, 1850 m. (Savoie), 5049; Mont Cenis, 2000 m. (Savoie), 5336, 5337.

ITALY. Aosta Valley, Chateau sur Nus, 1200 m., 5562; Gran Paradiso, 2200 m., 5626, 5638; Valnontey, 1800 m., 5655.

THE NETHERLANDS. Friesland, Island of Terschelling. a. Boschplaat, 7327—7332; b. Formerum, 5873—5879, 5891, 5894, 5895, 12877—12879, 12892—12903; c. Hoorn, 5796—5800, 5857—5867, 7333, 7334, 12910—12918, 12949—12953; d. Lies, 5855, 5856, 12933, 12934; f. Wytdune, 5785—5789, 5868—5872.

NORWAY. Near Sundvollen (between Oslo and Hönefoss), 11055.

Hieracium pilosella L. group **eupilosella** (2n=18)

ITALY. Valley of Aosta, near Ville sur Nus, 1400 m., 5840, 5841.

Hieracium pilosella L. group **eupilosella** (2n=36)

AUSTRIA. Deutschlandsberg (Steiermark), 6937, 6951.

BELGIUM. Eupen (Liège), 8258, 8259; De Panne (W. Vlaanderen), 11932, 11950.

DENMARK. Millinge (Fyn), 13093; Agger (Jylland), 13231; Ebeltoft (Jylland), 13175; Gladved (Jylland), 13182; Hennestrand (Jylland), 13245; Hvide Sande (Jylland), 13239; Klim (Jylland), 13210; Lögstör (Jylland), 13206; Lökken (Jylland), 13192; Rebild (Jylland), 13155; Slettestrand (Jylland), 13200; Stenbjerg (Jylland), 13229; Thorupstrand (Jylland), 13213; Stege (Mön), 13006; Lakolk (Römö), 13164, 13165; Helsingör (Sjaelland), 13034—13037.

FRANCE. Echenerex 700 m. (Ain), 10623; Virieu le Grand (Ain), 4913, 4935; Cap Blanc Nez (Artois), 11941—11946, 11953—11955; Nant (Aveyron), 8333; Plage de Loon (Flandres), 11935, 11948; Hohneck, Vosges, 1200 m. (Haut Rhin), 9469, 9470, 9471; Collobrières, Massif de Maures (Var), 8712, 8713.

W. GERMANY. St. Blasien, Schwarzwald (Baden-Württemberg), 10652; Borken (Nordrhein-Westfalen), 12290, 12294, 12298, 12299; Konzen (Nordrhein-Westfalen), 8242—8250; Monschau (Nordrhein-Westfalen), 8251—8256.

ITALY. Valley of Aosta, Ville sur Nus, 1500 m., 5586.

IRELAND. Killarney (Ct. Kerry), 9820, 9884; Furnace, Lough Feeagh (Ct. Mayo), 9824, 9912, 9916; Elphin (Ct. Roscommon), 9882; Lanesborough (Ct. Roscommon), 8753;

Longford (Ct. Roscommon), 9870, 9871, 9917; Benbulbin, 150 m. (Ct. Sligo), 9866, 9867.

LUXEMBOURG. Near Vianden, 9158.

THE NETHERLANDS. Friesland. Island of Ameland (various localities, see Fig. 5), 8152—8204; Oosterwolde, 13457; Island of Schiermonnikoog (various localities, see Fig. 5), 10070—10072, 10076—10080, 10085—10090, 10094—10096; Island of Terschelling (various localities, see Fig. 5), 5778—5784, 5790—5795, 5835—5854, 5880—5890, 5896—5899, 7895, 7995—8000, 8091, 8092, 12834, 12904—12906, 12943—12948; Island of Vlieland (various localities, see Fig. 5) 7821—7840.

Drente. Diphoorn, 4345—4347; Emmen, 4179, 7862, 13458; Noordsleen 4348, 4349; Oosterhesselen, 6336, 6337; Schoonebeek, 4172—4178; Sleen, 4350—4352.

Overijssel. Ommen, 13456.

Gelderland. Bennekom, 6043, 6044; Culemborg, 8273, 8275; Harderwijk, 7146—7148; Heelsum, 4448—4454, 4507; Opheusden, 8272; Speuld, 4013—4015; Winterswijk, 6150, 6151.

Utrecht. de Bilt, 4320—4323; Maarn, 586; Rhenen, 1765, 7878, 7879.

Noord Holland. Bergen, 4101—4103, 4107, 4582; Hilversum, 6045—6049; Laren, 4723—4728; Island of Texel (various localities, see Fig. 5), 6700, 6701, 6703—6729, 6732—6755, 6760—6768, 6771—6817, 6819—6841, 7928—7952, 7954—7958, 7960—7964, 7971—7984.

Zuid Holland. Island of Goeree, near Goedereede, 7181—7189; Voorne, 4300, 4301, 4306, 4335; Wassenaar, 6155—6161.

Zeeland. Oostkapelle, 6034.

Noord Brabant. Cromvoirt, 4225—4228; Drunen, 12387; Heesch, 7107—7109; Helvoirt, 4271, 4272; Lieshout, 7118—7120; Lage Mierde, 4187; Ossendrecht, 12307.

Limburg. Bemelen, 8233, 8235—8238; Brunssum, 8638—8640; Epen, 8070, 8071; Eys, 8046, 8052—8054, 8067—8069, 8267; Gulpen, 8047—8051, 8055, 8064—8066; Heerlen, 8648, 8649; Kunrade, 8269; Maastricht, 8260, 8261; Slenaken, 8239—8241; Terziet, 8641—8644, 8660—8664; Waubach, 8653—8659; Wittem, 8073, 8074, 8262—8264.

POLAND. Near Opole (Lublin), 10625, 10628.

NORWAY. Near Skjolden, 11084; near Oslo, 11559.

Hieracium pilosella L. group **eupilosella** ($2n=45$)

AUSTRIA. Bernstein (Burgenland), 6948; Oberwart (Burgenland), 6990.

IRELAND. Killarney (Ct. Kerry), 9883; Elphin (Ct. Roscommon), 9881; Port Runny Bay (Ct. Roscommon), 9822; Benbulbin, 200 m. (Ct. Sligo), 9879, 9880; Benbulbin, 600 m. (Ct. Sligo), 9863.

THE NETHERLANDS. Friesland. Island of Schiermonnikoog (various localities, see Fig. 5), 10058—10069, 10073—10075, 10081—10084, 10091—10093, 10097—10099; Island of Terschelling (various localities, see Fig. 5), 5747—5757, 7988, 8093, 8094, 12935, 12936; Island of Vlieland (various localities, see Fig. 5), 7801—7820, 7841—7845.

Gelderland. Near Winterswijk, 6152, 6153.

Noord Holland. Camperduin, 4111, 4112; de Slufter (Island of Texel), 6730, 6731, 6818; Oosterend (Island of Texel), 6756—6759.

Zuid Holland. Wassenaar, 6162.

NORWAY. Island of Borøya (Oslofjord), 11058, 11557; near Skjolden, 11073.

POLAND. Near Kurnice, 1250 m. (prov. Krakow), 9637.

SCOTLAND. Glen Affric Valley (Inverness), 13386, 13388; Loch Ness (Inverness), 13392; St. Cyrus (Kincardine), 13383; Ben Lawers mt. (Perth), 13398; Ben Eighe, Loch Maree (West Ross), 13393.

SWITZERLAND Val Verzasca, near Sonogno (Tessin), 8741; Jaun Pass, 7308; Breil (Graubünden), 10042, 10654, 10655.

Hieracium pilosella L. group **eupilosella** ($2n=54$)

AUSTRIA. Hebalm, NW. from Deutschlandsberg (Burgenland), 6935; Ruster Hügelland bei Oslip (Burgenland), 7003.

IRELAND. Strandhill near Sligo (Ct. Sligo), 9915.

THE NETHERLANDS. Friesland. Vuurboetsduin, Island of Vlieland, 7846—7850.

Noord Holland. de Slufter, Island of Texel, 6702, 7953.

ROMANIA. Near Bacau, 11535.

SWITZERLAND. Near Waltensburg, 1400 m (Graubünden), 10653.

YUGOSLAVIA. Near Mavrovo (Macedonia), 8990.

Hieracium pilosella L. group **incanum** (DC.) Zahn ($2n=45$)

FRANCE. Near Bonneval sur Arc, 1850 m. (Savoie), 5331; between Bonneval sur Arc and l'Ecot, 1950 m. (Savoie), 5360.

ITALY. National Park Gran Paradiso: near Rifugio Vittorio Sella, 5525; Between Valnontey and Rifugio Vittorio Sella, ca. 2200 m., 5619.

Hieracium pilosella L. group **incanum** (DC.) ZAHN (2n=54)

FRANCE. Between Bonneval sur Arc and l'Ecot, 1900 m. (Savoie), 4989, 5184, 5192, 5202, 5361; near Bonneval sur Arc, 1850 m. (Savoie), 5000; near Lac du Mont Cenis, 1850 m. (Savoie), 5112, 5152; near Bessans, 1700 m., (Savoie), 5156, 5352; Mont Cenis, 2500 m., (Savoie), 5408.

ITALY. National Park Gran Paradiso, between Rifugio Vittorio Sella and Valnontey, ca. 2200 m., 5636.

Hieracium pilosella × H. peleterianum (2n=27)

THE NETHERLANDS. Friesland, Island of Terschelling. Near ormerum, 5892, 5893, 7990—7994, 12881, 12887, 12890, 12891, 12900.

Pharmacognostic Screening of Plant Materials

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ABSTRACT

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Many different ways of approach have been taken in the search for natural products with biological activity. Phytochemical and biological screening procedures are described in this paper and examples of different methods are given. Some screening results are discussed, and a section is devoted to pharmacognostic field work. The importance of plant identification is pointed out.

INTRODUCTION

Although modern organic chemistry has provided us with an increasing number of synthetic compounds for medicinal use, the search for natural products with biological activity continues. The goal today is, however, to find not only therapeutically useful compounds. New sources of raw materials to be used in complicated chemical reactions are being sought, as well as new chemical structures which can serve as models for new drugs. The advanced techniques of modern chemistry have also made possible the isolation and characterization of a growing number of new compounds. Thus, in 1959 there were 2,175 known alkaloids, but only ten years later this figure had been doubled, giving a total of 4,350 alkaloids.

In this review we want to briefly present some methods used in the search for plants and plant products of pharmacological and chemical interest. The prospects of such investigations are promising, since it has been estimated that only 5—6 % of the world's flora has been studied chemically in any detail. The main purpose of the various screening methods is thus the selection of plant material for further study, but the results may also be of interest to taxonomists, biochemists and ethnobotanists.

Basically, there are two ways of looking for new biologically active compounds. We can either search for *the compound* or for *the effect* it produces. In the first case we speak of *phytochemical screening,* in the second of *biological screening.* The following discussion is divided into three sections, the first two dealing with biological and chemical screening methods with examples from recent research. In the third section we describe the methods we have used for plant screening in the field. An extremely thorough and extensive review of various screening procedures has been published by FARNSWORTH (1966), with more than 800 references to the literature. Before embarking on our main theme, we would like to cite FARNSWORTH (1966) regarding the personal training and background of investigators in this truly interdisciplinary field. "A great deal of common sense, a broad background in the medical sciences, and some knowledge of plant constituents and of chemotaxonomic relationships are all necessary for one to select the most promising plants for study." (FARNSWORTH 1966 p. 227).

BIOLOGICAL SCREENING

Pharmaceutical natural products research deals with pharmacologically active substances occurring in plants and also in animals. The first question the pharmacognosist asks is therefore: "Does this or that plant contain any substance with a biological effect?" The second question is: "What structure does the biologically active substance have?" It should be pointed out that both therapeutic and toxic effects are equally interesting at this stage of the investigation.

In order to test the biological effects of plant material simple screening methods have been worked out using mice and rats (SANDBERG 1966). This pharmacological screening can be performed in the field or, more usually, in the home laboratory.

Pharmacological screening as part of the field work was carried out by a research group headed by D. B. TAYLOR, M. D., Chairman of the Pharmacology Department at the University of California in Los Angeles. TAYLOR and his group made several collecting trips to Eastern Peru. A decade ago one of the authors (F. S.) met this group in Tingo Maria. Their procedure in the field was as follows: From plants growing in a region outside Tingo Maria small amounts of leaves, bark and/or root were collected at random. The taxonomist in the group collected sufficient herbarium material for reference, and checked the labels of the material to be used for extraction so that they coincided with the collection number of the corresponding herbarium sheets. The locality was indicated as accurately as possible. In the simple field laboratory in Tingo Maria a crude extract of the collected plant material was prepared and injected into mice for the screening procedure. If the screening showed any effect of interest, the TAYLOR group returned to the place where the plant was found in order to collect a large amount of plant material for further phytochemical and pharmacological research in the home laboratory in Los Angeles. This type of field work requires basic laboratory facilities for extraction and screening and mice must be flown out to the field base.

Another way of establishing the pharmacological effects of plants is to carry out the screening procedure on rats in the home laboratory. Our own experience is limited to folk-lore medicine from two regions in Equatorial Africa: The southwestern part of the Central African Republic (Berberati region) and the northern part of Congo/Brazzaville (Ouesso region) (SANDBERG 1965). With the aid of Swedish Baptist missionaries, who were well acquainted with the regions investigated, suitable persons were interviewed regarding plants used in native medicine, their mode of use and the vernacular names. This information had to be cross-checked in order to ensure that the data were reliable. The man who supplied the information on the use of a certain plant was asked to point out that particular plant in the field (Fig. 1). 1—3 kg of the plant part used (in Fig. 1 the bark of a tree) was collected, dried (Fig. 2), and sent by air to our laboratory in Stockholm where screening was performed on rats. A positive screening result confirms the value of the local use of a plant.

Another type of pharmacologic screening has been carried out in our department by SAMUELSSON (1966, 1969). Parasitic Loranthaceae species have been screened for their content of basic toxic proteins, tested by intraperitoneal injection in mice. The intraperitoneal toxicity method was also used to follow the purification of the basic proteins of viscotoxin type.

In all the above-mentioned examples the therapeutic and/or toxic effects on man and laboratory animals have been observed. Observations on the effects on domestic animals can also be used. They

Fig. 1 (top). Collection of bark for screening purpose from the tree to the extreme right, based on the information given by the man of the Pomo-tribe (no. two from the left), at the Sangha river north of Ouesso. — Fig. 2 (middle). Drying different types of plant material in the sun. Swedish Baptist Missionary Station in Ouesso, Congo/Brazzaville. — Fig. 3 (bottom). Field testing of cacti for alkaloids. A drop of the test solution is applied to the filter paper (see text). A group of *Lophophora diffusa* can be seen just behind the hat. Querétaro, Mexico.

react in two ways: either they avoid certain plants (a well known example being that cows do not eat *Ranunculus acris*) or they eat the toxic plants and get a specific disease: mouldy *Melilotus* gives "sweet clover disease" (internal bleeding), *Senecio* species produce severe destruction of the liver and so on. Recent examples have come from New Zealand and Colombia.

The empirical knowledge of toxic and medicinal plants gained by our ancestors was passed on from generation to generation by oral tradition, and was eventually annotated in the form of herbals and therapeutic manuals, as well as in herbarium notes and ethnobotanical studies. The retrieval of information from these sources can be both cumbersome and laborious, but the method has been used in varying degrees by several workers.

Under the auspices of the National Cancer Institute in Bethesda, Maryland, a survey of plants used to combat cancer has recently been carried out by HARTWELL (1967—71). This is very likely the most extensive "literature screening" that has ever been carried out in the search for new plant drugs. The world literature was systematically searched for references to cancer remedies since the beginning of writing. "Starting with *Chemical Abstracts* and *Index Medicus* for the first entries in the literature, one reference led to others so that eventually several thousand references embracing the whole history of medicine, pharmacology, materia medica, medical botany, ethnobotany and folk-lore were studied. At the same time, a lively and extensive correspondence was initiated to uncover unpublished material. As a result, the names of over three thousand different plant species were obtained." (HARTWELL 1967—71).

In a study of this type, a major problem is the validity of plant identification. As pointed out by HARTWELL (1967—71), the names given by the original authors have had to be accepted, unless specimens were available and could be identified.

In the same way it is impossible to know whether the "cancer" of the ancient authors was "cancer" as we now understand it.

The unequivocal identification of plants mentioned in the old herbals can however sometimes be accomplished through a careful study of text and illustrations.

The Mexican Badianus manuscript is an outstanding example. Written by an Aztec physician, MARTÍN DE LA CRUZ, in 1552 and with detailed colour illustrations, it still provides problems and furnishes possibilities for drug plant research. A new, richly commented edition of this book has recently appeared (DEL POZO 1967).

The advantage of securing information from herbarium notes is obvious. The data are first hand and there is usually no problem in identifying the plant. ALTSCHUL (1967) has collected 6,000 notes of medical interest from an examination of the Harvard University herbaria. In all, 2,500,000 herbarium sheets were studied.

SCHULTES (1967) has discussed the role of ethnobotany in the search for psychoactive drugs. First-hand knowledge of plant drugs still exists among the few remaining primitive peoples, but it is disappearing and will soon be lost altogether if efforts to collect this information are not made in the near future (SCHULTES 1967).

A very illustrative recent example connected with our own work is as follows: A Norwegian missionary — a physician (not a botanist!) — working in Zaire (Congo ex-Belge) learned of a plant, the leaves of which were used to facilitate child-birth. He wrote to the professor of pharmacognosy in Oslo, A. NORDAL, who asked him to collect a proper herbarium material of the plant. The taxonomist found the plant to be an *Oldenlandia* species (Rubiaceae). In the investigation from the Central African Republic (SANDBERG 1965 p. 27) the child-birth facilitating effects of this plant had already been established. Finally it should be mentioned that phytochemical and pharmacological investigations in Oslo have demonstrated the presence of a polypeptide with oxytocic effect.

PHYTOCHEMICAL SCREENING

The natural products that have received the greatest attention with regard to possible future medicinal applications are the alkaloids and saponins. Numerous papers have been published describing the screening for these two types of compounds. Some examples of phytochemical screening will be discussed in more detail, but first some general remarks.

The methods used to detect these compounds must be simple and rapid, but they should also be selective and easy to use. A field test for alkaloids has been described by RAFFAUF (1962), and found by us to be very useful. This test is based on a not completely specific reaction, which means that some compounds other than alkaloids will also give a positive result. Such false-positive reactions will probably have to be accepted in field screening, but by applying several different tests their number can be reduced. Herbarium material has also been tested with some success (RAFFAUF & ALTSCHUL 1968). The decomposition of alkaloids with time may however affect the results.

To avoid duplication of data, reference publications are available enumerating the plants known to contain certain compounds (e.g. RAFFAUF 1970, WILLAMAN & LI 1970).

Steroidal and triterpenoid saponins and sapogenins are important economic plant products. The possibility of using steroidal sapogenins for the synthesis of cortisone and related substances has lead to their extensive use in the pharmaceutical industry. Today, the synthesis of the above-mentioned drugs and the even more important anticonceptives depends almost entirely on plant sapogenins such as diosgenin (from *Dioscorea* species), stigmasterol (from soy beans) and hecogenin (from *Agave* species). The most important plant sources at present are the Mexican *Dioscorea* species, *D. composita* and *D. floribunda,* both of which have a high sapogenin content in the root tubers.

However, some of the *Dioscorea* species have probably been collected to the point of extinction (e.g. *D. sylvatica* of southern Africa), or are over-exploited as commercial sources of diosgenin (MARTIN 1969; HARDMAN 1969). Our possibility of handling the population explosion will certainly be greatly reduced if new plant sources of suitable steroidal sapogenins cannot be found.

For this and other reasons, many surveys have been carried out to detect saponins in plant material. Simple tests for saponins include the testing of the hemolytic activity of plant extracts as well as the formation of persisting froth when plant material is shaken up with water. These properties of the saponins are, however, common to both steroidal and triterpenoid saponins. A search for one of the two groups must utilize other methods, such as infra-red spectrophotometry analysis of the crude, isolated sapogenins to bring about a differentiation. HARDMAN & FAZLI (1972) have screened various *Trigonella* species for the presence of steroidal sapogenins in their seeds. The aim of their research is to find a plant rich in diosgenin or related compounds and that lends itself more easily to cultivation than the *Dioscorea* species. *Trigonella foenum-graecum* seeds are known to contain diosgenin and in the current investigation *T. coerulea, T. corniculata* and *T. cretica* were found to contain steroidal sapogenins, including diosgenin. The methods for assaying the seeds were blood haemolysis, colour reaction, infra-red spectrophotometry, and thin layer chromatography. The authors conclude that *Trigonella* "may prove to be a good source of steroidal sapogenins for the steroid industry and screening is continuing" (HARDMAN & FAZLI 1972).

In the Soviet Union, great problems have been encountered in supplying these raw materials for the steroid industry. *Dioscorea* does not occur in this country, and the interest of the Soviet research workers has therefore been focused on the screening of *Solanum* species as well as other plants. Some *Solanum* species contain the steroidal alkaloid solasodine, closely related to diosgenin. In a recent paper, RABINOWICH (1972) has discussed the introduction and cultivation of possible new drug crops of this type in the Soviet Union. *Solanum laciniatum* is already being cultivated for the isolation of solasodine. Other promising plants are *Dioscorea deltoidea* of Indian origin and *Yucca gloriosa,* which are now being tested as presumptive crops in southern Russia. From an economic point of view the cultivation of *D. deltoidea* and *Y. gloriosa* was deemed profitable (RABINOWICH 1972).

The role of alkaloid screening in the development of a folk medicine into a drug of therapeutic importance is exemplified by *Rauwolfia serpentina.* The root of this plant has been used for centuries in Indian medicine as a cure for insanity, epilepsy and high blood-pressure. In the 1930s Indian workers started an investigation of the plant and isolated several alkaloids. However, these alkaloids could not account for all of the interesting effects found in the plant extracts. The search for active principles continued, but not until 1952 was the alkaloid reserpine isolated and shown to possess all the main pharmacological properties of the root.

This discovery initiated an intensive screening for this therapeutically valuable alkaloid in the genus *Rauwolfia,* and subsequently also in other, closely related genera of the Apocynaceae. *Rauwolfia* is a genus of about 100 species, which are widely spread in the tropics, and alkaloid screening revealed the presence of reserpine in several of these. On the basis of this screening, *R. vomitoria* of Africa (Congo ex-Belge) and *R. tetraphylla* of America (the Caribbean) are now used for the commercial extraction of reserpine.

Reserpine was also found in more distantly related species, e.g. *Alstonia constricta,* and the search continues. The pharmacological properties of reserpine were also looked for in other *Rauwolfia* alkaloids and were found in rescinnamine and deserpidine.

In these *Rauwolfia* studies botanists, pharmacognosists, chemists and pharmacologists cooperated to a very high degree as ably shown in the *Rauwolfia* monograph prepared by WOODSON et al. (1957), and in the more popular report by KREIG (1964).

In contrast to the search for reserpine sources, the phytochemical screening for the occurrence of isothiocyanates and their parent glucosides in the families Cruciferae and Capparidaceae (KJAER 1960, KJAER & THOMSEN 1963) has no immediate therapeutic aspects. These compounds have however been discussed as a cause of poisoning in cattle. The restriction of this type of screening to one type of substance (not a single substance) within two families, gave within a reasonable period of time two results: first an excellent chemotaxonomic contribution to critical genera within these families, and secondly a decisive criterium in the choice of forage plants.

Phytochemical surveys of plants can also be made on a regional basis, as e.g. in the Argentine (BANDONI et al. 1972), but they are usually concerned with special families or genera. Some examples will be given in the following text.

By checking the available literature and by interviewing botanists and chemists in the Middle East it was found that most of the plants from the arid zones here were almost unknown phytochemically. Professor VIVI TÄCKHOLM, Cairo, invited one of the authors (F. S.) to start a phytochemical screening of desert plants in Egypt. With the help of the resources of the Desert Institute, Matariah, Cairo, the occurrence of alkaloids and saponins in desert plants was studied. This project was started in 1956 and has resulted in several important discoveries (SANDBERG et al. 1967 a). The family Chenopodiaceae was found to be promising: triterpenoid saponins were found in *Anabasis* species (SANDBERG & SHALABY 1960), and alkaloids of a new type in *Haloxylon* species (SANDBERG et al. 1967 b, CARLING & SANDBERG 1970).

Working within a single family, LÜNING (1967) has screened more than one thousand species of Orchidaceae for their alkaloid content. A systematic treatment of these alkaloid analyses was attempted but the distribution of alkaloids in Orchidaceae is rather complicated, different types of compounds being found in closely related species. The only way of coming to grips with this problem is to investigate the biosynthesis of these alkaloids. This also applies to other groups of plants, e.g. the Cactaceae, where the two main alkaloid groups, the phenethylamines and the tetrahydroisoquinolines, have been shown to have a common biosynthetic origin (AGURELL et al. 1971).

A screening procedure is not necessarily limited to the finding of and the preliminary characterization of given compounds. In a screening process for Cactaceae alkaloids and their biosynthetic intermediates, AGURELL (1969) and DE VRIES et al. (1971) have used the combination of gas chromatography and mass spectrometry for the rapid identification of already-known compounds in alkaloid extracts. This sensitive technique also makes it easy to observe new alkaloids and obtain information regarding their structures. Such a rapid screening process can presumably present valuable chemotaxonomic information that may be useful in the classification of this taxonomically difficult group (AGURELL et al. 1971).

In recent years the African species of the genus *Strychnos* have been the focus of interest of several workers using different approaches. LEEUWENBERG (1969) has published a botanical revision of the African *Strychnos* species, and also reviewed their use in Central African ordeal and arrow poisons (BISSET & LEEUWENBERG 1968). An excellent summary of the ethnobotany of these plants was compiled by BISSET (1970), and was followed by a thorough discussion of the alkaloids, including the screening of 180 herbarium samples (BISSET & PHILLIPSON 1971).

The screening of African species of *Strychnos* for alkaloids in this laboratory began with the information that the root bark of *Strychnos icaja* was used in arrow poisons and the root as an ordeal poison (SANDBERG 1965).

Phytochemical and pharmacological screening was carried out in our department (SANDBERG et al. 1969 a, SANDBERG et al. 1971) on a unique plant material of African *Strychnos* (well determined by Dr. A. J. M. LEEUWENBERG, Wageningen). A semi-quantitative estimation of the convulsant and muscle-relaxant effects was also made.

Continued pharmacologic screening of various fractions during the work-up of *S. icaja* led to the first isolation of strychnine from an African *Strychnos* species, and to the new alkaloid 4-hydroxystrychnine (SANDBERG et al. 1969 b). The first and second question of the pharmacognosist had thus been answered.

FIELD WORK

The accumulated experiences, positive and negative, of pharmacognostic field work in various parts of the world has made certain points clear.

The importance of the correct systematic determination of the plant material cannot be over-emphasized. For this reason appropriate herbarium material must be collected. A voucher specimen for reference should be kept in the department where the investigation is made and should be mentioned in the publication. The plant material is labelled with the collecting number of the voucher specimen, used by the pharmacognosist *or* the accompanying botanist (not both).

The amount required for phytochemical and/or pharmacological screening is 1—3 kg (See Figs. 1—2). When the screening has shown the presence of substances worthy of further investigation, larger quantities are required, about 10—20 kg. Quite a lot of work is involved in collecting this amount of an African *Strychnos* liane: the supporting tree has to be cut down, the lianes carefully "dissected", and the bark (which contains the active substances) removed from the stem.

The drying of plant material in the tropics often creates great problems. Therefore the dry season has to be chosen for collecting to allow the material to be dried in the sun (Fig. 2) or in a sheltered place, where possible. Transport to the home laboratory should be as quick as possible in order to avoid attack by mould and insects. Although expensive, we have found it necessary to send material by air (as un-accompanied luggage).

The investigation of folk-lore medicine is not easy for two main reasons: nowadays it is almost exclusively old people who have any knowledge of the local medicinal plants and their uses and they are often suspicious of foreigners and therefore liable to give faulty information or none at all. Our experience has taught us that nurses or physicians at missionary stations, who have the confidence of the population, are well suited to getting reliable information. However, the information thus elicited must be cross-checked.

In the search for cactus alkaloids, one of us (J. B.) has conducted field work in Mexico. Collecting trips were made in the company of botanists specialized in Cactaceae, and a field test (RAFFAUF 1962) was applied to the species encountered. Checklists of species known to contain alkaloids or to have medicinal uses were brought into the field and special attention was paid to the corresponding genera. In addition many helpful suggestions and a wealth of unpublished information came from the accompanying botanists.

The field test is used as follows (cf. Fig. 3). A small piece of a cactus (or any other interesting plant) is cut off and a drop of the sap pressed out and collected on a filter paper. A drop of the test solution, (a modified Dragendorff's reagent), is then added to the stain made by the sap. A red or orange colour indicates the presence of alkaloids.

Very small quantities of alkaloids, and some very simple alkaloids will not be detected by the reagent, but these limitations are only helpful in selecting the more interesting species. A special problem met with in cactus-testing is the high water-content of the plants. The results were checked by thin-layer chromatography in the laboratory.

CONCLUDING REMARKS

In conclusion, we hope to have demonstrated some starting-points for pharmacognostic research. We don't agree with RUSBY (1918), who believed in "the recognition at sight of poisonous and medicinal properties in unknown plants", but as seen from the above, many other different approaches are available, and many combinations of methods have been used.

However, if real progress is to be made, the enquiring phytochemist will have to rely to a great extent on the botanist. The correct identification of species must be the basis of all chemical studies. From this starting-point the natural products chemist can work on the isolation of and the structure of new compounds. But as pointed out by WITKOP (1971), this is still just a prologue: "The drama does not unfold until these children of nature are taken by man and are returned to participate in the dynamics of life in other systems."

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A New Rubus Species from the Canary Islands

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ABSTRACT

HANSEN, A. 1972. A new Rubus species from the Canary Islands. — Bot. Notiser 125: 379—382.

A new *Rubus* species, *R. palmensis* A. HANSEN, collected on the Island of La Palma, Canary Islands, in 1972 has been described and a survey of the *Rubus* species hitherto known from Macaronesia has been made.

Rubus palmensis A. HANSEN, sp. nov.

Subgenus *Eubatus,* sectio *Moriferi,* subsectio *Senticosi,* series ?*Grandifolii* (sensu FOCKE 1914).

DIAGNOSIS. Turiones robusti, arcuati, scandentes, plus minusve 5-sulcato-angulati, pilis pallidis, et setis glanduliferis validis, rigidis, rufo-subfuscis, ad 5 mm longis dense vestiti, setis aculeaceis, flavis nonnullis intermixtis. Folia quinata, magna (15—30 cm); petioli teretes, pilis et setis glanduliferis paucisque aculeis subcurvis vestiti; stipulae lineares, ad 2 cm longae. Foliola supra ut infra viridia concoloria, inaequaliter argute mucronato-serrata, terminale longe petiolulatum (4—5 cm), cordato-cuspidatum (ad 15 cm longum, 12 cm latum), lateralia minora, ovato-elliptica, saepe obliqua; omnia supra ut infra sparse pilosa, nervo medio ut lateralibus majoribus subtus pilos, setas glanduliferas, aculeos paucos gerentibus. Inflorescentia ampla, ad 40 cm longa, terminalis, pyramidalis, valde ramosa; axis principalis aculeis sparse armatus; ramuli infimi axillares, adscendentes (ad 20 cm longi), reliqui bracteis suffulti pedunculis divaricatis, patentibus, multifloris; pedunculi 2—4 cm longi, aculeis hamosis sparsis et pilis stellatis multis instructi; bracteae lineari-lanceolatae vel lineares, inferiores subpetiolatae, trifidae, ad 5 cm longae, omnes setis glanduliferis brevibus et pilis praesertim supra vestitae. Sepala oblongo-ovata, cava, mucronata, 5—7 mm longa, tomento cano praesertim extra induta, tempore florendi ut circa fructum reflexa; petala ovata vel obovata, alba 10—15×5—7 mm magna; stamina numerosa, ad 5 mm longa, glabra, antheris circiter 0.5 mm longis, cinnamomis; fructus subglobularis, 5—10 mm diam., e carpellis numerosis compositus imbricatis, glabris, circiter 3 mm longis, oblique ovalibus, mucronatis, crasse reticulate rugosis, maturis nigris, vix succosis. Floret VIII—IX.[1]

TYPUS. Canary Islands, Island of La Palma. Cumbre Nueva, on the eastern slope near the tunnel carrying the main road from Santa Cruz to Los Llanos right through the Cumbre, in about 1200 m, collected on September 1st, 1972. Holotypus, coll. no. 68, deposited at the herbarium of the Botanical Museum, Copenhagen (C).

Rubus palmensis is abundant in the *Laurus* forest covering the Cumbre Nueva in the fog zone, probably not at all rare on the island. It is probably endemic to the Island of La Palma.

Rubus palmensis is probably allied to the endemic Madeiran species *R. grandifolius* LOWE, but deviating in so many respects that its separation as a new, well-defined species seems to be justified. There seems to be no close relationship to any of the *Rubus* species hitherto known from the Canary Islands. However, some material of another probably unde-

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[1] Lektor TYGE CHRISTENSEN has kindly helped me with the Latin diagnosis.

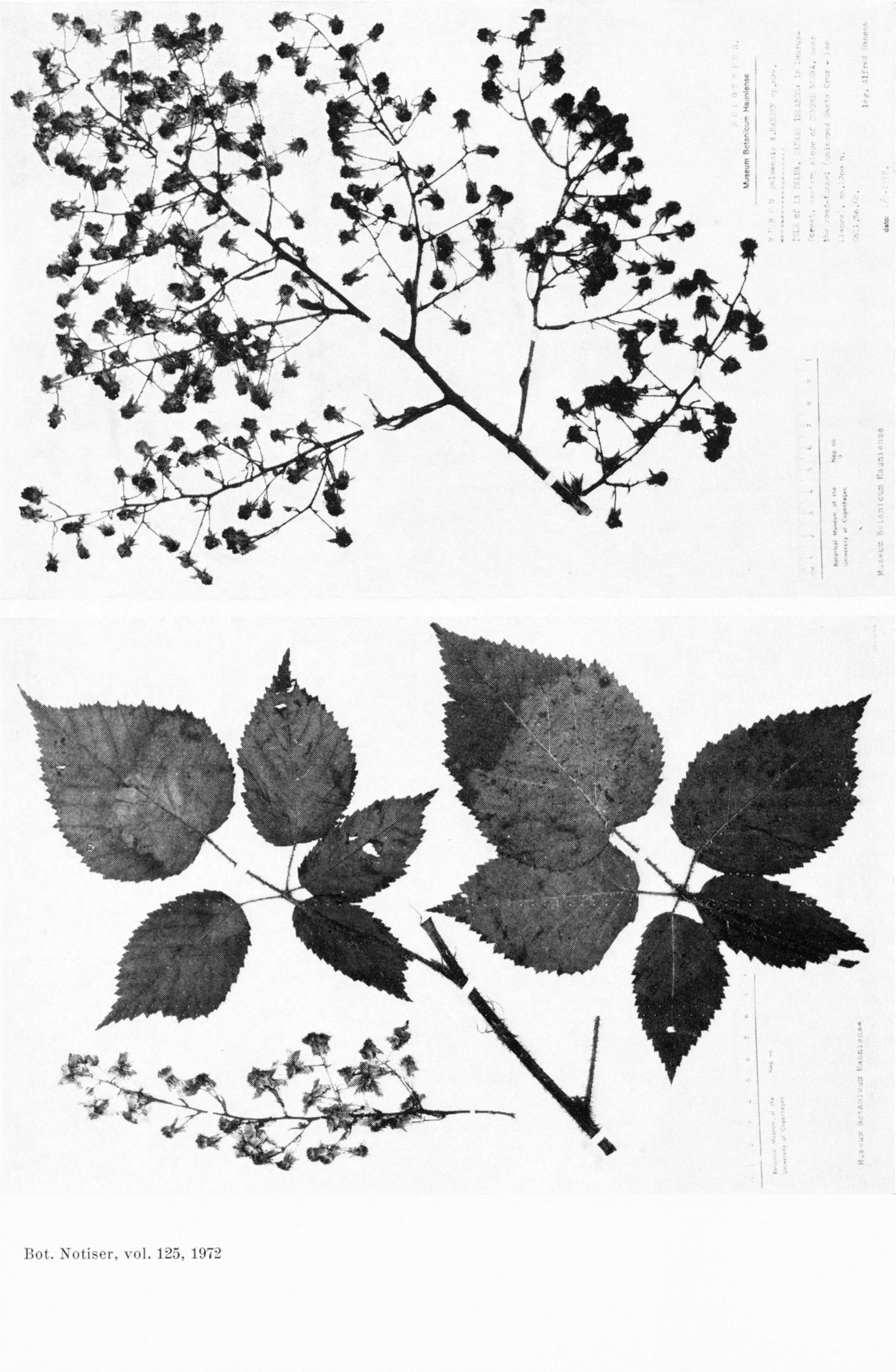

Fig. 1. *Rubus palmensis* A. HANS., sp. nov. (holotype).

scribed *Rubus* species has been collected by the present author on the Island of Tenerife (El Bailadero, Anaga Hills, October 1971, perhaps the same plant as *R. bollei* var. *murrayi* Focke, see below). Unfortunately this material lacks the flowering and fruiting stage, so that its description will have to wait until better and more representative material can be procured. It seems probable that *R. palmensis* is related to this undescribed species.

The *Rubus* flora of the Canary Islands, the Madeira Archipelago and the Azores is still insufficiently and badly known, cf. Gustafsson (1943), and undoubtedly much remains to be cleared up. The following taxa are at present recorded from the 3 groups of islands (on the Cape Verde Islands this genus is so far unknown).

CANARY ISLANDS (the 5 western islands only; C=Gran Canaria, T=Tenerife, G=Gomera, P=La Palma, H=Hierro).

R. bollei Focke, Abh. Nat. Ver. Bremen 9: 405, 1887; ibid. 12: 337, 1892 + var. *murrayi* Focke, Sp. Ruborum III: 118, 1914 (a doubtful variety). — C, T, G, P, H. Also on Madeira.

R. bornmuelleri Focke in Bornmüller, Engl. Bot. Jahrb. 33: 435, 1903; Sp. Ruborum III: 120, 1914. A somewhat doubtful species described only from non-flowering and non-fruiting material. — C.

R. canariensis Focke, Abh. Nat. Ver. Bremen 9: 405, 1887; ibid. 12: 338, 1892 (? *R. bollei* ×*ulmifolius*). — T, P. Focke (1914) also gives this species from Madeira, may be the same plant as *R.*×*suspiciosus* Mnzs., see below.

R. palmensis A. Hansen — P.

R. ulmifolius Schott, Isis 5: 821, 1818 (*R. rusticanus* Merc., *R. discolor* s. Syme, *R. amoenus* (Portenschl.) Focke). — Common on C, T, G, P, H, also on Madeira and the Azores.

MADEIRA-ARCHIPELAGO

R. bollei Focke, see above.

R. cf. *caesius* L., Sp. Pl. ed. 1: 706, 1753 or *R. corylifolius*-aggr. — Collected in 1968 in Ribeiro Frio at non-flowering stage, probably introduced or a garden-escape (Hansen 1969).

R. canariensis Focke, see above, perhaps= *R.*×*suspiciosus* Mnzs.).

R. concolor Lowe, Man. Fl. Mad., 249, 1868. — Madeira only (perhaps a variety of *R. bollei*).

R. grandifolius Lowe, Prim. Fl. Mad., 32, 1831. — Madeira only.

R. pinnatus Willd., Sp. Pl. II: 1081, 1779 (*R. pappei* Eckl. & Zeyh., *R. subulatus* Welw.). — Stated by Menezes (1914) as being a subspontaneous plant on Madeira (escaped from Funchal gardens, but not seen recently). A native of S. Africa and of some Atlantic islands: Saõ Tomé, Ascension, St. Helena). Perhaps identical with *R. rosaefolius* Sm. given by Bornmüller (1903): "Ad muros supra Fayal, subspont." A native of the tropics and subtropics from S. Africa and Madagascar to NE. Australia and S. Japan, elsewhere often cultivated and escaped.

R.×*suspiciosus* Menezes, J. Sc. Math. Phys. Nat. 2. Ser. 7, 28, 1909 (*R. bollei*×*ulmifolius* or *R. ulmifolius*×*vahlii*). — Madeira only.

R. ulmifolius Schott. — Common on Madeira and Porto Santo, also known from Deserta Grande. Some varieties have been described from Madeira by Menezes (1909).

R. vahlii K. Friedr., Bot. Tidsskr. 27: 108, 1905. — Madeira only.

AZORES

R. divaricatus P. J. Mueller, Flora 1858: 130 (*R. nitidus* Weihe & Nees). — Faial (Franco 1971).

R. hochstetterorum Seub., Fl. Azor. 48, 1844. — All islands except Graciosa and S. Maria.

R. ulmifolius Schott. — All islands.

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A Find of Nelumbo nucifera From Old Cyprus

With Some Notes on the History of the Species

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ABSTRACT

HJELMQVIST, H. 1972. A find of Nelumbo nucifera from old Cyprus. With some notes on the history of the species. — Bot. Notiser 125: 383—388.

Carbonized seeds and fruits of the Indian lotus, *Nelumbo nucifera,* were stated to occur in material from Salamis in Cyprus, dating from the 4th century B.C. The history of the species in the Mediterranean area is discussed with reference to the reports of several old authors. The latest records are apparently from the 13th century A.D.; after that the species has disappeared, which certainly to a great extent is due to the activity of man.

In a material of carbonized seeds and fruits from Cyprus, placed at my disposition by the Cypriote archaeologist Dr. V. KARAGEORGHIS, Nicosia, several seeds and fruits of the so-called Indian lotus, *Nelumbo nucifera* GAERTN., were stated to occur. The material derived its origin from an excavation in 1966 at Salamis and belonged to contexts of the 4th century B.C., about 325—300 B.C. It was made up mainly of fruits and seeds which, like those of *Nelumbo,* were edible and used by man, as olives, almonds, grapes, etc. The fruits of *Nelumbo* were, when whole, regularly oval to obovate, 13—13.5 mm long and 9—10.5 mm broad, but usually the fruit wall was absent and the seed divided into halves corresponding to the cotyledons[1], which were abruptly narrowed at the base and finely striated on the outer side. The cotyledons had a cavity on the inner side around the site of the plumule; the plumule itself was only occasionally present, provided with two unequal, doubly-bent leaf primordia. A comparison with recent seeds of *Nelumbo nucifera* showed good agreement in the details, as shown by Fig. 1 E—F.

The find of *Nelumbo nucifera* from old Cyprus is of a special interest, since the species is nowadays totally absent not only from this island but from the whole Mediterranean area. Its present distribution area extends over the warmer parts of Asia and Australia from Japan and the Australian archipelago in the east to the Caspian sea in the west. Owing to the frequent cultivation of the species, the spontaneous distribution area is often somewhat uncertain, but the most advanced occurrences in the west are Ghilan in northern Persia, the Kura estuary in Transcaucasia and the Volga delta. In the latter locality the lotus plant was referred to a separate species, *Nelumbo caspica,* by EICHWALD in 1831, but most of the differences given to characterize this

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[1] The fleshy nutritive tissue of the *Nelumbo* seed is made up of two partly coalescent cotyledons, as shown by WIGAND & DENNERT (1888) and by the thorough embryological investigation of LYON (1901).

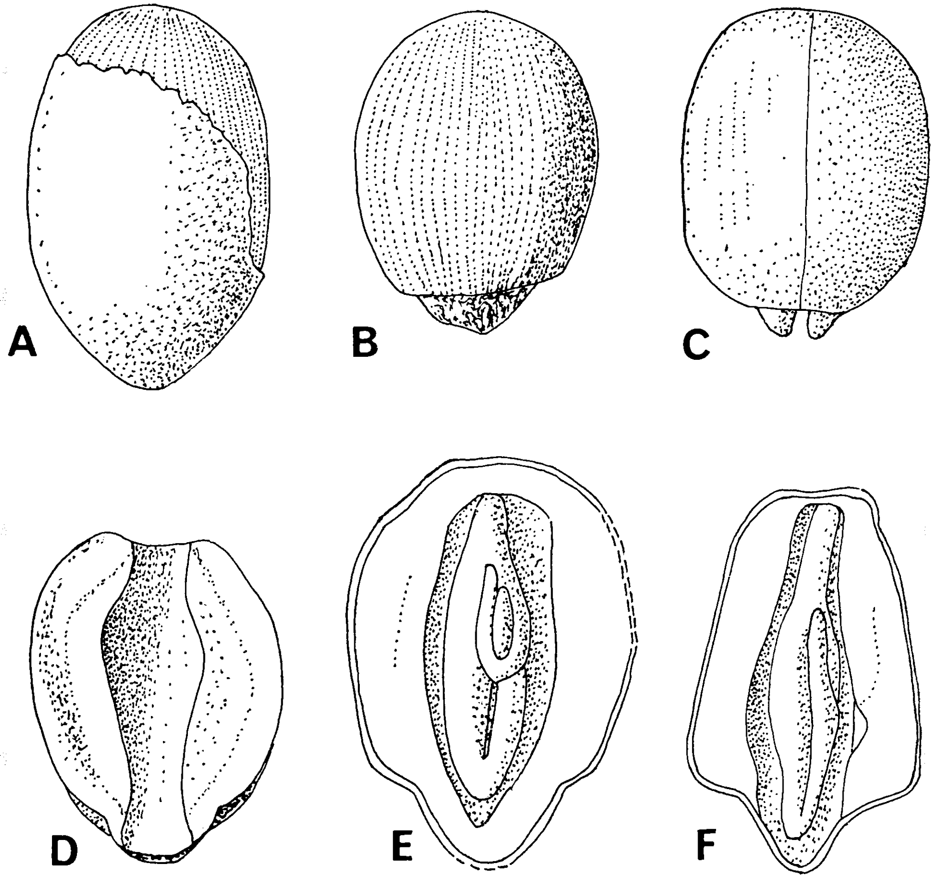

Fig. 1. *Nelumbo nucifera.* — A—E: Carbonized fruit and seeds from Cyprus. — A: Nut with the fruit wall partially removed. — B—C: Seeds from different sides, in C the longitudinal fissure visible. — D: Seed half, more exactly cotyledon, the plumule removed. — E: Seed half with plumule, bearing two leaf primordia. — F: Recent seed in longitudinal section, somewhat contracted owing to desiccation. — ×4.

taxon have not proved constant and it should not be separated from the species. A minor deviation is only that the number of nutlets in the receptacle is only 10—20, whereas in East Asia it is said to be 20—35 (KOMAROV & SCHISCHKIN 1937 p. 4).

Though the Indian lotus is at present absent from the Mediterranean area, the find of *Nelumbo* from ancient Cyprus is in good agreement with the statements of several classical authors that in their time this species occurred in the eastern Mediterranean. These records are in some cases so detailed and exact that there is no cause to doubt their correctness. Especially this is true about the extensive description of THEOPHRAST in his "Historia plantarum" or "Enquiry into plants", which dates from about 320 B.C. and thus is contemporary with the origin of the present find. THEOPHRAST describes the plant (book IV: 8: 7) in a way that shows that he knows it from own experience; i.a. he says that the "head" resembles a wasp's nest and that it in each cell, at most 30 in number, contains a "bean" that slightly projects above the surface, apparently a description of the receptacle with its nutlets. The flower is twice as large as a poppy and deep rose-coloured. The leaves are compared to broad-brimmed Greek hats; when the roots are said to be prickly and avoided by the crocodile, the spinose leaf stalks are apparently meant. He also knows that there is a bitter substance in the centre of the nut; obviously an allusion to the plumule with its bitter alkaloid content. The species is referred to the Egyptian plants, but outside Egypt it is said to grow in Syria, in Cilicia, and in Chalcidice, where it is found in a small lake at Torone. He says further that the roots are used for food by man but does not mention that the seeds are eaten. Mostly it grows spontaneously, but the seeds are sometimes also sown, having been mixed up with chaff, and then it retains its position permanently. In Chalcidice the plant develops quite ripe fruits, but in Syria and Cilicia it cannot ripen.

THEOPHRAST also reports that he has heard about a water-lily in the Euphrates, with flowers that sink beneath the water at night but in the morning are visible at the surface, and that the plant then opens its flowers, which go on rising so that they at last project far above the water level. THEOPHRAST apparently considers this plant to be the Egyptian lotus, *Nymphaea lotus,* but since this species is night-flowering and the plant of the Euphrates is said to open its flowers in the morning, it seems more probable that *Nelumbo nucifera* is meant. That the flowers of the water-lilies, when closed, had sunk beneath the water, was according to CONARD (1905) a common conception in old times; perhaps the submerged flower buds had been taken for flowers.

Still older than the description of THEOPHRAST is a note of HERODOTE (5th century B.C.) about *Nelumbo.* He says (book II: 92) that the Egyptians in addition to the Lotos (=*Nymphaea lotus*) also have other, water-growing lilies, the fruits of which resemble honey-cakes; in these there are numerous edible seeds of the size of olive kernels.

A later author who mentions the plant is STRABON, who lived 66 B.C.—24 A.D. He calls it *Nelumbo,* Egyptian bean, and says (Ch. 17: 1) that it is about ten feet high, has many flowers and leaves and has seeds that resemble the horse beans but differ from them in size and taste. It is possible to row with a boat in the *Nelumbo* forest and obtain shade from the gigantic leaves. From about the same time, at the beginning of our era, are the statements of DIODORUS SICULUS (book I: 34) that the plant "Ciborium", which bears the Egyptian beans, is found in great abundance in the Nile and the stagnant pools in its neighbourhood. The well-known naturalist DIOSCORIDES, in his book De materia medica (about 60 A.D.) also mentions *Nelumbo,* with the same name, Egyptian bean, as the preceding authors, but says (book II: 128) that it is also by some people called Pontic; the fruit is named Kiborion or Kibotion, the root Colocasia. It grows mainly in Egypt but is also found in Asia and Cilicia in stagnant waters. The seeds are said to have several medical qualities. Both seeds and roots are eaten. According to an author quoted by ATHENAEUS (book XV) at the time of Hadrianus (the 2nd century A.D.) *Nelumbo* grew together with the blue-flowered lotus (*Nymphaea caerulea*) in the brooks around Alexandria. In the works of ATHENAEUS (book III: 73 b—c) a further European locality is also mentioned for the plant. He quotes an earlier author, PHYLARCHUS (3rd century B.C.), who says that at the time of Alexander, the son of Pyrrhus, the species appeared in Thesprotia in Epeirus, where it "sprang up in a swamp near the Thyamis river", flowered, bore fruit and spread, but after a few years disappeared again, since the swamp dried up. In this connection PHYLARCHUS also mentions another locality, Aidepsus on Euboea, which had certain similarities to that of Thyamis. This has caused the statement that *Nelumbo* also grew in this place (FRIES 1845), but this is not said, and certainly not meant, by PHYLARCHUS; he compares the localities from other viewpoints. It is however possible that the species has also occurred in the Jordan River. In a passage (Ch. 40) in the Book of JOB (about 400 B.C.) it is said that the hippopotamus is shaded by lotus plants and that he is safe though a Jordan River rises against him. If the plant name really means a lotus, this must be *Nelumbo,* and the passage may indicate that the author knows the species from the Jordan River. Both the interpretation of the name and the localization are however somewhat uncertain.

The time of the disappearance of *Nelumbo nucifera* from the Mediterranean area is not known with certainty. The latest records of the species are apparently those given by two Arabian scholars. One of them, ABD-ALLATIF, who lived in the 13th century, says about the plant, which by him, in accordance with DIOSCORIDES, is called colocasia, the following (in translation by DE SACY 1810 pp. 23—24): "J'ai vu la colocasie à Damas; mais elle n'y est pas commune. — La feuille de la colocasie est ronde et grande, de la forme du pied d'un chameau, mais plus grande; son diamètre varie entre un et deux empans de longueur . . . elle n'a pas non plus de fruit". It has been assumed that this record meant the plant, in later times called colocasia, *Colocasia antiquorum,* but since the leaf is said to be round and large and its diameter is given, it seems to agree better with the orbicular lamina of *Nelumbo nucifera* than with the cordate one of *Colocasia antiquorum*; perhaps the former may also be said to remind of a camel's foot in shape. Thus the colocasia seen by ABD-ALLATIF at Damascus was probably *Nelumbo nucifera.* Another Arabian traveller from the same century, EBN-BEITHAR, mentions *Nelumbo* from Egypt in a way that indicates that he himself has seen the species there (DE SACY loc. cit. p. 97).

These two records seem to be the latest reliable statements about *Nelumbo* in the Mediterranean area. It must however be mentioned that there is also a report of much later date that has been assumed to mean the species (WOENIG 1897), though certainly incorrect. It is a note of the French author SAVARY, who in his "Lettres sur l'Égypte" (1785) mentions the lotus as a water-lily especially characteristic of Egypt and says that it consists of two species, one with white flowers and rounded, edible roots, the other with bluish flowers. He further says: "Les ruisseaux des environs de Damiette sont couverts de cette fleur majestueuse qui s'élève d'environ deux pieds au-dessus des eaux" and then he polemizes against the statements of PAW (1773), who says that it has disappeared from Egypt and further according to SAVARY gives a false description of the species. This polemic, as well as the note about a majestic flower that elevates itself 2 feet above the water level, has apparently given rise to the supposition that *Nelumbo* was meant, but this is certainly not the case. The two species described by SAVARY are undoubtedly *Nymphaea lotus* and *N. caerulea,* as shown by their characteristics, and the description of *Nelumbo* by PAW (1773 pp. 156—157), which mainly concerns the fruit, is quite correct; the statement of SAVARY that it is erroneous shows that he speaks about other species.

In the same way as in the Mediterranean area, *Nelumbo nucifera* has also in other regions shown a more or less marked retrogression. In the Aral Sea, where it was found by KARELIN in 1841, it has not been found again in later time; obviously it is extinct here (KOMAROV & SCHISCHKIN 1937). In the Volga delta it has decreased considerably in frequency, and according to STAUB (1891) in the last part of the 19th century it apparently was already in extinction. In India it has also receded in more recent times, in spite of the fact that it is regarded here as a holy plant; SUBRAMANYAM (1962), who states this fact, says that the collection of the edible fruits is one of the causes of the gradual disappearance.

The disappearance of *Nelumbo nucifera* from the Mediterranean area is also probably due largely to the activity of man. As for Egypt, WOENIG (1897) lays stress upon the cultivation of the Nile valley, the reduction of lakes and fens, and the accumulation of mud in the waters. The collection of fruits and rhizomes for food has of course also been of importance, and the common use of the flowers for different purposes in older times may have played a role. The statements that the species could not ripen its fruits in Syria and Cilicia may indicate that the climate has been of importance for the retrogression, at least in the northern parts, a possibility that was already discussed by DELILE (1813).

It is a common conception that the occurrence of *Nelumbo* in ancient Mediterranean was due to introduction by man and naturalization. Some older authors, as FRIES (1845), supposed that the species had been introduced at the beginning of the Egyptian culture, others, like SCHWEINFURTH (1884) and WOENIG (1897) meant that it was not much older than the first literary records, made in the 5th century B.C. by HERODOTE, or at least that an older existence was doubtful. This assumption is supported by the observation that in their opinion there are no reproductions of *Nelumbo* in the old Egyptian art, though the lotus motif is common. WOENIG, however, admits that it is difficult to identify the different species in the conventionalized ornaments. Thus the age and the nature of the occurrences are still somewhat uncertain.

Whether the *Nelumbo* fruits of the Cypriote find derive their origin from plants growing on Cyprus or have been introduced from elsewhere, in such a case probably from Egypt, is of course now impossible to decide. However, it is known that the "Egyptian beans" were imported from Egypt to Greece as a delicacy in classical time (BÖCKH 1886 p. 322), and this may also have been the case on Cyprus. In favour of the supposition of an introduction speaks the fact that there are very poor possibilities for the growth of water plants on Cyprus; according to HOLMBOE (1914) only a few small water phanerogams were found by him on the island. HOLMBOE, however, also draws attention to the fact that Cyprus during classical times, contrary to now, was rich in forests; certainly the climate was then more humid, and it seems possible that a water plant like *Nelumbo* may have grown there at that time. As a matter of fact, the lotus motif is not rarely found in old Cypriote art, which makes it probable that some waterlily grew on the island. Be that as it may, the occurrence of the *Nelumbo* fruits in an old context is a testimony among many others that this species in ancient times played an important role in the eastern Mediterranean.

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Das nordamerikanische Xanthium pungens Wallroth als Adventivpflanze anderer Kontinente

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ABSTRACT

WIDDER, F. J. 1972. Das nordamerikanische Xanthium pungens Wallroth als Adventivpflanze anderer Kontinente. — Bot. Notiser 125: 389—392.

The distinctly separated ser. *Glabrata* (sect. *Campylorrhyncha,* subgen. *Xanthium*) comprises four species. Of these, *X. pungens* WALLR., having its origin in SE. North America, is known as an adventitious plant from all continents. A list of the material seen by the author is given along with a map of the finds. In the map the native area of the species is also shown.

EINLEITUNG

Durch das Entgegenkommen von Frau Professor Dr. VIVI TÄCKHOLM wurde mir ein reiches Herbarmaterial der Gattung *Xanthium* aus Ägypten zugänglich. Darunter befand sich auch *X. pungens* WALLR., jene aus Nordamerika stammende Art, die oft als *X. pen(n)sylvanicum* WALLR. bezeichnet wird und unter diesem Namen als Paradebeispiel für Versuche über Photoperiodismus sehr bekannt geworden ist. Als ich seinerzeit von 1912 bis 1914 große europäische und nordamerikanische Herbarien, u.a. B, FI, G, GOET, L, LE, PRA, US, W, WU durchsehen konnte, fand ich darin zwar den nomenklatorischen Typus des *X. pungens* WALLR., sonst aber keinen einzigen außeramerikanischen Beleg dieser Art. Der nach dem ersten Weltkrieg verstärkt einsetzende Weltverkehr hat den mit ausgezeichneten Verbreitungsmitteln ausgerüsteten Klettdiasporen von *Xanthium*-Arten die Möglichkeit gegeben, die Grenzen ursprünglicher Areale gewissermaßen zu verwischen. Denn es wurde in manchen Fällen schwierig, über ein vermeintlich adventives Vorkommen einer anthropochoren oder zoochoren Sippe ein sicheres Urteil abzugeben. Eine neue Karte der Gesamtverbreitung von *X. pungens* WALLR. ist bisher noch nicht vorhanden.

XANTHIUM PUNGENS WALLR. IM SYSTEM DER GATTUNG

Die Gattung *Xanthium* umfaßt im subgen. *Xanthium* außer der sect. *Xanthium,* die neben anderen Arten den nomenklatorischen Typus der Gattung, *X. strumarium* L. enthält, noch die sect. *Campylorrhyncha* (WALLR. ex WIDD.) WIDD., deren Sippen meist braune Fruchtköpfchen mit deutlichen, oft gebogenen und an der Spitze in der Regel hakigen Schnäbeln besitzen. Innerhalb dieser Gruppe fallen die Sippen der ser. *Glabrata* WIDD. bei aller Verschiedenheit in Größe und Gestalt der Fruchtköpfchen durch deren Indument auf. Von völlig kahlen bis zu nur kurzdrüsigen und außerdem sehr kurzhaarigen Fruchtköpfchen, Hülldornen und Schnäbeln gibt es alle Zwischenstufen. Die kurzen, spitzen, einzellreihigen Haare sind stets kürzer als der mittlere Durchmesser der Hülldornen. Im Gegensatz dazu kommen den Sippen der ser. *Hispida* Widd. lange, spitze oder stumpfe, wenigstens zum Teil mehrzellreihige Haare zu, die den mittleren Durchmesser der Hülldornen nicht nur erreichen, sondern oft mehrfach überragen. Näheres über *X. pungens* Wallr. und dessen Nomenklatur ist aus Wallroth (1844 pp. 227, 231—232), Widder (1923 pp. 64—70, 164—167, 1967 pp. 186—187) zu entnehmen. Man beachte auch die zum Teil einander widersprechenden Ansichten von Millspaugh & Sherff (1919 pp. 17, 22, 23, 45) und besonders Löve & Dansereau (1959 pp. 176, 178, 180, 181) sowie Wagenitz (1968 pp. 265—266), wo das neuere Schrifttum zusammengestellt ist. Bei weiterem Artbegriff wird *X. pungens* Wallr. zuweilen mit der geographisch benachbarten und morphologisch nächst stehenden Antillen-Art *X. occidentale* Bertol. vereinigt. Zuweilen auftretende Mittelformen habe ich hier nicht besonders bezeichnet, sondern zu *X. pungens* Wallr. gezogen. Da Löve & Dansereau (1959 pp. 204—205) innerhalb der Gattung *X.* überhaupt nur 2 Arten anerkennen wollen, brauche ich auf die merkwürdige Kombination *Xanthium strumarium* L. ssp. *Cavanillesii* (Schouw) D. Löve & P. Dansereau var. *glabratum* (DC.) Cronq. ebensowenig einzugehen wie auf die „Notomorph *pensylvanicum* (Wallr.)“.

ADVENTIVE VORKOMMEN

In die folgende Liste sind nur jene Fundpunkte aufgenommen worden, von denen ich Belege selbst gesehen habe. Die Grundlagen boten die Herbarien, deren Kürzel zwischen Klammern gesetzt sind. Für öffentliche Sammlungen richten sie sich nach Lanjouw & Stafleu (1964). Für private Sammlungen kamen dazu: Ael = Aellen, Lou = Lousley, Sch = Schinz, Wid = Widder. Hinweise auf bloße Schrifttumsangaben wurden weggelassen, um die damit oft verbundene Unsicherheit zu vermeiden. Leider betrifft dies auch einen großen Teil Asiens, weil ich für die von Smoljaninova (1959) stammenden Angaben bisher noch keine Belege sehen konnte.

EUROPA

Portugal. Bei Santarem im Überschwemmungsbereich des Tejo, 1967, W. Forstner (Wid).

England. Grown from plant collected in Oct. 1958 from Southampton Docks, S. Hants., Vrc. 11, J. E. Lousley (Lou).

Schweden. Halland, Lindome, Dverred, mit Baumwolle eingeschleppt, 1937, C. Blom (Wid).

Deutschland. Ex ruderibus urbis petraeae ex seminibus fortuito disseminatis . . . per caudam Mel. Lotoris advestis elicitum, nec iterum h.l. visum, 1840?, Wallroth (PR).

Frankreich. Unter-Elsaß, Schuttstelle bei Souffenheim, 1953, P. Aellen (Ael, Wid).

Österreich. Steiermark, Leoben, an wüster Stelle in der Nähe des Kreuzfeldweges ein stattliches Exemplar, 1963, Melzer (GZU).

AFRIKA

Ägypten. Gebl Asfar, NE of Cairo in the fields as weed, 1926, G. Täckholm (CAI, Wid) — Gebl Asfar north of Cairo, 1955, M. Imam (CAI, Wid) — Giza, Faculty of Agriculture farm, 1971, Chrtek & Kosinova (CAI, Wid) — Giza, as weed in the School of Agriculture, 1926, M. Hassib (CAI, Wid) — Qalioub, Nile Delta, 1967, Täckholm, Imam, Nabil (CAI, Wid) — Faiyum, 1959, Batanouny (CAI, Wid) — Kafr Mahfuz, Beni Osman, Faiyum, 1968, Nabil (CAI, Wid) — Faiyum, 1967, Täckholm, Imam, Nabil (CAI, Wid) — Faiyum, Sennouris, 1967, Täckholm, Nabil, Ilal (CAI, Wid) — Markaz Sinnuris, Faiyum, 1968, Nabil (CAI, Wid) — Faiyum, 38 km from Medinet El Faiyum along the Lahun railway, 1967, Täckholm, Nabil, Imam, Konzalova (CAI, Wid) — El Sirw, Daqahlia, 1968, Täckholm, Nabil, Mahdi, Ibrahim (CAI, Wid) — Kharga Oasis, 1966, Nabil (CAI, Wid) — Assiut University ground, 1967, Nabil (CAI, Wid) — El Serroe, Gharbiya Province, 1968, M. Imam (CAI, Wid) — Assuan, 1969, L. Boulos (CAI, Wid) — Aniba, Nile valley, 1963, Täckholm, Boulos, Zahran (CAI, Wid) — Mit Abu Sheikha 6 km from Quesna Menoufia, 1967, Täckholm, Imam, Nabil (CAI, Wid).

Ostafrika. Ethiopia, Shoa province, Koka on banks of Awash R., 8°25′N, 39°03′E, alt. 1540 m, Rainf. c. 600 mm, Alluvium sub-

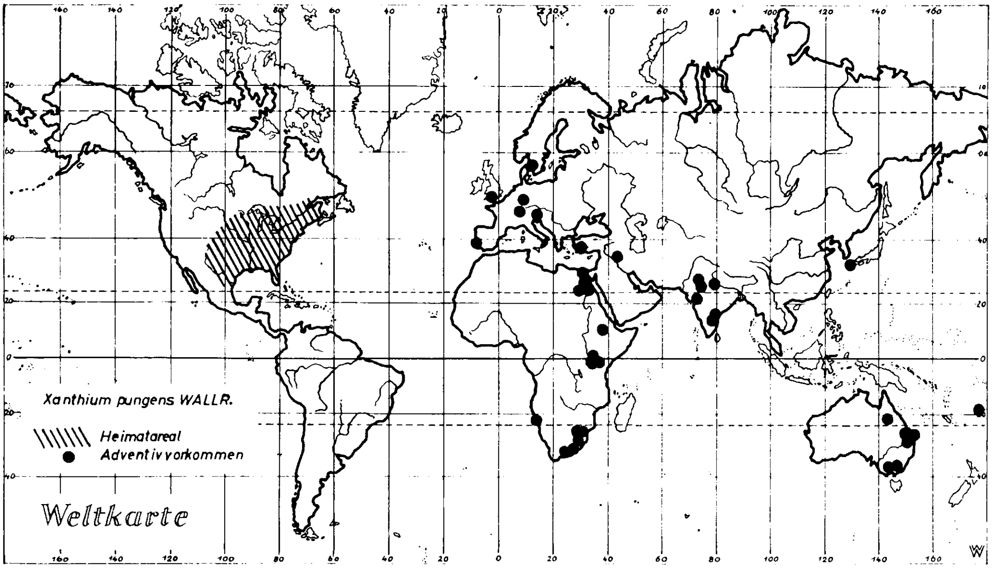

Fig. 1. Heimatareal und Adventivvorkommen von *Xanthium pungens* WALLR.

ject to flooding during rains, 1959, H. F. MOONEY 8178 (EA) — Near Kakamega, c. 0°16′N, 34°55′E, 1962, R. SCHOLES (EA) — Kenya, Nairobi, Ruderalstellen am University Way, sehr häufig und bodendeckend, 1967, F. J. WIDDER (K, Wid) — Kenya, Miwani Sugar Estate, 0°03′S, 34°58′E, weed in sugar cultivation, 1964, K. KAVANAGH 8 (EA).

Südwestafrika. Swakopmündung, 1964, W. GIESS 7799 (M).

Südafrika. Farm Schoonzicht, Pretoria, Transvaal, 1909, W. DEACON (K, PRE) — Brocklyn near Pretoria, 1918, Mss. CROSS (PRE) — The Thorns near Pretoria, 1917, Miss S. M. STENT (PRE) — Wonderboom, Pretoria, K. A. LANSDELL (PRE) — Mountain View, Aapjes River near Pretoria, 1911, WEEBER (K, PRE) — Potchefstroom, Transvaal, 1917, L. KRETSCHMAR (PRE, K, Wid) — Piet Retief, Transvaal, 1913, J. BEZUIDENHOUT (PRE) — Harrismith, MAGISTRATE (PRE) — Barberton, Transvaal, 1910, H. T. WALKINS (K, PRE) — Townlands round Barberton, Transvaal, 1912, C. E. LEGAT (K, PRE) — Natal, Umbilo ad catarrhactam, A. REHMANN, Exsicc. Africae austral. ex ann. 1875—1880 Nr. 8135 (Sch) — Queenstown, C. P., 1912, W. J. WIGGIL (PRE) — Queenstown, Cape of Good Hope, 1912, J. BURTT-DAVY (K) — Albany, (UZ).

ASIEN

Türkei. Bei den Sinterterrassen von Pamukkale, 1971, W. FORSTNER (Wid).

Irak. Weed in cotton-field, Zafraniya, in Baghdad Liwa, 1956, K. H. RECHINGER & F. NAIB, Exsicc. ex Herb. Univ. Baghdad No. 96 (GZU).

Indien. Oressa, along the river Raul, near Village Harlanga . . . 1964, J. L. KAPOOR et al. 71332 (LWG) — Surat, very common, 1955, G. S. SRIVASTAVA (LWG) — Trocken liegendes Bachbett bei Ellora, mittleres Vorderindien, 560 m, 1952, A. GILLI (W) — Bethamangala, Distr. Kolar, Mysore State, 8 miles from Kolar goldfield, a very rare seed, 1957, G. SARAN & party 40564 (LWG) — Adegmel, wild, 1954, PADENA (LWG) — Patiala, Rajpura, along the road, common near water, 1955, —, (LWG) — Delji Ridge, 1953, J. K. MAHESHWARI (LWG) — U. P. Lucknow, Sultanpur Road, near Ganjeria farm, 1959, J. G. SRIVASTAVA & al. (LWG) — Meerut, 1958, S. K. NERWAL (LWG).

Japan. Hakozaki, Fukuoka, 1935, HITOSHI KOJIMA (Wid).

AUSTRALIEN

N. S. Wales, 1966, F. EHRENDORFER (Wid) — Queensland, —, — (MEL, Wid) — Arcadia-Victoria, 1917, E. E. PESCOTT (MEL, Wid) — Stradbroke Island, off South East Coast of Queensland, 1915, C. T. WHITE

(BRI) — Kelvin Growe nr. Brisbane, 1927, W. G. WINCHESTER (BRI, Wid) — „Noogoora Burr" Gatton — a farm weed, 1926, C. T. WHITE 3305 (BRI, Wid).

FIDSCHI INSELN

Mauka of Belo, near Sigatoka, Viti Levu, naturalized in field, 1968, O. & I. DEGENER, Plants of Fiji 31909 (Wid) — Korotogo, Viti Levu, naturalized in pasture, 1969, K. & L. WASSON in: DEGENER's Plants of Fiji 31986 (Wid).

PUNKTKARTE DER ADVENTIV-VORKOMMEN

Die in der Fundortsliste aufgezählten Belege adventiver Vorkommen wurden in die Punktkarte (Fig. 1) zugleich mit dem schraffierten Heimatareal von *Xanthium pungens* WALLR. übernommen. In der Untergattung *Xanthium* ist *X. pungens* WALLR. auf dem Wege, ein Gegenstück zu dem berüchtigten *X. spinosum* L. der Untergattung *Acanthoxanthium* zu werden. *X. spinosum* L. hat sich von der südamerikanischen Heimat aus ein weltweites Adventivareal in solchem Umfang und mit sekundären Ausbreitungszentren erobert, daß die Heimat sogar angezweifelt wurde. Erst durch die eingehenden Untersuchungen von WEIN (1925) sind alle Einwände beseitigt worden. Vielleicht wird in Zukunft auch das Vordringen von *X. pungens* WALLR. aufmerksam zu kontrollieren sein.

Den Direktoren, beziehungsweise Vorständen oder Besitzern der im Text durch Kürzel genannten Herbarien, besonders Frau Professor Dr. VIVI TÄCKHOLM erlaube ich mir auch an dieser Stelle meinen aufrichtigen Dank zu sagen.

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Chromosome Numbers in Some Compositae from Egypt

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ABSTRACT

NORDENSTAM, B. 1972. Chromosome numbers in some Compositae from Egypt. — Bot. Notiser 125: 393—396.

Somatic chromosome numbers of 24 members of Compositae from Egypt are reported. Several of the species have not been cytologically investigated before, and some counts are at variance with earlier reports. The single known Egyptian population of *Taraxacum* is tetraploid (2n=32) and may represent an undescribed species allied to *T. minimum* GUSS.

INTRODUCTION, MATERIAL AND METHODS

The material used for this study originates from a botanical excursion in Egypt in March 1969, with participants from the Universities of Lund and Stockholm and under the guidance of Professor VIVI TÄCKHOLM. Her expert knowledge, and her enthusiasm and generosity made the excursion an unforgettable event, and this humble contribution to the knowledge of Egyptian plants is dedicated to her in deep gratitude.

In addition to herbarium material, a number of seed samples of vascular plants from various families were collected. Plants from the seeds were grown principally in the Botanical Gardens, Lund, and also in the Hortus Bergianus, Stockholm and used for chromosome counts. This report deals with the family Compositae only. Somatic chromosome numbers of 38 collections representing 24 different species have been determined.

The chromosomes were examined in root tip metaphases. After fixation in Navashin-Karpechenko's fixative (mainly the so-called Svalöf modification) the roots were embedded in paraffin and microtome-cut. The preparations were stained in crystal violet (in most cases with an addition of aniline) and permanently mounted. Voucher specimens of cultivated material are preserved at the Swedish Museum of Natural History, Stockholm (S). The original herbarium material from the field is preserved at the Botanical Museum, Lund (LD).

I am indebted to Prof. T. NORLINDH for determination of the *Calendula* material.

The results are given in Table 1.

Table 1. Chromosome numbers in some Compositae from Egypt.

Taxon	Locality	Coll. no.	2n
Aëtheorrhiza bulbosa (L.) CASS.	2 km E of Abu Sir	E. 937	18
Amberboa lippii (L.) DC. ssp. *tubuliflora* (MURB.) MURB.	El Quasr, c. 10 km NW of Mersa Matruh	E. 652	64
Artemisia monosperma DEL.	Cairo-Alexandria desert road, 141 km from A.	E. 957	34
„ —	Wadi Natroun	E. 958	34
Calendula aegyptiaca DESF.	21 km W of Alexandria (Mariut Road)	E. 202	c. 44
„ —	Abu Sir, sandy fields	E. 271	44

Taxon	Locality	Coll. no.	2n
Calendula aegyptiaca Desf.	Om el Racham village, NW of Mersa Matruh	E. 719	c. 44
„ —	Wadi Sheik Fayez, NW of Mersa Matruh	E. 853	c. 44
Calendula micrantha Tin. & Guss.	Fayoum, Lake Qaroun, in a garden	E. 28	44
„ —	15 km W of Mersa Matruh, junction of road to Siwa Oasis	E. 477 b	c. 44
Chrysanthemum coronarium L.	Abu Sir, sandy fields	E. 262	18
Conyza linifolia (Willd.) Täckh.	Alexandria, Pompejus' Pillar	E. 939	54
Crepis senecioides Del.	Mathsani village, c. 52 km W of Mersa Matruh	E. 493	8
Filago desertorum Pomel	65 km W of Alexandria (road to Mersa Matruh)	E. 290	c. 28
„ —	80 km E of Mersa Matruh (road to Alexandria)	E. 373	c. 28
„ —	El Alamein, the German cemetery	E. 896	c. 28
Hyoseris lucida L.	Abu Sir, sandy fields	E. 232	16
Ifloga spicata (Forsk.) Sch. Bip.	80 km E of Mersa Matruh (road to Alexandria)	E. 372	14
Launaea nudicaulis (L.) Hook. fil.	142 km E of Mersa Matruh (road to Alexandria)	E. 357	18
Launaea resedifolia (L.) OK.	El Quasr, c. 10 km NW of Mersa Matruh	E. 641	16
„ —	Ras el Hekma, 224 km W of Alexandria	E. 880	16
Leontodon hispidulus (Del.) Boiss.	Nigela village, 70 km W of Mersa Matruh	E. 541	12
„ —	84 km W of Mersa Matruh	E. 557	12
Matricaria chamomilla L.	Fayoum, Lake Qaroun, in a garden	E. 31	18
Notobasis syriaca (L.) Cass.	El Quasr, c. 10 km NW of Mersa Matruh	E. 648	34
Phagnalon rupestre (L.) DC.	120 km W of Alexandria (road to Mersa Matruh)	E. 311	18
Senecio desfontainei Druce	21 km W of Alexandria (Mariut Road)	E. 218	20
Sonchus asper (L.) Hill	Fayoum, El Shawashma at Lake Qaroun	E. 43	18
Sonchus oleraceus L.	El Quasr, c. 10 km NW of Mersa Matruh	E. 674	32
Sonchus tenerrimus L.	15 km W of Mersa Matruh, junction of road to Siwa Oasis	E. 433	14
„ —	Agiba Bay NW of Mersa Matruh, rocks near sea	E. 781	14
Taraxacum cfr *minimum* Guss.	Abu Sir, rocks at the fortress	E. 913	32
Thrincia tuberosa (L.) DC.	21 km W of Alexandria (Mariut Road)	E. 191	8
„ —	62 km W of Mersa Matruh	E. 529	8
„ —	Wadi Sheik Fayez, NW of Mersa Matruh	E. 807	8
„ —	62 km W of Mersa Matruh	E. 961, E. 962	8
Urospermum picroides (L.) Schmidt	15 km W of Mersa Matruh, junction of road to Siwa Oasis	E. 409	10

DISCUSSION

Only some of the more noteworthy counts will be commented upon here.

The ssp. *tubuliflora* of *Amberboa lippii* (also placed in *Centaurea* or *Volutaria*) is sometimes recognized as a species. It does not seem to have previously been studied cytologically. For *Volutaria lippii*, however, REESE (1957) reported 2n=32, and more recently *Centaurea lippii* was by CHOUKSANOVA et al. (1968) stated to have 2n=40 (erroneously quoted as 2n=36 in FEDOROV 1969). The latter record seems somewhat doubtful, and the evidence at hand suggests that ssp. *tubuliflora* has twice the chromosome number of ssp. *lippii*. Whether the basic number is x=8 as suggested by DARLINGTON & WYLIE (1955) or x=16 is an open question. Hitherto no related taxon with 2n=16 has been reported however.

2n=34 in *Artemisia monosperma* seems to be the first record for this species. The probably secondary basic number x=17 has also been found in some East Asiatic species.

Calendula taxonomy is very confused, and the varying chromosome numbers published for some taxa can undoubtedly be put down to taxonomic difficulties. Thus *C. aegyptiaca* has been reported to have 2n=14, 28, and 30, but here 44. According to MEUSEL & OHLE (1966), however, the first count refers to a taxon of the *C. algeriensis* complex. Further, the number 28 should be changed to 30. Finally, MEUSEL & OHLE's *C. aegyptiaca* PERS. is clearly a different taxon from *C. aegyptiaca* DESF. in the present paper. The former has small, concolorous capitula, narrow leaves and three-winged outer achenes. This taxon agrees with *C. platycarpa* COSS. and *C. aegyptiaca* ssp. *tripterocarpa* RUPR. My own material clearly belongs to two taxa. Plants referred to *C. aegyptiaca* DESF. have very short rays barely exceeding the involucre, a purplish disc and distinctly beaked marginal achenes. Specimens determined as *C. micrantha* TIN. & GUSS. have slightly longer ligules, a yellow disc and indistinctly or shortly beaked marginal achenes. Obviously there remain many taxonomic and nomenclatural problems in *Calendula*, including the correct interpretation of the name *C. aegyptiaca*.

Conyza linifolia (2n=54) is also known as *Erigeron linifolius* WILLD. Under the latter name two counts have been published, viz. 2n=52 and c. 54 (FEDOROV 1969). There is little doubt that 54 is the correct number. Multiples of 9 are known from various other members of the genus *Conyza*.

Filago desertorum POMEL has only recently been recognized as a widely spread Saharo-Sindic species also occurring in Egypt (WAGENITZ 1968). Unfortunately only approximate counts could be made. They indicate the number 2n=28, in agreement with all published counts in the genus.

The number 2n=14 in *Ifloga spicata* agrees with the only other count published for this genus, viz. n=7 in *I. fontanesii* CASS. (MEHRA et al. 1965).

Taraxacum is a fairly recent discovery in Egypt and one which to my knowledge has not been published. The single known population (from Abu Sir) has been identified as *T. minimum* GUSS. The chromosome number of the latter species has been reported by RICHARDS (1969) to be 2n=16. The Egyptian specimens deviate in chromosome number, and also morphologically in certain respects, from the plants referred to *T. minimum* by RICHARDS and probably belong to a different, perhaps undescribed species. A thorough investigation is necessary, however, before a new *Taraxacum* can be published from this region.

In *Thrincia tuberosa*, which is sometimes included in *Leontodon*, 2n=8 was found in four different populations. The same number was recently reported in *L. tuberosus* L. from Greece (DAMBOLDT 1971). In *Leontodon* sensu lato various basic numbers are known, viz. at least x=4, 5, 6 and 7. My count on *L. hispidulus* (2n=12) appears to be the first report.

In an early report *Urospermum picroides* was said to have n=4 (MARCHAL 1920), but NEGODI (1938) later found 2n=10. The higher number was confirmed by SVESHNIKOVA (in FEDOROV 1969), by DELAY (1970), and has now been confirmed by me. The other species of the genus, *U. dalechampii* (L.) DESF., has 2n=14 (NEGODI 1938, LARSEN 1956, DELAY 1970).

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Notes on the Variation and Taxonomy in the Scirpus maritimus Complex

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ABSTRACT

NORLINDH, T. 1972. Notes on the variation and taxonomy in the Scirpus maritimus complex. — Bot. Notiser 125: 397—405.

From the *Scirpus maritimus* complex several taxa have been segregated at specific level, e.g. *Scirpus compactus* HOFFM. (1800) and *S. affinis* ROTH in ROEM. & SCHULT. (1817). They have also been treated as infra-specific units of *S. maritimus* by various authors. The Eurasian forms are investigated, above all with regard to the ramification of inflorescence and styles, and the morphology of achenes. Field studies have been carried out in several places along the Swedish coast. There has proved to be a pronounced irregularity in the ramification of inflorescence (compact or expanded), the number of style branches (3- or 2-stigmatic) and shape of achenes (often dimorphous in the spikelet). The conclusion is that *S. compactus* has to be regarded merely as a synonym and *S. affinis* as a subspecies of *S. maritimus*.

INTRODUCTION

When working up the material of *Scirpus* collected by Swedish expeditions in Central Asia, e.g. in Mongolia and Sinkiang, I have met with considerable difficulties in the taxonomic treatment of the *Scirpus maritimus* complex. This especially applies to the evaluation of those form series, which have been named *Scirpus* (*Bolboschoenus*) *compactus* HOFFM. and *S. affinis* ROTH. In this paper I have confined myself mainly to the Eurasian forms. For other forms I beg to refer to ERIC HULTÉN's interesting distribution map of the *Scirpus maritimus* complex with comments (HULTÉN 1962, p. 180, map 169).

The fact that several authors have recently treated the above-mentioned form series as separate species or infra-specific taxa has induced me to make a closer study of the herbarium material and literature of the *Scirpus maritimus* complex in order to try to determine whether its division into two or more species really is motivated. Further I have studied populations of the species in nature in some parts of the Swedish coastal regions. This has enabled me to form an opinion of the variation amplitude of the biotype group on which LINNAEUS originally founded his *Scirpus maritimus*.

Herbarium abbreviations are according to LANJOUW & STAFLEU (1964).

SCIRPUS MARITIMUS IN THE SENSE OF LINNAEUS

LINNAEUS (1753) described the inflorescences of *Scirpus maritimus* as "panicula conglobata". In the specimen in LINN (sheet 71: 43, lectotype), the inflorescence has proved to be almost compact, thus closely agreeing with the form later described as *Scirpus compactus* HOFFM. In his Flora Svecica (1745, p. 15, nr 39) LINNAEUS had already given its habitat "in littoribus marinis Roslagiae & c." ("Roslagen" is the eastern part of the province of Uppland and Stockholm) and there the form with a compact inflorescence is not uncommon.

In addition to his diagnosis LINNAEUS cited authors who had described the inflorescence (panicula) as "compacta" as well as those who called them "subsessili" (GUETTARD) and "sparsa" (BAUHINIUS and MICHELI). Thus, even LINNAEUS included in his *S. maritimus* forms with a compact inflorescence as well as forms with an expanded inflorescence, but the latter have as a rule been considered to be the true *S. maritimus* by the botanists who have separated these forms as taxa, for instance GODRON (1844) who named it *S. maritimus* var. *genuinus*. In this connection it is well to point out that there is a specimen of *S. maritimus* in the Linnaean herbarium of Stockholm with an expanded inflorescence.

SCIRPUS MARITIMUS IN THE SWEDISH COASTAL REGIONS

A study of populations of *S. maritimus* in the field during the years 1962—1964 in many places along the coasts of Sweden, e.g. in the provinces of Gästrikland, Uppland, Småland and Skåne, showed that inflorescence characters were of little or no taxonomic value. Culms with an expanded inflorescence and culms with a compact inflorescence proved to be completely mixed in the reeds of this species and all forms of transition between them occurred.

Observations on the rhizome connections between culms with inflorescences of different types of branching have been carried out by me in 1963 in a coastal area of Skåne in the parishes of Bunkeflo and Limhamn. In September, when the inflorescences had reached the final stage of development, I set about the laborious task of uncovering some rhizomes. It then appeared that from single older, widely extended rhizomes there emanated culms with expanded inflorescences as well as ones with more or less compact inflorescences (NORLINDH, Sept. 1963, nr. 5452, S). This varying development of the mature inflorescences in one and the same specimen would seem to be due to variation in the dampness and nutriment resources of the soil infiltrated by the rhizome. The fact is that a rhizome sometimes penetrates wet nutritious soil, where it mostly develops culms with expanded inflorescences, and sometimes relatively dry and sandy ground, where it produces culms with more or less compact inflorescences. Thus, in this case the variation in inflorescence type is in all probability due to modification induced by varying substrata.

The question of age of the inflorescences must also be taken into consideration. Early in the flowering season (June, in southern Sweden) the culms with a more or less compact inflorescence are often dominant. However, during the development from the flowering to fruiting stage the proportion between culms with different inflorescence types changes considerably in favour of those with expanded inflorescences. More or less elongate rays with one to several glomerulate spikelets can in many cases develop secondarily from inflorescences which were compact or almost so at the flowering stage. Thus, in some localities the frequency of culms with expanded inflorescences increases during development from the flowering to the fruiting stage. As in some cases I have observed that both culms with compact inflorescences and culms with expanded inflorescences arise from the same rhizome, I consider these characters to be of no taxonomic value.

The number of style branches and the shape of the achenes have not been treated by LINNAEUS in his description of *Scirpus maritimus*.

However, as style and achene characters have been much used in the classification of the *S. maritimus* complex in some other countries I have closely studied them in the Swedish populations as well. For a more detailed investigation of the styles of this species I have chosen a couple of populations situated in more northerly parts of the country (see HULTÉN 1971, p. 74, map 296), viz. those at Båtviken and Norrönningsviken on the island of Iggön in the Gulf of Bothnia, about 25 km NNE. of the town of Gävle. *Scirpus maritimus* is pronouncedly protogynous and the investigation was therefore carried out at an early flowering stage (July 5, 1964), when the style branches were optimally developed, but anthers and filaments still hidden by the glumes. One spikelet in each inflorescence was examined. The number of spikelets in the inflorescences varied in the abovementioned stands from 3 to 13.

The investigation gave the following results:

(1) All spikelets examined proved to have flowers with 3 as well as 2 style branches, irrespective of whether the inflorescence was expanded or more or less compact.

(2) The upper flowers of the spikelets had, as a rule, 3 style branches while the lower ones had 2. — However, at least one exception has been established, where a couple of apical flowers in the spikelets have 2 style branches.

(3) In the spikelets the number of flowers with 3 style branches were as a rule in excess of those with 2 style branches, but the ratio between them varied considerably. As an example it may be mentioned that in the most extreme cases the ratio between 3-branched and 2-branched styles was 20: 2 and in the least pronounced 12: 10. Further, ratios such as 12: 6, 14: 4, 6: 4 and 8: 5 occurred. — However, one exception to this predominance of flowers with 3-branched styles has been found. In an inflorescence of the expanded type, in one of the nine spikelets the great majority of flowers had 2 style branches.

As understood from the discussion above on expanded and compact inflorescences in *Scirpus maritimus* it is impossible to decide at an early flowering stage whether or not a more or less compact inflorescence will later develop into an expanded one. The *Scirpus maritimus* reeds in the northerly latitude of Iggön (60° 52′), which develop late, showed a large number of culms with inflorescences of the *compactus* type at anthesis in the beginning of July 1964. I have not completed my investigations there statistically, but it is my intention to publish square analyses from the Iggö localities later on, and this may elucidate the changes that take place in the ratio between the abovementioned types of inflorescences from the flowering to the mature stage.

The style characters of *Scirpus maritimus* populations in the other abovementioned parts of Sweden have not been as methodically investigated as those on Iggön. However, I have been able to establish that there too the spikelets in many cases had flowers both with 3 style branches and ones with 2 and that as a rule there are only a few of the latter in the spikelets. In some inflorescences with 3 style branches reductions in length occurred in one of them, but only fresh material is suitable for such a study. Some styles appear to be 2-branched, but on closer observation it is possible to detect the rudiments of a third branch. Herbarium material of this species is hardly suitable for the investigations of styles, as the withered style branches are extremely brittle and are easily broken.

The result of this investigation in the Swedish population of *Scirpus maritimus* clearly indicates that style characters cannot be used in distinguishing taxa.

The shape of the ripe achenes in the spikelets of the Swedish biotypes of *Scirpus maritimus* is trigonous and/or plane-convex (Fig. 1 A, B). The former achenes are presumed to have developed from pistils with 3-branched styles, the latter from pistils with 2-branched styles. Sometimes it is almost impossible to decide whether the achenes should be designated as trigonous or plane-convex, because there can be an almost imperceptible suggestion of an angle on the outer convex surface.

In her excellent work "Atlas of Seeds" 2 (1969), pl. 5: 1, GRETA BERGGREN has illustrated the achenes of the North-west European *Scirpus maritimus*. In her morphological description (op. cit. p. 14) she also mentions that biconvex achenes occur, though rarely. However, in the biconvex achenes the dorsal surface is usually considerably less convex than the ventral one, thus closely agreeing with the achenes of var. *digynus* (p. 401), described by GODRON as slightly convex on the dorsal and more convex on the ventral side.

SCIRPUS COMPACTUS AND CORRESPONDING TAXA

Scirpus compactus was originally described from Europe, and as it was published in "Deutschlands Flora" it must be considered to be based mainly on specimens from Germany even though an illustration of a Danish plant was also cited by the author. HOFFMANN's diagnosis (1800) is too brief and incomplete to give any information of value. He described the spikelets as being sessile and the involucre as two-leaved and unequal. He gave no information about the number of stigmas or the appearance of achenes, nor about the locality where it was collected. However, thanks to his two quotations "Krock. Sil. 1 t. 15" and "Fl. dan. t. 937" his description is indirectly supplemented by several fairly important statements.

In the former, Flora Silesiaca by KROCKER (1787), tab. 15, the plant was named *Scirpus maritimus* "Varietas minoris" and it was reported from four localities in Silesia and Saxonia. KROCKER described the inflorescence (panicula) as compounded of 4—10 more or less conglobate spikelets. Unfortunately KROCKER's drawing of the plant is not sufficiently detailed to give any information about the number of style branches and the shape of fruits. However, HOFFMANN's fellow-countryman and contemporary ROTH wrote (cf. p. 403) that the achenes of *S. compactus* are triquetrous, thus of about the same shape as the trigonous achenes which usually occur together with plane-convex achenes in the spikelets of the Swedish *compactus* forms of *S. maritimus*. It is probable that ROTH, when describing a closely allied taxon from India as *S. affinis*, compared it with an authentic specimen of *S. compactus* received from HOFFMANN. From ROTH's statement that *S. compactus* has triquetrous achenes it also follows that it had 3-branched styles.

In the other quotation, Flora Danica (1787), vol. VI, tab. 937, the detailed drawing of the flowers clearly shows that the style is 2-branched, but there were probably also flowers with 3-branched styles in the spikelets of this plant, just as there usually are in the corresponding forms in Sweden. The involucre, according to this picture, is not two-leaved as HOFFMANN wrote in his diagnosis of *S. compactus*, but three-leaved. However, the number of involucral bracts usually varies from 2 to 3 and this character is thus of no significance. The excellent drawing also shows that the rhizome of this plant produces runners and thick corm-like enlargements.

There seems to be no herbarium specimen preserved that can be chosen as the type of *Scirpus compactus*, at least not in the Göttingen Herbarium, where HOFFMANN worked at the time he described it. Therefore the picture in KROCKER's Flora Silesiaca, tab. 15, cited by HOFFMANN, must be chosen instead as the nomenclatural type.

The French botanist GODRON was probably the first to observe a form of *S. maritimus* having, as he thought, flowers with 2-branched styles only. He described this form as a variety (GODRON 1844), naming it *Scirpus maritimus* var. *diggynus*. GODRON, who based it on specimens from a locality near Nancy in France, stated that it is very rare there. He also pointed out that the fruits of this distigmatose variety are compressed, slightly convex on the dorsal and more convex on the ventral surface and that its spikelets are usually congested into one compact head. At the same time he distinguished a variety, *genuinus,* of *S. maritimus,* characterized by tristigmatic styles and trigonous fruits with the dorsal surface flat. GODRON gave two reasons for not having treated *diggynus* as a distinct species. He had observed that not all the fruits in his specimens of var. *diggynus* were of the shape described above, but that some were trigonous, and that in var. *genuinus* not all the flowers were tristigmatic, but that some were distigmatic. However, the occurrence of some trigonous achenes in his var. *diggynus* suggests there is every probability that there were also some flowers with tristigmatic styles, although he had not observed them. On the whole the variation in both his varieties coincides with the variation in the Swedish material.

LITWINOV (1922) established a new taxon, *Scirpus compactus* var. *orientalis,* basing it on a collection from the Nerczinsk district in Transbaical (Schedae ad Herbarium Florae Rossicae n. 2792). LITWINOV stated that in this variety the achenes were compressed and the styles distigmatic, as did GODRON concerning his var. *diggynus* of *S. maritimus*. There seems to be no reason for treating these plants as separate taxa.

LITWINOV considered the number of stigmas to be far more essential a character than the ramification of the inflorescence. The present writer quite agrees with LITWINOV that the ramification of the inflorescence is not an essential character, but contrary to him I do not consider the number of style branches to be an essential character either. In his discussion of *S. compactus* var. *orientalis* he writes that the form occurring in the same area (Transbaical), which has distigmatic styles and compressed achenes and which owing to its ramified inflorescence has been included in *S. maritimus,* ought rather to be classified as *S. compactus* var. *orientalis* f. *decompositus* LITW. The latter form actually has its close counterpart in a form found on Iggön in Sweden (p. 399) as it has an expanded inflorescence and flowers with almost only distigmatic styles, but the shape of its achenes is unknown.

In the Flora URSS III (1935 p. 57), ROSHEVITZ maintains *Scirpus compactus* at specific level, but under the name of *Bolboschoenus compactus* (HOFFM.) DROB. In his key of the genus he inadvertently attributes it the incomplete character stigmas 2, instead of stigmas 2—3. However, according to his description the typical form of the species, which is predominant in the west, has ovaries with 3 stigmas, while the dominant form in the eastern part of the Soviet Union is characterized by having 2 stigmas. Further, according to him the achenes of the former are plano-convex, subtrigonous (tab. III: 12) and those of the latter more or less globular (tab. III: 13). The so-called typical form of *S.* (*B.*) *compactus* is undoubtedly nothing but the *compactus* form of *S. maritimus,* which frequently occurs in Scandinavia and which normally has both 3- and 2-branched styles in the spikelets. It has been shown (p. 399) that the flowers with 3-branched styles normally greatly outnumber the 2-branched ones, which are usually found in the basal part of the spikelet. I therefore regard *S. compactus* to be merely a synonym of *S. maritimus.*

The above-mentioned Asiatic form series, called *S.* (*B.*) *compactus* var. *orientalis,* has been characterized by 2-branched styles and compressed or more or less globular achenes. Bearing in mind the ir-

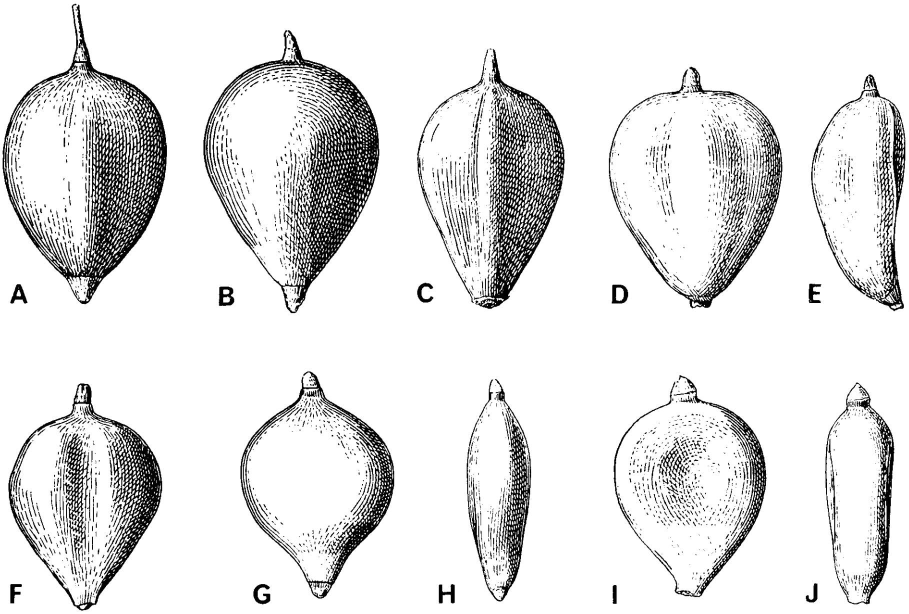

Fig. 1. Fruit forms of *Scirpus maritimus* L. — A—F: ssp. *maritimus*. — G—J: ssp. *affinis* (Roth in R. & S.) T. Norl. — A trigonous and B plane-convex achene from one and the same specimen, the former with a not very distinct ventral angle, the latter without, both seen from the ventral side. — C: Trigonous achene, with pronounced angle on ventral side. — D: Plane-convex achene, seen from ventral side and E the same from the margin. — F: Plane-convex achene with ventral side slightly longitudinally depressed in the middle. — G: Achene compressed, biconvex, seen from side, H the same from the margin. — I: Achene compressed, with a shallow concavity on both sides and J the same seen from margin.

A, B: Sweden. Skåne, parish of Bunkeflo, coast of Öresund, Norlindh, 1962, n. 5451 (S) — C: Germany. Bavaria. Ad ripas fluvii "Regnitz" prope "Bamberg", 240 m s. m., Harz, 1908, n. 5350 (Herb. Normale ed. Dörfler) (S) — D, E, F: Czechoslovakia. Moravia. Im Mitterteich bei Eisgrub, Zimmermann, 1910, n. 411 (Fl. Bohem. et Morav. exsicc. F. Petrak, sub nom. *S. maritimus* var. *digynus* Godr.) (S) — G, H: India orientalis. Malabar, Concan etc. Regio trop., Stocks, Law etc., s. n. (Herb. Ind. Or. Hook. fil. & Thomson) (C) — I, J: Mongolia australis: prov. Ning-hsia, Tsaghan-tokhoi, Söderbom, 1928, n. 7168 (S). — A—J ×10.

regularity of the occurrence of flowers with 2- and 3-branched styles in the spikelets of corresponding European biotypes in the complex, I consider it most probable that in certain cases at least single flowers with 3-branched styles may also occur in var. *orientalis*.

As regards the above-mentioned description of the achenes of var. *orientalis* I should prefer to call them biconvex, as both the dorsal and the ventral sides are convex although the dorsal side is usually less so than the ventral. I consider var. *orientalis* to be identical with *S. maritimus* var. *digynus*.

With regard to the shape of the achenes of var. *orientalis* and other *compactus* forms I also wish to refer the reader to the discussion (p. 403) on *S. maritimus* ssp. *affinis*.

SCIRPUS AFFINIS AND CORRESPONDING TAXA

Scirpus affinis ROTH had already been validly published in 1817 in ROEMER & SCHULTES, Systema Vegetabilium, which seems to have been overlooked by several botanists who have treated this taxon. This first description was followed by the reference "ROTH nov. plant. spec. MS". Exactly the same diagnosis was given in 1821 by ROTH in his own work on new plant species from East India. In both cases the descriptions were followed by an account of the differences between his new species and the very closely allied form described as *Scirpus compactus,* but the distinguishing characters are more exhaustively treated in the latter publication. As regards *S. affinis,* ROTH pointed out, among other things, that the glumes are discolorous with the margins silvery-membranaceous, that the achenes, which he called nuts, are subrotundate-compressed (which might correspond to the present term compressed biconvex) and that the style is constantly bifid and not trifid. By contrast he described the glumes in *S. compactus* as being concolorous and the achenes as triquetrous. His description of the achenes as being triquetrous is of great interest, because from that we conclude that it was the form with trifid styles he had in view.

During the 19th century the East Indian *S. affinis* was generally considered to be either a synonym of or an infra-specific taxon of *S. maritimus.* Thus, in LEDEBOUR's Flora Rossica (1853) it is included as a synonym of *S. maritimus* var. *compactus* and in HOOKER's Flora of British India (1894) as var. *affinis* C. B. CL. of *S. maritimus.* However, MEINSHAUSEN (1900) again raised it to the rank of species and then characterized its achenes as flattened biconvex in contradistinction to those of *S. maritimus,* which he described as flattened subtrigonous. Among other characteristics of the species he pointed out that it had hard, rigid culms and pale spikelets. Since then botanists have often treated *affinis* as a species. DROBOV (1916) transferred it to *Bolboschoenus,* a small genus segregated from *Scirpus.*

In several later publications the name *Scirpus* (*Bolboschoenus*) *affinis* has been changed to *Scirpus strobilinus,* which was validly published in 1820, although prior to this as a nomen nudum in 1814. This is due to the fact that the earliest publication of *S. affinis* ROTH in R. & S. in 1817 (not 1821) had been overlooked.

Judging from the herbarium material it is not possible to clearly delimit *S. affinis* from the forms of *S. maritimus* with compact inflorescences. All the Indian specimens of *S. affinis* that I have hitherto seen are quite characteristic with regard to the shape of the achenes and the colour of the spikelets. However, in central and eastern Asia forms transitional between these taxa occur. The essential distinguishing character is not the shape of the achenes, but the colour of the glumes.

The achenes in *S. affinis* are described as lenticular or compressed biconvex. A closer study of achenes in specimens from India, for instance those of STOCKS, LAW etc. from Malabar, Concan etc. (C, LD, S), shows that the sides are not always strictly convex, but that the central part of the faces may be almost completely flat or not rarely with a shallow cavity. However, in their general aspect these achenes may still be described as lenticular (Fig. 1 G—J). They show close agreement with certain types of achenes, which according to Flora URSS III (p. 57) occur in *Bolboschoenus* (=*Scirpus*) *compactus,* viz. those described as being flat on both sides or concave. Only in the colour of the glumes of the spikelets do these taxa show some differences, the glumes of *S. maritimus* being dark brown or ferruginous, and those of *S. affinis* whitish-yellow, stramineous or silvery-membranaceous.

In my opinion the above-mentioned biotypes occurring in Asia are more closely allied to *S. affinis,* which was described from India, than to *S. maritimus* with compact inflorescences (*S. compactus*), which was based on specimens from Germany. As the distributional areas of *S. maritimus* and *S. affinis* partly overlap, and as there are forms transitional between them, I consider the latter to be only a geographical race, a subspecies of the polymorphous *S. maritimus.* Therefore I now form the following new combination:

Scirpus maritimus ssp. **affinis** (ROTH in R. & S.) T. NORL., comb. nov.

Basionym: *Scirpus affinis* ROTH in ROEMER & SCHULTES, Syst. Veg. II (1817) p. 140.

A typo differt: glumis spicularum pallide luteis, stramineis vel argenteo-membranaceis.

I have not yet been able to trace any specimen of *S. affinis* that could be chosen as lectotype. Such a specimen was probably preserved in the Botanical Museum of Berlin, but it must have been destroyed when the Museum was damaged during World War II. However, I have now selected a neotype in the collection of *S. affinis* from India, which shows all the characteristic features of this taxon, viz. the specimen in Copenhagen (C) from India orientalis. Malabar, Concan etc. Regio trop., STOCKS, LAW etc., s. n., (Herb. Ind. Or. HOOK. FIL. & THOMSON). — Fig. nostrae 1 G, H.

SUMMARY AND CONCLUSIONS

From my investigations of the *Scirpus maritimus* complex I have arrived at the following results.

The ramification of the inflorescence is a non-essential character. Even in the Scandinavian populations there is a variation from compact to expanded inflorescences and both types can be found in culms arising from one and the same rhizome. In extreme cases the inflorescences are reduced to solitary spikelets, for instance in the modification described as *S. maritimus* var. *monostachys* LGE (Flora Danica, vol. XVI, 1867, tab. 2702).

The number of style branches has often been seen to vary irregularly in the spikelets, either 3-branched only, or 3- and 2-branched together, or 2-branched only, so that this character cannot be used to distinguish taxa either. Thus, I cannot accept *S. maritimus* var. *digynus* GODR. as a taxonomic unit, as it was mainly based on the character of styles being distigmatic. The occurrence, according to GODRON (1844), of some trigonous achenes in var. *digynus* suggests there is every probability that a few flowers with tristigmatic styles also existed in the spikelets. The ordinary fruits of this variety, developed from distigmatic styles, were described by GODRON as slightly convex on the dorsal and more convex on the ventral side. Thus the achenes of this plant are in reality dimorphous, which is often the case in *S. maritimus.*

It is very likely that two plants in Flora Danica, viz. the *compactus* form of *S. maritimus* (op. cit., vol. VI, 1787, tab. 937) and the *monostachys* form cited above, which are drawn with 2-branched styles, in reality also had a few 3-branched styles in their spikelets, just as other similar forms in the Scandinavian species populations usually have.

The two common achene types in the Scandinavian *S. maritimus,* the trigonous and the plane-convex (Fig. 1 A, B), may not infrequently occur together in the spikelets of the compact as well as in the expanded inflorescences and they thus cannot be used for distinguishing taxa.

In my view *Scirpus compactus* HOFFM. does not deserve to be treated neither as a species nor as an infra-specific taxon.

I consider *Scirpus affinis* ROTH to be only a geographical race in the above complex and have therefore reduced it to a subspecies, *S. maritimus* ssp. *affinis* (ROTH) T. NORL., comb. nov.

The variation in the ramification of inflorescence, the number of style branches and shape of achenes in the *Scirpus* *maritimus* complex is remarkable and makes any division into clear-cut entities rather difficult.

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LITERATURE AND NOMENCLATURE OF SCIRPUS MARITIMUS L.

The list is mainly applied to the Eurasian species populations.

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Variation in the Chromosome Complement of Leopoldia comosa (L.) Parl. (Liliaceae) in the Aegean (Greece)

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ABSTRACT

BENTZER, B. 1972. Variation in the chromosome complement of Leopoldia comosa (L.) Parl. (Liliaceae) in the Aegean (Greece). — Bot. Notiser 125: 406—418.

The basic karyotype of *L. comosa,* 2n=18, from a number of localities in the Aegean is described. The occurrence and consequences of a widespread apparently balanced heteromorphism in a particular chromosome pair is discussed. Autotriploid populations were found on Kriti. Hybridization between *L. comosa* and tetraploid *L. weissii,* 2n=36, is frequent when the species occur sympatrically. The variation in satellite position and number is briefly discussed.

INTRODUCTION

Leopoldia comosa is a pan-Mediterranean plant which is widely distributed in Greece, especially in biotopes influenced by agricultural activities. It is mainly allogamous and comprises a number of continuous morphological types. The variation range within populations is sometimes considerable. Due to this the taxonomy has become extremely confused. Morphological studies and taxonomical considerations will, however, be dealt with elsewhere. The present paper treats *L. comosa* s.l. and includes taxa which have earlier been recognized as distinct species, viz. *L. holzmanni* (HELDR.) HELDR., *Muscari charrelii* (HELDR.) ex HAL. & NADJI, *Muscari cousturieri* GANDOG., *L. curta* HELDR., and *L. sartoriana* HELDR.

A large number of chromosome counts of *Leopoldia comosa* have been made all confirming 2n=18, e.g. GUIGNARD (1889), WUNDERLICH (1936, 1937), FERNANDES et al. (1948), D'AMATO (1950, 1952), POLYA (1950), LARSEN (1956, 1960), GADELLA et al. (1966), GARBARI (1967), STUART (1970), and DAHLGREN et al. (1971). The chromosome morphology has been studied by DELAUNAY (1915, 1923, 1927), SATO (1942), GARBARI (1966, 1968, 1969) and BENTZER (1969) etc. The present study confirms the previous results and contributes some new data, e.g. triploidy, hybridization and widely distributed structural heterozygosity.

MATERIAL AND METHODS

Specimens from about 50 local populations mainly from the Aegean Archipelago have been cultivated (Fig. 1). Between 1967 and 1972 living material has been brought to Lund by a number of colleagues, viz. Prof. H. RUNEMARK (R), Dr. I. BJÖRKQVIST (Bt), Dr. S. SNOGERUP (S), Dr. A. STRID (St), Mr R. VON BOTHMER (B), Mr L. ENGSTRAND (E), Mr M. GUSTAFSSON (G), Mr B. HÄGERHÄLL (Hl), and Mr J. PERSSON (P). My own collections are designated (Be). A code to the collections used in the present study is given in an appendix.

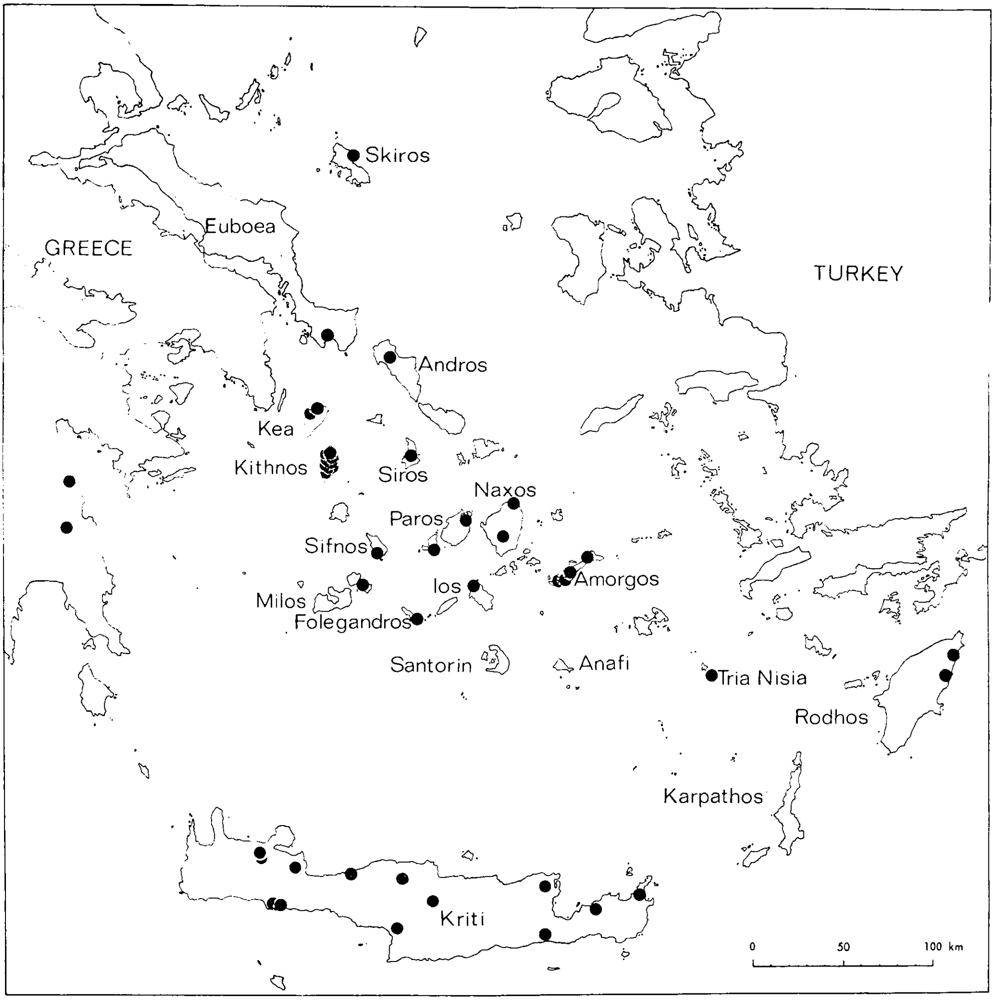

Fig. 1. Distribution of cytologically investigated diploid *Leopoldia comosa*. A few populations studied are from outside the area shown.

Chromosome preparations were made according to Bentzer (1969, 1972). Male fertility was estimated by calculating the percent stainable pollen in cotton blue. At least 200 grains were counted. Some figures given are means from 3 independent calculations on the same specimen. However, since the different values obtained in that way appeared fairly constant it was later on found sufficient to make only one count. The majority of values given are based on a single count.

The spelling of geographical names follows The Times Atlas (Bartholomew 1956), and the marine charts of the British Admiralty. Descriptions of centromeric positions follow Levan et al. (1964).

Drawings were made with the aid of a binocular camera lucida (Leitz) mounted on a Leitz Orthoplan microscope. Photos were taken with a Nikon AFM camera. The film used was Scientia 39 C 56.

Fig. 2. Karyotypes of diploid *Leopoldia comosa*. — A: Kriti, no. 507. — B: Naxos, no. 320. — C: Rodhos, no. 514. — D: Rodhos, no. 512. — E: Kithnos, no. 322. — Heteromorphic pair within rectangle. Chromosome designation for each group is given.

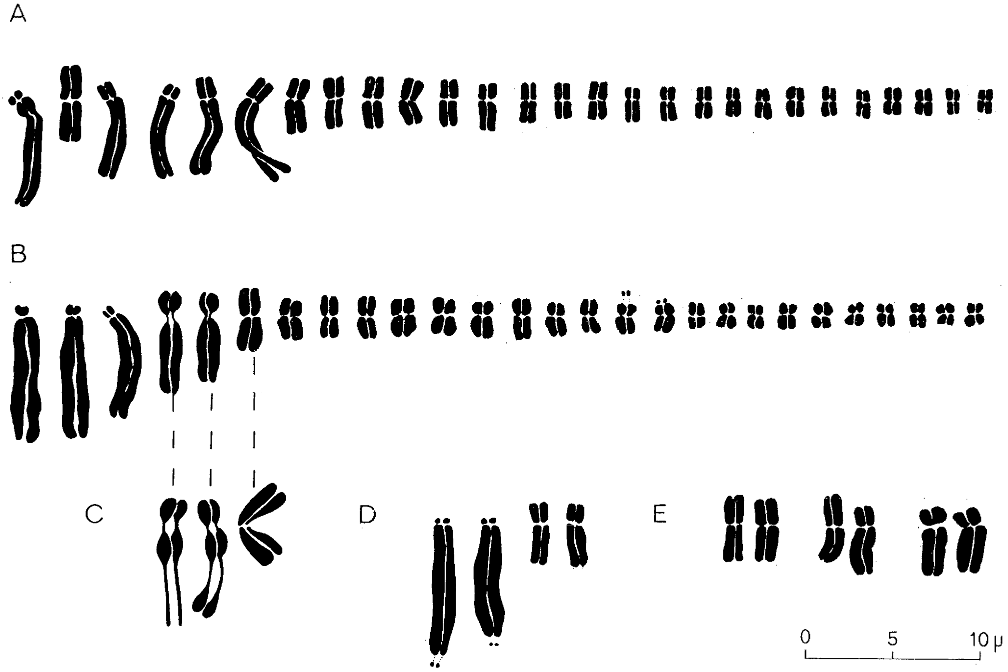

Fig. 3. A: Hybrid karyotype of *Leopoldia comosa* (2n = 18) × *L. weissii* (2n = 36). — B: Autotriploid *L. comosa* from Kriti. — C: (L) m-st chromosomes from the same autotriploid specimen as B but less contracted. — D: (L) t and (L) m-st chromosomes of no. 313 from Kithnos. — E: The different combinations of (L) m-st chromosomes found in population no. 322 from Kithnos.

RESULTS

Basic Karyotype

The karyotype of *Leopoldia comosa,* 2n = 18, is trimodal and comprises 3 groups of chromosomes. The first of these have 4 long (L) chromosomes with 2 t ones, r-values exceeding 10, and 2 shorter m-st ones, r-values 1.1—4.0. The second group comprises 6 medium-sized (M) msm chromosomes and the last group includes 8 short (S) m chromosomes (Fig. 2). In some specimens the distinction between the 2nd and 3rd group is vague.

Satellites are normally present on 2 (S) chromosomes. They are always small. It is likely that satellites sometimes escape notice because of their small size. Occasionally satellites are attached to the long arm of one or both of the (L) t chromosomes, e.g. populations no. 313, 502, 506 and 512 (Fig. 3 D). Due to the variations in number and position the satellites are hardly useful as chromosome markers in comparisons between specimens or populations. The number of nucleoli varied between one and two at interphase.

In many cells the (L) t chromosomes have a secondary constriction on the long arm c. 1/4-way down from the centromere (Fig. 2 D, E). The constriction sometimes only occurs in one of the homologues, e.g. in one specimen from population no. 55. Sometimes another 2—3 weak constrictions are present more distally on the long arm.

In chromosome sets that are poorly contracted the (L) t chromosomes have a

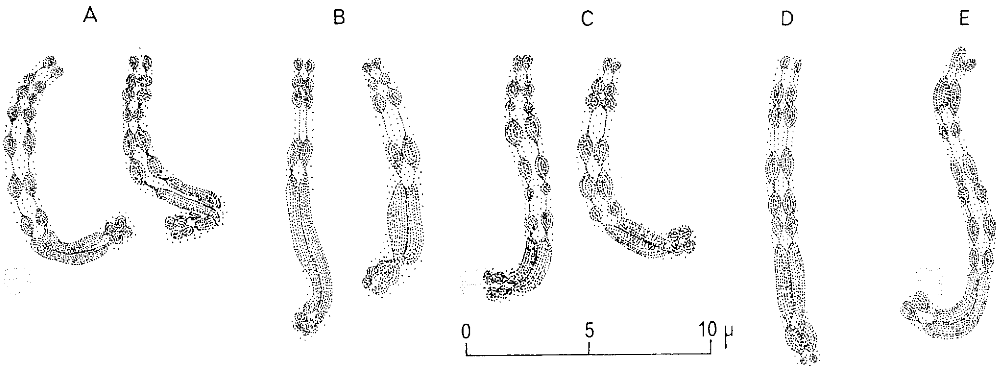

Fig. 4. Composition of differentially stained segments in (L) t chromosomes. — A: Kithnos, no. 322. — B: Kriti, no. 502. — C: Rodhos, no. 512. — D: Kriti, no. 500 (only one homologue). — E: Kriti, no. 506 (only one homologue).

number of segments which are much more contracted than the intermediate ones. The number of such segments seems to be fairly constant between homologues. Between specimens pronounced differences are present. However, the semidistal parts of the long arms are essentially identical in all (L) t chromosomes studied (Fig. 4). A similar case of morphological differentiation of chromosomes into chromomeres in rye without prior cold treatment was reported by Heneen (1962).

On the (L) m-st pair, st chromosomes often have a secondary constriction in the middle of the long arm. On (L) m chromosomes this constriction never occurs.

There seems to be a difference in contraction rate in an (L) m-st pair depending on whether the chromosomes are (L) m or (L) st; the former generally contract more rapidly than the latter. The long arm of (L) st chromosomes especially has a large segment which contracts late (Fig. 3 C). This gives rise to a certain degree of uncertainty in the determination of r-values for these chromosomes and also in the calculations of relative length.

The distal parts of the (M) and (S) chromosomes contract later than the proximal parts and appear as long thin weakly stained threads, while the proximal parts are thick and heavily stained.

A striking feature of interphase cells is the occurrence of Feulgen-positive heteropycnotic bodies. These bodies are normally 2 in number (Fig. 5) but in some cells another one or two usually smaller bodies occur. According to what has been noticed in contracting sequencies of entire chromosome sets the 2 larger allocyclic bodies seem to contain the large semidistal segment of the (L) t chromosomes (Fig. 4). Heteropycnotic interphase bodies are not found in other species of *Leopoldia*.

Structural Heterozygosity

In a number of populations the (L) m-st homologues are heterozygous for a large segment (Fig. 3 E). The populations no. 312, 322, 507 and 512 all include three different chromosome compositions, viz. (1) basic homologues with r-values c. 1.1—1.6; (2) one basic homologue and one homologue with r-value c. 2.5—4.0; (3) two homologues with r-values c. 2.5—4.0. In the total material (135 specimens) 46 % were heterozygous, 39 % basic homozygous and 15 % homozygous for the re-

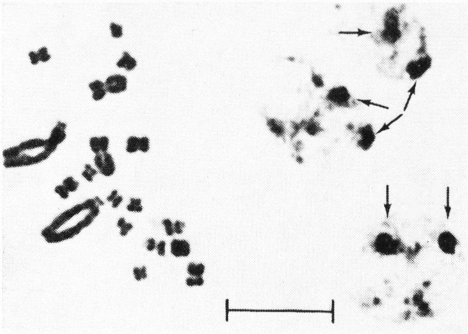

Fig. 5. Feulgen-positive heteropycnotic bodies at interphase indicated by arrows. Scale unit equals 10 μ.

arrangement. These figures agree closely with the expected Hardy-Weinberg frequencies. The relative length of the chromosomes remain essentially the same independent of r-values. Those differences in length which have been found are probably caused by a somewhat different heterochromatin content which accompanies the allocycly, a phenomenon that would likewise explain the variation in r-values.

In the area investigated the three groups are more or less equally distributed and growing in similar biotopes (Table 1). Outside the area similar heterozygosity has been observed in material from Italy (Garbari 1966, 1969) and Egypt (Bentzer unpublished). Sato (1942) reported a similar heterozygosity but the origin of his material is unknown.

The reduction of pollen stainability is not due to heteromorphism in the (L) m-st pair. For all three chromosome compositions the pollen stainability normally exceeds 90 % (Table 2). The values lower than 90 % pollen stainability are probably caused by factors other than the polymorphism here discussed since specimens with reduced pollen stainability seem to be in proportion equally distributed independent of chromosome combination.

Table 1. Number of specimens with different rearrangement compositions in the (L) m-st pair from a number of populations. bHo: Basic homozygous. He: Heterozygous. sHo: Structural homozygous.

Population	Type		
	bHo	He	sHo
Skiros, no. 524	—	1	—
Euboea, no. 528	—	—	1
Giona, no. 335	4	2	—
Parnon, no. 451	1	—	—
Erymanthos, no. 453	1	—	—
Paralia Tiro, no. 437	2	2	—
Andros, no. 344	1	—	—
Kea, no. 412	—	1	—
Kithnos, no. 302	—	5	—
Kithnos, no. 312	3	1	1
Kithnos, no. 313	1	1	—
Kithnos, no. 322	2	2	2
Kithnos, no. 323	—	1	—
Kithnos, no. 330	—	2	—
Kithnos, no. 409 b	—	1	—
Kithnos, no. 446	—	1	—
Skiros, no. 347	1	1	—
Naxos, no. 16	3	1	—
Naxos, no. 320	2	1	—
Paros, no. 11	4	—	—
Andiparos, no. 57	—	1	—
Sifnos, no. 65	—	1	—
Poliaigos, no. 55	3	1	—
Folegandros, no. 81	3	—	—
Ios, no. 419	—	1	—
Amorgos, no. 58	—	—	1
Amorgos, no. 79	1	—	—
Amorgos, no. 424	2	2	—
Amorgos, no. 429	—	—	1
Tria Nisia, no. 92	6	1	—
Rodhos, no. 509	—	1	—
Rodhos, no. 512	3	2	3
Rodhos, no. 514	—	8	—
Kriti, no. 400	—	1	3
Kriti, no. 401	—	2	—
Kriti, no. 403	—	—	3
Kriti, no. 501	2	2	—
Kriti, no. 502	—	1	3
Kriti, no. 504	1	2	—
Kriti, no. 506	—	3	1
Kriti, no. 507	2	2	1
Kriti, no. 516	2	4	—
Kriti, no. 517	—	2	1
Kriti, no. 518	2	2	—
Total:	52	62	21
Expected frequencies according to the Hardy-Weinberg law:	51	64	20

Table 2. Number of specimens with different pollen stainability.

(L) m-st chromosome composition	% pollen stainability															
	0	10	20	30	40	50	55	60	65	70	75	80	85	90	95	100
Basic homozygotes		1			1		1		1		1	1	3	4	16	
Structural heterozygotes							1		1		1		2	4	20	
Structural homozygotes												1		1	5	
"Autotriploids"								1		1						
L. comosa×*L. weissii*			3	4	1			1								

Vegetative propagation via bulbils is common in *Leopoldia comosa* but its occurrence does not seem to be correlated with the structural heteromorphism.

Triploids

Two populations from Kriti, no. 500 and 520, were found to be triploid, i.e. 2n=3x=27. The chromosome morphology indicates autotriploidy s.l. (Fig. 3 B). The same composition of the (L) m-st chromosomes was found in all specimens investigated, i.e. one (L) m and two (L) st chromosomes. In early metaphase the single (L) m homologue was heavily contracted while the two (L) st chromosomes were poorly contracted in long segments on their long arms (Fig. 3 C). Distally on the long arm of one of the (L) st homologues a segment was relatively strongly contracted. The difference in appearance probably indicates a certain difference in heterochromatin content between the homologues.

Pollen stainability has only been studied in two specimens from no. 500 both of which have reduced stainability, i.e. 64 % and 74 % respectively.

Hybrids

Chromosome morphology gives important data about the frequency of hybridization with other taxa. Hybrids with tetraploid, i.e. 2n=36, *L. weissii* (Freyn) Freyn ex Heldr. are common whenever these taxa occur sympatrically. The different chromosome sets of the two species are readily identifiable on their long (L) chromosomes (Fig. 3 A). The karyotype for diploid *L. weissii* is given in Bentzer (1972). A few other *Leopoldia* species in the Aegean are theoretically possible as counterparts to *L. comosa* in hybridization with the same hybrid karyotype as result. In the natural hybrids found so far, *L. weissii* is, however, the most likely counterpart owing to its sympatric occurrence with *L. comosa*.

The hybrids have reduced pollen stainability, i.e. 20—65 % (Table 2) but they are capable of vegetative propagation via bulbils. This makes the constitutional hybrid karyotype persistent for very long periods of time. Now and then backcrossing presumably takes place giving rise to introgressive offspring. Such cases have been found on the island of Sirna (Bentzer 1969), where *L. comosa* formed introgressive swarms presumably with *L. weissii*. The introgressive hybrids were easily identified on their karyotypes.

Meiosis in the Diploid Material

Meiosis was studied in a few sample preparations representing specimens with different mitotic karyotypes. The pairing of homologues was normal. Only very occasionally were univalents and multivalents found, i.e. in less than 1 % of the cells studied. Apparent chromatin connections between bivalents at diakinesis were observed in some cells.

The (L) m-st bivalents were unequally

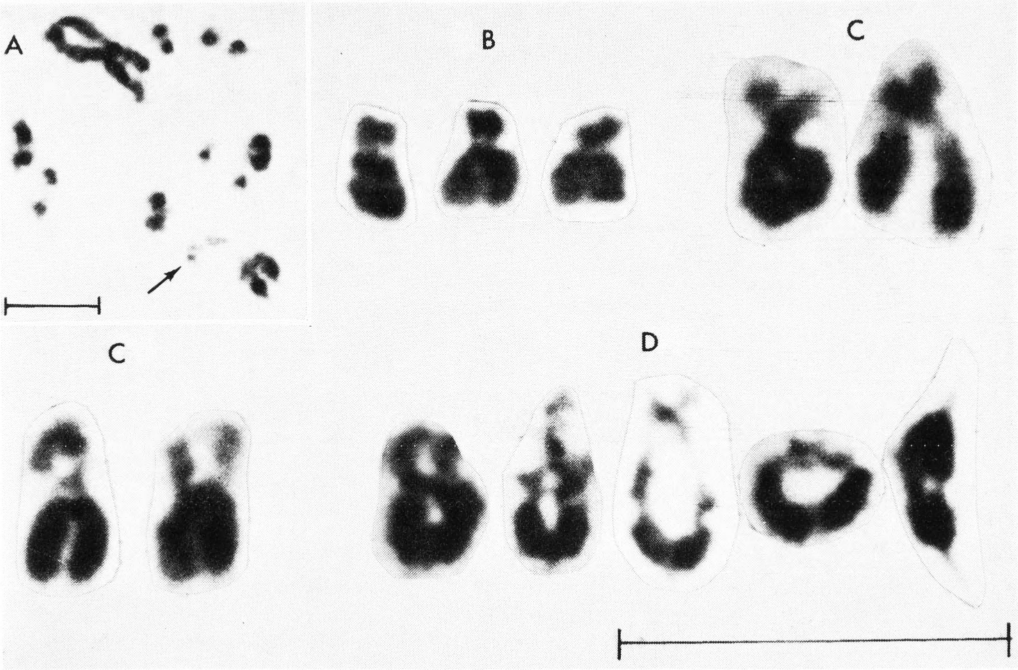

Fig. 6. A: Cell at diakinesis from Mt. Giona, no 335. Arrow indicates weakly contracted part of the homozygous (L) m-st bivalent. — B—D: (L) m-st bivalents at diakinesis and metaphase. — B and C: Structural homozygous bivalents from Mt. Giona, no. 335. — D: Structural heterozygous bivalents from Kriti, no. 401. The last bivalent is in metaphase. — Scale units equal 10 μ.

contracted at diakinesis independent of the presence or absence of structural heterozygosity (Fig. 6). The distal or semidistal parts of the bivalents were less contracted than the rest, a fact that may indicate the presence of a certain amount of distal heterochromatin. A distal heterochromatic segment was also indicated in some mitotic cells (Fig. 3 C).

Heteromorphism in the (L) m-st chromosomes did not affect the normal pairing and chiasma formation. The bivalents formed between 1 and 3 chiasmata; one or two terminal and generally one interstitial.

The (L) t bivalent had between 1 and 4 chiasmata; normally 2—3 (Table 3). The chiasmata were often interstitial. In the (M) and (S) bivalents the number of chiasmata is difficult to determine but never more than 2 were observed in any cell. The chiasmata always seemed to be terminal.

In a few cells at anaphase I apparent sub-chromatid exchanges were observed (Fig. 7 A—C), indicated by the fact that no acentric fragments were found.

A pericentric inversion is a possible explanation of the heteromorphism in the (L) m-st chromosomes. However, analyses of relative chromatid length of separating (L) m-st chromosomes at anaphase I and chromatid arm length at anaphase II were not possible owing to technical difficulties and hence analyses of chiasmata in the suspected pericentric inversion segment are lacking.

Table 3. The minimum, mean and maximum number of chiasmata/bivalent is given for each specimen. bHo: Basic homozygous. He: Heterozygous. sHo: Structural homozygous.

Population and specimen no.	Composition of (L) m-st homologues	Number of cells studied	Chiasmata per bivalent		
			(L) t	(L) m-st	(S) & (M)
16-5	—	14	1—2.2—3	2—2.1—3	1—1.4—2
16-6	—	30	1—2.3—4	1—1.8—2	1—1.2—2
92-4	bHo	14	1—1.7—2	2—2.0—2	1—1.3—2
335-4	He	38	1—2.4—3	1—2.0—3	1—1.2—2
400-1	sHo	26	1—2.0—3	2—2.2—3	1—1.3—2
401-2	He	7	2—2.1—3	2—2.2—3	1—1.2—2
424-2	He	16	1—2.3—4	2—2.3—3	1—1.2—2
		Total: 145	Means: 2.1	2.1	1.2

Meiosis in Triploid Hybrids

In hybrids between *Leopoldia comosa* and tetraploid *L. weissii* the meiosis was very disturbed with a number of univalents, bridges, laggards etc. (Fig. 7 D—F).

DISCUSSION

Structural Polymorphism

Structural polymorphism in chromosomes is a common phenomenon in plants (see, for example, Darlington 1965, John & Lewis 1968 for references). In the Aegean region structural heterozygosity has been observed in *Allium* (Bothmer 1970), *Elymus* (Heneen & Runemark 1962, 1972), and *Leopoldia* (Bentzer 1969, 1972) for example.

However, cases of identical polymorphism previously described originate from either isolated specimens or different populations which are moderately separated, viz. *Leopoldia weissii* (Bentzer 1972). In the case of *L. comosa* the conspicuously wide distribution of apparently the same balanced structural heteromorphism seems to be unique.

Only speculations can be made about the origin of the heteromorphism.

The (L) m-st chromosomes may contain a balanced heteromorphism for a pericentric inversion and in addition to that a large allocyclic segment of somewhat different shape and size (Fig. 8). The available data on meiotic pairing and chiasma formation supports such a composition.

Theoretically a shift could give rise to the same chromosome morphology as a pericentric inversion. In the Y_2 chromosome of *Rumex acetosa,* Kuroki & Kurita (1970) found a morphological chromosome variation between two populations which was very similar to that found in the (L) m-st pair of *L. comosa.* Without meiotic data they concluded that the origin of that variation might be caused by a decrease in heterochromatic material or by a shift. However, a shift is hardly a plausible possibility in *L. comosa* since in that case the complete terminalization of any chiasma would be impossible. In all bivalents studied at least one chiasma was terminal.

Different ways in which structural rearrangements are established and distributed in natural populations have been shown. Especially in *Drosophila* species a number of rearrangements have been investigated according to their value for the increased fitness of the population (e.g. Carson 1967). For instance in *Drosophila willistoni* about 50 different inversions

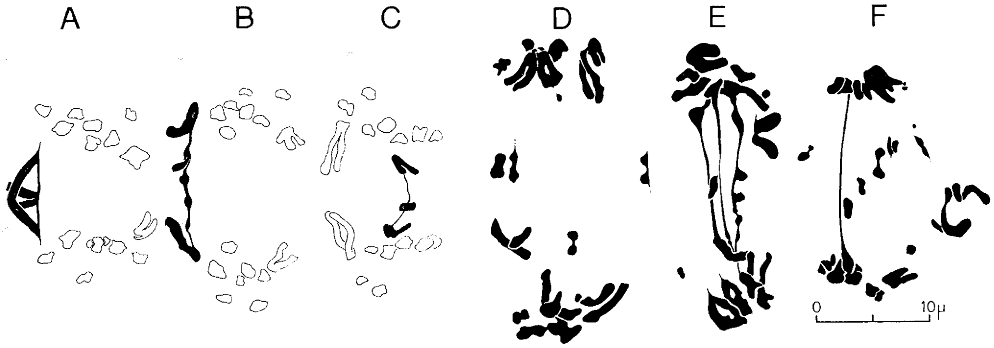

Fig. 7. A—C: Presumed sub-chromatid bridges in diploid *Leopoldia comosa* from Kriti, no. 401. — D—F: Late A I in hybrid between *L. comosa* (2n=18) and *L. weissii* (2n=36).

have been found in natural populations. The inversions are more common in central than in peripheral populations. It is claimed that in the central populations the inversions are favoured because they limit the range of variation in the large gene pool, i.e. they prevent favourable heterozygotic combinations from breakdown. In margin populations structural homozygotes with their larger recombination ability are favoured (LEWIS & JOHN 1963).

A case of apparently selective advantage caused by rearrangement was described by ISING (1969). He found a pericentric inversion in *Cyrtanthus* (Amaryllidaceae) which seemed to increase male fertility as well as seed production.

Three main avenues for the preservation of structural rearrangements have been proposed: (1) Inbreeding in normally outbreeding species favours the establishment of structural heterozygotes (CLELAND 1949, DARLINGTON & LA COUR 1950, LEWIS & JOHN 1957, REES 1961, HENEEN & RUNEMARK 1962 and CARSON 1967); (2) In outbreeding populations structural heterozygotes are sometimes favoured since they prevent favourable gene sequencies from breaking down (e.g. LEWIS & JOHN 1963); (3) Structural heterozygotes are selectively neutral and appear in ratios that agree with HARDY-WEINBERG's law.

In natural populations of the mainly allogamous *L. comosa* the genetic heterozygosity is on the one hand increased by outcrossing but is on the other hand relatively decreased by proliferation. Proliferation is very common in cultivated specimens but appears to be more limited under natural conditions. However, since the genetic background for proliferation obviously exists one may assume that even in natural populations the rate of proliferation increases under certain condi-

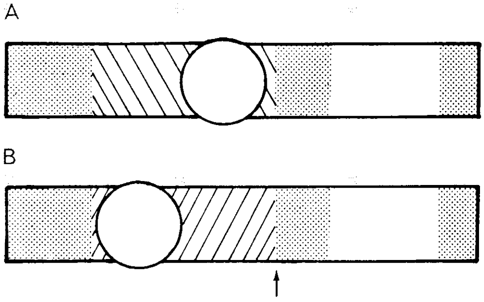

Fig. 8. Idealized structure of heterozygous (L) m-st pair. — A: Normal (L) m chromosome. — B: Rearranged (L) st chromosome. Dotted and lined areas indicate euchromatic segments. White areas indicate heterochromatic segments. Lined areas indicate segments which are involved in a pericentric inversion. Arrow indicates site of secondary constriction.

tions. *L. comosa* preferentially appears in biotopes which are continually changed, i.e. cultivated fields, and vegetative propagation is likely to be most efficient under such circumstances. This would imply that in many populations the basic number of genotypes is limited and that a certain amount of inbreeding is unavoidable. In such populations it should be the alternative (1) that favours heterozygosity.

In biotopes which are comparatively unaffected one may suspect that the number of basic genotypes is high and that sexual reproduction plays a more active role compared with proliferation. In such populations the alternative (2) would favour heterozygosity.

Since the heteromorphism is widely distributed in different kinds of population structures and biotopes it may be of adaptive significance in either of the ways discussed above, or it may in fact be selectively neutral. The total distribution of the different karyotypes in the (L) m-st pair agrees closely with the expected HARDY-WEINBERG distribution (Table 1). However, in order to check the general application of the HARDY-WEINBERG law, the distribution of the heteromorphism must be investigated in a large number of specimens from some different biotopes. Not until such studies have been made can one state that the heteromorphism is selectively completely neutral independent of biotopes.

Secondary Constrictions

Secondary constrictions are generally considered to be reliable chromosome markers which often contain nucleolar organizers (DARLINGTON 1965 pp. 35—40). However, in some plant materials it has been found that the size, number and position of satellites varies between populations and sometimes between specimens (e.g. HENEEN & RUNEMARK 1962, 1972, GARBARI 1969, STRID 1969, BOTHMER 1970, BENTZER 1969, 1972, BENTZER et al. 1972). In *L. comosa* the discrepancies in position and number may either be a result of competition between different potential nucleolar organizing regions (NAVASHIN 1934) or it may be the result of minor translocations which do not reduce fertility as was postulated to be the case in *Nigella* (STRID 1969), or due to difficulties in the detection of such small satellites.

ACKNOWLEDGEMENT

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APPENDIX. Origin of cultivated populations

Cultivation number is given in boldface and chromosome number within brackets. **4** (18): Poliaigos, in the NW part, fields, volcanic ground, R & Be, 1967. — **11** (18): Paros, 2 km SE Naousa, fields, serpentine, R & Be, 1967. — **16** (18): Naxos, 1 km S Apollon, fields, R & Be, 1967. — **55** (18): Poliaigos, the NW cape, fields, volcanic ground, R & Be, 1967. — **57** (18): Andiparos, the most SW part, R & Be, 1967. — **58** (18): Amorgos, the Bay of Langadhia, fields, R & Be, 1967. — **65** (18): Sifnos, Taxiarkhis, N of the bay, fields, R & Be, 1967. — **79** (18): Amorgos, N Oros Korax, fields, 200 m. s.m., R & Be, 1967. — **81** (18): Folegandros, near the harbour village in the E-most part, fields, R & Be, 1967. — **92** (18): Tria Nisia, the W island, 40 m. s.m., R & Be, 1967. — **302** (18): Kithnos, the valley NE Ag. Louka, fields, R & E, 1968. — **312** (18): Kithnos, Ormos Flambourion, fields, phrygana, R & E, 1968.

— **313** (18): Kithnos, 3 km N Loutra, R & E, 1968. — **320** (18): Naxos, between Moni and Sifones, c. 550 m. s.m., R & E, 1968. — **322** (18): Kithnos, N Chora, fields, bulbils often found, R & E, 1968. — **323** (18): Kithnos, Chora, R & E, 1968. — **330** (18): Kithnos, roadside S Dhriopis, R & E, 1968. — **335** (18): Mt. Giona, near Sthromi, cliffs, E, 1968. — **344** (18, 27): Andros, 1.5 km S—SSE the peak of Mt. Ag. Saranda, in the valley, 150—200 m. s.m., S & B, 1968. — **347** (18): Siros, near Kiperoussa, in the valley, 150—300 m. s.m., S & B, 1968. — **400** (18): Kriti, Chania, 0.5 km SW Mournies close to the road to Malaxa, fields, Be, 1969. — **401** (18): Kriti, Chania, 0.5 km SW Mournies close to the road to Malaxa, fields, Be, 1969. — **403** (18): Kriti, Sfakion, in the village of Anopolis, fields, Be, 1969. — **407** (18): Kriti, Sfakion, Frankokastello, fields, Be, 1969. — **408 a** (18): Kithnos, S Merikha Bay, 80 m. s.m., Be, 1969. — **409 b** (18): Kea, the bay N Ormos Kalogeros, phrygana, Be, 1969. — **412** (18): Kea, near Otzia, fields, 0—15 m. s.m., Be, 1969. — **415** (18): Folegandros, 0.5 km E the harbour village on the E part of the island, fields, Be, 1969. — **419** (18, 27): Ios, 2 km N Akr. Gremnos, fields, 50 m. s.m., Be & G, 1969. — **422** (27): Anafi, near the monastery in the E part of the island, Be & G, 1969. — **424** (18): Amorgos, along the road between Katapola and Chora, c. 200 m. s.m., Be & G, 1969. — **425** (27): Amorgos, along the road between Katapola and Chora, c. 200 m. s.m., Be & G, 1969. — **429** (18, 27): Amorgos, 2 km SW Katapola, old fields, 200 m. s.m., Be, 1969. — **437** (18): Peloponnisos, just S Paralia Tiro on the E coast, fields, R & Be, 1969. — **443** (18): Kithnos, NE Merikha, phrygana, 50 m. s.m., R, St, and G, 1969. — **446** (18): Kithnos, close NE to Merikha Bay, phrygana, fields, 60 m. s.m., Be, 1969. — **451** (18): Peloponnisos, Mt. Parnon, E side of the northern part of the southernmost massive, 3 km S Platanakion, fields, 1200 m. s.m., P, 1969. — **452** (18): Peloponnisos, Mt. Taïyetos, forest road in the northern part, 3 km S of the peak Xerovouna, 1250 m. s.m., P, 1969. — **453** (18): Peloponnisos, Erimanthos, 1 km E Kalentzion, 1200 m. s.m., P, 1969. — **500** (27): Kriti, 1 km E Adele, 75 m. s.m., Bt & Hl, 1971. — **502** (18): Kriti, 0.5 km E Mouliana, c. 40 m. s.m., Bt & Hl, 1971. — **504** (18): Kriti, near Moni Toplou, c. 175 m. s.m., Bt & Hl, 1971. — **506** (18): Kriti, 2 km NW Kalogeri, c. 350 m. s.m., Bt & Hl, 1971. — **507** (18): Kriti, 2 km W Fourni, c. 300 m. s.m., Bt & Hl, 1971. — **509** (18): Rodhos, 2 km N Arnitha, c. 100 m. s.m., Bt & Hl, 1971. — **512** (18): Rodhos, 3 km N Mt. Tsambika, Bt & Hl, 1971. — **514** (18): Rodhos, 1 km N Kalithies, Bt & Hl, 1971. — **516** (18): Kriti, 1 km S Klima, c. 100 m. s.m., Bt & Hl, 1971. — **517** (18): Kriti, 2 km N Siva (18 km SSW Heraklion), c. 280 m. s.m., Bt & Hl, 1971. — **518** (18): Kriti, 1 km W Makrigiani, vineyard, Bt & Hl, 1971. — **520** (27): Kriti, E Grimbithiana, c. 25 m. s.m., Bt & Hl, 1971. — **524** (18): Skiros, Molos, 0—10 m. s.m., S & G, 1971. — **528** (18): Euboea, 1—2 km NNE Karystos, 50—250 m. s.m., S & G, 1971.

Chromosomal Polymorphism in Isolated Populations of Elymus (Agropyron) in the Aegean

I. Elymus striatulus sp. nov.

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ABSTRACT

Heneen, W. K. & Runemark, H. 1972. Chromosomal polymorphism in isolated populations of Elymus (Agropyron) in the Aegean. I. Elymus striatulus sp. nov. — Bot. Notiser 125: 419—429.

Elymus striatulus is a diploid littoral species (2n=14) found in the Aegean area. A brief taxonomic treatment of the species is presented. Twenty-six individuals representing six populations were studied cytologically. The chromosomes have a small range of length, but can be easily identified into pairs. Two pairs have characteristic satellites. The seven pairs are very similar to, and may correspond to, the seven largest pairs in *E. farctus* ssp. *boreo-atlanticus* and *E. rechingeri*. Chromosomal polymorphism expressed as slight differences in the appearance of the satellited chromosomes was found. Three of the variant satellited types corresponded to variant types found in *E. rechingeri*. Meiosis was apparently normal, but fertility was low.

INTRODUCTION

Elymus striatulus is one of three new *Elymus* species found by Runemark in the Aegean. *E. striatulus* is a diploid whereas the other two species, *E. rechingeri* and *E. diae*, are tetraploid and octoploid, respectively. Morphologically the three species together with *E. farctus* (= *Agropyron junceum*) constitute a closely related group.

The present work deals mainly with the cytology and briefly with the taxonomy of *E. striatulus*. The occurrence of chromosomal polymorphism in this species was pointed out in an early report (Heneen & Runemark 1969). Chromosomal polymorphism also characterizes the other two Aegean species *E. rechingeri* and *E. diae* (Heneen & Runemark 1962, in prep. a and b).

TAXONOMY

Elymus striatulus Runemark, sp. nov. (Fig. 1)

Orig. coll.: Greece. Cyclades. Mikonos, the bay E. of Ormos Ornos 18.6. 1960 Runemark & Nordenstam 16157 (LD holotype).

Agropyron elongatum (L.) BEAUV. var. *aegaea* RECHINGER FIL. 1939 p. 544. — Orig. coll. Greece. Thracia. Porto Lagos 16.6. 1936 RECHINGER 9636 (W lectotype).

DIAGNOSIS. *Elymo farcto* (*Agropyro junceo*) similis, sed omnibus partibus minor, caespitosus, foliis striatulis et numero chromosomatum 2n=14. Holotypus: Graecia, Cyclades, Mikonos 1960 RUNEMARK et NORDENSTAM 16157 in Museo Botanico Lundensi.

DESCRIPTION. A densely caespitose perennial, 12—35 cm high, at least often also developing long rhizomes. Culms erect to slightly curved. Basal internodes often inflated. Vegetative shoots not developed during flowering.

Leaves convolute, straight or slightly curved, 1—2 mm in diameter. Abaxial surface longitudinally striate, glabrous. Adaxial surface with prominent ribs, densely covered with short, stiff, spreading hairs. Basal part of the blade without auricles. Sheaths smooth, glabrous, basal ones persistent, membranaceous, brown or exceptionally brownish-black, finally fibrous. Ligule 0.5—1 mm, truncate, minutely fimbriate at apex.

Epidermal cells of the abaxial side of the leaves square in transverse section. Sclerenchymatous tissue not forming a continuous layer inside the epidermis but restricted to the regions around the veins.

Spike erect, more or less slender, 3—12 cm and with 3—10 solitary spikelets. 1—3 of the basal spikelets often reduced and sterile. Rhachis flattened, smooth, fragile and disarticulating when mature. Internodes of the rhachis in lowermost part as long as or longer than the spikelets, in upper part often shorter than the spikelets. Spikelets 8—14 mm with 3—5 florets. Glumes subequal 7—12 mm, obtuse, asymmetrically keeled, and with 3—5 veins not reaching the apex, glabrous. Lemma 6—9 mm, obtuse, 3—5-veined, glabrous except for the minutely pubescent margins. Palea somewhat shorter than the lemma, folded along the two pubescent veins, slightly emarginate. Anthers 4—5 mm, yellow. Caryopsis 5—7 mm, brown. Chromosome number 2n=14.

VARIABILITY. Morphologically *Elymus striatulus* is fairly invariable.

AFFINITIES. *Elymus striatulus* belongs to the series *Junceae* established (within *Elytrigia*) by NEVSKI. It is the single diploid member known within this complex. It is not closely related to *E. elongatus* (*Agropyron elongatum*) as suggested by RECHINGER (1939).

Material of series *Junceae* from the Black Sea region (e.g. the Crimea, Sudak 1896 CALLIER distributed as Herbarium Normale no. 3397 by DÖRFLER) resembles *E. striatulus*, but all parts are larger and it has larger epidermal cells. An experimental and cytological analysis of material from this area is urgently needed.

ECOLOGY. On mobile sand and gravel in the littoral zone, never found in closed plant communities.

DISTRIBUTION. Scattered localities all over the Aegean.

Known localities

GREECE. Thracia. Porto Lagos 1936 RECHINGER 9636 (W) — Macedonia. Kavalla, Kalamitsa 1936 RECHINGER 10157 (W) and 1960 RUNEMARK cult. no. 3675 (LD) — Northern Sporades. Skiros, N.E. of the town 1960 RUNEMARK & NORDENSTAM 19600, 19602, 19603 (LD) — Cyclades. Mikonos: Ormos Ornos 1960 ibid. 16060 (LD), Tershana Pt 1960 ibid. 16259 (LD), the bay E. of Ormos Ornos 1960 ibid. 16157 (LD), the bay inside Agrelos Pt 1960 ibid. 16173 (LD) — Naxos, W. of Mitria 1958 RUNEMARK cult. no. 1500 (LD) — Crete. Iraklion, Gazi 1960 RUNEMARK & NORDENSTAM 16531 (LD) — Pedeada, Cap Chersonisos 1960 ibid. 16546 (LD) — Sitia, Grandes Bay 1960 ibid. 16582 (LD).

CYTOLOGICAL MATERIAL AND METHODS

A total of 26 plants of *Elymus striatulus* were studied cytologically. These plants were raised from seeds collected from nine localities on the Aegean islands. Each of these nine localities was represented by one to four plants that were grown in greenhouses. The localities (Fig. 2) from which the seeds were collected are the following:

Fig. 1. *Elymus striatulus* (holotype). Habit ×0.8; detail of spike ×2.

Macedonia. Kavalla, Kalamitsa (cult. no. R-3725). In mobile sand.

Northern Sporades. Skiros, N.E. of the town (cult. no. R-3629, 3646, 3647, 3649). The four localities are situated within 1 km and represent different morphological types as well as minor differences in habitat (mobile sand to hard, coarse gravel). They may represent the variation within a rather large and widespread population.

Cyclades. Naxos, W of Mitria (cult. no. R-1500). A rather small population confined to sand. — Mikonos, Ormos Ornos (cult. no. R-3654, 3658). R-3654 represents material from sand and R-3658 material from gravel mixed with small stones from a rather small population.

Crete. W. of Gazi (cult. no. R-3605). A small population on coarse sand. — Cap Chersonisos (cult. no. R-3674). A small population on gravel.

Feulgen-squash preparations were made from root-tips using the method described by ÖSTERGREN & HENEEN (1962). For pollen mother cells, Carnoy fixative (alcohol: chloroform: acetic acid; 6: 3: 1) was used, and staining was by the Feulgen method. Lactophenol acid fuchsin was used as a pollen stain.

CYTOLOGICAL RESULTS

Karyotype

The diploid chromosome number 2n= 14 was found in *Elymus striatulus* (Fig. 3). The chromosomes vary in length between 6 and 8 μ which is approximately the size range of the largest chromosomes in the tetraploid species *E. farctus* ssp. *boreo-atlanticus* and *E. rechingeri* (HENEEN 1962, HENEEN & RUNEMARK in prep. a). Besides similarity in size, the chromosomes of *E. striatulus* also have morphological characteristics in common with the seven largest pairs in these two species. Fig. 3 C shows a karyotype in which the chromosomes are designated with the Arabic numerals 1—7.

Pair 1 — The largest pair in the complement, with submedian centromeres.

Pair 2 — Large chromosomes, slightly shorter than pair 1, with median or nearly median centromeres.

Pair 3 — Large chromosomes with a small satellite on the short arm. This pair has the lowest short/long arm ratio in the complement.

Table 1. Constitution of the satellited chromosomes in six populations of *Elymus striatulus*.

Localities	Satellited chromosomes					
	A_2A_2 B_1B_1	A_2A_2 B_1B_5	A_2A_2 B_1B_4	A_2A_2 B_1B_3	A_2A_2 B_1B_6	A_6A_6 B_1B_4
Kavalla						
R-3725 . . .	1	–	–	–	–	–
Skiros						
R-3629 . . .	3	–	–	–	–	–
R-3646 . . .	3	–	–	–	1	–
R-3647 . . .	–	4	–	–	–	–
R-3649 . . .	–	–	–	1	–	1
Mikonos						
R-3654 . . .	2	–	–	–	–	–
R-3658 . . .	2	–	–	–	–	–
Naxos						
R-1500 . . .	–	–	2	–	–	–
Crete, Gazi						
R-3605 . . .	3	–	–	1	–	–
Crete, Cap Chersonisos						
R-3674 . . .	2	–	–	–	–	–
Sum	16	4	2	2	1	1

Pair 4 — The chromosomes are of about the same length and arm ratio (submedian centromeres) as pair 5, with no detectable secondary constrictions, however. Pairs 4 and 5 are intermediate in length between the relatively longer and shorter chromosome pairs nos. 1—3 and 6—7 respectively.

Pair 5 — The chromosomes have large satellites; the short arm being divided by a clear secondary constriction into two almost equal parts. Occasionally a faint secondary constriction was visible near the end of the long arm.

Pair 6 — One of the two smallest pairs, with median or almost median centromeres.

Pair 7 — The chromosomes are equal in size to or slightly smaller than pair 6. The centromere is submedian.

The two satellited pairs (nos. 3 and 5) are morphologically similar to those found in *E. farctus* ssp. *boreo-atlanticus* (HENEEN

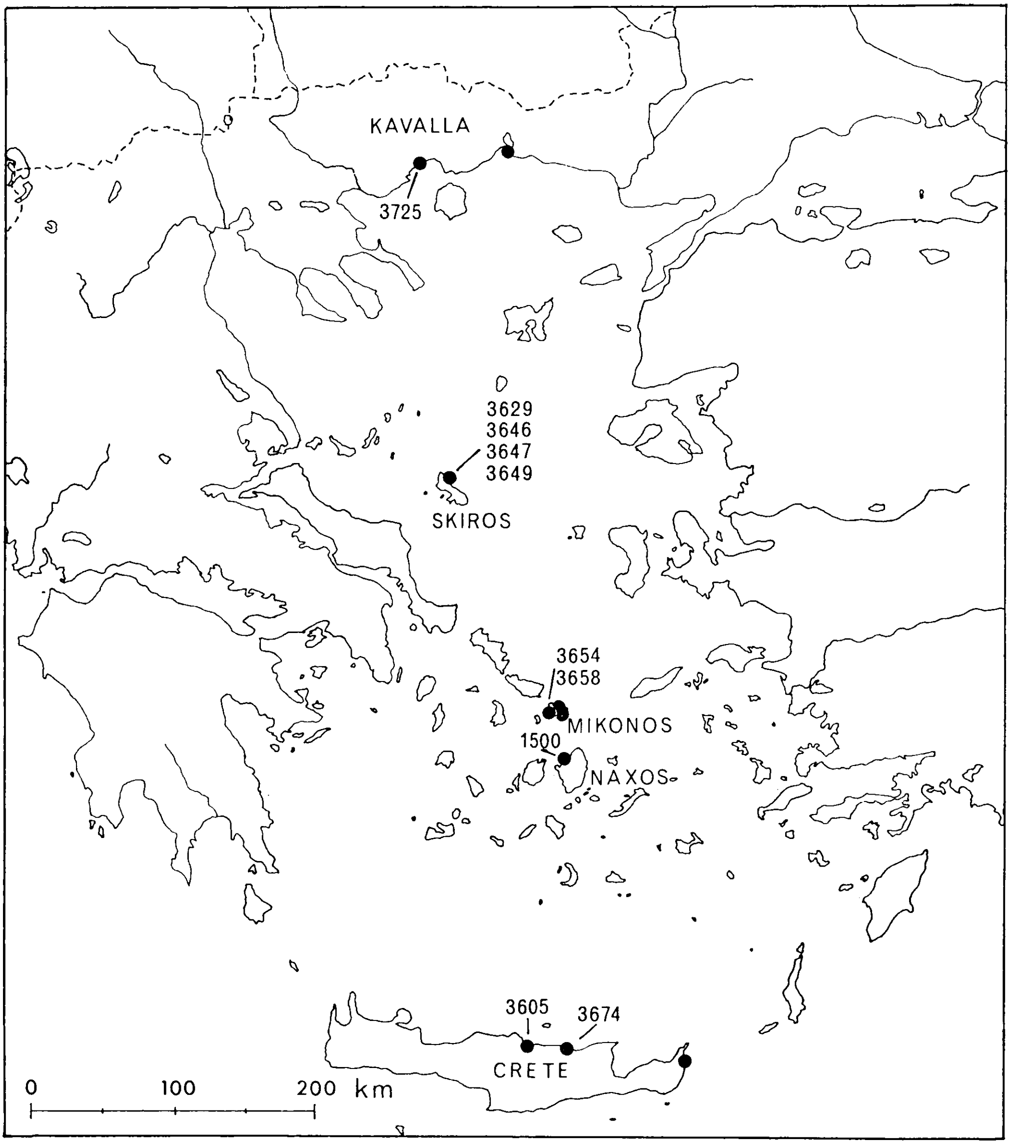


Fig. 2. A map of the Aegean showing all known localities of *Elymus striatulus* and six populations represented in the present study.

1962) in which the pair with the large satellite also exhibited an occasional faint secondary constriction at the end of the long arm. Further, they are similar to the satellited chromosomes referred to as pairs AA and BB in *E. rechingeri* (HENEEN & RUNEMARK 1962, in prep. a).

It appears as if not only the two satellited pairs but even the rest of the chromosomes in *E. striatulus* might correspond to specific chromosomes in *E. farctus* ssp. *boreo-atlanticus* and *E. rechingeri*. Thus, comparison between the seven pairs of *E. striatulus* with pairs 1—7 (the largest pairs) in the complements of the other two species (HENEEN 1962, HENEEN & RUNEMARK in prep. a) shows a striking similarity in chromosome size and position of centromere.

Chromosomal Polymorphism

Variations in the appearance of the satellited chromosomes were observed among the 26 individuals which represented six populations. The different types of satellited chromosomes found are shown in Fig. 4. The types of satellited chromosomes described under the karyotype section (pairs 3 and 5) were the commonest, being found in 16 individuals (Table 1), and probably represent the species. They are referred to as pairs, A_2A_2 B_1B_1 in Fig. 4 because of their similarity to the largest satellited pairs of *E. rechingeri* ($2n=28$) where such designations were adopted (HENEEN & RUNEMARK 1962, in prep. a). The variant satellited types are designated B_3, B_4, B_5, B_6 and A_6. As can be seen in Table 1, satellited chromosome constitutions other than A_2A_2 B_1B_1 occur sporadically.

The satellited types B_3, B_4 and A_6 have been observed in *E. rechingeri* which also exhibits chromosomal polymorphism (HENEEN & RUNEMARK in prep. a). The secondary constriction in B_3 is faint and hardly detectable whereas in B_4 it divides the short arm into two unequal segments, the satellite segment being slightly smaller than the proximal segment. Chromosome A_6 is characterized by the smallness of its long arm, being about two-thirds the normal size.

The satellited types B_5, B_6 are new. Contrary to B_4, the satellite segment in chromosome B_5 is slightly longer than the proximal region of the short arm. In chromosome B_6 the constriction is in the middle of the short arm; however, the short arm as a whole is longer than usual.

The differences between the different types of chromosome B in different individuals or populations are small though constant. Pair A_6A_6, on the other hand, differs markedly from the usual A_2A_2 constitution. In spite of the limited number of individuals studied it seems that variations in satellited chromosome constitutions occur both between and within populations.

Meiosis

Meiosis, studied in pollen mother cells was generally found to be normal. Pairing data from four individuals are presented in Table 2. The majority of the cells had seven bivalents that were usually ring-shaped (Fig. 5 A). A maximum of two univalents was sometimes observed (Fig. 5 B). The frequency of cells with univalents varied in different individuals and ranged between 0.4 and 13.2 % (Table 2).

Anaphase I was generally normal. Occasional abnormalities such as separation difficulties (Fig. 5 C), breakage, and lagging of chromosomes were encountered. About 99 % of the pollen looked normal. Seed-setting was however very poor under greenhouse conditions. One and 15 seeds were obtained from 10 and 143 spikes after isolation or open pollination, respectively. The poor seed-setting may be largely due to the inadequate conditions for cross-fertilization provided by the limited material in the greenhouse. Low fertility was also observed in natural populations.

DISCUSSION

The *Elymus* (*Agropyron*) complex consists mainly of polyploid species, the origin of which has always been the subject of investigation and experimentation. The discovery that *Elymus striatulus* is a diploid, and is morphologically and cytologically related to a certain group of

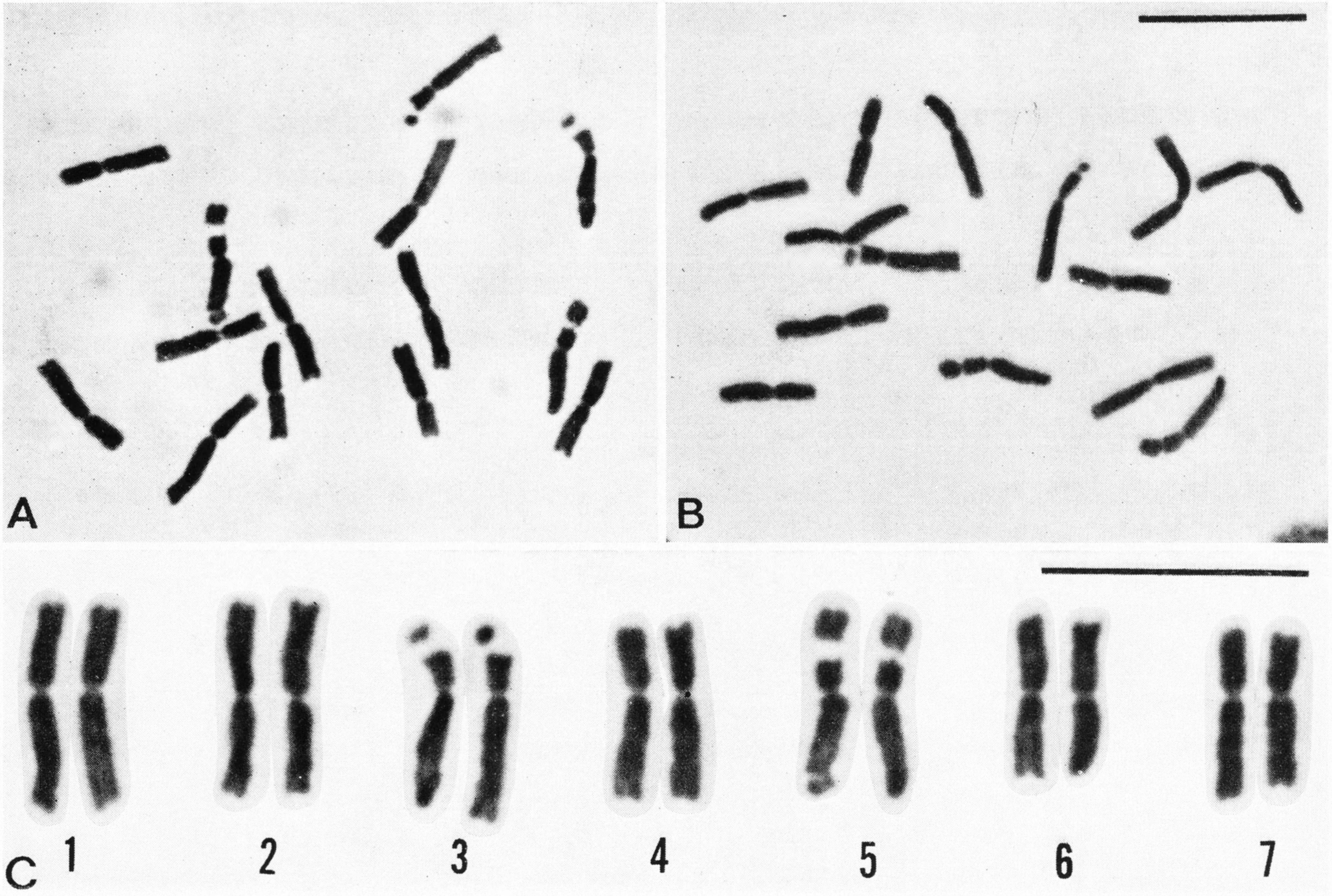
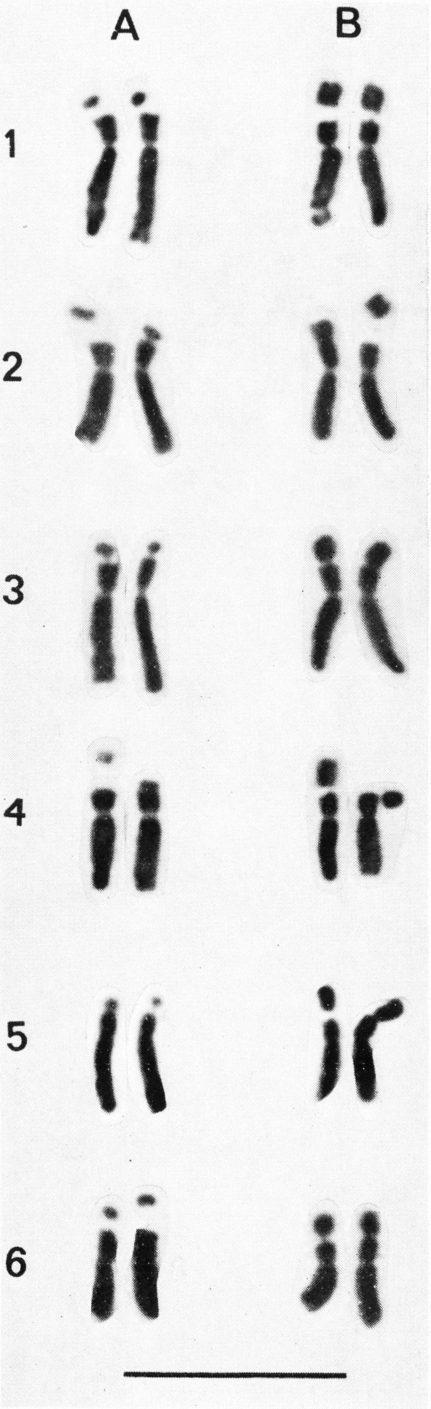


Fig. 3. *Elymus striatulus*. Somatic metaphase chromosomes. — A and B: Complements with the satellited chromosome constitutions A_2A_2 B_1B_1 and A_2A_2 B_4B_1, respectively. — C: Karyotype of the metaphase cell shown in A. — Scale equals 10 µ.


A
B
1
2
3
4
5
6

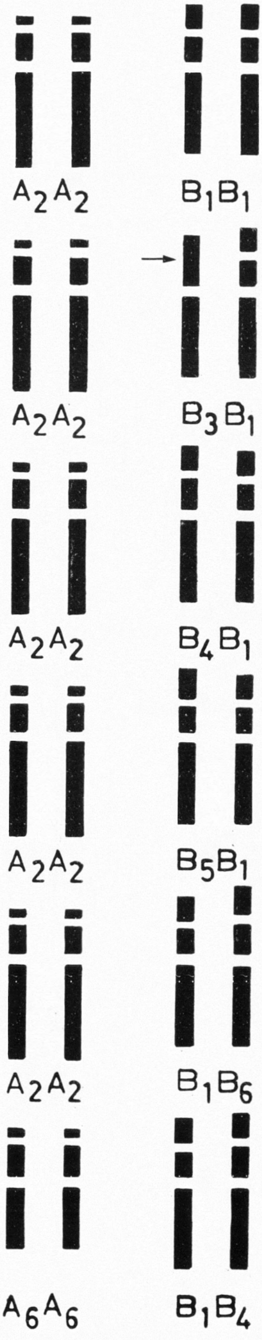

A_2A_2
B_1B_1
A_2A_2
B_3B_1
A_2A_2
B_4B_1
A_2A_2
B_5B_1
A_2A_2
B_1B_6
A_6A_6
B_1B_4

Table 2. Types and frequencies of metaphase I configurations in pollen mother cells of four individuals of *Elymus striatulus*.

Plant No.	Metaphase I configuration							Total No. of cells	% cells with univalents
	Only bivalents			Bivalents and univalents					
	Ring	Rod	No. of cells	Ring	Rod	I	No. of cells		
1	6.75	0.25	268	6.00	0.00	2	1	269	0.4
2	6.74	0.26	92	5.00	1.00	2	1	93	1.1
3	6.27	0.73	51	5.67	0.33	2	3	54	5.5
4	5.58	1.42	66	4.30	1.70	2	10	76	13.2

species is of value in determining the constitution and possible origins of genomes in certain polyploid species. The other Mediterranean diploid taxa in this complex are *E. elongatus* ssp. *elongatus* and ssp. *haifensis* (HENEEN & RUNEMARK 1972).

That *Elymus striatulus* is more closely related to *E. farctus* (=*Agropyron junceum*), *E. rechingeri* and *E. diae* than to *E. elongatus, E. caninus* and *E. repens* is indicated by the appearance of the satellited chromosomes (HENEEN 1962, HENEEN & RUNEMARK 1962, 1972, in prep. a and b, RUNEMARK & HENEEN 1968). These similarities and differences agree with the morphological and taxonomical findings (RUNEMARK, in prep.).

The possibility that the chromosomes of *E. striatulus* correspond to the seven largest pairs in the tetraploid species *E. farctus* ssp. *boreo-atlanticus* and *E. rechingeri* suggests that its two genomes are represented in these tetraploid taxa. *E. farctus* ssp. *boreo-atlanticus* has been given the genome formula J_1J_1 J_2J_2 (ÖSTERGREN 1940, CAUDERON 1958). A genome formula for *E. striatulus* may thus be expressed as J_1J_1. It would be of interest to analyze pairing relationships in triploid hybrids between these diploid and tetraploid species if such hybrids could be obtained. In the few trials made, no hybrids were acquired (HENEEN in prep.). The differences between on the one hand *E. striatulus, farctus, rechingeri* and *diae*, and on the other hand *E. elongatus, E. caninus* and *E. repens* are found in the morphology of the satellited chromosomes as well as in the size and centromeric position of the other chromosomes in the complement.

The polymorphism of the satellited chromosomes found in *E. striatulus* was not associated with morphological diversity such as that found in *E. rechingeri* (HENEEN & RUNEMARK 1962, RUNEMARK in prep.). A point worth mentioning in this respect is the fact that the variations in the appearance of the satellited chromosomes in *E. striatulus* were much less pronounced than those observed in the polyploid species *E. rechingeri* and *E. diae* that are also found in the Aegean (HENEEN & RUNEMARK in prep. a and b). A point of interest is the discovery that three of the five variant satellited chromosome types were similar to variant types found in *E. rechingeri*. This, and similar observations on the occurrence of the same type of variant satellited or marker chromosomes in *E. rechingeri* and *E. diae* are discussed elsewhere (HENEEN & RUNEMARK in prep. c).

The seeds of *E. striatulus* used in the present investigation were collected from

Fig. 4. Different satellited chromosome constitutions represented in the material of *Elymus striatulus* studied. Scale equals 10 μ.

Fig. 5. Meiosis in pollen mother cells of *Elymus striatulus*. — A: Metaphase I, 7 II. — B: Metaphase I, 6 II+2 I. — C: Anaphase I, a lagging bivalent exhibiting separation difficulties. — Scale equals 10 μ.

localities that are somewhat different ecologically. Whether the chromosomal polymorphism observed can be attributed to ecological differences or to other factor(s) remains to be elucidated. However, the main factor influencing the choice of biotopes may well be low competition capacity, as *E. striatulus* has always been found in localities devoid of or almost devoid of other plants.

A low degree of fertility characterizes *E. striatulus,* both in the field and in the greenhouse, in spite of the apparently normal meiosis observed and the high percentage of morphologically good pollen. Apart from possible genetic factors, the low degree of fertility could perhaps be attributed to inadequate conditions for cross-fertilization, especially in clones and in small populations.

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We want to thank Dr. GUNNAR WEIMARCK for providing the drawing of the holotype of *Elymus striatulus.*

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Separation Difficulties During Anaphase I in Elymus (Agropyron) Species

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ABSTRACT

HENEEN, W. K. 1972. Separation difficulties during anaphase I in Elymus (Agropyron) species. — Bot. Notiser 125: 430—438.

Instances of separation difficulties during anaphase I were observed in a number of *Elymus* species and were especially frequent in *E. rechingeri.* The abnormality is expressed terminally or interstitially in one or both chromatids of the separating chromosomes. The interstitial types appeared as side-arm bridges either with both side-arms on the one side or one on each side of the bridge. Breakage occurred in the middle between the two side-arms and/or between side-arms and centromeres. The abnormality is most likely a result of sub-chromatid exchanges. The possibilities that sub-chromatid breakage and reunion may take place at half- and other partial-chromatid levels and that the configurations observed may represent defective chiasmata are discussed.

INTRODUCTION

Side-arm bridges at anaphase have been described during mitosis and meiosis in a variety of material (see EVANS 1962, CROUSE 1961, MELANDER 1963, HENEEN 1963 a, LEWIS & JOHN 1966, NEWMAN 1967, BRANDHAM 1969, 1970). This type of aberration represents a common expression of pseudo-chiasmata and is generally attributed to sub-chromatid exchanges that lead to separation difficulties at anaphase. In addition to being inducable by a variety of agents, the phenomenon seems to be of common occurrence in several plant and animal groups.

In the course of a cytological study on different *Elymus* species, configurations portraying this type of abnormality were encountered at meiotic anaphase. Separation difficulties at anaphase I were especially common in *E. rechingeri* (HENEEN & RUNEMARK 1962). In the present paper, the morphology of chromosomes undergoing separation difficulties are described, and the nature of sub-chromatid breakage is also further discussed.

MATERIAL AND METHODS

Species nomenclature in the present paper is in accordance with the system recommended by RUNEMARK and HENEEN (1968). The *Elymus* species investigated are the following:

E. elongatus (HOST) RUN. ssp. *elongatus* (2n = 14) and ssp. *flaccidifolius* (BOISS. & HELDR.) RUN. (2n = 28).

E. striatulus RUN. (2n = 14).

E. rechingeri (RUN.) RUN. (2n = 28).

E. farctus (VIV.) ssp. *farctus* (2n = 42) and ssp. *boreo-atlanticus* (GUIN. & SIMONET) (2n = 28).

E. repens (L.) (2n = 42).

E. diae RUN. *nomen nudum* (2n = 56).

The material of *Elymus elongatus, striatulus, rechingeri, farctus* ssp. *boreo-atlanticus* and *repens* that was studied is the same as that reported in HENEEN (1962) and HENEEN & RUNEMARK (1962, 1972 a and b). The material of *E. farctus* ssp. *farctus* and *diae* is of Mediterranean origin. Detailed information on the collections studied of these two species, and also of additional material of *E. rechingeri* will be presented elsewhere. *E. diae* is an Aegean new species found by RUNEMARK and preliminarily referred to in HENEEN & RUNEMARK (1962).

Meiosis was studied in pollen mother cells of spikes fixed in Carnoy (ethyl alcohol-chloroform-acetic acid; 6: 3: 1). Staining was according to the Feulgen method and the plastic coverslip method (ÖSTERGREN & HENEEN 1962) was used to make the slides permanent.

RESULTS

The meiotic aberrations that will be dealt with here represent a specific kind of irregularity that has frequently been encountered in *Elymus rechingeri* (Fig. 1), and occasionally in the other *Elymus* species studied (exemplified by Fig. 2). The affected bivalents exhibit separation difficulties at anaphase I and usually lag behind the rest of the chromosomes that have already separated. The abnormality is usually accompanied by chromatin stretching, bridge-formation and subsequent breakage in the attenuated regions of the separating chromosomes. No free fragments were found in association with these bridges which were mainly of the type referred to as side-arm bridges. In *E. rechingeri,* anaphase I cells showing separation difficulties amounted to 24 % (HENEEN & RUNEMARK 1962).

The segregating chromosomes that exhibit separation difficulties can be placed in different categories depending on whether the point at which they are hindered from complete separation is terminal or interstitial, and whether one or both chromatids are involved. This classification is approximate and is only meant to give an idea of the morphological expressions of this phenomenon in a pollen mother cell population. As will be pointed out later, interstitial types may appear as terminal types in later stages of anaphase I. Separation difficulties are usually encountered in only one chromosome arm. In chromosomes with distinctly unequal arms, the aberration is frequently observed in the long arm.

Two Chromatids Involved Terminally or Interstitially

In terminal types, the separating chromosomes are held together at the distal ends (Fig. 3 A—F). At early stages of anaphase, the two separating chromosomes appear as a dicentric with a constriction in the middle region (Fig. 3 A—B). At later stages, attenuation of chromatin occurs in interstitial regions of the separating arms (Fig. 3 C—F). This is manifested in one or both arms and in the latter case, usually at corresponding points. The progression of centromere movements towards the poles in such bivalents leads to a continuous thinning of the attenuated regions and their subsequent breakage. When breakage occurs in only one arm the result will be a deficient chromosome moving to one pole, whereas the distal segment of this chromosome associated with the other homologue will be included in the other polar region (Fig. 3 E—F).

In the region of association between the separating chromosomes shown in Fig. 3 G—H, the distal segments of each chromatid diverge slightly. This may indicate that the points of separation difficulties are not at the distal ends but in their proximity.

In configurations of the interstitial type that involve two chromatids (Fig. 3 I—K), the separating chromosomes exhibit two dicentric chromatid bridges with chromatin material as side-arms on these bridges. Fig. 3 L may represent a situation in which separation difficulties are at an interstitial point in one chromatid and at a terminal point in the other chromatid.

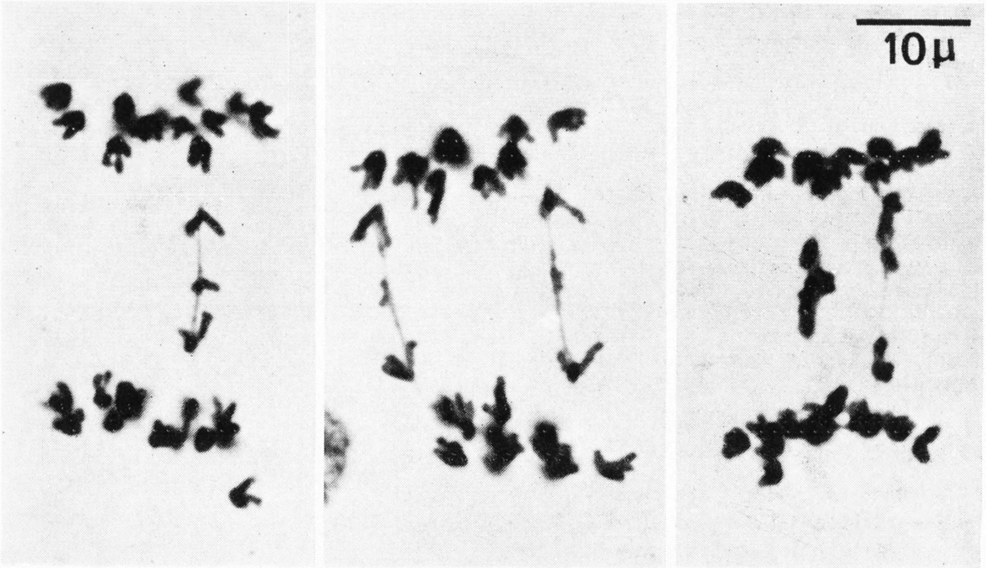

Fig. 1. Separation difficulties at anaphase I in three pollen mother cells of *Elymus rechingeri* (2n=28).

One Chromatid Involved Terminally or Interstitially

In these configurations, only one dicentric chromatid holds the separating chromosomes together. The examples shown in Fig. 3 M—N may represent terminal types, whereas Fig. 3 O—X shows interstitial types which were commoner. The positions of the side-arms in relation to each other and in relation to the attenuated parts of the bridge vary, thus leading to a diversity of appearance of the interstitial types. The two side-arms were either adjacent and touching each other (Fig. 3 O—S) or in parallel positions and separated by part of the bridge (Fig. 3 T—X). The side-arms were either both on the same side of the bridge (Fig. 3 S—V) or one on each side (Fig. 3 W—X).

Breakage of the bridge can take place at any point, either in the middle between the two side-arms or between the side-arms and the centromeres. When the bridge is broken between the two side-arms, these may change their position and instead of continuing to lie perpendicular to or at an angle to the bridge, they take up a position parallel to the attenuated chromatin. The appearance of the lower side-arm in the configuration shown in Fig. 3 V probably illustrates such a condition. If both side-arms behave in this way, the configuration will thus appear as a terminal type at an advanced anaphase stage in spite of its interstitial origin.

The two chromatid segments representing the side-arms were approximately equal in size. Different configurations of separation difficulties, however, exhibited varying sizes of side-arms.

DISCUSSION

Anaphase I bridges have been interpreted in the literature as representing three different conditions with chromosome breakage and reunion as a common

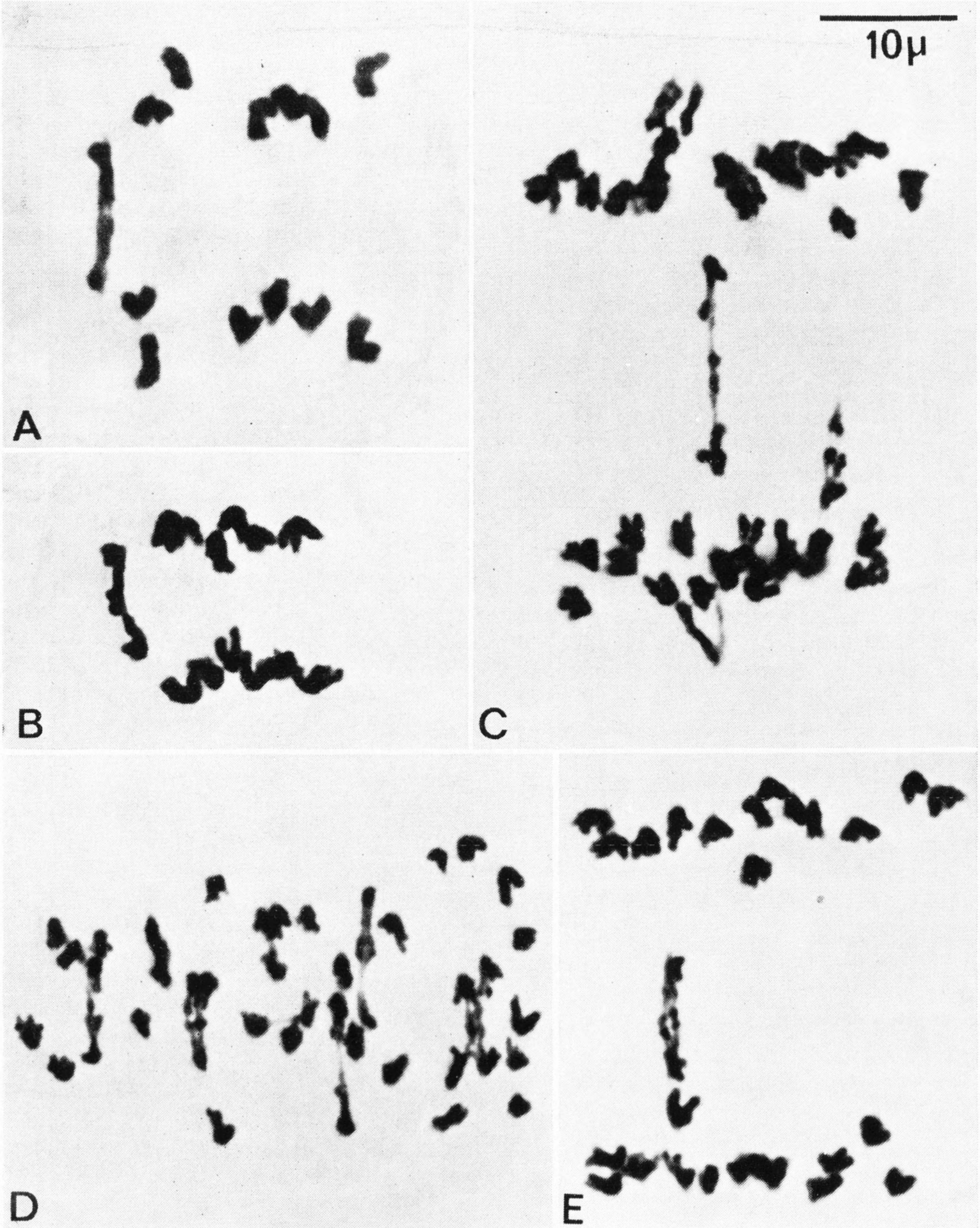

Fig. 2. Separation difficulties at anaphase I in pollen mother cells of different *Elymus* species. — A: *E. striatulus* (2n=14). — B: *E. elongatus* ssp. *elongatus* (2n=14). — C: *E. farctus* ssp. *farctus* (2n=42). — D: *E. repens* (2n=42). — E: *E. elongatus* ssp. *flaccidifolius* (2n=28).

denominator: (1) Crossing-over in the pairing loop of paracentric inversion heterozygotes (McClintock 1931). (2) Chromatid breakage and reunion (Matsuura 1950, Walters 1950, Haga 1953). (3) Sub-chromatid exchanges (La Cour & Rutishauser 1953, 1954, Wilson et al. 1959).

Free fragments are associated with the first two types of bridges only, with which we are not concerned in the present context. In the third type there may occur chromatin material connected to the bridge in the form of side-arms. Such configurations are referred to as side-arm bridges or pseudo-chiasmata (see Evans 1962). The aberrations described here are designated as separation difficulties (Walters 1957) in order to cover both terminal and interstitial events. Such a designation would also leave the door open for finding out if mechanisms other than sub-chromatid exchanges are involved in the evolvements of these abnormalities. Besides sub-chromatid exchanges and among other proposed interpretations of pseudo-chiasmata (see Melander 1963), stickiness might be another likely explanation. That stickiness and sub-chromatid exchanges induced by irradiations are two different and independent phenomena has been argued by Fox (1966).

The aberrations observed in the present *Elymus* material portray terminal and interstitial separation difficulties that most likely reflect a sub-chromatid exchange etiology. The interstitial types resemble the side-arm bridges, attributed to sub-chromatid exchanges and observed in a variety of material (e.g. John et al. 1960, Crouse 1961, Lewis & John 1966, Newman 1967, Brandham 1969, 1970). That sub-chromatid exchanges could give rise to terminal types of separation difficulties has also been pointed out (e.g. Brock 1955).

The interesting hypothesis that breakage-reunion events during meiosis represent errors in crossing-over has been forwarded by Darlington & La Cour (1952), Rees & Thompson (1955) and Lewis & John (1966). The testing of this hypothesis gave evidence favouring a related origin of chiasmata and chromatid and sub-chromatid exchanges (Jones 1968, 1969, Brandham 1970). A great number of meiotic anaphase aberrations may thus result from different patterns of reunions at sub-chromatid and chromatid levels on sites of defective crossing-over.

Elucidative schematic drawings showing possible origins of side-arm bridges following sister or non-sister sub-chromatid exchanges in the presence or absence of chiasmata can be found in Wilson et al. (1959), John et al. (1960), Crouse (1961), Lewis & John (1966) and Brandham (1970). In these models as well as in other reports (see Evans 1962), the sub-chromatid unit of exchange has usually been referred to as a half-chromatid. The subdivision of chromatids into half-chromatids has been pointed out in various material (see John & Lewis 1969). Such a subdivision in meiotic chromosomes has been disputed by Whitehouse (1968), however. The organizational pattern of chromatin fibres inside the chromosome is still an open question (Comings & Okada 1970).

Manifestation of sub-chromatid aberrations at other levels than at the half-chromatid level cannot be excluded (see e.g. Heneen 1963 b). Discussing meiotic errors and sub-chromatid exchanges, Darlington & La Cour (1952) and La Cour & Rutishauser (1953, 1954) pointed out the possible prevalence of partial effects that are a result of incomplete breakage and reunion.

Partial breakage and reunion is compatible with the above-mentioned concept that sub-chromatid and chromatid exchanges are presumably an expression of defective chiasmata and random patterns of reunion of breakage surfaces. It is also well established that breakage leading to sub-chromatid aberrations takes place

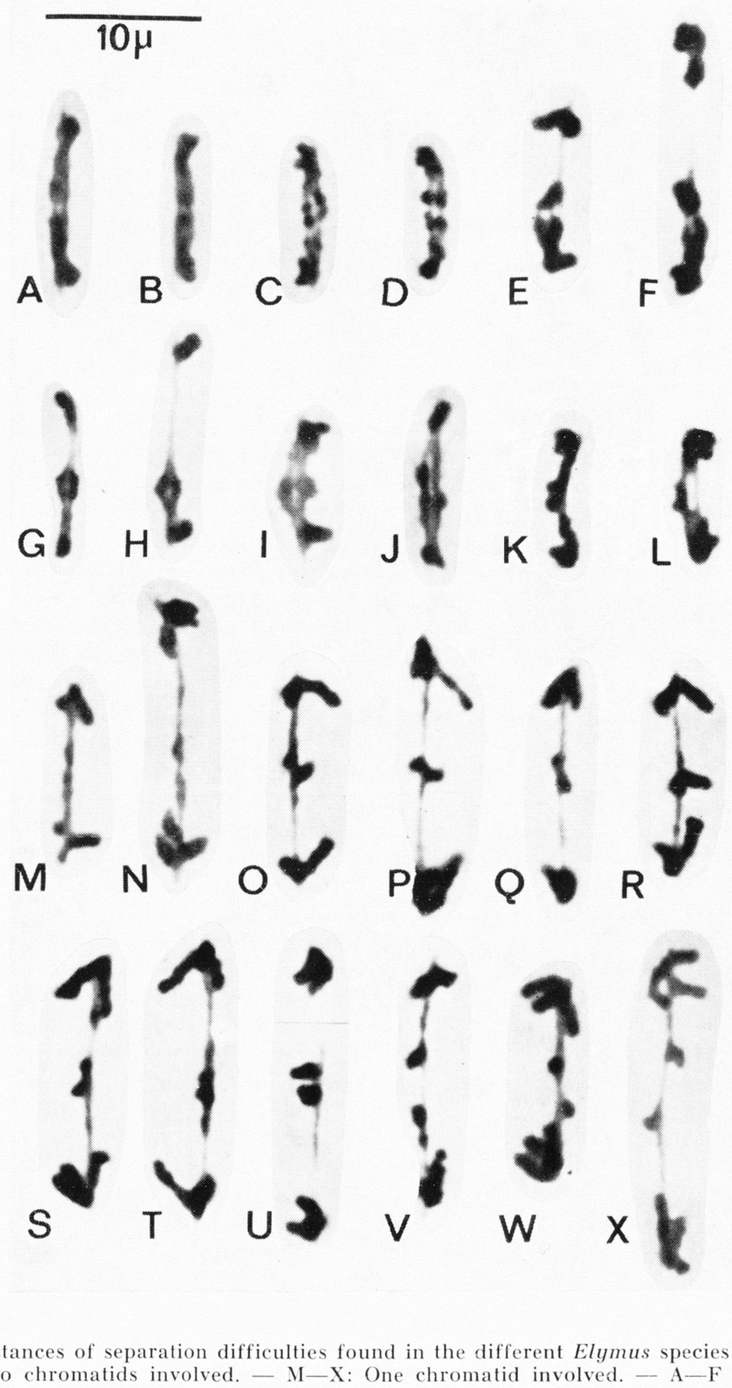

Fig. 3. Instances of separation difficulties found in the different *Elymus* species studied. — A—L: Two chromatids involved. — M—X: One chromatid involved. — A—F and M—N: Terminal types. — G—L and O—X: Interstitial types.

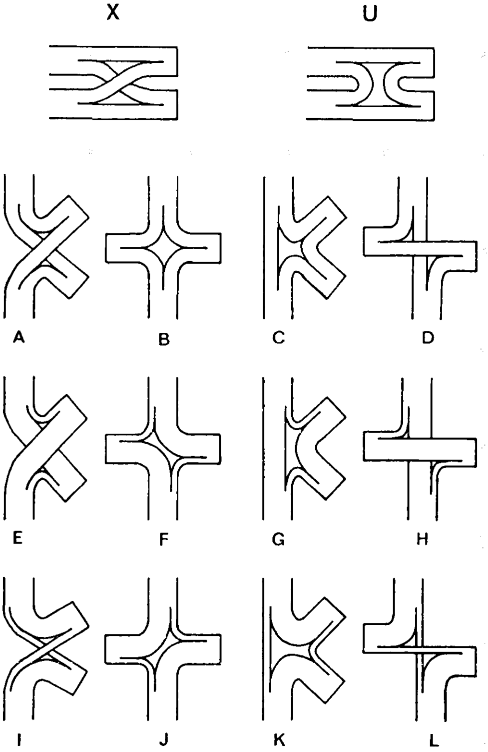

Fig. 4. Schematic drawings depicting X- and U-types of sub-chromatid exchanges. — A—D: Half-chromatids involved. — E—H: More than half-chromatids involved. — I—L: Less than half-chromatids involved. — In both the X- and U-types, side-arms are either on the same or different sides of the bridge.

in stages between pachytene and metaphase I (Evans 1962). These stages cover a wide range of chromosome condensation which might influence the expression and the extent of breakage and reunion. A partial effect is also the cytological expression if it is a question of complete fibre breakage and reunion in a spiralized (Östergren & Wakonig 1954) or folded (Kihlman & Hartley 1967, Kihlman 1970) fibral system. Partial exchanges at chromatid level and complete exchanges at fibral level might thus appear as partial-chromatid aberrations. This would explain the variation in appearance of side-arm bridges as regards side-arm positions and breakage points along the bridge.

Schematic drawings depicting side-arm bridges resulting from sub-chromatid reunions that involve both half- and partial-chromatids are presented in Fig. 4. "Half-" and "partial-chromatids" do not here refer to sub-chromatid organizational units. These terms are used in the sense that expression of breakage and reunion may involve any portion of the chromatid's cross-section, irrespective of the organizational nature of the fibres in the chromatid at different condensation levels. The drawings in Fig. 4 demonstrate bridges that result from X- and U-type exchanges. These diagrams also illustrate the position of the two side-arms, whether these are on one or both sides of the bridge. The appearance of bridges resulting from exchanges that involve more than or less than chromatid halves (Fig. 4 E—L) may be indicative of the most probable configurations to be expected at a later anaphase stage.

The U-type exchanges are especially informative in this respect. Thus the pattern presented in Fig. 4 G would give rise to a bridge that probably has continuous or parallel side-arms on the same side and breakage points between side-arms and centromeres (Fig. 3 S—T). Breakage in the middle of the bridge (Fig. 3 V) would be expected in the case of the pattern shown in Fig. 4 K. Similarly, the pattern in Fig. 4 H would give rise to a configuration with side-arms that originate at the same point and where breakage occurs between this point and the two centromeres (Fig. 3 R). The pattern in Fig. 4 L, on the other hand, would give rise to a bridge with side-arms on different sides and a breakage point between the side-arms (Fig. 3 W).

Separation difficulties of the terminal type could also be explained as being due to terminal partial-chromatid exchanges. Breakage in one chromatid or at corresponding positions in the two separating chromatids might take place at especially weak points along the two homologous chromosomes. That some of the terminal types are of interstitial origin is also possible. In such a case an interstitial exchange would involve a small fraction of the chromatid thus giving rise to thin bridges between separating chromosomes that might be classified as instances of terminal separation difficulties. Here also, secondary constrictions or attenuated regions would occur at corresponding points in the chromatids of the separating chromosomes.

It might be pointed out here that chromosomal polymorphism characterizes many of the species studied (HENEEN & RUNEMARK 1962, 1969, 1972 a and b) and may thus be among the factors that lead to the expression of the anomalies described. Incomplete homology between pairing chromosomes might interfere with proper chiasma formation and terminalization.

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Studies in the Flora of Northern Morocco

I. Some Poor Fen Communities and Notes on a Number of Northern and Atlantic Plant Species

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ABSTRACT

DAHLGREN, R. & LASSEN, P. 1972. Studies in the flora of Northern Morocco. I. Some poor fen communities and notes on a number of northern and Atlantic plant species. — Bot. Notiser 125: 439—464.

A number of poor fens with *Sphagnum auriculatum* SCHIMP. on four different mountains of the sandstone range of Jebala have been studied. The composition of the species found is described. Regularly occurring in the *Sphagnum* fens are especially *Anagallis crassifolia* THORE, *Eleocharis multicaulis* (SM.) SM., *Juncus bulbosus* L., *Agrostis castellana* BOISS. & REUT., *Agrostis juressii* LINK, and *Sieglingia decumbens* (L.) BERNH. These poor fens with *Sphagnum* are compared with two other spring and fen communities in the Sebta region and in Central Rif.

Soil samples show that the *Sphagnum* fens have a low content of organic matter. The pH values are around 5. Values of exchangeable cations are normal for poor fens.

Observations are also made on the occurrence and distribution of the following species in the Tanger—Rif region: *Polystichum aculeatum* (L.) ROTH, *Sieglingia decumbens* (L.) BERNH., *Molinia caerulea* (L.) MOENCH, *Nardus stricta* L., *Eleocharis multicaulis* (SM.) SM., *Carex echinata* MURR., *Carex leporina* L., *Carex oederi* RETZ. coll., *Carex paniculata* L., *Juncus bulbosus* L., *Genista anglica* L. ssp. *ancistrocarpa* (SPACH) MAIRE, *Frangula alnus* MILL., *Hypericum humifusum* L., *Viola persicifolia* SCHREB., *Chamaenerion angustifolium* (L.) SCOP., *Calluna vulgaris* (L.) HULL, *Erica ciliaris* L., *Anagallis crassifolia* THORE, *Gratiola officinalis* L., *Pinguicula lusitanica* L., and *Littorella uniflora* L. Some of these are new to the region. Localities are presented on maps.

REGION INVESTIGATED

Our study of the flora of Northern Morocco was started in 1970. Plant collections were then made in about 100 localities distributed over the Tingitanean Peninsula and the Rif Mountains, from Larache—Tanger in the west to the Beni Snassen Mountains in the east.

In the spring and summer of 1972, the research programme was continued when more intensive studies were carried out on the flora of the Tingitanean Peninsula (Tanger—Arzilah—Tetouan—Sebta—Tanger) and on the montane flora of the Rif Mountains, especially in the *Cedrus* and *Abies* zones, from Jbel Bou Hassim in the west to Jbel Oursane (south of Targuist) in the east. The former investigation was chiefly carried out by R. DAHLGREN, the latter by P. LASSEN.

In the course of our field work in 1972,

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[1] Analysis of some soil samples is presented by Mr. BO WALLÉN, Department of Plant Ecology, Ö. Vallgatan 14, S-223 61 Lund, Sweden.

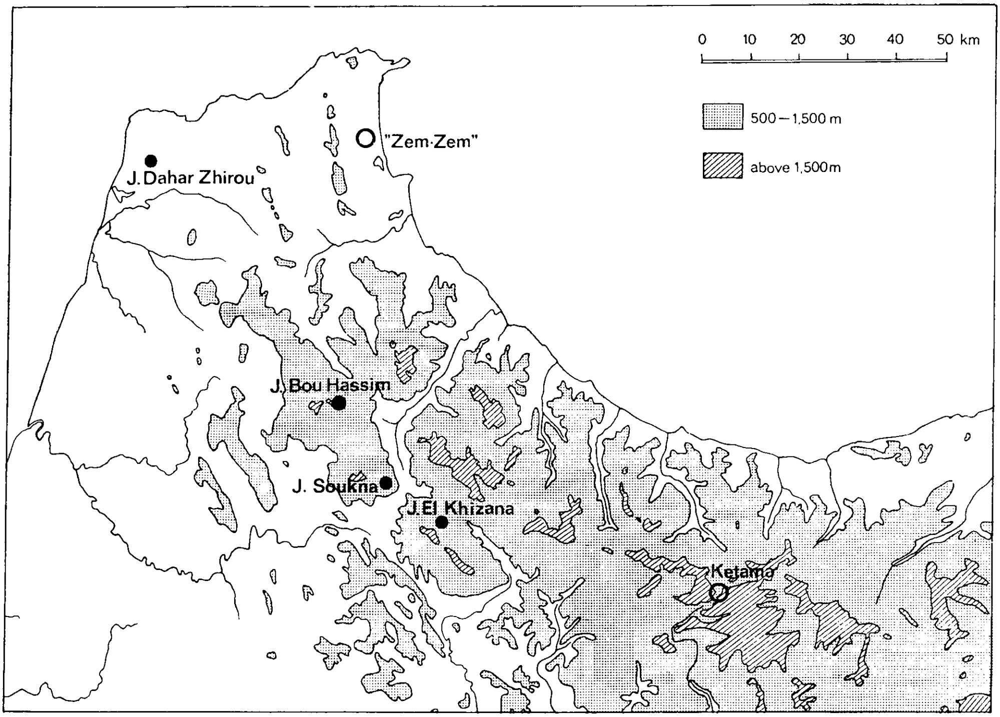


Fig. 1. Geographical situation of the four mountains where poor fens with *Sphagnum auriculatum* have been studied (dots) and of two other fens given in the text for comparison (circles).

we were attracted by the northern and Atlantic elements found particularly in the small patches of fen vegetation along the mountain range of Jebala. Taking the occurrence of *Sphagnum auriculatum* SCHIMP. as being an indication of poor fens, an unpretentious comparison of the species composition in similar fens is presented here together with the report of some finds of northern and Atlantic plant species in Northern Morocco. The names used are taken from the 1: 50,000 scale maps.

POOR FENS WITH SPHAGNUM IN NORTHERN MOROCCO

The four mountains where poor fen communities with *Sphagnum auriculatum* have hitherto been studied (Fig. 1) are all located along the Jebala Range with its extensions towards the north-west. The *Sphagnum* fens seen by us are at altitudes of between 700 and 1,250 m above sea level except on Jbel Dahar Zhirou, where the altitude is only about 150 m.

The Jebala Range consists largely of siliceous sandstones, which is reflected in the poorness of the soils (see "Analysis of soil samples", p. 461). Jbel Dahar Zhirou and Haouta Bern Mediar, which are very low mountains, belong to the "étage humide" of SAUVAGE (in EMBERGER 1964) with a precipitation of about 800—1,000 mm per annum (IONESCO & STÉPHANESCO 1967). Jbel Bou Hassim, Jbel Soukna and Jbel El Khizana (Bou Hachem, Sougna and Khessana in earlier literature) are much higher and are entirely exposed to the Atlantic winds from the west. During the period September 1971 to May 1972 the precipitation at the Forestry Office of Bou Hassim, close to a *Sphagnum* locality, was registered as c. 2,100 mm (personal communication), and during the summer period June—August there is still plenty of mist and even rain, although EMBERGER (1964) described the region as having a "Mediterranean" climate.

Owing to the permeability of the ground and the predominantly steep inclination, fens are however small and easily overlooked. This would explain the scarcity of previous records of some of the plants listed below.

STÉPHANESCO (in IONESCO & STÉPHANESCO 1967 p. 33) called the *Sphagnum* site on Jbel Dahar Zhirou a "tourbière", an expression used also by EMBERGER & MAIRE (1941 p. 953) for a *Sphagnum* fen on Jbel Soukna, but there is no question of raised bogs. All sites (except, perhaps, the "pool" on Jbel Bou Hassim) are poor fens with moving water. As will be shown below, the soil samples contain relatively little organic material.

Jbel Dahar Zhirou

Jbel Dahar Zhirou is not more than 280 m high. It is situated only about 8 km from the Atlantic coast. The *Sphagnum* occurrence on this mountain has previously been described by STÉPHANESCO in 1967. It is located on the northern side of the mountain on the gentle north-western slope of a broad valley open towards the north, at an altitude of 150 m. According to our estimation the site is about lat. 35°41′10″, long. 5°52′00″, which does not deviate much from STÉPHANESCO's statement. The slopes of the valley have an Atlantic "matorral" vegetation with species of *Erica, Calluna vulgaris* (L.) HULL, *Genista triacanthos* BROT., *Agrostis setacea* CURT., and *Drosophyllum lusitanicum* (L.) LINK. *Cistus crispus* L. is also common on the slopes, and shrubs of *Cistus populifolius* L. are found on the upper parts of the ridge.

The valley is partly cultivated, and small ditches occur. *Sphagnum auriculatum* grows in a water-pit, where it covers some 5 m². The rest of the pit is occupied by *Eleocharis multicaulis* (SM.) SM., growing to a height of 30—40 cm, by *Juncus bulbosus* L. and *J. conglomeratus* L., and floating *Panicum repens* L. *Anagallis crassifolia* THORE grows in the *Sphagnum* mat as well as on the bare wet soil. The pit is partly bordered by *Osmunda regalis* L., and *Gnaphalium luteo-album* L. grows on the walls of the pit. On the dry, upper margin there are shrubs of *Teline linifolia* (L.) WEBB & BERTH. — Noteworthy components common also to the more natural eastern fens with *Sphagnum* are *Eleocharis multicaulis, Juncus bulbosus* and *Anagallis crassifolia.*

Tufts of *Molinia caerulea* (L.) MOENCH occur in a ditch some 50 m from the *Sphagnum* pit, more abundantly near a spring about 600 m west of this, on the easterly slopes of the same valley. At this spring are also found: *Agrostis juressii* LINK in SCHRAD., *Anagallis crassifolia, Erica ciliaris* L., *Hypericum perforatum* L., *Juncus bulbosus, Pinguicula lusitanica* L., and *Sieglingia decumbens* (L.) BERNH.

Jbel Bou Hassim

The fens on Jbel Bou Hassim were studied in greater detail than any of the others. *Sphagnum auriculatum* was found in three places in this area. Two of these will be described below.

The Pool. One locality is a small pool (Fig. 2) situated in a small basin on the northern slopes of the mountain at an altitude of c. 1,210 m. The site is c. 3,400 m south of the little village of Tayenza, lat. 35°15′23″, long. 5°25′04″.

The pool is bordered on the western side by a rather steep slope covered with *Quercus canariensis* WILLD. and *Q. pyrenaica* WILLD., on the southern side by relatively flat ground with densely growing *Pteridium aquilinum* (L.) KUHN, and on the

Fig. 2. A small pool on Jbel Bou Hassim described in the text. *Sphagnum* (s) at the southern end, *Pteridium* in the foreground, and a few trees of *Quercus suber* to the right. The slope in the background with *Quercus canariensis* and *Q. pyrenaica*.

eastern side by a "matorral" with *Pteridium, Cistus salviifolius* L., *C. crispus, Erica arborea* L., and *Tolpis nemoralis* F.-Q., with sparse examples of *Quercus suber* L.

The pool is only about 60 cm deep in the deepest part and has gently sloping sides. It has a distinct shore zone of temporarily wet soil. *Sphagnum* is found only on the southern side, where it covers an area of 10—20 m^2.

The following species occur in the pool, where the water seems to be permanent and at the time of our visit was of some depth:

Agrostis castellana Boiss. & Reut.
Baldellia ranunculoides (L.) Parl.
Eleocharis multicaulis (Sm.) Sm.
Gratiola officinalis L.
Juncus bulbosus L.
Lythrum portula (L.) D. A. Webb
Mentha pulegium L.
Ranunculus tripartitus DC.

Sterile *Polytrichum* covers part of the bottom of the pool.

The temporarily wet soil along the margin of the pool is inhabited by:

Agrostis castellana Boiss. & Reut.
Cicendia filiformis (L.) Delarbre
Carex distans L.
Eleocharis multicaulis (Sm.) Sm.
Gratiola officinalis L.
Isoëtes histrix Dur.
Juncus bulbosus L.
Lotus subbiflorus Lag.
Ormenis sp.
Ornithogalum unifolium (L.) Ker-Gawl.
Plantago coronopus L. ssp. *cupani* (Guss.) Pilger
Ranunculus bulbosus L. coll.
Sieglingia decumbens (L.) Bernh.
Simethis planifolia (L.) Gren. & Godr.
Thrincia tuberosa (L.) DC.

Of these, *Plantago coronopus, Eleocharis multicaulis,* and in certain parts, *Ornithogalum unifolium* and *Isoëtes histrix* are dominant. *Hypericum humifusum* L. is found in somewhat drier parts, usually together with *Polytrichum.* Above this zone, *Moenchia erecta* (L.) GAERTN. and *Luzula multiflora* (EHRH.) LEJ. occur on dry tufts and tree-roots.

Patches of *Sphagnum auriculatum* are found in the shallow, southern part of the pool. Associated species are:

Eleocharis multicaulis (SM.) SM.
Galium palustre L. (narrow-leaved forms)
Genista anglica L. ssp. *ancistrocarpa* (SPACH) MAIRE
Hypericum humifusum L.
Oenanthe lachenalii C. C. GMELIN
Ormenis sp.
Potentilla erecta (L.) RÄUSCH.
Prunella vulgaris L.
Sieglingia decumbens (L.) BERNH.

Genista anglica in this locality is only about half a metre high (cf. below). A few examples of *Salix atrocinerea* BROT. occur in the same part of the pool, as do *Juncus conglomeratus* L. and *Montia lusitanica* SAMP.

Fens on the Lower North-Western Slopes. A system of fens is scattered over the lower north-western slopes of Jbel Bou Hassim, most of them approximately between lat. 35°15′10″, long. 5°25′25″ and lat. 35°15′30″, long. 5°25′50″, at an altitude of 1,060 to 1,100 m. Most fens are small, often only 10—20 m in diameter. The majority of them are scattered on slopes covered with an Atlantic heath-"matorral" vegetation, which is commoner on the Tingitanean Peninsula. *Cistus crispus, Erica umbellata, E. arborea, Tuberaria lignosa* (SWEET) SAMP., and species of *Halimium* are characteristic components. The fens vary somewhat in character, from those that are apparently rather poor like those with *Sphagnum,* to be described first, to those of a more intermediate character.

Two of the poorest fens where *Sphagnum auriculatum* is found, are situated near the Forestry Office at an altitude of about 1,090 m. The site is about lat. 35°15′10″, long. 5°25′26″. They have a distinct, oval to circular shape and are rather sharply delimited from the surrounding vegetation. They also differ from the other fens by being partly surrounded, especially on the upper (western) side, by a pine plantation with a dense undergrowth of *Pteridium* at the margins. Towards the north-east the fens border on more open "matorral" vegetation. A brooklet runs down the mountain. It partly ends up between the fens, but ground water doubtless supplies these all along their upper border.

The northern fen surface is about 25× 15 m, with the greatest length at right angles to the slope. In the vegetation above the fen *Pteridium* is dominant. *Genista anglica* ssp. *ancistrocarpa,* which here is up to more than one metre high, and *Erica ciliaris* form the characteristic border-zone of the fen which is seen in Fig. 3. In addition, the following species are occupants of this zone:

Agrostis castellana BOISS. & REUT.
Anthoxanthum odoratum L.
Carex distans L.
Holcus lanatus L.
Potentilla erecta (L.) RÄUSCH.
Rubus ulmifolius SCHOTT. FIL.
Sieglingia decumbens (L.) BERNH.

On the lower, north-eastern side of the fen, which is drier, the scrub largely consists of *Cistus crispus, Erica arborea,* and species of *Halimium.*

The vascular plants inhabiting the fen surface are:

Agrostis castellana BOISS. & REUT.
Agrostis juressii LINK in SCHRAD.
Anagallis crassifolia THORE
Carex echinata MURR.
Carex oederi RETZ. coll.
Eleocharis multicaulis (SM.) SM.
Juncus acutiflorus EHRH. ex HOFFM.
Juncus bulbosus L.
Pinguicula lusitanica L.
Potentilla erecta (L.) RÄUSCH.
Sieglingia decumbens (L.) BERNH.

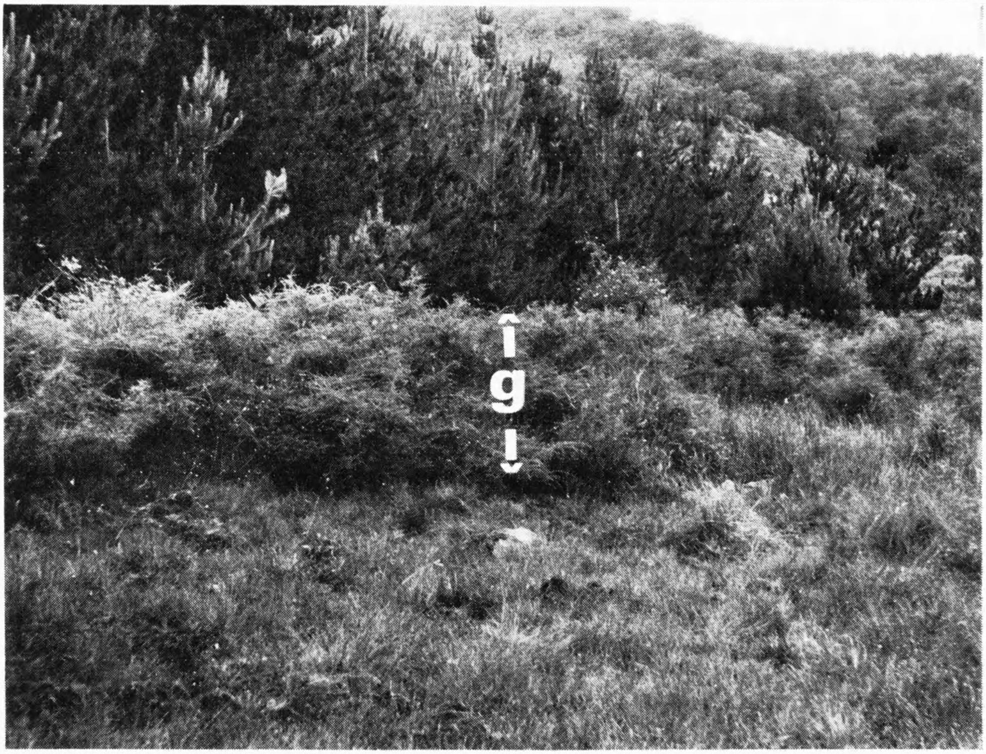


Fig. 3. A poor fen on the northern slope of Jbel Bou Hassim, the picture taken from a *Sphagnum* mat in the fen centre, showing the upper parts and the border zone. *Eleocharis multicaulis, Sieglingia decumbens,* etc. inhabit the fen surface in the foreground. The *Genista* border (g) is prominent and more than one metre high.

Anagallis crassifolia and *Agrostis juressii* are mainly found in the *Sphagnum* mats, which are concentrated to the central parts of the fen surface, whereas the soil of the upper marginal parts is more or less bare with scattered specimens of the two species of *Juncus* and with *Eleocharis multicaulis* and *Sieglingia*. Apart from *Sphagnum,* mosses are on the whole rare in the fen. Isolated specimens of *Dactylorhiza maculata* (L.) Soó coll. and *Lobelia urens* L. occur chiefly along the margins of the fen.

A somewhat larger fen surface, about 30 metres square, is located to the south of the above fen, and is separated from it by the above-mentioned brooklet. Unlike the more northerly fen it lacks a distinct upper margin, and joins up with the vegetation along the stream. *Sphagnum auriculatum* covers most of the central parts of the fen and is mainly associated with *Carex echinata, Eleocharis multicaulis* and *Anagallis crassifolia.* In addition to the species found on the surface of the more northerly fen, the following species also occur:

Anthoxanthum odoratum L.
Baldellia ranunculoides (L.) PARL.
Briza minor L.
Galium palustre L.
Lotus pedunculatus CAV.
Lythrum junceum BANKS & SOL.
Viola persicifolia SCHREB. (growing on the margin)

Fig. 4. The same fen as in Fig. 3 shown from the upper margin towards the north-west. *Genista* border, *Pteridium* and fen surface shown. Isolated rocks are seen in the centre The hills towards the north-west are rather denudated.

In the other fens on the slope, situated chiefly in the open "matorral", the conditions seem to be slightly richer than in the *Sphagnum* fens mentioned. Some are very wet and inhabited by *Ranunculus peltatus* and *tripartitus* and *Apium inundatum* (L.) RCHB. FIL., for example.

Unfortunately the area is being planted with pines; holes have been dug for this purpose all over the slope. Thus within a few years the natural vegetation will probably have been destroyed.

Besides the species recorded from the *Sphagnum* fens above, the following additional species occur:

Apium inundatum (L.) RCHB. FIL.
Apium nodiflorum (L.) LAG.
Callitriche cf. *hamulata* KÜTZ. ex KOCH
Carex divulsa STOKES
Carex flacca SCHREB.
Carex leporina L.
Eleocharis palustris (L.) R. BR.
Epilobium tetragonum L. ssp. *tournefortii* (MICH.) LÉVEILLÉ
Glyceria spicata GUSS.
Hypericum humifusum L.
Hypericum perfoliatum L.
Hypericum undulatum SCHOUSB. ex WILLD.
Juncus bufonius L.
Juncus capitatus WEIG.
Juncus conglomeratus L.
Juncus heterophyllus DUF.
Laurentia michelii DC.
Lythrum portula (L.) D. A. WEBB
Moenchia erecta (L.) GAERTN. ssp. *octandra* (ZIZ) COUT.
Montia lusitanica SAMP.
Myosotis welwitschii BOISS. & REUT.
Ranunculus bulbosus L. coll.
Ranunculus ophioglossifolius VILL.
Ranunculus peltatus SCHRANK
Ranunculus tripartitus DC.
Rumex conglomeratus MURR.
Salix atrocinerea BROT.
Scrophularia aquatica L.
Serapias lingua L.
Silene laeta (AIT.) GODRON

Sisymbrella aspera (L.) SPACH ssp. *boissieri* (COSS.) HEYW.
Trifolium repens L.
Trifolium strictum L.

Jbel Soukna

Sphagnum auriculatum was found in a fen about 20 metres square, located in a basin on an eastern extension of Jbel Soukna, c. 2,500 m WNW of the village Akarate, at about lat. 35°06′18″, long. 5°20′32″, north of the road between Dardara and Tanakoub, at an altitude of about 735 m.

The fen is situated in an open landscape and is surrounded by scrub of *Erica arborea*. *Pteridium aquilinum* is abundant on the slopes. *Sphagnum* covers only part of the fen surface. It is associated with the following species:

Agrostis castellana BOISS. & REUT.
Anagallis crassifolia THORE
Anthoxanthum odoratum L.
Eleocharis multicaulis (SM.) SM.
Holcus lanatus L.
Hypericum undulatum SCHOUSB. ex WILLD.
Juncus acutiflorus EHRH. ex HOFFM.
Juncus bulbosus L.
Lotus pedunculatus CAV.
Lythrum junceum BANKS & SOL.
Typha latifolia L.

The composition of the species, although less complete, is similar to that on Jbel Bou Hassim.

Another fen on Jbel Soukna, with for example *Sphagnum auriculatum*, was reported by FONT-QUER as early as 1934 (p. 57). It was said to be at an altitude of 1,350—1,400 m, which is considerably higher than ours. Besides some of the species mentioned above, FONT-QUER also listed *Carex leporina*, *Potentilla erecta*, *Hypericum humifusum*, *Athyrium filix-femina*, and *Polytrichum* (*commune*), i.e. species found by us on the other mountains in the Jebala Range.

Jbel El Khizana

In a locality on this mountain we found greater amounts of *Sphagnum auriculatum* than on the other mountains. The *Sphagnum* grows in small fens on northerly slopes of the north-eastern side of the mountain, c. 4,000 m SSW of Bab Taza and c. 1,500 m due west of the little village of Beni Ouetli, lat. 35°02′21″, long. 5°12′48″. The altitude is about 1,160 m.

The hills above the fens are covered with a heath-"matorral" vegetation which includes *Cistus crispus*, *Erica umbellata*, *Tuberaria lignosa*, and species of *Halimium*.

The fens are supplied with water from more or less localized springs. The species in a representative fen are:

Agrostis castellana BOISS. & REUT.
Agrostis juressii LINK in SCHRAD.
Agrostis salmantica (LAG.) KUNTH
Anagallis crassifolia THORE
Asperula laevigata L.
Baldellia ranunculoides (L.) PARL.
Blechnum spicant (L.) ROTH
Briza minor L.
Carex distans L.
Carex echinata MURR.
Carex leporina L.
Cicendia filiformis (L.) DELARBRE
Crataegus monogyna JACQ.
Cuscuta epithymum (L.) NATHORST
Cyperus longus L. ssp. *badius* (DESF.) MURB.
Dactylorhiza maculata (L.) SOÓ coll.
Eleocharis multicaulis (SM.) SM.
Eleocharis palustris (L.) R. BR.
Galium palustre L.
Genista anglica L. ssp. *ancistrocarpa* (SPACH) MAIRE
Glyceria spicata GUSS.
Holcus lanatus L.
Hypericum humifusum L.
Hypericum undulatum SCHOUSB. ex WILLD.
Isolepis setacea (L.) R. BR.
Juncus articulatus L.
Juncus bufonius L.
Juncus conglomeratus L.
Juncus effusus L.
Juncus foliosus DESF.
Juncus tenageia EHRH.
Lotus pedunculatus CAV.
Lythrum junceum BANKS & SOL.
Lythrum portula (L.) D. A. WEBB
Mentha pulegium L.
Montia lusitanica SAMP.
Myosotis welwitschii BOISS. & REUT.
Nardus stricta L.
Oenanthe lachenalii C. C. GMELIN
Parentucellia viscosa (L.) CARUEL
Potentilla erecta (L.) RÄUSCH.

Prunella vulgaris L.
Ranunculus bulbosus L. coll.
Ranunculus tripartitus DC.
Sieglingia decumbens (L.) Bernh.
Trifolium dubium Sibth.
Trifolium repens L.

Genista anglica ssp. *ancistrocarpa* borders the upper margin of the fen, and in the grass just above the fen are found *Nardus stricta, Sieglingia decumbens, Potentilla erecta, Dactylorhiza maculata,* and *Blechnum spicant.* Some of these species are also found in the actual fen.

Galium palustre, Eleocharis multicaulis, Juncus bulbosus, Carex echinata and the three species of *Agrostis* are found on the fen surface nearest to the upper margin and in close connection with *Sphagnum,* with which *Anagallis crassifolia* is otherwise most closely associated.

The lower part of the fen merges into patches with only temporarily wet, bare soil. On these patches are found, e.g., *Juncus tenageia, J. bufonius, J. foliosus, Isolepis setacea,* and also isolated specimens of *Parentucellia viscosa* and *Ranunculus bulbosus. Isolepis setacea* is also associated with *Cicendia filiformis* and *Montia lusitanica* on bare sandy soil with water seeping through.

In deeper water, often in close association with *Sphagnum* tufts, the above-mentioned species are substituted by *Baldellia ranunculoides, Ranunculus tripartitus, Glyceria spicata,* and *Galium palustre,* for example. *Carex distans* and *C. leporina* line the sides of springs and streams.

Adjacent fens with deeper water contain the following additional species: *Gratiola officinalis, Juncus bulbosus* (floating forms), *J. heterophyllus, Ranunculus ophioglossifolius, Nasturtium officinale* R. Br., and *Rumex conglomeratus.*

The water from the fens continues as streams, in which are found *Potamogeton polygonifolius* Pourr. and *Fontinalis. Sphagnum auriculatum* covers a considerable area, i.e. hundreds of square metres, on relatively flat ground near these watercourses.

The vegetation of the poor fens on Jbel El Khizana is largely the same as that on Jbel Bou Hassim. An additional component (also found on Jbel Soukna, see Mathez & Sauvage 1970 p. 95) is *Nardus stricta,* which is commoner at high altitudes in Central Rif.

Fen and pool vegetation, apparently of a richer character, have also been studied at higher altitudes in the deciduous oak region on Jbel El Khizana. It contributes a number of other species (but *Sphagnum* is missing): *Alopecurus aequalis* Sobol., *Apium inundatum, Callitriche* cf. *platycarpa, Isoëtes velata* A. Br., *Juncus pygmaeus* Rich., *Myriophyllum alterniflorum* DC., and *Oenanthe fistulosa* L.

Conclusive Remarks

In general it can be said of the localities described above that they are situated on slopes with sandy soil and in a surrounding vegetation containing species which are more or less calcifuge, such as *Pteridium aquilinum, Erica umbellata* and *arborea, Cistus crispus,* and *Tolpis nemoralis. Quercus suber* is sometimes present, but not *Q. ilex.*

In the *Sphagnum* fens themselves a series of species are quite characteristic, occurring in all or almost all localities visited. These species include *Eleocharis multicaulis, Juncus bulbosus, Agrostis castellana, Agrostis juressii, Anagallis crassifolia, Anthoxanthum odoratum, Sieglingia decumbens* and *Pinguicula lusitanica.*

COMPARISON WITH OTHER FEN AND SPRING COMMUNITIES

Fens on the Tingitanean Peninsula

The fen and spring communities of the Tingitanean Peninsula are usually small in size and each one often displays only a fraction of the many species of moist habitats found in the region. The following community has been selected as it provides a rather representative list.

It is situated west of Restinga, on the eastern slope of a small sandstone mountain with the name "Zem-Zem" on the 1: 50,000 scale map (Tetouan sheet). The situation of the spring is about lat. 35°44′40″, long 5°22′50″, at an altitude of about 190 m. (N. B.: this Zem-Zem must *not* be confused with the well-known Jbel Zem-Zem which is situated south-east of Tanger, and which is cited many times in Jahandiez & Maire's Catalogue and mentioned several times below.)

The spring community comprises the following species:

Agrostis semiverticillata (Forsk.) Christ.
Anagallis crassifolia Thore
Anthoxanthum odoratum L.
Apium nodiflorum (L.) Lag.
Briza minor L.
Carex flacca Schreb.
Carex punctata Gaud.
Cicendia filiformis (L.) Delarbre
Eleocharis multicaulis (Sm.) Sm.
Erica ciliaris L.
Fuirena pubescens (Poir.) Kunth
Holcus lanatus L.
Hypericum humifusum L.
Isoëtes histrix Bory
Isolepis cernua (Vahl) Roem. & Schultes
Juncus articulatus L.
Juncus bulbosus L.
Juncus capitatus Weig.
Juncus fontanesii Gay ssp. *pyramidatus* (Lah.) Snog.
Juncus hybridus Brot.
Juncus pygmaeus Rich.
Juncus striatus Schousb.
Juncus tenageia Ehrh.
Laurentia michelii DC.
Lotus subbiflorus Lag.
Lythrum junceum Banks & Sol.
Ornithopus pinnatus (Miller) Druce
Parentucellia viscosa (L.) Caruel
Pinguicula lusitanica L.
Plantago coronopus L. coll.
Polypogon monspeliensis (L.) Desf.
Radiola linoides Roth
Ranunculus bulbosus L. coll.
Samolus valerandi L.
Scilla mauritanica Schousb.
Serapias parviflora Parl.
Sieglingia decumbens (L.) Bernh.
Silene laeta (Ait.) Godron
Simethis planifolia (L.) Gren. & Godr.
Trifolium dubium Sibth.

Each of these species has its own particular distribution and preference within the spring community, which shows a striking resemblance to that on Jbel Dahar Zhirou (see above) although it is richer in species and lacks *Sphagnum auriculatum.*

Spring and fen communities like the one described here have also been studied on Jbel Kebir, Jbel Zem-Zem (proper), Haouta Bern Mediar, Jbel Sidi Habib and other places, and the list could easily be complemented with many species. The following are among the rather common ones:

Agrostis castellana Boiss. & Reut.
Agrostis salmantica (Lag.) Kunth
Cyperus longus L. ssp. *badius* (Desf.) Murb.
Cyperus mundtii (Nees) Kunth
Eleocharis palustris (L.) R. Br.
Hypericum perfoliatum L.
Juncus conglomeratus L.
Juncus effusus L.
Myosotis welwitschii Boiss. & Reut.
Panicum repens L.
Prunella vulgaris L.
Ranunculus ophioglossifolius Vill.
Schoenus nigricans L.

There are relatively few species common to both the fens of the Tingitanean Peninsula and the montane pastures in the higher parts of the Rif Mountains (see below). Some of these species are *Anthoxanthum odoratum, Eleocharis multicaulis, Holcus lanatus,* some species of *Juncus, Radiola linoides,* and *Ranunculus bulbosus* coll.

The similarities between the vegetation of the springs and fens of the Tingitanean Peninsula and the Jebala Range (Jbel Bou Hassim, Jbel Soukna, Jbel El Khizana, etc.) are far greater. Most species in the lists above are, in fact, common to the two regions except perhaps *Carex punctata, Fuirena pubescens* and *Scilla mauritanica,* which are western.

Fens in Central Rif

Most watercourses in the montane zone are seasonal streams drying up very soon after the snow has melted and leaving a furrow practically free of vegetation. However, where the water supply is more permanent, such as on the slopes below springs, quite extensive surfaces of turf may form, kept wet by seepage and containing a number of species characteristic of fens and more or less wet meadows. Dominating species in these montane pastures are often *Festuca ovina* L. and *Nardus stricta.*

This type of vegetation is represented by a locality situated by the stream draining "Plateau d'Isagen" (=Issârhene), 1 km south of Ketama in the Tidighin region, at an altitude of about 1,500 m. The site is on a slope with water seeping from a small spring. The upper part is almost bare peat trampled by grazing sheep, and the lower part is a closed grass turf dominated by *Festuca ovina.* Other species occurring in the turf are:

Anagallis tenella L.
Carex distans L.
Carex echinata MURR.
Dactylorhiza maculata (L.) SOÓ coll.
Eleocharis multicaulis (SM.) SM.
Isolepis setacea (L.) R. BR.
Nardus stricta L.
Potentilla erecta (L.) RÄUSCH.
Ranunculus paludosus POIR.
Viola palustris L.

Additional species on the bare peat are *Carex oederi* coll., *Glyceria spicata, Juncus articulatus,* and *Juncus foliosus.*

In similar communities on the northern slopes of Jbel Tidighin and adjacent mountains, at altitudes of 1,700—1,800 m, some other interesting, more or less northern species occur, such as *Botrychium lunaria* (L.) SWARTZ, *Carex nigra* (L.) REICH., *Eleocharis quinqueflora* (F. X. HARTM.) O. SCHWARZ, *Pinguicula vulgaris* L., and *Veronica serpyllifolia* L. None of these species were found in the *Sphagnum* fen communities in the Jebala Range. Common to both regions are, however, a few species, such as *Carex echinata, C. oederi* coll., *Eleocharis multicaulis,* and *Potentilla erecta,* beside such common species of most wet places like *Isolepis setacea* and *Carex distans.*

However, most of the species in these moist meadows and fens in Central Rif do not extend far to the west or to lower altitudes, *Nardus stricta* only just reaching the *Sphagnum* localities on Jbel El Khizana and Jbel Soukna.

OCCURRENCE AND DISTRIBUTION OF SOME NORTHERN AND ATLANTIC SPECIES

The species presented below have been selected on the following grounds:

(1) they are new or especially noteworthy in the region
(2) they have a distribution that shows a particular pattern and indicates preference for a given climate and soil type.

The maps are based on our own material complemented with sufficiently exact locality statements from the literature, in particular JAHANDIEZ & MAIRE's "Catalogue des plantes du Maroc" (1931, 1932, 1934) abbreviated "J. & M."

Sphagnum auriculatum SCHIMP. The relatively few finds of *Sphagnum* in Morocco and the southern part of the Iberian Peninsula have often been referred to as *S. rufescens* (NEES & HORNSCH.) WARNST. However, most taxonomists to-day agree that *S. rufescens* cannot be upheld as a species. In ISOVIITA 1966 p. 234 it is included without discrimination under *S. auriculatum* SCHIMP., which has been accepted here.

The first record of *Sphagnum* in Morocco was made by PITARD (1913 p. 128) from "Djebel Darziro entre Tanger et Arzila". It was reported under the name *S. rufescens,* and some of the material was even considered by PITARD to correspond to var. *turgidum* (C. MÜLL.) WARNST. of this taxon, no doubt being a case of modification within the material. *Sphagnum*

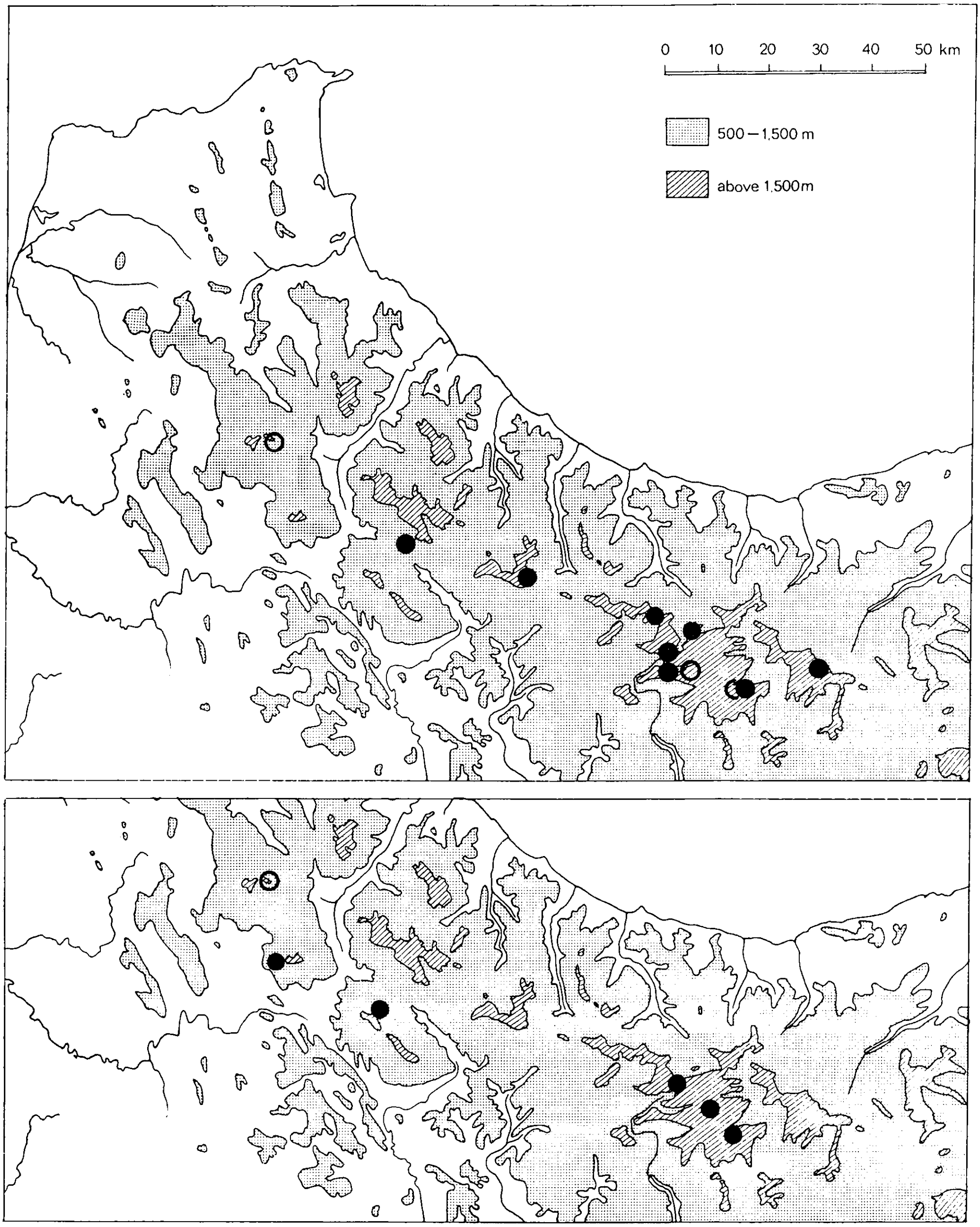


Fig. 5. Documented finds of — top: *Polystichum aculeatum* (circles) and a species with comparable distribution in Northern Morocco, *Ophioglossum vulgatum* (dots) — bottom: *Viola persicifolia* (circle) and *Nardus stricta* (dots).

was later searched for in this mountain, but not refound until 1964 by STÉPHANESCO, who described the locality in IONESCO & STÉPHANESCO 1967 p. 33. The place is doubtless the same as that visited by us (see above).

The next report of Moroccan *Sphagnum* is by FONT-QUER (1934 p. 57) from Jbel Soukna. MATHEZ & SAUVAGE (1970) later recorded *Sieglingia decumbens, Juncus bufonius* and *Nardus stricta* from *Sphagnum* sites on Jbel Bou Hassim, Jbel Soukna and Jbel El Khizana, respectively. Finally, Dr. S. LÆGAARD, Aarhus, collected *Sphagnum auriculatum* on Jbel Bou Hassim in 1969.

In the course of our field work in 1972, *Sphagnum* was found on the four mountains mentioned (Fig. 1) although at that time we were not aware of any previous records except that on Jbel Dahar Zhirou.

According to Mrs. BODIL LANGE, Copenhagen, who has examined our Moroccan *Sphagnum* material, this has a fairly wide range of variation, but the variation does not follow a regional pattern. It agrees with other south-western material of the species.

Polystichum aculeatum (L.) ROTH [=*Dryopteris setifera* ssp. *lobata* of J. & M. (1931 p. 3)] is a northern species with an Atlantic tendency, occurring only on mountains in the southern part of its range. It is known from Middle and Great Atlas but not previously from the Rif. *P. aculeatum* was found by us in a ravine in deciduous oak forest on Jbel Bou Hassim and along small brooks in the cedar forests on the northern slopes of Jbel El Arz and Jbel Tidighin (Fig. 5).

Sieglingia decumbens (L.) BERNH. was reported by J. & M. (1931 p. 57) from a few localities in Morocco, such as Jbel Kebir and Jbel Zem-Zem in the Tanger region and from Bab Amegas in the Rif. In MATHEZ & SAUVAGE 1970 (p. 92) the species was reported from Bou Hassim. However, the species has proved to be a relatively common component of the "matorral" vegetation on the sandstone mountains in the west where there is sufficient moisture. It is also found in the actual fens and in the communities bordering the fens in Western Rif (Fig. 6). — The north-Moroccan *Sieglingia decumbens* has been divided into two subspecies. These were reduced to variety rank by MATHEZ & SAUVAGE 1970. The variation in our material is certainly wide. Further studies will show whether or not subdivision of the species is justified. In Algeria the species has been recorded from La Calle only, in the north-east. It is absent from Middle and Great Atlas.

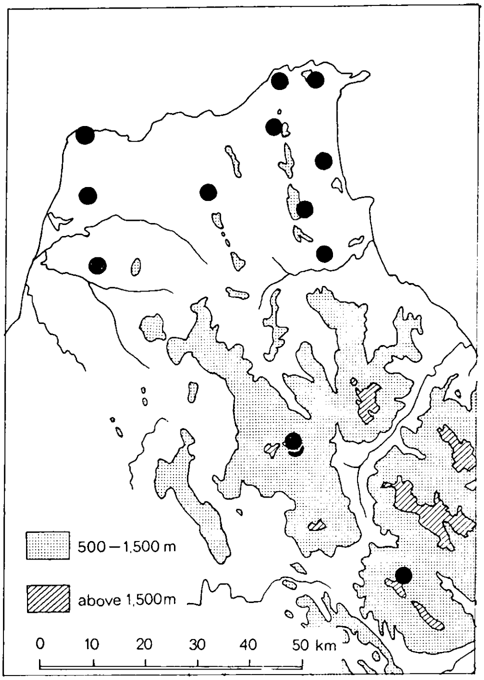


Fig. 6. Documented finds of *Sieglingia decumbens* in Northern Morocco.

Molinia caerulea (L.) MOENCH according to MAIRE 1955 p. 29 was reported by BONNET & BARRATTE from the Tanger region, based on collections by SCHOUSBOE without locality statement. It has been doubted whether they in fact were collected in Morocco. Later SAUVAGE & VINDT (1955 p. 224) reported *Molinia* from one place in Great Atlas. It was also found by us in two places in the western parts of the Tingitanean Peninsula, on Jbel Dahar Zhirou and on Haouta Bern Mediar (Fig. 9). There it grows together with *Sieglingia decumbens, Erica ciliaris* and *Eleocharis multicaulis.* On Haouta Bern Mediar (arrow on the map), *Molinia* is rather plentiful on a moist slope facing south-west, growing along a brook below the Forestry Office. A soil sample (see below) from this place indicates poor, well-drained moor soil. — The species is also known from a few localities in Algeria and Tunisia.

Nardus stricta L. was reported by J. & M. 1931 (p. 84) from one locality in Northern Morocco, "Mont Tidighin" in Central Rif, and by MAIRE (1955 p. 298) from "Plateau d'Isagen" near this mountain. It was also later found on Jbel Soukna (MATHEZ & SAUVAGE 1970 p. 9). *Nardus* is, in fact, a characteristic component of moist pastures at high elevations in the Rif Mountains, the westernmost localities on Jbel Soukna and Jbel El Khizana being from margins of fens with *Sphagnum auriculatum* (Fig. 5). The species is also known from one place in Great Atlas, but not from Algeria.

Eleocharis multicaulis (SM.) SM. was recorded by MAIRE 1957 (p. 77) from the Tingitanean Peninsula and also from the Rif Mountains eastwards to Tizi Ifri. It is also found in poor fens in the west, e.g., in the Mâmora Forest north of Rabat, and north of Lalla Mimouna (DEL VILLAR & WERNER 1952 p. 45). Its distribution in Northern Morocco appears to be similar to that of *Juncus bulbosus,* and our studies indicate that it is a characteristic component of the vegetation of poor fens as well as damp acidic ground in general (Fig. 8). It is thus regularly present in the *Sphagnum* fens mentioned above. In Algeria it is known from a few places mainly in the north-east.

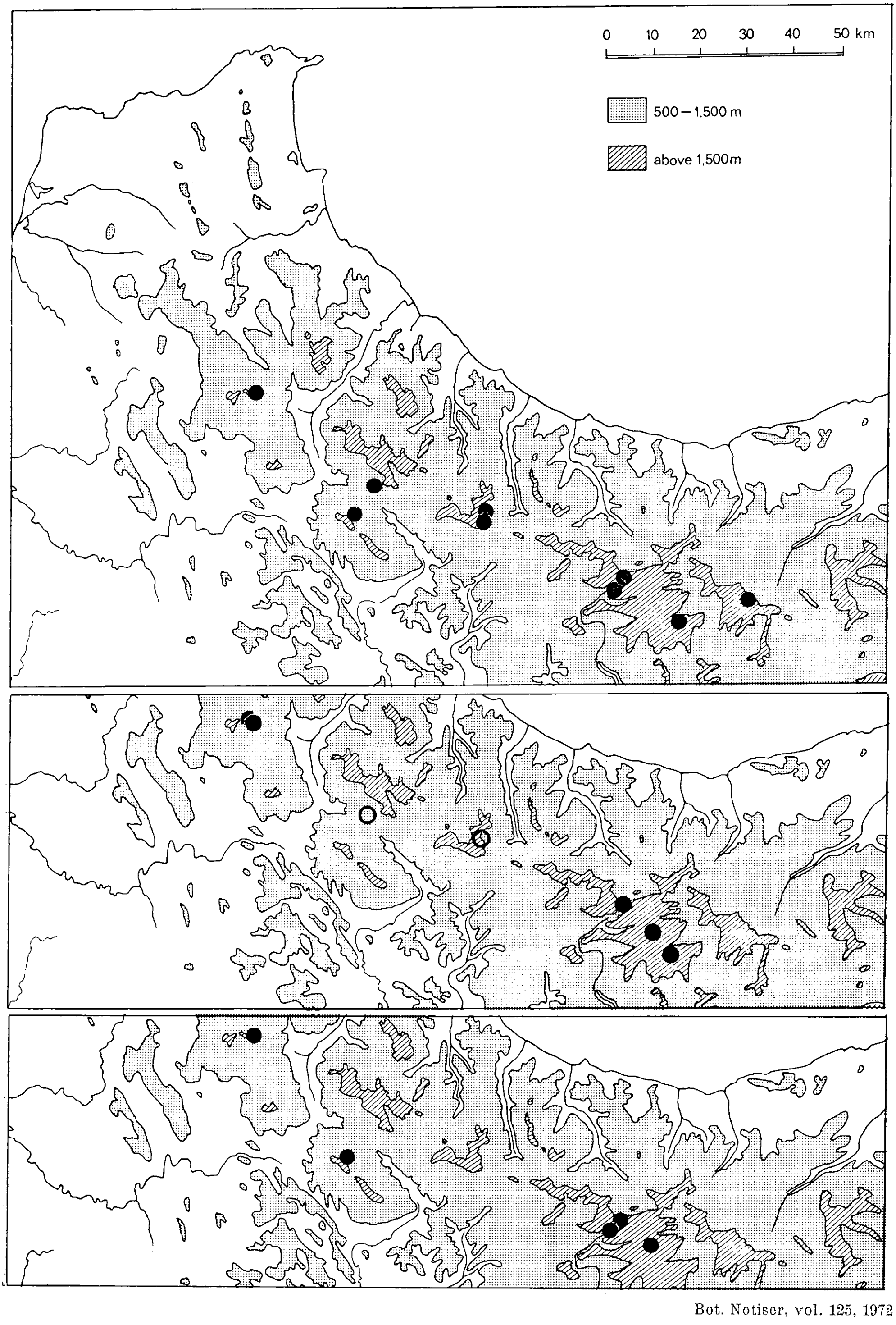
Carex echinata MURR. has been recorded from Jbel Tidighin in Central Rif and from "Azib de Ketama" west of this mountain (MAIRE 1957 p. 118). It is fairly characteristic of the poorest fens in the Rif Mountains and is often associated with *Sphagnum.* It is known to occur at least from Jbel Bou Hassim in the west to Jbel Tidighin in Central Rif in the east (Fig. 7). Its distribution in Northern Morocco though more restricted may be referred to the same group as that of *Carex leporina* and also resembles that of *Nardus stricta. Carex echinata* is known from Great Atlas but is absent from Algeria.

Carex leporina L., like the preceding species, was reported by J. & M. (1931 p. 100) from two localities in the Rif, namely Bab-Amegas and Jbel Tidighin, and by FONT-QUER (1934 p. 57) from Jbel Soukna, but has been shown to be widely distributed throughout the sandstone mountains. It ranges at least from Jbel Bou Hassim in the west to Jbel Oursane (south of Targuist) in the east (Fig. 7). Its habitat in the Rif is margins of brooks and fens in non-calcareous regions. — The Rif forms agree well with ssp. *leporina* [=ssp. *ovalis* (GOOD.) MAIRE], whereas forms in Great Atlas are referred to ssp. *atlasica* LINDB. The species is known from one place in Algeria only.

Carex oederi RETZ. coll. (Fig. 7). In Morocco this variable complex is treated by MAIRE (1957 p. 170) as a subspecies of *C. flava* L.: ssp. *oederi* (RETZ.) SYME, with the var. *oederi* (RETZ.) DC., var. *nevadensis* (BOISS. & REUT.) BRIQ., and var. *brevirostris* ASCH. & GR.

Most of our collections (dots on the map) agree with the diagnosis and description of *Carex nevadensis* BOISS. & REUT. (1852 p. 118), although they are

Fig. 7. Documented finds of — top: *Carex leporina* — centre: *C. oederi* coll., forms resembling *C. tumidicarpa* (dots), forms more like *C. oederi* s.str. (circles) — bottom: *C. echinata.*


0 10 20 30 40 50 km
500—1,500 m
above 1,500m

mostly taller, which is not surprising as they were collected at rather low altitudes, about 1,100—1,500 m, whereas the type locality for *C. nevadensis* is "in pratis turfosis regionis alpinae et nivalis Sierra Nevada". The description of var. *nevadensis* in MAIRE 1957 (p. 170) does not fit our material, however, as female spikes and utricles are said to be very small, etc.

On the other hand, our material of the "*nevadensis* type" bears a striking resemblance to the taxon which in northern Europe has recently been treated as *C. tumidicarpa* ANDS. They have in common the 2.5—3 mm broad basal leaves which are shorter than the stems, the very similar arrangement of the female spikes which are subtended by rather long and broad leaves not sharply deflexed, the lowermost female spikes mostly remote from the others in the axil of a cauline leaf with a long sheath, and the size and shape of the utricles. These are 3—4 mm long and have a rather slender beak about 1/3 the length of the utricle and slightly deflexed. Apart from possible differences in leaf colour and texture, which are difficult to observe in pressed material, the only obvious difference from North European populations of *C. tumidicarpa* is a tendency in our Moroccan material to shorter male spikes with shorter peduncles. Our collections of this type are from poor fens, often in or in the vicinity of *Sphagnum* fens in the western part of the region investigated, or together with *Nardus stricta* in the Tidighin region of Central Rif.

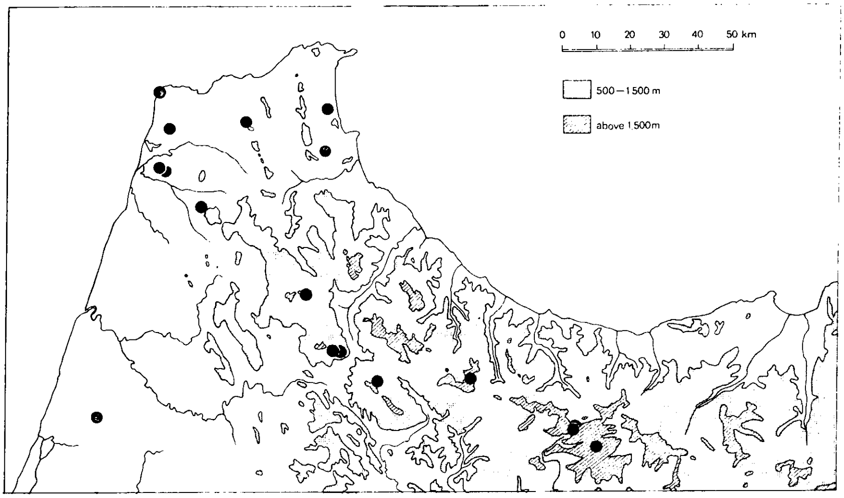
Two collections of *C. oederi* coll. (circles in the map), deviate from those described above. They agree more closely with European forms belonging to *C. oederi* s. str., still a variable complex, however (see HYLANDER 1966 p. 166). They have narrower leaves, c. 2 mm broad, almost as long as or longer than the stems, and smaller, densely clustered spikes; the utricles are also smaller, only about 2.5 mm long, and have a short beak. One of these collections was made in a montane spring community containing lime deposits, the other grew by a small fen on sandstone but with luxuriant vegetation and obviously not of poor character. It is uncertain which of the varieties mentioned in MAIRE 1957 (pp. 169—171) this type corresponds to.

Carex paniculata L. has to our knowledge not been previously found in the Rif Mountains. It has been recorded from Middle Atlas and from two localities in Rharb near the Atlantic coast (MAIRE 1957 p. 114). However, it also grows on Jbel Bou Hassim in Western Rif (Fig. 9) by the side of a stream near the *Sphagnum* fens described above. Species growing associated with *C. paniculata* along the stream are, e.g., *Athyrium filix-femina, Blechnum spicant, Carex echinata, C. oederi, Osmunda regalis,* and *Potentilla erecta. Carex paniculata* is not known from Algeria.

Juncus bulbosus L. was recorded by MAIRE (1957 p. 291) from the Tingitanean Peninsula, the sandstone ranges of the Rif, and Mount Outka. Our field studies show that it is a characteristic and not at all rare component of wet, acidic habitats (Fig. 8). Thus it is frequent in some of the fens containing *Sphagnum* and also in other fens with high water level, floating forms occurring where water is fairly deep. In Algeria the species is recorded only from the north-east.

Genista anglica L. ssp. **ancistrocarpa** (SPACH) MAIRE (Fig. 9) was mentioned by J. & M. (1932 p. 354) from Atlantic fens south of Larache, from fens north of Lalla Mimouna, and from some more place further south, all places being near the Atlantic coast. It was also reported by SAUVAGE (1961 p. 86) from the Mâmora

Fig. 8. Documented finds in Northern Morocco of — top: *Eleocharis multicaulis* — centre: *Juncus bulbosus* — bottom: *Hypericum humifusum.*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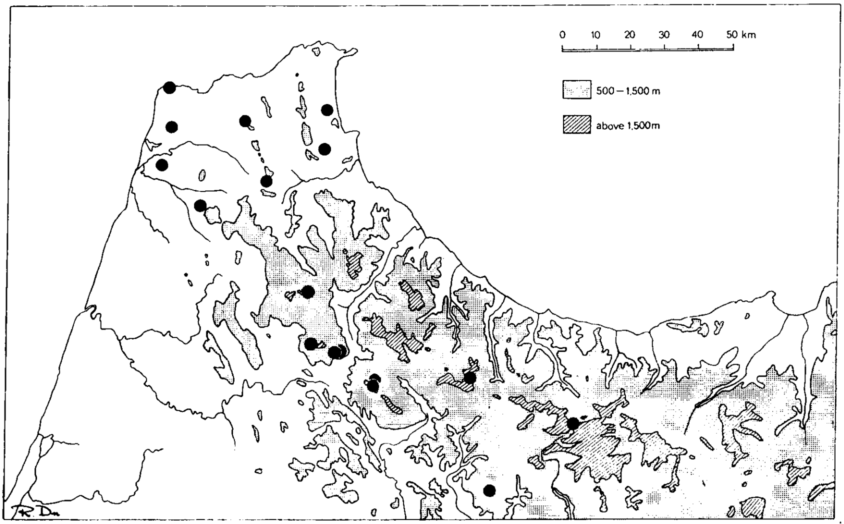
above 1.500m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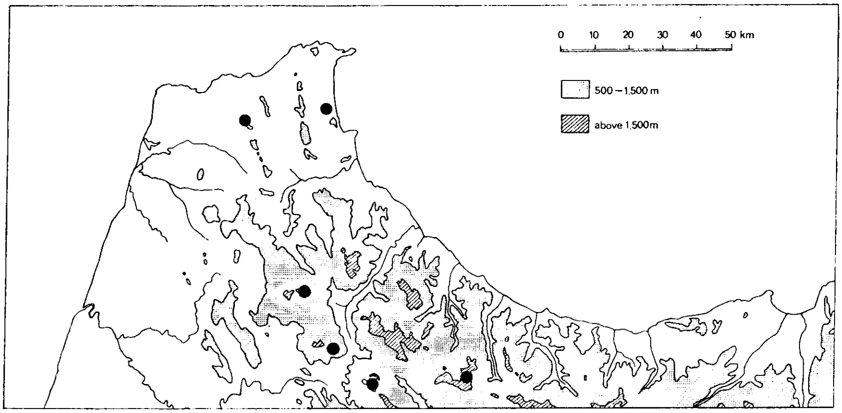
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Forests north of Rabat. SAUVAGE indicated that it has a considerable occurrence in Northern Morocco, but we have few exact records of the species. As described above, it is a striking member of the fen margin vegetation on Jbel Bou Hassim and Jbel El Khizana in north-western Rif, which serves to illustrate the Atlantic character of the fen communities described from these mountains. In the latter fens the species is usually associated with *Erica ciliaris*.

Ssp. *ancistrocarpa* has simple as well as trifoliolate, sessile leaves, the trifoliolate leaves being often dominating; furthermore, the legumes are relatively long and many-seeded, and the shrubs may be up to 150 cm high. These and other features give the subspecies an appearance rather different from that of ssp. *anglica*, which it replaces in the south. It was originally described as a species, *Genista ancistrocarpa* SPACH, from Portugal. It is absent in Algeria.

Frangula alnus MILL. (=*Rhamnus frangula* L.) was reported by J. & M. (1932 p. 475) from fens ("marais") in Northern Rharb and part of the Jebala Range as well as from Central Rif: "Badou". Our finds are mainly from rivulets and more or less shady, humid ravines. The species occurs, for example, along streams on Haouta Bern Mediar in the west as well as in the Rif Mountains (Fig. 11) up to high elevations, where it is sometimes associated with *Betula pendula* EHRH. It has also been found in a steep ravine on the north-western side of Jbel Tisirene together with *Euonymus latifolius* SCOP. (not previously known from the Rif) and *Sambucus ebulus* L.

Hypericum humifusum L. has previously been recorded from Jbel Soukna and Jbel El Khizana by J. & M. (1932 p. 484), and has also been collected by us on these mountains. It occurs in non-calcareous, somewhat moist habitats in Western Rif as well as on the Tingitanean Peninsula. All the places are characterized by sandstone or sandy ground, and the species is often associated with *Polytrichum*. Its known distribution in Northern Morocco (Fig. 8) shows resemblance to those of *Juncus bulbosus* and *Eleocharis multicaulis*. — *H. humifusum* is not known from Middle or Great Atlas, nor from Algeria. — The occasional nomenclatural fusion between *Hypericum australe* TEN., which shows a preference for calcareous soils, and *H. humifusum* is not supported by our experience from Northern Morocco.

Viola persicifolia SCHREB. (=*V. stagnina* KIT.) according to our knowledge has not previously been reported from Morocco (or other parts of Northern Africa). It occurs in relatively poor fens on the northern slopes of Jbel Bou Hassim in Western Rif (Fig. 5), where it is associated with *Sphagnum auriculatum* (see under Jbel Bou Hassim above), for example. Our material was collected in the post-floral stage, but there is no doubt of its identity.

Chamaenerion angustifolium (L.) SCOP. (=*Epilobium angustifolium* L.), like the previous species, does not seem to have previously been recorded from Northern Africa. It was found on the northern slopes of Jbel Bou Hassim (Fig. 9) at an altitude of about 1,500 m. The slopes are covered with huge rocks (a monkey habitat!) with trees of *Quercus canariensis* growing in between. *Chamaenerion* grows in porous, humus-rich soil in shady places between the rocks. A limited population of cedars is found somewhat lower down.

Calluna vulgaris (L.) HULL was not given many records in Northern Morocco by J. & M. (1934 p. 559), namely Jbel Kebir, Jbel Zem-Zem, the hills above Sebta, etc. In SAUVAGE & VINDT 1952 (p. 4) it is reported from "Tangerois" and "moitié occ. du Rif S.-O." In SAUVAGE 1961 (p. 146) the species is, furthermore, re-

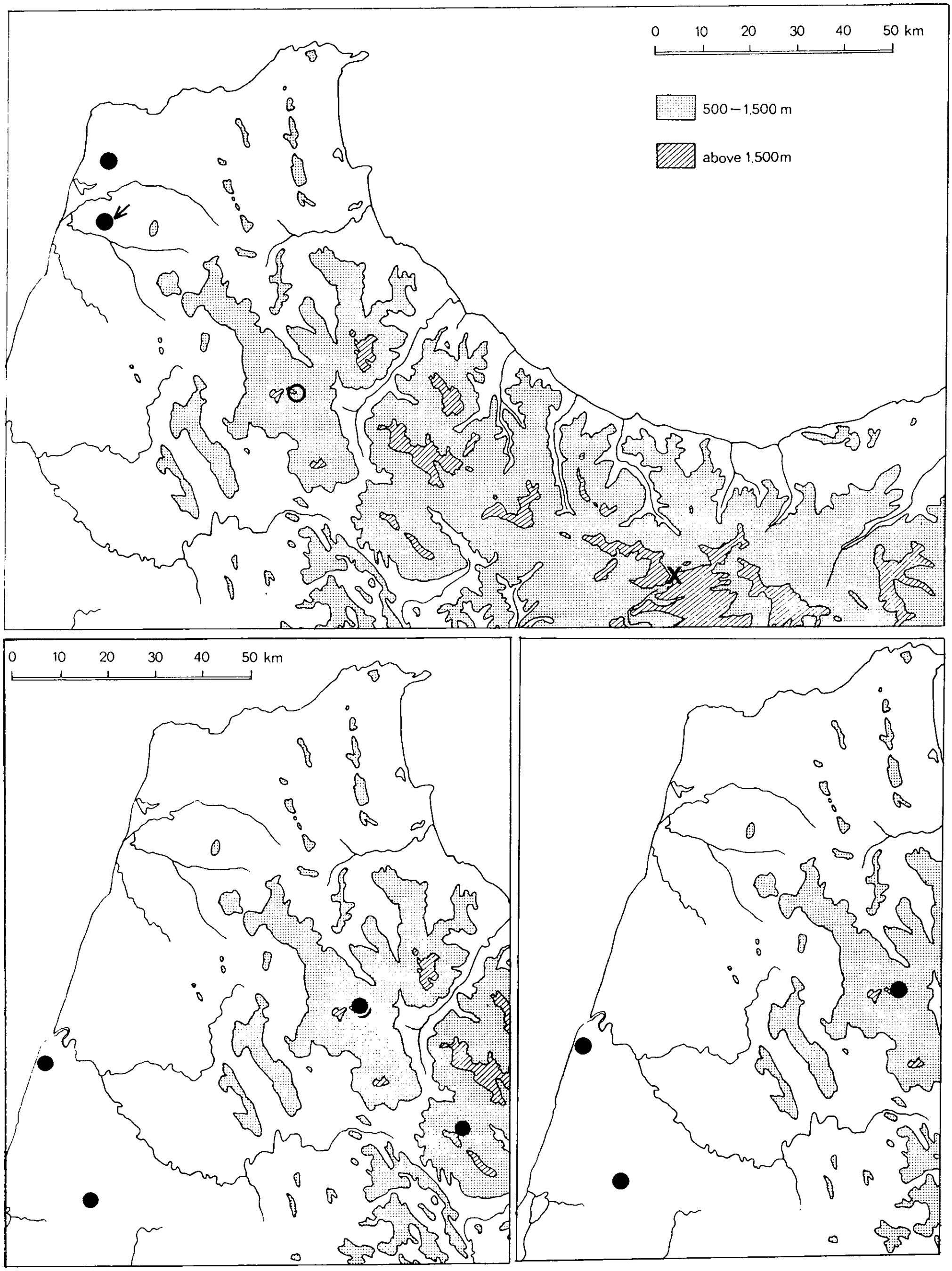

Fig. 9. Documented finds in Northern Morocco of — top: *Molinia caerulea* (dots; the arrow indicates site of soil sample), *Chamaenerion angustifolium* (circle), and *Littorella uniflora* (cross) — bottom left: *Genista anglica* ssp. *ancistrocarpa* — bottom right: *Carex paniculata.*

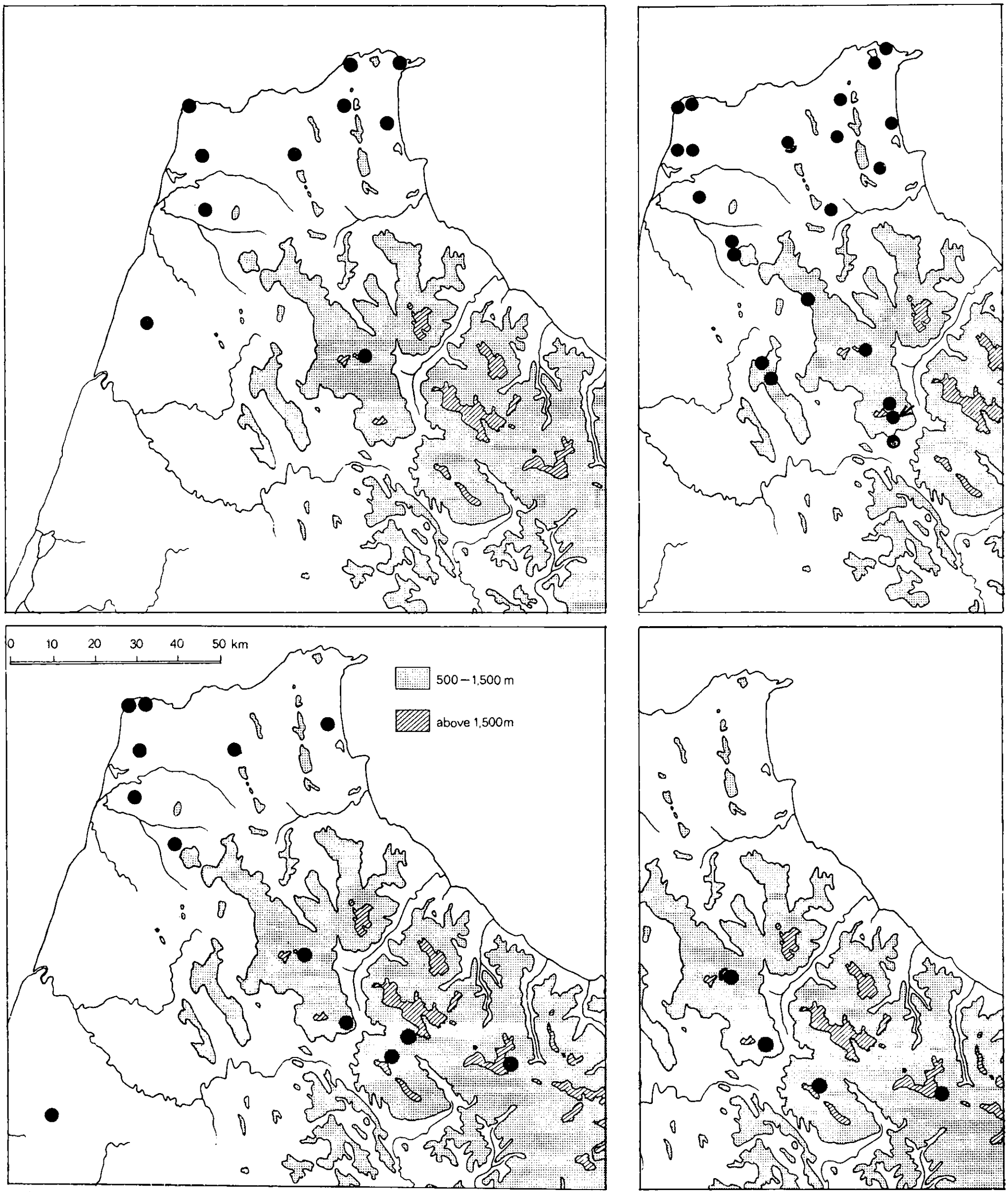

Fig. 10. Documented finds in Northern Morocco of — top left: *Erica ciliaris* — top right: *Calluna vulgaris* (the arrow indicates site of soil sample) — bottom left: *Anagallis crassifolia* — bottom right: *Gratiola officinalis*.

corded from several localities in the Jebala Range as far as Soukna and in the ranges south of Jbel Sidi Habib. Our records represent no extension of range, but Fig. 10 serves to show that *Calluna* belongs to the characteristic Atlantic elements such as, for example, *Erica ciliaris*. In fact *Calluna* is regionally very common

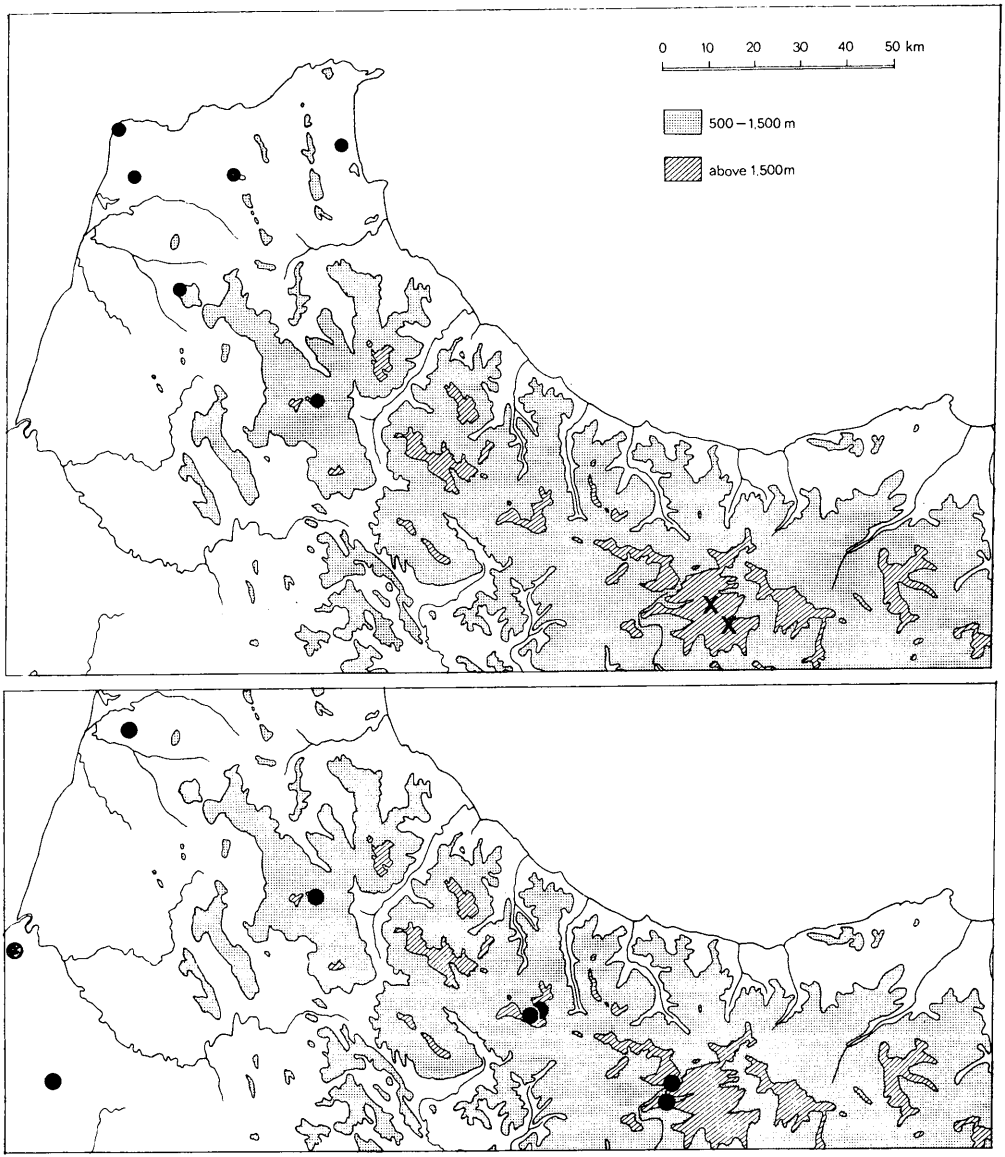

Fig. 11. Documented finds in Northern Morocco of — top: *Pinguicula lusitanica* (dots) and *P. vulgaris* (crosses) — bottom: *Frangula alnus*.

on non-calcareous ground on the Tingitanean Peninsula. It is generally associated here with *Erica umbellata, E. scoparia, Cistus crispus, Genista triacanthos, Tuberaria lignosa, Agrostis setacea, Festuca caerulescens, Halimium* spp., etc. in a community in which one will often also find *Drosophyllum lusitanicum.*

Eastern outposts of *Calluna* in Northern Morocco were found in relatively moist habitats, on Jbel Bou Hassim near a rivulet in association with *Erica arborea,* and on an extension of Jbel Soukna (arrow on the map) on a moist slope in association with, among other species, *Eleocharis multicaulis, Agrostis castellana,* and *Hypericum humifusum.* A soil sample taken from this place is commented on below.

Calluna vulgaris has not been recorded from the southern ranges of the Atlas Mountains or from Algeria.

Erica ciliaris L. normally grows in moister habitats than *Calluna,* but shows a similar distribution pattern in Northern Morocco (Fig. 10). It was recorded by J. & M. (1934 p. 560) and SAUVAGE & VINDT (1952 p. 8) from a few localities in the northern parts of the Tingitanean Peninsula, and by MATHEZ & SAUVAGE (1970 p. 105) from Northern Rharb. In these regions the species grows along brooks in humid valleys, often together with *Osmunda regalis, Carex pendula,* and *Athyrium filix-femina,* but it is also found in spring and fen communities, such as on Jbel Dahar Zhirou and Haouta Bern Mediar, where it is associated with *Molinia caerulea* and *Eleocharis multicaulis. Erica ciliaris* also continues into the Jebala Range at least as far as Jbel Bou Hassim, where it is associated with *Genista anglica* in fen margins. It is not known from Algeria or the more southern parts of Morocco.

Anagallis crassifolia THORE was reported by SAUVAGE & VINDT (1952 p. 18) from the region of Tanger and from the western, humid region of Northern Rharb, but in J. & M. 1934 (p. 563) also from Rif without particulars and in the same year by FONT-QUER from Jbel Soukna. The species is in fact a characteristic and common component of the *Sphagnum* fens of the country, frequently actually growing in the *Sphagnum* mats. It is also found on bare sandy soil that is permanently wet due to seepage, i.e. a habitat similar to that of *Pinguicula lusitanica* which has a similar distribution. *Anagallis crassifolia* ranges from the western part of the Tingitanean Peninsula as far as Mont Tisirene in the east (Fig. 10). In Algeria, the species occurs in very few places, for example at La Calle in the north-east.

Gratiola officinalis L. was not included in the Catalogue of J. & M. 1934. However, the doubtfully distinct *Gratiola linifolia* VAHL has been reported from Mount Outka, south of the Rif proper. — *G. officinalis* has been found by us in a number of places, especially margins of pools and other, permanent occurrences of water, chiefly stagnant, with a vegetation denoting intermediate or relatively poor status. The distribution as documented by us is shown in Fig. 10. According to QUEZEL & SANTA 1963, the species does not occur in Algeria, but it is found on the Iberian Peninsula.

Pinguicula lusitanica L. has an Atlantic distribution in Northern Morocco. It was recorded by J. & M. 1934 (p. 700) from Jbel Kebir, Jbel Dahar Zhirou, and Jbel Zem-Zem, and has also been found by us in the eastern part of the Tingitanean Peninsula and along the Jebala Range: on Jbel Sidi Habib and Jbel Bou Hassim (Fig. 11). The habitat is non-calcareous ground where seepage occurs, usually on the very margin of springs breaking through on slopes. The habitat resembles to some extent that of *Pinguicula vulgaris* L. (crosses on the same map), which has a high-montane distribution in the Rif, occurring mainly in fens with permanent seepage in cedar forests at relatively high altitudes. None of the two species seem to occur in the other parts of the Atlas Mountains, nor in Algeria.

Littorella uniflora L. has, to our knowledge, not been previously recorded from Morocco (or Algeria). It occurs, however, on the "Plateau d'Isagen" at Ketama in Central Rif, at an altitude of 1,400—1,500 m on sandy ground along the watercourses near the Ketama cross-roads (Fig. 9). It is associated in this place with *Jun-*

cus squarrosus L., *Eleocharis palustris, Ranunculus flammula* L., and *Isoëtes histrix,* and also with the endemic species *Deschampsia crassifolia* F.-Q. & MAIRE and *Genista nociva* PAU & F.-Q.

Concluding Remarks

The species mentioned above represent only a fraction of the Atlantic and "northern" elements in the vegetation of the regions studied, but some of them play an important role in the fens described above.

Some of the species seem to be new to the region: *Polystichum aculeatum, Molinia caerulea, Viola persicifolia, Chamaenerion angustifolium, Gratiola officinalis,* and *Littorella uniflora.*

Species with an *Atlantic* distribution in Northern Morocco as well as in Europe are *Genista anglica, Calluna vulgaris, Erica ciliaris, Anagallis crassifolia,* and *Pinguicula lusitanica.* They occur on the Tingitanean Peninsula or somewhat further south and have outposts in the humid north-western parts of the Jebala Range of the Rif Mountains. *Sphagnum auriculatum, Sieglingia decumbens,* and *Hypericum humifusum* may also be placed in this group, although they extend far into the Jebala Mountains.

Other species, common in north-western Europe, are strictly limited in Northern Morocco to the Rif Mountains, sometimes only to the very central and highest parts. They are often also found at higher elevations in the more southern ranges of the Atlas Mountains. They are chiefly *northern* in distribution and may be classed as "boreal" in Morocco. Such species are *Polystichum aculeatum, Nardus stricta, Carex echinata, C. leporina, C. oederi* p.p., *Pinguicula vulgaris,* and *Littorella uniflora.* Many other species found in fens and pastures in the cedar zone and not particularly commented upon above belong to this group, such as *Betula pendula, Juncus squarrosus, Ranunculus flammula,* and *Viola palustris.*

Some species have a somewhat wider distribution which is a combination of the previous two types. Such species are *Eleocharis multicaulis* and *Juncus bulbosus.*

Several of the species mentioned are absent from Algeria, especially those having an Atlantic distribution. Some are, however, found in this country and then usually in the extreme north-eastern corner in the region of "La Calle", which is one of the most humid parts of Algeria.

ANALYSIS OF SOIL SAMPLES [1]

Methods

The sampling has been done on a volume basis. On each sampling site one sample was cut out vertically from the soil surface with a sampling cylinder (385 cm^3, 10 cm). In sites 2 and 5 the living *Sphagnum* layer was included in the sampling. The chemical properties have been expressed on the fine earth content per volume unit. That means that weights of roots and particles greater than 2 mm in diameter are not included in the calculation. From all samples 25 g of fresh fine earth was extracted for 3 hours in 150 ml 1 M NH_4Ac, 50 ml 0.2 M KCl and 50 ml of distilled water respectively. In the KCl and distilled water extracts the pH was measured electrometrically with separate reference and glass electrodes. In the NH_4Ac extracts the metallic cations Ca^{2+}, Mg^{2+}, Fe^{2+} and Mn^{+} were determined by atomic absorption spectrophotometry, Na^{+} and K^{+} by flame photometry and H_3O^{+} by measuring the pH. The percentage of neutralization gives the sum of extractable metallic cations Ca^{2+}, Mg^{2+}, Na^{+}, K^{+} in percentage of the extractable cations Ca^{2+}, Mg^{2+}, Na^{+}, K^{+} and H_3O^{+}. The total nitrogen analysis has been carried out on dry samples by a semi-micro Kjeldahl method. The water content and loss of ignition have been determined gravimetrically.

Description of Soil Samples

SAMPLES 1—5. Taken on Jbel Bou Hassim (see p. 443) near the Forestry Office. Fens below pine plantation.

SAMPLE 1. Fen surface with wet, bare soil without *Sphagnum,* taken 0.5 m from upper

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[1] By BO WALLÉN, Department of Plant Ecology, Ö. Vallgatan 14, S-223 61 Lund, Sweden.

Table 1. Chemical properties of soil samples from Northern Morocco. Samples 1—5 from Jbel Bou Hassim, sample 6 from an eastern *Calluna vulgaris* site on Jbel Soukna, and sample 7 from a *Molinia caerulea* site on Haouta Bern Mediar.

Sample	Weight g/dm³	pH H_2O	pH KCl	% Neutralization	Extractable with NH_4Ac mmol/dm³						
					H^+	Ca^{2+}	Mg^{2+}	Na^+	K^+	Fe^{2+}	Mn^+
1	1351	5.18	4.18	6.7	53.0	0.77	0.58	0.52	0.58	0.04	0.01
2	850	5.40	4.30	35.0	25.9	1.00	5.29	0.44	0.60	0.04	0.37
3	1210	5.17	4.20	6.4	64.3	0.86	0.80	0.55	0.52	0.02	0.19
4	916	4.82	3.67	18.8	110.8	7.38	3.93	0.88	2.15	0.05	0.16
5	1199	5.20	4.26	10.3	72.7	1.05	1.70	1.20	1.62	0.01	0.82
6	1571	5.10	3.90	7.8	79.9	1.75	1.07	0.58	0.54	0.02	0.01
7	1620	5.25	3.97	25.1	79.0	3.75	6.96	2.10	3.00	0.02	0.01

Sample	Extractable with NH_4Ac ppm						Ca/Mg	N % of org. matter	Water cont. % fresh matter	Loss of ignition % dry matter
	Ca^{2+}	Mg^{2+}	Na^+	K^+	Fe^{2+} $\times 10^3$	Mn^+ $\times 10^3$				
1	0.019	0.024	0.023	0.015	0.7	0.2	1.33	2.63	65.1	15.6
2	0.025	0.218	0.019	0.015	0.7	6.7	0.19	2.04	84.2	30.4
3	0.021	0.033	0.024	0.013	0.4	3.4	1.07	2.65	67.6	22.7
4	0.184	0.162	0.038	0.055	0.9	2.9	1.88	2.71	62.8	19.9
5	0.026	0.070	0.052	0.041	0.2	14.9	0.62	2.50	84.3	37.5
6	0.044	0.044	0.025	0.014	0.4	0.2	1.64	2.24	27.8	6.6
7	0.094	0.286	0.092	0.077	0.4	0.2	0.54	2.44	29.4	8.3

margin with *Genista anglica*. Adjacent plant species: *Juncus bulbosus, Eleocharis multicaulis,* and *Potentilla erecta*. Sample reaching down into mineral soil containing stones and sand. Colour brown. Consistency creamy. The sample contains some fibres and roots.

SAMPLE 2. Centre of fen surface, in a *Sphagnum* tuft. Adjacent plant species: *Eleocharis multicaulis* and tufts of *Carex echinata*. Isolated specimens of *Agrostis juressii, Sieglingia decumbens, Potentilla erecta* and *Pinguicula lusitanica*. Sample contains brown-coloured, highly humified *Sphagnum* remnants and mineral soil.

SAMPLE 3. Fen surface, bare soil next to the upper *Genista* margin. Taken near sample 1, but from firmer ground. Adjacent plant species: *Sieglingia decumbens, Juncus acutiflorus* and *Eleocharis multicaulis*. (Near the sample, on looser soil: *Agrostis juressii, Juncus bulbosus* and *Anagallis crassifolia*.) Sample reaching into the mineral soil containing sandstone products. Structure and colour as in sample 1. Dense penetration of roots and fibres.

SAMPLE 4. Drier ground above the fen surface, c. 4 m from its upper *Genista* border, in *Pteridium* association. Other adjacent plant species: *Erica ciliaris, Potentilla erecta, Agrostis castellana* and *Holcus lanatus*. Colour of soil sample greyish-brown. Crumbly consistency. High content of roots and fibres.

SAMPLE 5. Taken on southern, wider fen surface. A wet sample from the centre of a *Sphagnum* mat. Similar in character to sample 2. *Eleocharis multicaulis* subdominant. Adjacent plant species: *Carex echinata, Agrostis juressii, A. castellana, Baldellia ranunculoides* and *Galium palustre*. Brown-coloured mixture of high- and low-humified *Sphagnum* remnants and mineral soil. Some root penetration.

SAMPLE 6. Taken on Jbel Soukna, eastern outpost for *Calluna vulgaris*. On the upper part of a south-eastern ridge extending from the mountain, ESE of the Ahlalech village. A moist slope with easterly aspect. The site of tall-growing *Calluna*, associated with *Pteridium aquilinum, Cistus salviifolius, Agrostis castellana* and *Carex distans*. Adjacent plant species: *Eleocharis multicaulis, Anagallis crassifolia, Hypericum humifusum, Erica arborea* and also *Erica umbellata, Lavandula stoechas* and *Inula viscosa.* — A dark brown cement-like soil with a rather dense penetration of shrub roots.

SAMPLE 7. Taken on Haouta Bern Mediar, Tingitanean Peninsula, in *Molinia caerulea—Eleocharis multicaulis*-vegetation. A humid valley facing south-west, below the Forestry Office. Sandstone ground. Some seepage. — The sample was taken from bare soil between tufts of *Molinia caerulea.* Adjacent species are: *Eleocharis multicaulis, Erica ciliaris, E. scoparia, Calluna vulgaris, Myrtus communis* and *Cistus populifolius.* — A black-coloured, cement-like soil with some penetration of grass roots but mainly shrub roots.

Chemical Properties

SAMPLES 1—5. The soils under discussion have, in spite of their peaty character a high content of inorganic matter. The relatively low content of organic matter (especially in samples 2 and 5, taken in *Sphagnum* peat) indicates a considerable mixing with the underlying mineral soil, partly due to the sampling method. The sampling cylinder has penetrated into the underlying mineral soil. The water content is relatively closely related to the content of organic matter.

The pH varies little between the samples. The highest is found in sample 2, which also shows the highest degree of neutralization. Sample 4 differs from the other samples in having a relatively low pH and at the same time showing a relatively high degree of neutralization. This is due to a high cation exchange capacity (the sum of H_3O^+, Ca^{2+}, Mg^{2+}, Na^+ and K^+) in the sample.

The values of exchangeable cations are in general normal for poor fen soils. The values of Ca^{2+} are extremely low, probably due to the fact that the underlying mineral soil is very poor in Ca^{2+}. Sample 4 is, with its higher Ca^{2+} content, an exception in this case.

The nitrogen contents of the samples vary little. The values are fairly normal for these soil types.

SAMPLE 6. The sample can be characterized as a poor, well-drained moor soil with a very low content of organic matter. The pH value, 5.1, is relatively high. The degree of neutralization is very low, due to very low contents of Ca^{2+} and K^+. The Ca/Mg ratio is normal for this type of soil. The value of nitrogen is also normal.

SAMPLE 7. The sample can, like sample 6, be characterized as a poor, well-drained moor soil with a very low content of organic matter. The pH value is, as in sample 6, relatively high. The degree of neutralization is in this sample higher than in sample 6, partly due to the rather high Mg^{2+} content. The Ca^{2+} content is very low. As a result of this the Ca/Mg ratio is very low.

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Sur quelques Arenaria d'Europe et d'Asie occidentale

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ABSTRACT

FAVARGER, C. 1972. Sur quelques Arenaria d'Europe et d'Asie occidentale. — Bot. Notiser 125: 465—476.

Seventeen taxa of the genus *Arenaria* have been studied from a cytological point of view. Twelve chromosome numbers have been reported for the first time, whereas two differ from those which have been published for the same taxa. The origin of *A. pungens* must be found in North Africa, that of *A. tetraquetra* (sensu stricto) in the Baetic range of South Spain. The author proposes a hypothesis to explain the origin of *A. ligericina,* a pyreneo-cevenol endemic. *A. huteri* is almost certainly a paleopolyploid.

In the subgenus *Eremogone,* the chromosomes are generally larger than in the subgenus *Arenaria* and the most widely represented basic number is x=11. Polyploidy is very frequent in this subgenus. An accurate cytotaxonomical study of the species related to *A. graminifolia* SCHRAD. will probably allow to give some light to the taxonomy and phylogeny of this difficult group.

INTRODUCTION

Dans un travail antérieur (FAVARGER 1962), nous avons montré que le genre *Arenaria* L. se signalait à l'attention par la grande variété de ses nombres chromosomiques de base (x=9, 10, 11, 12, 13, 14, 15 et x'=23). Il paraissait tentant d'utiliser ce critère dans la recherche — fort difficile — des affinités entre espèces. D'autre part nos études sur les populations alpiennes du groupe de l'*Arenaria ciliata* (FAVARGER 1960, 1963, 1965) ont montré que la polyploïdie avait joué un rôle important dans la naissance de races morphologiquement assez peu distinctes mais géographiquement bien définies. Le présent travail a pour but d'approfondir l'étude cytotaxonomique du genre *Arenaria* en étendant les recherches à des espèces qui, pour la plupart, n'ont pas été étudiées jusqu'ici à ce point de vue.

Nous sommes heureux de dédier cette étude à notre éminente collègue Madame VIVI TÄCKHOLM, le savant auteur de la Flore d'Égypte et de nombreux travaux de taxonomie. Madame TÄCKHOLM s'est toujours intéressée à nos activités et ses encouragements nous ont été très précieux. Qu'elle veuille bien accepter ce travail en déférent hommage.

MATÉRIEL ET MÉTHODES

Le matériel qui sert de base aux présentes recherches a été récolté (et parfois fixé) sur place par des collègues ou collaborateurs ou par nous-même. D'autre part, nous avons utilisé des plantes récoltées en général dans la nature par les soins de divers jardins botaniques. La plupart des espèces étudiées ici sont en culture au jardin botanique de Neuchâtel; des exsiccata (témoins de fixation) sont conservés dans notre herbier personnel. Les fixations ont toujours été faites à l'alcool acétique (3: 1) avec mordançage, et les colorations au carmin acétique par la méthode d'écrasement. Pour certains polyploïdes élevés, nous avons dû procéder à un prétraitement de deux heures au monobromonaphtalène, qui nous a donné de bons résultats (la

Tableau 1. Nombres chromosomiques de quelques *Arenaria.*

Taxon	Lieu de récolte	No de culture	n	2n
A. pungens CLEMENTE	Erdouz, Maroc, 2200 m	—	14	28
„ —	Mulhacen, Sierra Nevada, Espagne, 3100 m	—	28	—
„ —	J. bot. Lausanne	57/393	28	—
A. tetraquetra L.	Prado Llano, Picacho de Veleta, Sierra Nevada, Espagne, 3000 m	—	20	—
„ —	Guara, Prov. Huesca, Espagne, 1850 m	71/770	—	ca 120[1]
„ —	Versant E. du Turbon, Prov. Huesca, Espagne, 1800 m ..	71/768	—	ca 120[2]
„ —	Port de Vénasque, Prov. Huesca, Espagne, 2350 m ..	68/98	—	120[3]
A. ligericina LECOQ & LAMOTTE	Pic de Casamanya, Andorre, 2300 m	69/1897	40	—
„ —	Montpellier-le-Vieux, Aveyron, France, 500 m	70/1813	40	—
A. cinerea DC.	Les Scaffarels, Basses Alpes, France, 750 m	72/1361	20	—
A. bertolonii FIORI	Mte Corazi, Sardaigne	—	—	30
„ —	Gran Sasso, Italie, 2150 m ..	71/1651	15	—
A. biflora L.	Wöllaner Nock, Gurktaler-Alpen, Autriche, 2000 m ..	69/1708	—	22[4]
A. gracilis WALDST. & KIT. ..	Kamesnica, Yougoslavie, 1800 m (J. bot. Lausanne)	70/1254	—	24
„ —	Biokova, Croatie, 1450 m (J. bot. de Graz)	70/1403	—	24
A. huteri KERNER	Val Cimoliana, Italie, 1000—1100 m	72/1670	—	88
A. cucubaloides SMITH	Arménie (J. bot. d'Erevan) ..	69/587	11	22
A. dianthoides SM.	Arménie (J. bot. d'Erevan) ..	68/339	33	—
A. lychnidea M. BIEB.	Caucase (J. bot. de Moscou)	61/66	11	—
A. longifolia M. BIEB.	Russie d'Europe (J. bot. de Moscou)	69/80	44	ca 88
A. polaris SCHISCHK.	J. bot. de Moscou	57/100	55	—
„ —	J. bot. de Kirovsk	66/245	ca 55	—
A. koriniana FISCH.	Province d'Aktubin (J. bot. de Moscou)	67/111	—	44
A. syreistschikovii SMIRNOV ..	J. bot. de Moscou	60/39	11	—

[1] Compté 2n=127.

[2] Compté 2n=123—125.

[3] Compté parfois aussi 2n=123—126.

[4] Deux chromosomes sont porteurs d'un satellite.

méthode ne réussit cependant pas dans tous les cas).

Toutes les figures ont été dessinées avec une chambre claire de Levallois (Paris) au même grossissement (Oculaire 25×, Objectif 100×), à l'exception des Fig. 1 O et 2 A (Ocul. 15×).

Les resultats sont résumés au tableau 1.

DISCUSSION

ARENARIA PUNGENS CLEMENTE. Cette espèce ibéro-atlasique a été étudiée par QUEZEL (1957). Cet auteur a compté n=30 chez les ssp. «*eu-pungens* EMB.» du Toubkal et *boissieri* EMB. de Bou

Naceur et n=15 chez le ssp. *parviflora* sous-espèce nouvelle que QUEZEL a décrite d'après une récolte des environs de m'Semrir (haute vallée du Todhra, versant sud du Grand Atlas central).

L'auteur français est le premier à avoir décelé chez *A. pungens* de la polyploïdie intraspécifique. Selon lui, les ssp. «*eu-pungens*» (calcifuge) et *boissieri* (calcicole) sont des orophytes dérivés par multiplication du génome d'un taxon (le ssp. *parviflora)* localisé à une altitude relativement faible. Laissant de côté pour l'instant la question du nombre de base, nous ferons observer que la plante récoltée à l'Erdouz par Mme A. CAUWET et étudiée à Neuchâtel, appartient selon toute vraisemblance au ssp. *parviflora,* puisqu'elle est diploïde et offre des fleurs un peu plus petites que, par exemple, les plantes de la Sierra Nevada. Puisque l'Erdouz se trouve au N. du Grand Atlas, à environ 240 km à vol d'oiseau de la station de m'Semrir, il est vraisemblable que l'*Arenaria pungens* diploïde est assez répandu dans le Ht Atlas, où des prospections systématiques permettront sans doute de circonscrire exactement son aire. En revanche, les populations de la Sierra Nevada semblent uniformément tétraploïdes.

Il paraît des plus vraisemblable que l'*A. pungens* est né en Afrique du Nord où subsistent encore (peut-être à l'état plus ou moins relictuel) des populations diploïdes. Les races tétraploïdes, nées plus tardivement et plus conquérantes, ont envahi le Ht Atlas, peut-être au Pliocène, et ont gagné la Sierra Nevada. Si l'on se refuse à admettre une telle migration vers le Nord, de l'*A. pungens* tétraploïde, il faudrait supposer une origine polytopique des tétraploïdes, *à la fois* dans le Ht Atlas et dans le Sud de l'Espagne; dans ce cas, il deviendrait difficile de comprendre pourquoi la race diploïde ne se rencontre plus actuellement en Sierra Nevada.

Parmi les orophytes ibéro-atlasiques, qui ont un nombre de chromosomes plus bas en Afrique du Nord qu'en Europe, QUEZEL (1957 p. 398) cite l'exemple de l'*Alyssum spinosum*=*Ptilotrichum spinosum,* qui accompagne souvent l'*Arenaria pungens* dans les garrigues altimontaines à xérophytes épineux. Ce taxon est diploïde en Afrique du Nord (QUEZEL, loc. cit.); en revanche, et cela contrairement à l'opinion de QUEZEL (loc. cit.)[1] les populations de Sierra Nevada sont tétraploïdes, comme celles de la Sierra de Javalambre et des Pyrénées orientales (KÜPFER 1972). Nous pensons qu'*Alyssum spinosum* a pris naissance en Afrique du Nord et qu'il est devenu polyploïde au cours d'une migration (polyploïdie de migration, FAVARGER 1967) qui l'a conduit d'abord dans la chaîne bétique et de là jusqu'au Languedoc et au Roussillon. BAUDIÈRE (1970) qui s'est intéressé tout particulièrement à la population du Malaza (Pyrénées orientales) écrit à ce propos (p. 87): «le sens de la migration ne fait aucun doute». Il est des plus vraisemblable qu'*Arenaria pungens* accompagnait l'*Alyssum spinosum* dans sa première migration au Sud de l'Espagne, car ainsi que le remarque QUEZEL (1957 p. 411) au sujet de la flore atlasique «les orophytes y sont parvenus en groupes, en gardant en quelque sorte leur constitution en associations végétales». Cette opinion s'applique aussi, à notre avis, à une migration vers le Nord d'éléments nord-africains. Seule l'époque de cette migration est difficile à préciser. En tout état de cause, nous pensons qu'on peut considérer le ssp. *parviflorum* diploïde d'*A. pungens* comme un taxon patroendémique d'Afrique du Nord (FAVARGER & CONTANDRIOPOULOS 1961).

Il reste le problème du nombre de base de cette espèce. Sur le matériel d'Erdouz, fixé par Mme A. CAUWET, nous n'avons jamais pu observer plus de 14 bivalents à la diacinèse; à la métaphase somatique, on compte 2n=28 (Fig. 1 A). Les individus,

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[1] Nous ne savons pas sur quel comptage précis s'est appuyé QUEZEL pour affirmer «qu'en Afrique du Nord *et en Sierra Nevada* (c'est nous qui soulignons), *Alyssum spinosum* s'est montré caractérisé par 8 paires de chromosomes».

fixés par M. PH. KÜPFER, deux années consécutives (1967 et 1968) à la Sierra Nevada nous ont permis de compter 28 bivalents sur des métaphases I. Certes, le comptage n'est pas toujours facile, et parfois on a l'impression qu'il y a un bivalent (métaphase I) ou un chromosome (métaphase II) de plus. Enfin, sur une plante cultivée à Neuchâtel et venant du jardin botanique de Lausanne, nous avons compté à plusieurs reprises et *exactement* n=28 (Fig. 1 B) tant sur des métaphases I et II que sur des anaphases I de la microsporogénèse. Nos comptages sont donc en désaccord avec ceux de QUEZEL (1957). Le nombre gamétique n=14 existe dans le genre *Arenaria*; nous l'avons déterminé en particulier chez *A. montana* L. (FAVARGER 1962). Il est vrai que, tout récemment, FERNANDES & LEITAO (1971) ont compté 2n=30 chez une plante de cette espèce croissant au Portugal. En revanche, SCHOTSMAN (1970) a confirmé le nombre n=14 sur du matériel de Sologne et du Gard. Il n'est pas exclu que dans ces deux espèces d'*Arenaria,* il puisse y avoir des individus tétrasomiques. Il n'y a guère d'affinités entre *A. pungens* et *A. montana,* (à part le nombre chromosomique de base). Ces deux espèces sont placées par MCNEILL (1962) dans des sous-genres différents.

Les affinités de l'*A. pungens* restent très obscures. C'est une espèce isolée pour laquelle MCNEILL (op. cit.), qui la place dans le sous-genre *Eremogone,* se demande s'il ne conviendrait pas de créer un sous-genre particulier. La seule espèce affine est l'*A. dyris* de l'Atlas, sur laquelle QUEZEL (1957) a compté n=20. A notre avis, ce nombre demande confirmation. MCNEILL (1962 p. 127) ne parle pas de l'*Arenaria dyris* mais cite comme espèce proche de l'*A. pungens,* l'*A. mairei* EMBERGER. Cependant, d'après MAIRE (1963), cette dernière espèce n'appartient pas à la section *Eremogone.*

ARENARIA TETRAQUETRA L. Ce binôme est pris ici dans le sens où l'entendent CHATER & HALLIDAY (1964) dans Flora Europaea, c'est-à-dire au sens restreint. Sur le matériel de la Sierra Nevada, récolté par M. PH. KÜPFER, et appartenant au var. *granatensis* BOISS., nous avons compté avec précision 20 bivalents à la métaphase I (Fig. 1 C). Ce taxon est donc diploïde.[2] En revanche, les populations du Nord de l'Espagne, correspondant au var. *pyrenaica* BOISS. sont polyploïdes. Nous n'avons pu étudier ici la méiose, et avons dû nous contenter des mitoses somatiques des pointes radiculaires. Comme les chromosomes sont très nombreux, nous avons utilisé un prétraitement (cf. p. 465). Le matériel du Port de Vénasque nous a permis de compter à deux reprises, exactement 2n=120 (Fig. 1 D). Il est vrai que sur d'autres racines de la même provenance, nous avons compté une fois 126 et une autre fois 123 chromosomes. Le même phénomène s'est présenté dans la plante du Turbon: 2n=123—125 et dans celle de Guara: 2n=127. Nous pensons que le taxon du Nord de l'Espagne est un hexaploïde à 2n=120, mais que son nombre chromosomique varie quelque peu, par suite d'anomalies méiotiques ou

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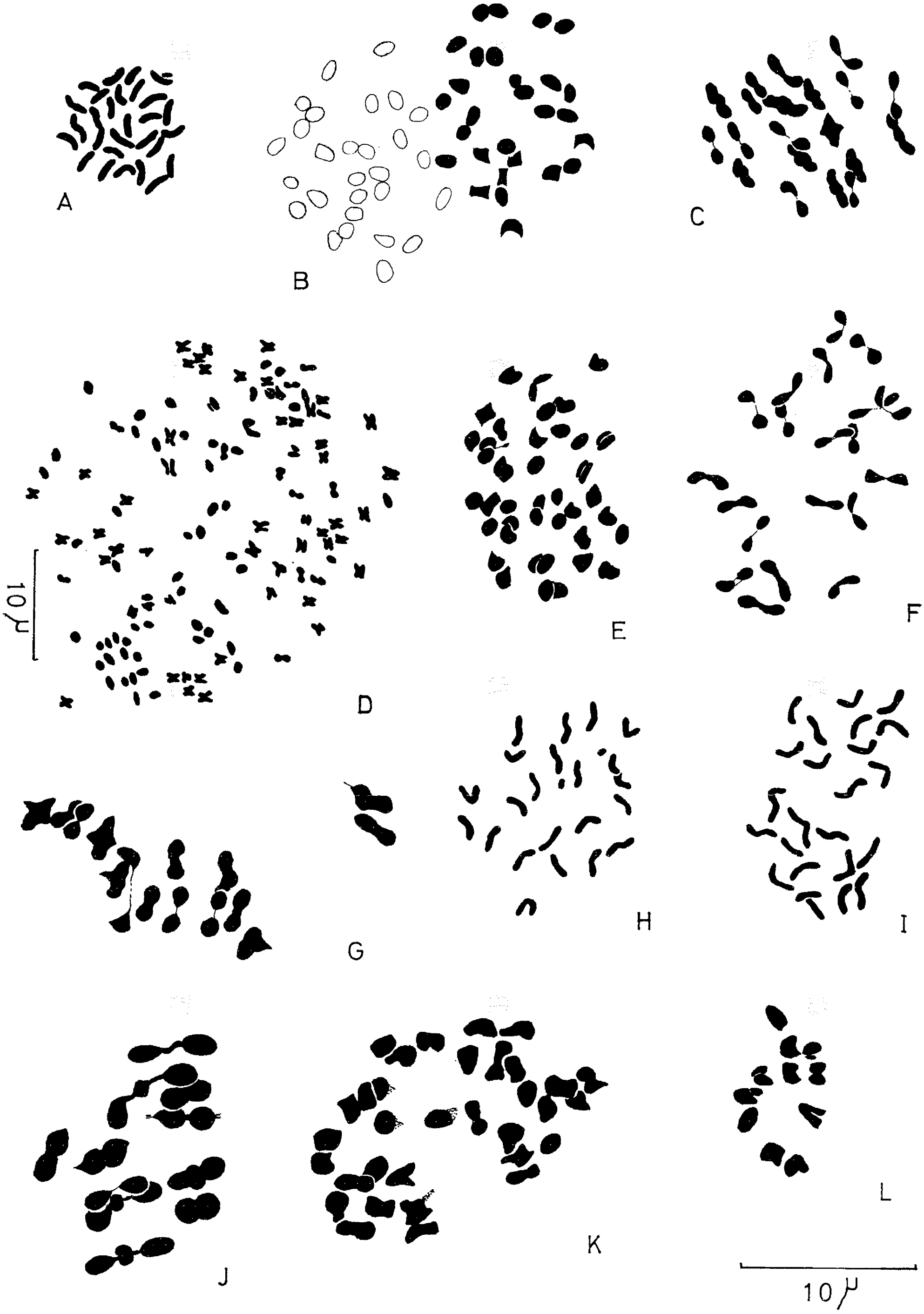
[2] On pourrait évidemment le considérer comme tétraploïde, en supposant un nombre de base x=10. Toutefois, ce nombre n'a pas été observé jusqu'ici dans le groupe d'espèces dont fait partie *A. tetraquetra* (section *Plinthine* (RCHB.) MCNEILL).

Fig. 1. A: *Arenaria pungens* (Maroc). Métaphase somatique de pièce florale. — B: *A. pungens* (J. bot. Lausanne). Anaphase I, les 2 groupes sont dans 2 plans différents. — C: *A. tetraquetra* (Sierra Nevada). Métaphase I. — D: *A. tetraquetra* (Pyrénées). Métaphase somatique d'une racine (prétraitement au monobromonaphtalène). — E: *A. ligericina* (Aveyron). Anaphase I. — F: *A. cinerea.* Métaphase I. — G: *A. bertolonii* (Gran Sasso). Métaphase I. — H: *A. biflora.* Métaphase somatique du méristème radiculaire. — I: *A. gracilis* (Biokova). Métaphase somatique du méristème radiculaire. — J: *A. cucubaloides.* Métaphase I. — K: *A. dianthoides.* Anaphase I. — L: *A. lychnidea.* Anaphase I.


A
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peut-être même mitotiques, comme cela arrive souvent dans les polyploïdes élevés.[3]

L'*Arenaria tetraquetra* L. (sensu stricto) n'a pas été étudié jusqu'ici au point de vue cytologique. Nos recherches montrent que le taxon de la Sierra Nevada diffère de celui des Pyrénées centrales et des Prépyrénées aragonaises, non seulement par des détails morphologiques (fleurs plus petites, à 5 pétales, anthères plus petites, etc.) mais aussi par le nombre de chromosomes. Ces différences justifient amplement pour les deux taxons un statut de sous-espèces. C'est bien le statut que leur a donné FONT QUER (1948) mais en les incluant dans une grande espèce collective: *Arenaria aggregata* L. comprenant presque toutes les espèces de la section *Plinthine*. Là-dessus, LAINZ (1960), se conformant à la règle d'antériorité, a transféré tous les taxons de FONT QUER, sous le pavillon de l'*Arenaria tetraquetra* L. «sensu lato».

Nous ne pensons pas qu'il soit très «naturel» de réunir dans une même espèce des taxons tels l'*Arenaria tetraquetra* var. *granatensis* (n=20) et le groupe comprenant l'*A. aggregata* (L.) LOISEL.=*A. capitata* LAM. et l'*A. armeriastrum* BOISS.=*A. armerina* BORY dont le nombre de base paraît être x=15.[4] Nous préférons personnellement le traitement taxonomique adopté par CHATER & HALLIDAY (1964) et par MCNEILL (1962) qui distinguent respectivement 6 et 9 espèces dans la section *Plinthine*. En attendant que des études cytotaxonomiques précises s'étendent à l'ensemble de cette section du genre *Arenaria,* nous croyons qu'il est justifié de donner au binôme *Arenaria tetraquetra* L. un sens restreint. A l'intérieur de cette espèce, il y a deux taxons principaux, à savoir:

l'*Arenaria tetraquetra* L. (sensu stricto, non sensu LAINZ 1960) ssp. *imbricata* (LAG. & RODR.) FONT QUER ex LAINZ, basionyme: *A. imbricata* LAG. & RODR. An. C. N. 5: 278—1802, syn. *A. t.* var. *granatensis* BOISS., sous-espèce diploïde, à corolles pentamères, du S. E. de l'Espagne; et

l'*Arenaria tetraquetra* L. ssp. *tetraquetra* (=*A. t.* var. *pyrenaica* BOISS.), taxon hexaploïde du N. de l'Espagne, à corolles tétramères et fleurs plus grandes.

Les données cytologiques obtenues ici donnent à penser que le ssp. *imbricata* représente le taxon ancestral et que le ssp. *tetraquetra* est devenu polyploïde lors d'une migration qui l'a conduit du S-E. de l'Espagne dans le Nord de la péninsule. KÜPFER (à l'impression) compare ce cas à celui du *Silene boryi* qu'il a étudié en détail et pense que la migration vers le Nord des races polyploïdes de ces espèces oroméditerranéennes a eu lieu au Tardiglaciaire. Dans le cas particulier de l'*A. tetraquetra,* ce phénomène nous paraît plus ancien, car il y a une grande lacune entre l'aire des diploïdes et celle des polyploïdes. Quoiqu'il en soit, le ssp. *imbricata* est un taxon patroendémique du S-E. de l'Espagne, et le ssp. *tetraquetra* un apoendémisme des Pyrénées centrales et des Prépyrénées aragonaises.

ARENARIA LIGERICINA LECOQ & LAMOTTE. Le nombre chromosomique de cette espèce est rapporté ici pour la première fois. Grâce aux récoltes de M. PH. KÜPFER, nous avons pu étudier deux populations, l'une des Causses de l'Aveyron, et l'autre du Pic de Casamanya en Andorre. Sur les deux matériels, nous

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[3] Les nombres différant de 2n=120 peuvent s'expliquer, en partie, par des difficultés techniques, car on peut prendre parfois les deux chromatides d'un chromosome métaphasique raccourci pour deux chromosomes en superposition.

[4] Chez *A. aggregata* (L.) LOIS., nous avions compté n=ca 15 (FAVARGER 1962). Ce nombre a été précisé et confirmé par GUINOCHET & LOGEOIS (1962) et par PUECH (1963); d'autre part, le nombre gamétique de l'*A. armeriastrum* BOISS. semble être de n=30 (FAVARGER 1962) mais ce dernier nombre, compté sur du matériel de jardin botanique, devra être confirmé sur des plantes spontanées.

avons compté exactement n=40 à la métaphase I ou à l'anaphase I de la microsporogénèse (Fig. 1 E). Dans l'ensemble, la méiose est régulière; cependant, le matériel du Pic de Casamanya montre parfois à la métaphase I quelques univalents ou pseudo-univalents, c'est-à-dire des bivalents séparés précocement.

L'histoire de cette espèce est intéressante. Longtemps elle fut considérée comme endémique des Cévennes. En 1901, une plante assez semblable «exhalant sur le vif une odeur spéciale qui rappelle celle de l'*A. lesurina* LORET des Causses et des Cévennes», fut découverte à la Sierra del Cadi par GAUTIER et l'Abbé COSTE. Elle ne fut pas reconnue d'emblée comme l'*A. ligericina* par COSTE mais décrite par COSTE et SOULIÉ (1911) comme une forme spéciale de l'*A. ciliata,* à savoir le var. *canescens* COSTE & SOULIÉ. C'est FONT QUER (1946) qui, le premier,[5] comprit que la population du Coll de Jou se rapportait à l'*A. ligericina.* La plante espagnole différait cependant de celle des Causses «par sa robustesse, ses calices plus longs et ses pétales dépassant peu le calice». Il en fait l'*A. ligericina* var. *canescens* (COSTE & SOULIÉ) F. Q. Ce taxon fut découvert ensuite en Andorre par LOSA et MONTSERRAT (1951). Ces auteurs constatent que la plante du Pic de Casamanya est identique à celle des Cévennes et diffère de la population de la Sierra del Cadi (var. *canescens*) par une pubescence moins forte. Grâce à l'amabilité du Dr L. GRANEL DE SOLIGNAC (Montpellier) et du Professeur O. DE BOLOS (Barcelone) que nous remercions vivement ici, nous avons pu examiner le matériel de la Sierra del Cadi. Si les échantillons de COSTE et SOULIÉ (MPU) sont plus hirsutes que ceux du Pic de Casamanya (legit KÜPFER, NEU), cette différence est loin d'être constante et l'échantillon récolté par FONT QUER et CUATRECASAS en 1926 (BCC) n'est pas plus pubescent que ceux de l'Andorre. En revanche, tous les individus récoltés en altitude diffèrent des plantes des Causses de l'Aveyron par un port plus ramassé, des hampes florales moins hautes et moins ramifiées et des sépales plus longs. Pour la plante de montagne, il nous semble qu'on peut garder le nom de var. *canescens* en se reportant aux différences signalées par FONT QUER (1946).

L'étude cytologique, en montrant que les plantes des Causses et celles de l'Andorre ont le même nombre de chromosomes, apporte un argument de plus à l'opinion de FONT QUER, selon laquelle ces plantes sont conspécifiques. Mais elle permet, à notre avis, d'aller plus loin. L'examen comparatif des *Arenaria moehringioides* (=*A. ciliata* ssp. *moehringioides*) des Pyrénées, de l'*A. hispida* des Cévennes et de l'*A. ligericina,* montre que cette dernière espèce est morphologiquement intermédiaire entre les deux autres. Comme l'*A. hispida* a 2n=40 (FAVARGER 1962) et l'*A. moehringioides* aux Pyrénées (comme d'ailleurs aux Alpes) aussi 2n=40 (FAVARGER & KÜPFER 1968 et KÜPFER, non publié), nous pensons que l'*A. ligericina* est né par amphidiploïdie à partir de ces deux taxons.

Les choses ont pu se passer de la façon suivante: l'*A. hispida* occupait probablement à la fin du Tertiaire une aire plus vaste au N. de l'Espagne et dans les Cévennes. Au moment des glaciations, l'*A. moehringioides* des Pyrénées est «descendu» en plaine et s'est croisé avec l'*A. hispida.* Par redoublement du nombre des chromosomes, l'hybride a produit l'*A. ligericina.* Lors du retrait des glaciers quaternaires, l'*A. ligericina* qui devait posséder de par sa nature hybridogène une grande amplitude altitudinale, a suivi les glaciers jusqu'en Andorre et à la Sierra del Cadi. Aux Pyrénées, son aire ne s'est pas étendue, à cause de la concurrence de l'*A. moehringioides* qui vit dans les mêmes biotopes. Une partie des populations est restée dans les Causses où ne

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[5] Selon FONT QUER (1946) la véritable identité de la plante avait été reconnue par PAU, *in schedis.*

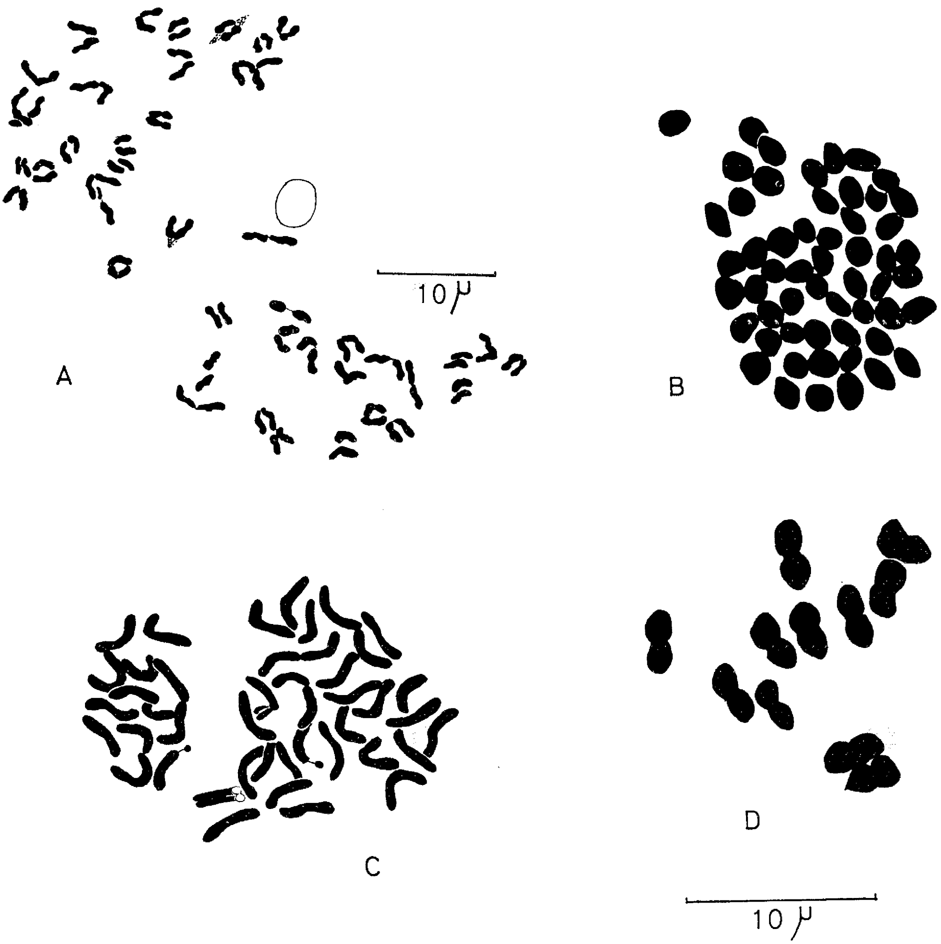

Fig. 2. A: *Arenaria longifolia*. Diacinèse. — B: *A. polaris*. Métaphase I. — C: *A. koriniana*. Métaphase de pièce florale. — D: *A. syreistschikovii*. Métaphase I.

croît pas actuellement l'*A. moehringioides*. Ainsi donc, cette espèce, sans être très ancienne (apoendémisme pyrénéo-cevenol datant des glaciations), possède actuellement un caractère relictuel. Il sera fort intéressant de vérifier cette hypothèse par la voie expérimentale.

ARENARIA CINEREA DC. Le nombre chromosomique de cette espèce endémique de Provence est rapporté ici pour la première fois: il est de n=20 (Fig. 1 F) comme celui de l'*A. hispida* et de l'*A. moehringioides*. BRAUN-BLANQUET (1923) pense que les *A. cinerea, hispida* et *ligericina* «seraient les descendants d'une espèce méditerranéo-montagnarde de souche tertiaire». Son opinion est peut-être exacte pour les *A. cinerea* et *hispida* que l'on pourrait à la rigueur considérer comme des espèces schizoendémiques.[6] En revanche, le nombre chromosomique de

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[6] L'*A. cinerea* est cependant assez différente de l'*A. hispida* par l'absence de poils glanduleux, par ses sépales ciliés au bord, etc.

l'*A. ligericina* prouve que cette espèce n'est pas née par spéciation graduelle. Sa ressemblance avec l'*A. moehringioides* n'est pas pour nous le résultat d'une convergence. C'est pourquoi nous pensons que l'*A. moehringioides* est affine de ce groupe, bien qu'elle ait un caractère orophile plus prononcé. McNeill (1962) a placé les *A. ciliata* et *cinerea* dans la même section (*Rariflorae*). En revanche, il place les *A. hispida* et *ligericina* dans une autre section (*Orientales*). Cette façon de procéder ne nous paraît pas très naturelle. En définitive, nous pensons qu'il faut se garder d'un jugement hâtif; les taxons correspondants de l'*A. cinerea* sont encore à trouver. Peut-être faut-il regarder du côté de l'*A. valentina* dont le nombre chromosomique n'est pas connu?

ARENARIA BERTOLONII Fiori=A. SAXIFRAGA Fenzl. Nous avons publié en 1962 le nombre chromosomique n=15 déterminé sur du matériel de Corse. Les recherches présentes montrent que l'espèce est diploïde et possède le même nombre de chromosomes dans les diverses parties de son aire (à l'exception de la Sicile d'où nous n'avons pu encore obtenir du matériel) (Fig. 1 G). Le matériel corse, récolté à la Punta delle Fornello par J. Contandriopoulos, appartient au var. *burnatii* Briq., celui de Sardaigne, au var. *salisii* Briq. Quant aux plantes du Gran Sasso, elles se rapportent au var. *italica* Briq. Nous doutons un peu que ces variétés soient plus que des populations locales. En particulier, la pubescence des feuilles est bien variable, tant dans l'Apennin qu'en Sardaigne.

ARENARIA BIFLORA L. Nous confirmons ici nos comptages antérieurs (Favarger 1949, 1962) sur du matériel des Alpes.

Sur une métaphase du méristème radiculaire, nous avons observé deux chromosomes satellitifères, portant un assez gros satellite (fig. 1 H). Si nous mentionnons

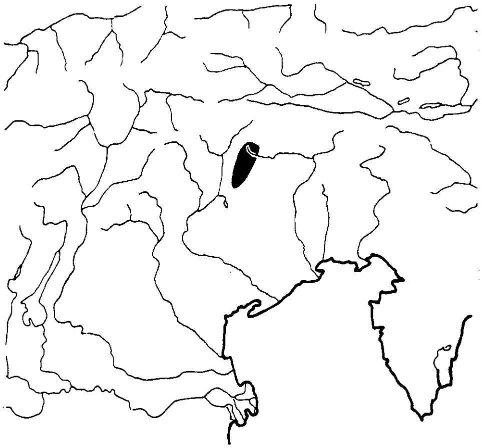

Fig. 3. Aire approximative de l'*Arenaria huteri* dans les Alpes.

ici cette espèce, c'est que lors d'une excursion en Autriche à laquelle assistait notre jardinier-chef en 1969, cette plante avait été désignée par un des organisateurs comme étant l'*A. rotundifolia* Bieb. Nous n'avons pas connaissance de la présence en Autriche de cette dernière espèce pour laquelle nous avons publié en 1962, n=22.

ARENARIA GRACILIS Waldst. & Kit. Le nombre publié ici (Fig. 1 I) confirme sur des plantes croissant à l'état spontané en Yougoslavie, celui que nous avions publié en 1962 pour cette espèce. La présence de l'*A. gracilis* à n=12 dans la section *Rariflorae* Williams, à côté de plusieurs espèces à x=10 (*A. cinerea, A. ciliata,* etc.) a quelque chose d'un peu insolite.

ARENARIA HUTERI Kerner. Cette espèce est une des endémiques alpiennes dont l'aire est la plus restreinte. (Carte fig. 3.) Ascherson & Graebner (1919) pensaient qu'elle était affine de l'*A. gracilis* et d'*A. grandiflora,* cependant que Chater & Halliday (1964) la comparent à l'*A. bertolonii.*

Bien que nous n'ayons eu à notre disposition que des stolons et quelques racines, nous avons pu faire un comptage sur un méristème radiculaire, après prétraitement au monobromonaphtalène. Le nombre zygotique de l'espèce est 2n=88. Il s'agit donc d'un polyploïde sur la base de x=11, dont les affinités sont à rechercher peut-être du côté de l'*Arenaria orbicularis* Vis. du Velebit (2n=44) ou d'autres taxons balkaniques affines.

Non seulement l'*A. huteri* est extrêmement localisée, mais elle semble avoir une écologie stricte. Dans la partie inférieure du Canale de Cimolais, entre 800 et 1100 m d'altitude, elle croît exclusivement dans les fentes des rochers dolomitiques, en station fraîche ou à l'ombre. Elle est assez abondante dans ses stations où elle côtoie *Spiraea decumbens, Phyteuma comosum, Paederota bonarota,* etc. Elle donne l'impression d'une espèce ancienne, dont les taxons correspondants ont peut-être disparu. Jusqu'à plus ample informé, nous la considérerons comme un paléopolyploïde, endémique des Alpes vénitiennes.

Les espèces suivantes appartiennent au sous-genre *Eremogone* dont McNeill (1962 p. 120) dit qu'il remplace plus ou moins le subgenus *Arenaria* en Asie et à l'ouest de l'Amérique du Nord.

ARENARIA CUCUBALOIDES Smith. Cette belle espèce du Caucase, de l'Arménie et du Kurdistan est diploïde avec n=11 ou 2n=22 (Fig. 1 J). À côté de figures normales comme celle que nous reproduisons ici, nous avons relevé dans notre matériel diverses anomalies méiotiques telles que: manque de simultanéité (coexistence des stades pachytène, métaphase I, stade à 4 noyaux), cytomixie conduisant à des cellules mères à chromosomes nombreux, plus ou moins éparpillés ou disposés en petits groupes, tétrades inégales, etc. Nous ne pouvons nous prononcer sur le déterminisme de ces anomalies.

ARENARIA DIANTHOIDES Smith. On note ici la présence de 33 bivalents (Fig. 1 K). Notre matériel est donc hexaploïde.

Avec *A. gypsophiloides* L. (n=11, Favarger 1962), les deux espèces précitées sont classées par McNeill (1962) dans la section *Glomeriflorae* Fenzl ex Williams. Le nombre de base de cette section est x=11.

ARENARIA LYCHNIDEA M. Bieb. L'espèce est diploïde, avec n=11 (Fig. 1 L). Notre matériel offrait de nouveau un certain nombre d'anomalies méiotiques à côté de diacinèses et d'anaphases I tout à fait normales. *A. lychnidea* est placé par McNeill (1962) dans la section *Capillares* qui selon cet auteur serait le groupe le plus primitif du sous-genre *Eremogone.* Le nombre chromosomique de 2n=22 a été compté par Zhukova (1966) dans *A. capillaris* Poir. Il semblerait donc que le nombre de base de cette section soit aussi de x=11. Cependant, Löve & Kapoor (1967) puis Löve, Löve & Kapoor (1971) ont publié 2n=40 pour *A. fendleri* A. Gray. Est-ce un indice que le nombre x=11, si fréquent dans le sous-genre *Eremogone,* dérive de x=10, nombre de base fort répandu dans le sous-genre *Arenaria,* qui selon McNeill serait plus primitif que *Eremogone,* cela n'est pas impossible. Toutefois, il convient d'étudier la cytologie d'un nombre plus grand d'espèces, avant de se prononcer.

ARENARIA LONGIFOLIA M. Bieb. Le nombre gamétique n=44 a été compté à la diacinèse (Fig. 2 A). Ce taxon est donc octoploïde. Comme les suivants, il appartient à la section *Eremogone.*

ARENARIA POLARIS Schischk. Dans le matériel du jardin botanique de Moscou, nous avons compté n=55, à la métaphase I (Fig. 2 B). Sur le matériel de Kirovsk, le nombre gamétique est très probablement le même, bien que les difficultés techniques ne nous aient pas permis de faire un comptage précis. Ce taxon est subordonné par CHATER & HALLIDAY (1964) à *A. procera* ssp. *glabra* (=*A. graminifolia* SCHRAD.), non sans quelque doute sur le rang (sous-espèce?) qu'il convient de lui attribuer. Au point de vue morphologique, l'*A. polaris,* en culture à Neuchâtel, nous a paru différer de l'*A. graminifolia,* d'une façon constante, par ses tiges moins hautes, ascendantes et non dressées et ses jeunes pousses courbées en faux. Son nombre chromosomique qui révèle un polyploïde élevé (décaploïde) serait un argument de plus pour en faire au moins une sous-espèce. En effet, l'*A. graminifolia* SCHRAD. possède soit 2n=22 (matériel du Burgenland, TITZ 1966), soit 2n=44 (matériel d'U.R.S.S., FAVARGER 1962).

ARENARIA KORINIANA FISCH. Sur une mitose de pièce florale, nous avons dénombré 2n=44 chromosomes dont une paire d'éléments satellitifères (Fig. 2 C). Ce taxon paraît très voisin de l'*A. graminifolia.*

ARENARIA SYREISTSCHIKOVII SMIRNOV. Les plantes qui nous ont été envoyées sous ce nom par le jardin botanique de Moscou se sont révélées diploïdes avec n=11 (Fig. 2 D). Pour CHATER & HALLIDAY (1964) ce binôme est synonyme de l'*A. procera* ssp. *glabra*=*A. graminifolia* SCHRAD. Les résultats présentés ici donnent à penser que l'*A. graminifolia* possède au moins deux «races chromosomiques», l'une diploïde (Burgenland, selon TITZ (1966), et U.R.S.S.), l'autre tétraploïde (FAVARGER 1962). Cette dernière est peut-être identique à l'*Arenaria koriniana.* TITZ (1966) pense qu'il conviendrait de soumettre l'*A. graminifolia* à une étude cytotaxonomique précise. Nous partageons entièrement l'opinion de notre collègue autrichien, qui rejoint ce que nous écrivions déjà en 1962 (p. 74).

Les présentes recherches sur 7 taxons de la section *Eremogone* confirment ce que nous avions noté chez deux d'entre eux en 1962. Tout d'abord, les chromosomes dans cette section sont notablement plus grands que dans le sous-genre *Arenaria.* Il suffit pour s'en convaincre de comparer par example, les Fig. 1 J, 2 C et D (*Eremogone*) et les Fig. 1 C, F et I (*Arenaria*). D'autre part, il semble bien que le nombre de base soit ici de x=11 [7], de façon préférentielle, sinon exclusive (cf. p. 474). Enfin, il est intéressant de constater que la polyploïdie a joué un rôle important dans la différentiation des *Eremogone* chez lesquelles nous avons décelé des taxons tétra-, octo-, et décaploïdes, à côté de diploïdes. Les troubles méiotiques qu'offrent certaines espèces méritent également un examen attentif. En 1962, nous les avions attribués à une hybridation qui se serait produite, au moins en partie, dans les jardins botaniques. Cependant, ceux que nous avons mentionnés ci-dessus se rencontraient dans des espèces apparemment pures et diploïdes (*A. cucubaloides, A. lychnidea*) récoltées en nature. De plus, ils ne se présentaient pas constamment. Il serait fort intéressant de rechercher la cause de ces anomalies et de voir si elles s'accompagnent ou non de stérilité.

REMERCIEMENTS

Nous tenons à remercier les amis et collaborateurs qui nous ont procuré du matériel, en particulier Mme A. CAUWET (Perpignan), MM. PH. KÜPFER, assistant et P. CORREVON, jardinier-chef (Neuchâtel). Notre gratitude va aussi à Mmes M. TISSOT et B. EMERY, qui nous ont aidé à préparer notre manuscrit et les figures.

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[7] Aux comptages mentionnés plus haut, il convient d'ajouter ceux de ZHUKOVA (1966) et de YURTSEV et ZHUKOVA (1972) sur *A. tschuktschorum* RGL: 2n=22. Cette espèce est classée par MCNEILL dans la section *Sclerophyllae* (BOISS.) MCNEILL.

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Studies on the Changes of the Inner Micro-structure During the Chloroplast Development in Chlorophyllous Roots of Wheat

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ABSTRACT

FADEEL, A. A. & AL-SANI, N. 1972. Studies on the changes of the inner micro-structure during the chloroplast development in chlorophyllous roots of wheat. — Bot. Notiser 125: 477—482.

The developmental sequence of the chloroplast has been studied in illuminated excised wheat roots. The formation of the mature chloroplast usually takes place as the tissues expand in light. The mature chloroplasts are developed from proplastids through different changes in their inner micro-structure.

INTRODUCTION

The formation of well developed chloroplasts in root tissues and their distribution have been studied by several authors under the light microscope. These studies have established which tissues of various species are capable of differentiating chloroplasts, what pigments are present in green roots, and whether such chloroplasts are photosynthetically competent (BURSTRÖM & HEJNOWICZ 1958, FADEEL 1962, 1963, BJÖRN 1967, and HELTNE & BONNET 1970). LANCE-NOUGARÈDE & PILET (1965) published electron micrographs showing the fine structure of the mature chloroplast in the roots of *Lens culinaris* L. However, the study of the origin of the chloroplast in root tissues has only recently received some interest. HELTNE & BONNET (1970) suggested that the formation of a developed chloroplast in roots goes through a sequence of stages: the initial stage (leucoplast), three intermediate stages, and a final stage (mature chloroplast).

WILKIE (1964) suggested that proplastids are present in the meristematic cells of roots but they are apparently unable to develop into mature chloroplasts when exposed to light. He also suggested that some internal factors hold the developmental potential of the proplastids in check. However, it is now a well established fact that chloroplasts are developed in root tissues when subjected to light and the addition of auxin to the nutrient media (FADEEL 1962).

In the present paper an attempt has been made to study the different developmental stages of the root chloroplasts. For this purpose illuminated excised roots have been used in which chloroplast development was induced by the addition of 1-NAA to the nutrient media.

MATERIAL AND METHODS

Excised wheat roots were used as the standard material in the present investigation. Wheat grains of the "Pompe" variety (*Triticum aestivum*) obtained from Weibulls,

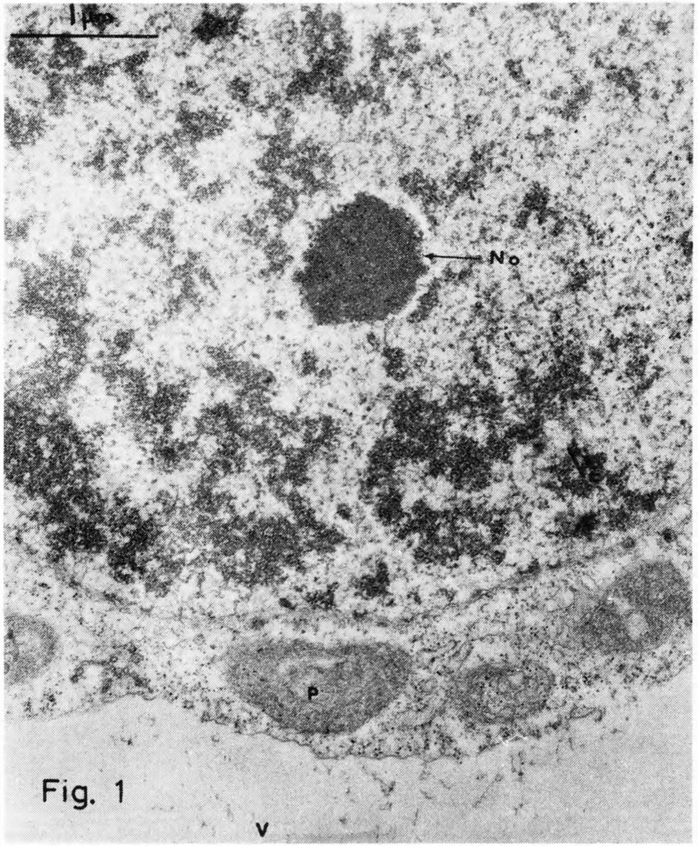


Fig. 1

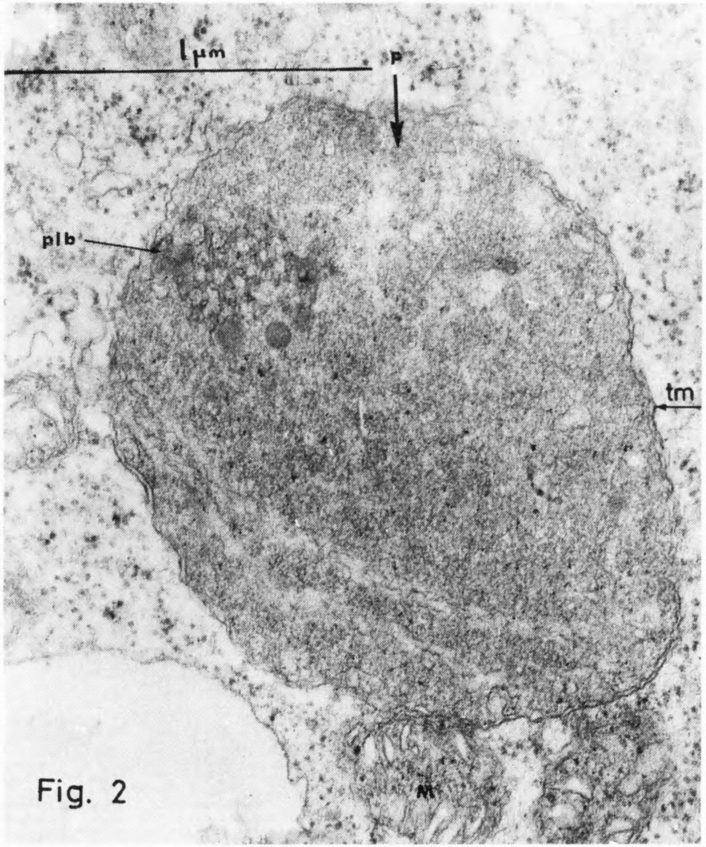
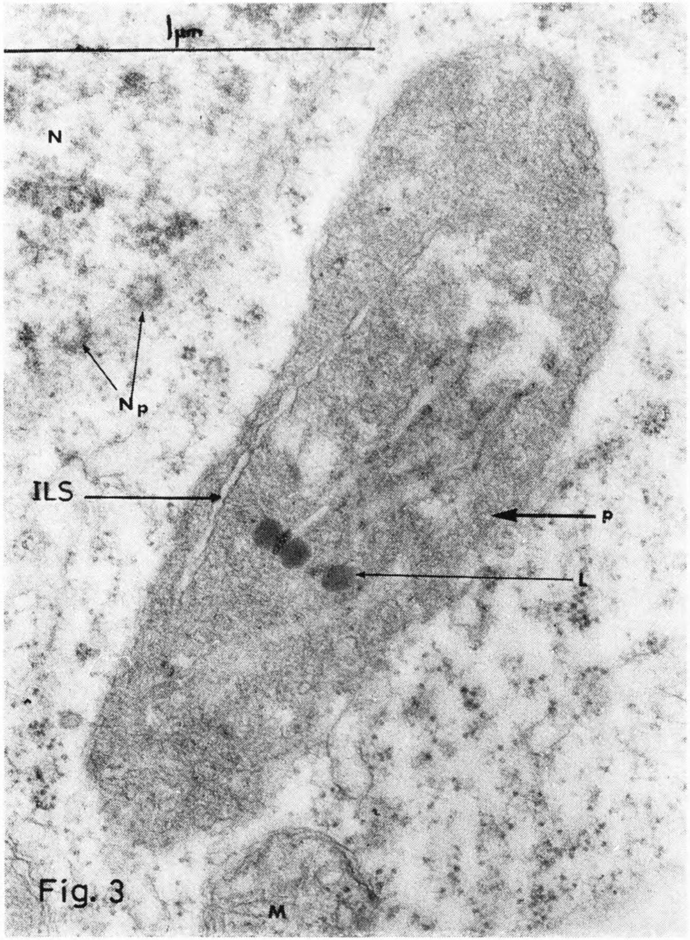


Fig. 2

Fig. 1. Early stage of proplastid (P), nucleolus (No), and vacuole (V).

Fig. 2. Intermediate stage of proplastid (P), prolamellar body (plb), twin membrane (tm), and mitochondrion (M).



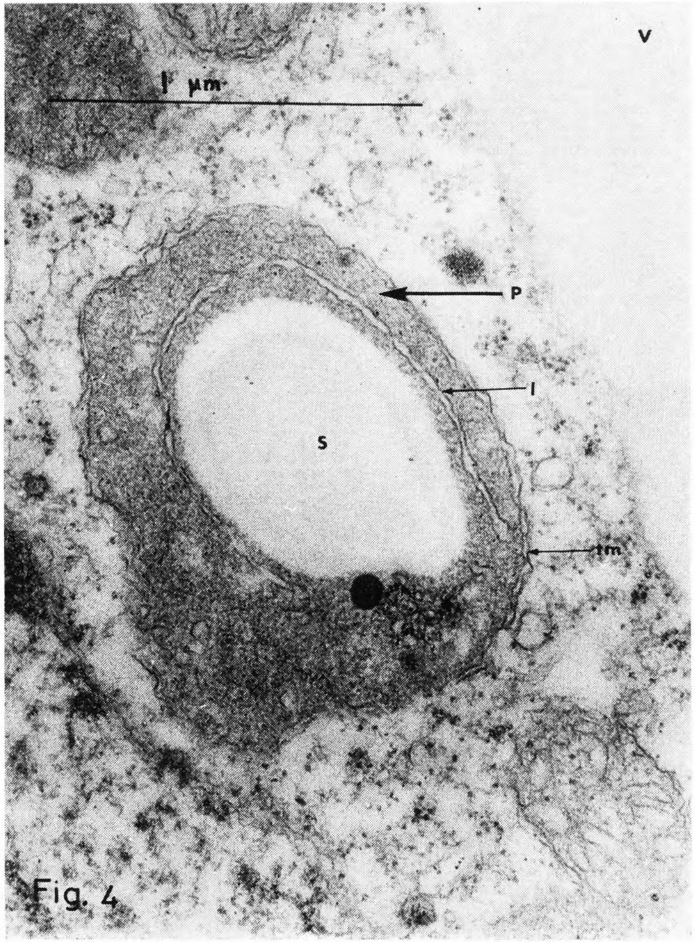


Fig. 3. Intermediate stage of proplastid (P), lipid droplet (L), irregular lamellar structure (ILS), nucleus (N), nuclear pore (Np), and mitochondrion (M).

Fig. 4. Late stage of proplastid (P), twin membrane (tm), lamella (l), and a large starch grain (S).

Landskrona, Sweden, were cultivated in the manner described earlier (FADEEL 1963). After 7 days of illumination the length of the excised root was about 20 mm. Segments 1.5—2 mm long were processed for electron microscopic examination (Figs. 1—4). The root segments were fixed in glutaraldehyde, prefixed in OsO_4, and embedded in Araldite mixture according to the technique described by JUNIPER et al. (1970) and modified by H. G. DICKINSON of the Department of Botany, University College, London.

RESULTS AND DISCUSSION

In the present investigation it has been noticed that in wheat root sections studied under the light microscope, the mature chloroplasts first appeared about 8—10 mm from the root tip. The chloroplasts were strictly located to the two innermost cortical layers and outside the endodermis (see Figs. 5 and 6). Few starch grains were also observed in the cortical cells that were devoid of chloroplasts. Proplastids could not, however, be seen under the light microscope in the younger tissues, i.e. 0—8 mm from the root tip. Due to the limited resolution of the light microscope it would be misleading to draw any conclusions in regard to the appearance of the proplastids in the meristematic tissues. Nor was it possible to decide which of the root tissues of a specific age are competent to differentiate the chloroplasts. Since the electron microscope could provide better ways of resolving the micro-structure of the cell organelle, it was possible to study the developmental sequence of the chloroplast along the root axis and at different distances from the root tip.

Fig. 1 shows the minute undifferentiated proplastids during the early stage of their development. This initial stage of proplastid formation appears in the second segment at 2—3 mm from the root tip. The first detectable change in the inner structure of the proplastid was observed in sections made through the third segment at 4—5 mm from the root tip (Fig. 2). The appearance of the prolamellar body as well as the formation of the double or twin membrane indicate an intermediate stage in the chloroplast development. This finding tallies with the results published by other workers (HYDE et al. 1963, and HELTNE & BONNET 1970). Two more intermediate stages could be identified in the present work. During those stages further detailed micro-structure could be seen. Fig. 3 shows the appearance of irregular lamellar structure and the formation of lipid droplets. Fig. 4 shows the development of the double lamella, the twin membrane surrounding the proplastid, and the formation of a large starch grain.

From the above-mentioned discussion it is possible to conclude that the formation of the mature chloroplast usually takes place as the tissues expand in light. During the subsequent development, the inner binding membrane of the proplastid seems to introvert to form a rudimentary lamella which appears in the early stages as a prolamellar body. This structure first resembles the mitochondrial cristae. At a later stage the lamella breaks away from the bounding membranes, proliferates, and then assumes the double lamellar structure (see Figs. 3 and 4).

The light micrographs, Figs. 5 and 6 show the structure and the distribution of the mature chloroplasts. It was found that the mature chloroplasts in green roots were always uniform in size and with well organized grana. We believe that most of the chlorophyll appears during this last stage of development.

From the results reported it can be inferred that, in principle, the chloroplasts in the chlorophyllous roots are developed from proplastids through different changes in their inner micro-structure. Since morphological criteria are not sufficient for identifying the origin of the organelle, it is on our programme to approach the problem of the biosynthesis of the proplastid on a biochemical and a physiological basis. Other aspects of this problem, including the investigation of the inter-

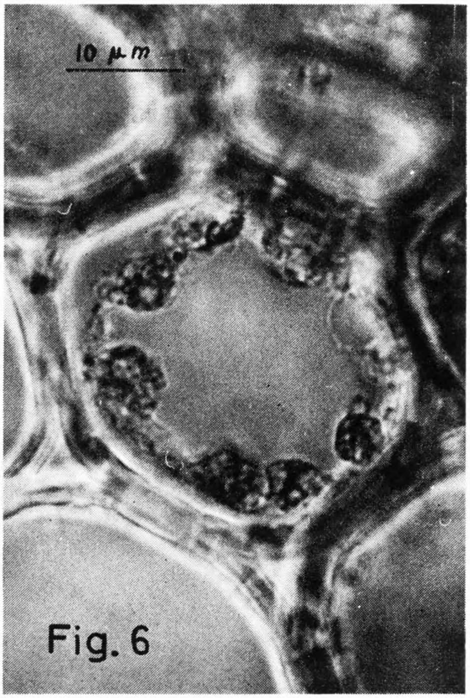


Fig. 5. Hand transverse section in fresh unstained material showing the distribution of mature chloroplasts.

Fig. 6. A single cell from the cortical region showing the uniform chloroplasts in surface view and also the size of the well developed grana in relation to the total size of the chloroplast.

mediate stages in relation to the rate of protein synthesis in the root cells, are also under consideration.

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Ecology, Taxonomy and Rational Land Use in Africa

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ABSTRACT

HEDBERG, I. & HEDBERG, O. 1972. Ecology, taxonomy and rational land use in Africa. — Bot. Notiser 125: 483—486.

International aid projects in developing countries have mostly had unforeseen and sometimes disastrous side effects. Ecological pre-investment studies are urgently needed to avoid or mitigate undesirable effects from, for instance, damming enterprises and other changes in land use. A necessary prerequisite for adequate ecological studies is that the flora and fauna of the area concerned are sufficiently known. Lack of taxonomic and ecological knowledge and of trained specialists with relevant tropical experience present the most severe obstacles to the effectuation of the ecological studies required in most developing countries.

The term ecology was coined in the 1870s, being the study of the relations between organisms and their living and non-living environment. That each organism is directly dependent upon its environment has long been known, but the extremely complicated manner in which the life histories of different organisms are interwoven in nature is something we have only begun to realize in recent years. Within each ecosystem, that is the complex of organisms in a defined *milieu* together with their non-living environment, there exists a dynamic equilibrium between the different species of producers (photosynthesizing plants), and between them and the primary consumers (herbivorous animals), the secondary consumers (carnivores, insectivores, etc), and the decomposers (bacteria, fungi, etc). The elimination of a species from the ecosystem or the introduction of a new one may cause catastrophic changes — such as those induced by the introduction of *Opuntia* and rabbits into Australia.

Man cannot escape from his dependence upon the ecosystems in which he lives — although he has greater possibilities of modifying them than any other species has. The composition of the ecosystems in which he is involved varies widely from the Arctic habitat of the Greenland Eskimoes to the lowland rain forest of the Congo Pygmies. But wherever he lives man attempts to crop his ecosystems as efficiently as possible. Ideally he should try to do so on a sustained yield basis, so as not to hazard his future existence, but unwise exploitation leading to the large-scale deterioriation of ecosystems has become far too common. Awareness of this catastrophic development has made biologists and other scientists as well as politicians all over the world realize that the land will have to be put to more prudent use in the future.

The complicated pattern formed by different ecosystems in a tropical or subtropical area that has not become too heavily depleted by human action often mirrors the changes in soil conditions as regards soil texture, chemical composition, slope, exposure, drainage, etc. Consequently it is often possible to make a better prediction of land use potential in an undeveloped area from an adequate study of the local ecosystems, notably the vegetation, than from soil analyses however detailed. The most fundamental prerequisite for rational land use in such an area is therefore an adequate ecological study of the ecosystems concerned. Detailed studies of this kind often show that each ecosystem or plant association is characterized by a number of plant species exclusive to it and which can serve as ecological markers. Studies of this sort, however, have only been made in comparatively few cases, and they are rendered difficult in most tropical and subtropical countries because of insufficient knowledge of the flora of the areas concerned. It may be worth while recalling that, from tropical Africa alone, roughly 300 new species of angiosperms are described every year. An essential part of the infrastructure for improved land use in a country is therefore an adequate taxonomic revision of its flora so that plant species can be determined and information about them properly utilized.

It is true that large amounts of taxonomic and ecological information have been assembled in Africa in recent years by scientists working in connection with forestry, agriculture and national parks, as well as by members of FAO missions and others. The accelerating Africanization in most tropical African countries after the close of the colonial period has unfortunately interrupted much of this work, however, and in most African countries the number of adequately trained indigenous taxonomists and ecologists is still quite insufficient to cope with the urgent problems arising out of actual changes in land use. In the industrialized countries, too, the number of adequately trained taxonomists and ecologists that are specialized in tropical and subtropical developing countries is still comparatively small, whereas the number of urgent research tasks is large.

Government circles in Africa as well as in other parts of the world have previously shown little understanding for the ecological viewpoint. It is only in the last few years, and then largely through the influence of IUCN and UNESCO, that the World Bank and similar financing agencies have demanded that adequate ecological pre-investigations should be carried out before making decisions concerning major development schemes and other changes in land use in tropical countries.

What practical implications can then an ecological investigation have for rational land use in Africa? The scope is indeed wide, and we shall only mention two examples dealing with "rangeland" and inland waters, respectively.

The term "rangeland" has been employed for the dry grasslands of tropical Africa with varying amounts of trees and shrubs too dry for regular agriculture. Originally this was the home of the famous "savanna" fauna of East Africa, now surviving mainly in the national parks. Except for game cropping this ecosystem has mainly been utilized for nomadic cattle-keeping. For the nomadic tribes concerned cattle constitute their main means of existence and their main property. Accordingly they strive to keep their herds of cattle as large as possible. This has given rise to pronounced over-grazing in many areas, especially during years of severe drought, and this again has caused serious soil erosion over vast areas with the accompanying silting up of downstream reservoirs. Comparative studies of wild game and cattle have shown that in many cases an area of rangeland is able to carry up to 3—4 times more live weight of game than of cattle per unit area, and that game causes far less soil erosion. In order to obtain the maximum yield of protein and to conserve the soil, it might therefore in many cases be preferable to go in for game ranching rather than nomadic cattle-breeding. Admittedly there are considerable difficulties connected with methods of cropping, meat transport, and marketing, but successful experiments have been made in East Africa indicating that these difficulties can be overcome. A more difficult problem seems to be poaching. For the scheme to be economically attractive to the government or any other organizing body cropping should obviously be reserved for the organizer, but during the trials carried out so far large-scale poaching seems to have occurred, much reducing the organizer's gains. From the point of view of ecology one might argue that it does not matter so much who derives economic benefit as long as a high yield of protein is obtained for the people of the country, but this type of reasoning will scarcely appeal to the governments concerned — and besides, illegitimate cropping is probably not compatible with optimum yield. Further scientific studies and a more stringent control of poaching will therefore be necessary to ensure the desirable development of game ranching in lieu of nomadic cattle keeping in tropical African rangeland areas.

The larger part of Africa is arid or semi-arid — water supply is therefore a matter of crucial importance in most countries. Permanent streams and wells are scarce, and any possibility of tapping underground water or making a small dam for water storage will be attractive to the local population. In recent years there have been a large number of household water schemes, aided, for instance, by development grants from Sweden. Damming up and boring must not be carried out indiscriminately, however, but should be preceded by hydrological and ecological pre-investigations and directed by regional planning. Some of the early bore-holes sunk in NE. Kenya led to such a crowding of cattle around them that all vegetation within walking distance for cattle was annihilated. In the present development programme for this area, great care is being taken to limit the number of people and cattle utilizing each block by the suitable rationing of the amount of water made available. It has been found that some of the earlier household dams in Tanzania silt up much more quickly than was originally anticipated — thus the term of life of the Ikowa Dam in Tanzania looks like being only about 30 years. The future constructions of dams of this sort will certainly have to be preceded by more adequate hydrological studies, but ecological studies are also desirable. The rising of the water-table round an impoundment of this sort may lead to changes in vegetation and changes in the distribution of disease vectors. The number of dams built along each river must be limited — in some cases so much water has been impounded that nothing is left for the lower reaches, which may prove catastrophic to downstream populations.

Particular ecological problems have been caused by the impoundment of large lakes for hydro-electric purposes, the most important in tropical Africa being Lake Kariba, Lake Nasser, and Lake Volta — not to speak of the regulation of Lake Victoria at Owen Falls. Each such large enterprise has a number of side effects — the population inhabiting the area to be impounded must be shifted, the distribution of disease vectors is often extended, extensive and sometimes unforeseen vegetation changes may take place, etc. Thus in Lake Kariba the adjustment of the population shifted to a new environment created a number of problems, and the occurrence of a small water weed caused great difficulties for the fishing industries. The damming up of Lake Nasser caused a very large increase in bilharzia frequency, the retention of 75 % of the water and silt of the Nile in the impoundment has caused severe degradation of the Nile delta, etc. The most alarming prospect for Lake Nasser as well as for the other large lakes mentioned, may prove to be invasion by the South American weed *Eichhornia crassipes,* the water hyacinth, which occurs in adjoining areas, and which has caused a great deal of trouble in other parts of the world. A very instructive example of smaller dimensions is provided by the Nyumba ya Mungu Lake on Pangani River, not far south of Kilimanjaro. The main purpose of this impoundment was to regulate the course of the river for two hydro-electric plants downstream, and to provide water for irrigation. Because of the salinity of the surrounding soils their utilization for irrigated agriculture has proved more difficult than anticipated, however. On the other hand the occasional inplanting of fish (Lake Victoria *Tilapia*) together with the immigration of other fish species from surrounding waters quite unexpectedly gave rise to luxuriant fisheries — at present more than 30,000 people are said to live on fishing here. Because this had not been foreseen no proper planning had been undertaken for the development of fisheries, hence organization got out of hand. The selection of suitable crops for the saline soils and the reorganization of fisheries are now presenting some difficult problems to Government authorities — problems which might have been lessened or avoided by more detailed pre-investment studies.

The above examples may well serve to stress the point that in order to achieve rational large-scale improvements in land use one should always start with a thorough ecological survey of the area concerned. On the basis of such a survey it should be possible to undertake multipurpose planning, taking into consideration as many different aspects and potential uses as possible. One-purpose projects concentrating, for example, on water power or agriculture alone, may sometimes have unexpected ecological side effects and often neglect important sidelines of considerable economical importance. It should also be evident that no reliable ecological studies can be carried out unless the flora (and fauna) of the area in question is already reasonably well known, and the determinations of the plant (and animal) species concerned are carefully checked and documented. Ecology and taxonomy must therefore work hand in hand.

Cytotaxonomic Studies in Galium hercynicum Weig.

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ABSTRACT

KLIPHUIS, E. 1972. Cytotaxonomic studies in Galium hercynicum Weig. — Bot. Notiser 125: 487—492.

Within *Galium hercynicum* WEIG., diploids with 2n=22 chromosomes and tetraploids with 2n=44 chromosomes were observed. The difference in chromosome number is correlated with certain differences in morphology, which are described and discussed. The two cytotypes are formally proposed as subsp. *vivianum* KLIPHUIS subsp. nov., and subsp. *hercynicum,* respectively.

INTRODUCTION

Galium hercynicum WEIG. is a typically European Atlantic species (see HULTÉN 1958 map 133), extending from southern Scandinavia to northern Spain and Portugal, the British Isles, Iceland, eastward to the Karelian Isthmus (POBEDIMOVA 1958), in Central Europe sporadically to Bohemia and the Transsylvanian Alps (ROUY 1903; EHRENDORFER 1956) and in the south to the Jura Mountains (BONNIER 1921). It has been introduced into Greenland, Newfoundland and the Azores (EHRENDORFER 1956). It prefers acid soil in light forests, near forest edges, sunny hills, moist, rocky places with short turf (GABRIËLS 1965). It is also typical of moorland and swamps where its non-flowering stems may form dense carpets. In most floras it is described as morphologically uniform, apart from some minor differences in habit. ROUY (1903) distinguished four varieties, based mainly on characters of habit, like height, branching and shape of the inflorescence. COUTINHO (1939) reported two of them from Portugal, these are var. *genuinum* ROUY and var. *riparium* ROUY. FONTES (1948) compared them again and arrived at the conclusion that they are nothing but extremes in habit, connected by all possible intermediates.

Two cytotypes of *Galium hercynicum* are known. Diploids with 22 chromosomes occur in Portugal (KLIPHUIS 1962, 1967) and Spain (KÜPFER 1969), tetraploids with 44 chromosomes throughout the area of distribution of the species (FAGERLIND 1934, 1937; EHRENDORFER 1956; KLIPHUIS 1962, 1967; GADELLA & KLIPHUIS 1963; PIOTROWICZ 1964). The diploid is distinguished from the tetraploid by a more fragile habit, more slender shoots, smaller leaves and flowers, and by the fact that it flowers about two weeks earlier than the tetraploid. Culture experiments extending over several years showed these differences to be genotypically founded (KLIPHUIS 1967).

In a general cytotaxonomic survey of some species of *Galium, G. hercynicum* was also included. More material from its whole area was used in this study in which the position of the two cytotypes was investigated in more detail.

Many authors have placed *Galium hercynicum* WEIGEL in the synonymy of *Galium saxatile* L.. This goes back to the interpretation given by SCHINZ & THELLUNG (1909) when they refuted KERNER's assertion (1884) that *Galium hercynicum* is the correct name. HYLANDER (1945) again delved into the problem and, adducing new details, in his turn rejected SCHINZ's and THELLUNG's conclusion; his opinion, however, has not been universally followed. In the present author's opinion HYLANDER's argumentation is correct, so the name must be *Galium hercynicum* as described by WEIGEL in 1772.

MATERIAL AND METHODS

Living plants as well as seed samples were collected. The seeds were sown in the Botanical Gardens of the State University of Utrecht. Chromosome counts were made from root tips of potted plants. The tips were fixed in Karpechenko's fixative, embedded in paraffine wax, sectioned at 15 micron and stained according to Heidenhain's haematoxylin method. Drawings of the metaphase plates of root tip cells were made with the aid of an Abbe camera lucida; microscope used: Zeiss, type Standard Junior.

Measurements of leaves, flowers and fruits were treated according to the normal statistic methods for calculating the mean ($\bar{x}$), the standard deviation (SD), and the standard error of the mean (SE).

RESULTS

Cytology

The results of the counts are assembled in an appendix at the end of this paper. The material is arranged in accordance with the alphabetical sequence of the countries of provenance. In the Dutch material about 10 plants per population were used in the study.

Diploids with 2n=22 as well as tetraploids with 2n=44 chromosomes were observed. The latter is the commonest cytotype, occurring throughout the distributional area of the species. The diploid was only met with in the north-west of the Iberian Peninsula.

The chromosome portraits of the two cytotypes show a normal pattern (Fig. 1). No B-chromosomes or satellites were observed.

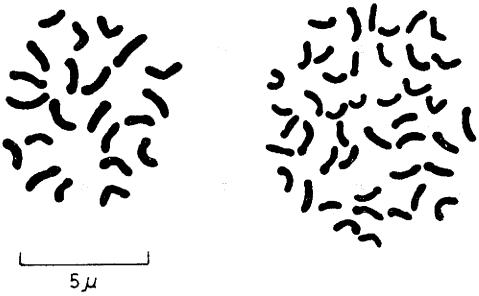

Fig. 1. Mitotic metaphase plates from root-tips of *Galium hercynicum*. — Left: ssp. *vivianum* (2n=22) from the Tras-os-Montes region in Portugal. — Right: ssp. *hercynicum* (2n=44) from the coastal dunes of Oost-Voorne in the Netherlands.

Morphology

Galium hercynicum is a perennial, mat-forming plant with prostrate non-flowering shoots. Stem glabrous, quadrangular; leaves in whorls of 4—6, most often 6, glabrous, flat, entire, with small weak spines on the edge, unicostate, finely veined, acuminate, on the flowering shoots the upper lanceolate to oblong-lanceolate (type I), the middle ones obovate-oblanceolate (type II) and the lower obovate, obtuse (type III), on the non-flowering shoots obovate (type IV). Flowers in cymes mostly assembled in an interrupted panicle; pedicels straight. Petals ovate, acuminate, white. Stamens 4, inserted on the corolla; anthers yellow. Stigma bifid. Ovary inferior, bipartite; fruit densely verruculose-scabrous.

This description holds for both the diploid and the tetraploid. The morphological difference is mainly in a more slender habit and slender shoots of the diploid, as compared with the tetraploid (Fig. 2). This remains constant during the years of cultivation. Measurements of leaves, flowers, internodes and fruits show striking differences.

LEAVES. *Galium hercynicum* has four different types of leaves, three on flowering (types I, II, III) and one on non-

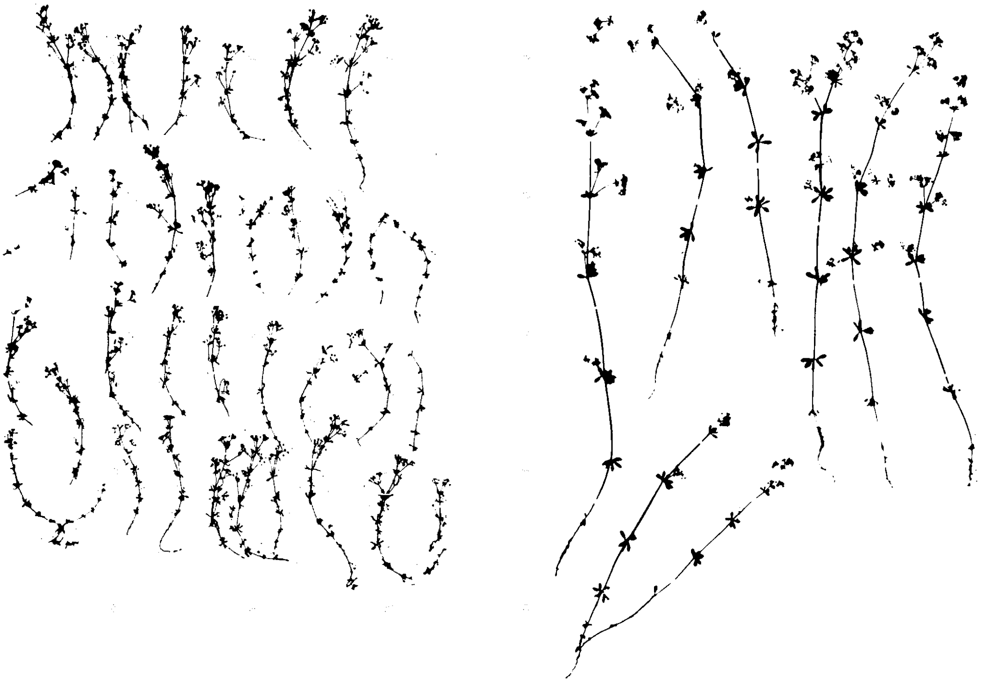

Fig. 2. *Galium hercynicum,* habit of plants, fourth year of cultivation. — Left: ssp. *vivianum* (2n=22) originating from Tras-os-Montes, Portugal. — Right: ssp. *hercynicum* (2n=44) originating from Skjern, Denmark.

flowering shoots (type IV). The size of the leaves of all types, both in the diploid and in the tetraploid plants, fluctuates from one year to the other. This emerged from measurements of length and width of leaves of two plants from both cytotypes in three subsequent years of cultivation (Kliphuis 1967). Nevertheless those of the tetraploids are distinctly and permanently larger than those of the diploids (Kliphuis 1967). Further measurements of the length and width of leaves of ten diploid and ten tetraploid plants confirmed this.

Fifty leaves each of type I, II and IV were measured per plant, and the mean (x̄), the SD and the SE were determined. The results of these measurements and their evaluation are brought together in Table 1. Leaves of type III were left out of account as there are only few per plant and these are, moreover, often wilted. Their average length in the tetraploids is ± 3.80 mm, their width ± 1.50 mm, in the diploids ± 2.50 mm and ± 0.85 mm, respectively.

PETAL SIZE. The size of the flowers fluctuates notably little from one year to another. As shown by measurements of six diploids and six tetraploids, there is a distinct difference in size of the flowers of the two cytotypes. In all, length and width were measured in 400 flowers of the diploid and in 600 flowers of the tetraploid. The length of the diploids fluctuated from 2.10 to 3.80 mm, with a mean of $\bar{x}=2.85 \pm 0.02$ and a SD of 0.30, the width fluctuated from 0.50 to 1.10 mm, with a mean of $\bar{x}=0.78 \pm 0.01$ and a SD of 0.15. For the tetraploids the values are for the length 3.20—4.90 mm ($\bar{x}=4.70 \pm 0.01$; SD=0.24), for the

Table 1. Size in mm of three types of leaves from diploid (ssp. *vivianum*) and tetraploid (ssp. *hercynicum*) plants of *Galium hercynicum*.
Number of observations: 500 of each type.

leaf type		I			II			IV		
		$\bar{x}$	SD	SE	$\bar{x}$	SD	SE	$\bar{x}$	SD	SE
2n=22	length	4.40	1.00	0.04	4.44	1.05	0.05	4.09	1.42	0.06
	width	0.71	0.20	0.01	1.03	0.34	0.02	1.49	0.28	0.01
2n=44	length	5.79	1.23	0.06	7.08	1.53	0.07	5.28	1.30	0.06
	width	0.96	0.31	0.01	2.01	0.41	0.02	1.43	0.39	0.02

width 0.60—1.40 mm ($\bar{x}=1.05 \pm 0.01$; SD=0.10).

INTERNODE LENGTH. In 10 diploid and in 25 tetraploid plants the internodia were measured. In the diploids they are up to 3 (exceptionally up to 4) cm long, in the tetraploids up to 6 (exceptionally up to 8) cm.

FLOWER NUMBER. The number of flowers in the inflorescences of the diploid and the tetraploid cytotypes are not the same. For each part of the interrupted panicle it is 2—10, usually 3—6 in the diploid, 4—20, usually 6—14 in the tetraploid.

FRUITS. Measurements of the length of 150 fruits of diploid and as many of tetraploid plants yielded the following results: diploid plants $\bar{x}=1.00 \pm 0.01$; SD=0.16, tetraploid plants: $\bar{x}=1.40 \pm 0.01$ and a SD=0.13. The minimum and maximum values were 0.80—1.50 mm, and 1.10—1.80 mm, respectively.

CROSSING EXPERIMENTS

Attempts at crossing the two cytotypes have so far remained unsuccessful. This result agrees with what has been found for other *Galium* species. Inside the genus there is a strong reproductive barrier between various levels of ploidy, inter- as well as intraspecifically.

DISCUSSION

As shown by the cytotaxonomic studies the two cytotypes differ greatly in their distribution. Samples taken from a large part of the distributional area of the species show the tetraploids to be widely distributed, whereas diploids have only been met with in the north-west of the Iberian Peninsula. The two cytotypes probably do not occupy separate areas; e.g., a diploid and two tetraploid samples hail from the same area between La Coruña and Santiago (prov. La Coruña) by the road on a slope overgrown with *Ulex europaeus* L. and *Erica australis* L. This also seems to indicate that the two cytotypes have the same ecological preference, but this requires much more cyto-ecological research.

In the experimental garden both cytotypes show a remarkable uniformity in growth habit, leaf shape on both flowering and non-flowering stems, petal shape, and number of leaves per node. As argued above, the diploid cytotype differs in having a more slender appearance, much smaller leaves, flowers, and fruits, shorter internodes, and fewer flowers per inflorescence.

Study of herbarium material from Utrecht (U), Leiden (L), the Institute of Botany, Lisboa (LISU), Instituto Superior de Agronomia, Lisboa (LISI), Porto (PO), Coimbra (COI), and Elvas (ELVE) from the entire distributional area of the species showed that plants with the characters of the tetraploid occur throughout the distributional range, whereas in the material studied plants with the features of the diploid could only be demonstrated in Portugal. The little material available from Spain showed the characters of the tetraploid. The origin of a diploid in the province of La Coruña, Spain, and also the find of KÜPFER (1969) from one in the Sierra de Gredos points to a wider distribution of the diploid on the Iberian Peninsula.

Galium hercynicum is not subdivided in WILLKOMM & LANGE's Spanish Flora (1870). The two varieties treated by COUTINHO (1939) in his Portuguese Flora do not agree in their morphological characters with any of the cytotypes. FONTES' (1948) opinion that they are only extremes in habit is probably correct. Cultivation experiments are, however, required to confirm this.

Taking into account the differences in cytology, morphology, and to a certain extent also in distributional area, and the reproductive barrier, we may conclude that we are concerned with two taxa. As the differences are not very profound, the rank of subspecies seems to be indicated for them.

Galium hercynicum WEIGEL ssp. **hercynicum**

Plant forming mats; leaves on non-flowering shoots obovate, up to 6×3 mm, on flowering shoots the lowermost ones obovate, up to 5×2 mm, the middle ones obovate-lanceolate, up to 8×2.5 mm, the upper ones lanceolate to oblong-lanceolate, up to 6×1.25 mm. Internodes up to 8 cm. Flowers in terminal panicles consisting of 15-(exceptionally to 20-)-flowered cymes. Petals up to 4×1 mm; fruit verruculose, up to 1.5 mm in diameter. 2n = 44.

Galium hercynicum WEIGEL ssp. **vivianum** KLIPHUIS ssp. nov.

Planta caespitosa; folia ramulorum sterilium obovata, ad 4.25×2 mm, ramulorum floriferorum inferiora obovata, ad 3×1 mm, media oblanceolata, ad 5×1 mm, superiora lanceolata vel oblongo-lanceolata, ad 5×0.75 mm. Internodia haud ultra 3 cm. Panicula terminalis cymos ad 6-(vel ad 10-)-floros gerens. Petala longitudinem 3 mm et latitudinem 3/4 mm haud attingentia. Fructus verruculosus, usque 1 mm. diam. 2n = 22.

Typus: M. BELIZ, GONCALVES & RUIVO nr. 1263, 17. 7. 1953; Beira-Alta, Serra da Estrela, Portugal (LISU).

The subspecies is named in honour of Professor VIVI TÄCKHOLM.

ACKNOWLEDGEMENTS

The author wishes to express his gratitude to Dr. K. U. KRAMER for his assistance in translating the Dutch text, to Mr. A. KUIPER for the photographs, and to Mr. H. RIJPKEMA for the drawings of the chromosome portraits.

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APPENDIX

Cytologically investigated material of Galium hercynicum

TETRAPLOIDS, 2n=44 (ssp. *hercynicum*)

BELGIUM. K 394 — Ardennes, Brume, Bois de Rakiers; K 395 — Ardennes, Brume, Trois-Point; K 398 — Reinherdtstein, Robertsville; K 1232 — Valley of the Amblève.

DENMARK. Jutland: K 202 — near Tarm; K 208 — near Alkjaersig; K 238 — near Skjern; K 362 — collected in the field, precise locality unknown; K 1197 — near Madum; K 1198 — near Rebild; K 1203 — between Vrads and Hjøllund; K 1205 — near Viborg; K 1206 — near Hobro; K 1210 — near Löve; K 1204 — between Viborg and Hjøllund.

ENGLAND. K 1140 — Dartmoor, between Two Bridges and Princetown; K 1141 — Dartmoor, near Yelverton; K 1178 — Lake district, near Ullswater Hotel; K 1179 — Lake district, Ulpha Fell; K 1180 — Derbyshire near Hathersage; K 1181, K 1187 — Peak district.

FRANCE. K 297 — near Rouen; K 557 — Roc Trévézal, Finistère; K 558 — Lopérée, Finistère; K 602 — Vosges, Hohneck; K 603, K 770 — Vosges, Grande Fosse; K 787 — Grand Ballon, Ht. Rhin.

GERMANY. K 164, K 165 — Eifel, near Schleiden; K 304 — Harz, Brocken; K 718 — W. Erzgebirge, Oberwildental.

ICELAND. K 1051 — Seldalur.

IRELAND. K 1109 — Slieve Bawn, near Roscommon; K 1135 — Co. Wicklow, Wicklow Mountain; K 1136 — Co. Kerry, Blackwater; K 1137 — Co. Sligo, Ben Bulbin; K 1138 — Co. Roscommon, Lough Ree; K 1139 — Co. Kerry, Lough Caragh; K 1178, K 1179 — Achill Islands, Meewin cliffs.

THE NETHERLANDS. Province of Drente: K 137 — near Weerdinge; K 251 — near Vledder; K 735 — near Hooghalen; K 793 — between Hooghalen and Halerbrug; K 794 — between Hooghalen and Grollo; K 795 — near Grollo; K 796 — between Grollo and Schoonlo; K 797 — between Schoonlo and Schoonoord; K 798 — near Schoonoord; K 809 — Odoornerveld; K 810 — near Odoorn; K 811 — between Odoorn and Exlo; K 813 — between Odoorn and Valthe; K 815 — between Valthe and Kleindijk; K 816 — near Emmerschans; K 952 — near Zweelo; K 953 — near Sleen; K 954 — near Diphoorn; K 976 — De Klencke, near Oosterhesselen; K 978 — between Sleen and Schoonoord; K 979 — near Schoonoord; K 1009 — near Oud-Schoonebeek; K 1010 — near Midden-Dorp, Schoonebeek; K 1228 — near Norg; K 1229 — near Westervelden. Province of Friesland: K 252 — Duurswoude, estate of Corabibi; K 414 — near Beetsterzwaag; K 985 — Oosterend, Isle of Terschelling. Province of Gelderland: K 415 — Hoge Veluwe, near Kröller-Müller Museum. Province of Noord-Holland: K 662 — de Koog, Isle of Texel. Province of Zuid-Holland: K 196 — near Westenschouwen; K 363, K 364, K 365 — near Oost-Voorne. Province of Limburg: K 386 — near Vylen. Province of Overijssel: K 1128 — near Ommen. Province of Utrecht: K 153, K 627, K 628 — near Maarn; K 622 — near Schalkwijk; K 1000 — near Woudenberg; K 1002 Ridderoordse bossen, Bilthoven; K 1094 — near Rhenen, Grebbeberg.

NORWAY. K 1143 — near Fjellspollen, Isle of Sotra; K 1144 — Øvsthunfoss, Nordheimsund; K 1147 — Isle of Sotra, south of Fell; K 1149 — Hattvik, NE of Osöyri.

PORTUGAL. K 478, K 577 — collected in the field, precise locality unknown; K 1015 — Serra da Estrela, 1850 m; K 1016 — Serra da Estrela, 1900 m.

SPAIN. K 1022, K 1025 — Prov. of La Coruña, between La Coruña and Santiago.

DIPLOIDS, 2n=22 (ssp. *vivianum*)

PORTUGAL. K 106, K 244 — Tras-os-Montes; K 1017, K 1018 — near Pisoes, prov. of Tras-os-Montes; K 1020 — Serra do Gerez, 850 m., Leonte Lisca do Alvao.

SPAIN. K 1021 — Prov. of La Coruña, between La Coruña and Santiago.

Verbascum spathulisepalum (Scrophulariaceae), eine neue Art aus Nordost-Griechenland

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ABSTRACT

GREUTER, W. & RECHINGER, K. H. 1972. Verbascum spathulisepalum (Scrophulariaceae), eine neue Art aus Nordost-Griechenland. — Bot. Notiser 125: 493—496.

A description, illustration and discussion of this new species, which is related to *V. humile* JANKA from Bulgaria, is given with some comments on the inflorescence of *Verbascum*.

Bei Durchsicht der westthrazischen Ausbeute, die Frau ELLI STAMATIADHOU, Sammlerin am Naturhistorischen Museum GOULANDRIS, im Frühjahr 1972 eingebracht hat, fiel uns ein *Verbascum* zunächst durch den scharfen Kontrast zwischen den weissfilzigen, reichblätterigen Basalrosetten und dem kahlen, praktisch blattlosen, dünnästig-lockeren Blütenstand auf. Bei näherer Untersuchung traten weitere in dieser Gattung seltene, sonst nirgends in dieser Kombination auftretende Merkmale zutage, insbesondere die spateligen, kahlen Kelchzipfel, die aussen kahlen Korollen und die einzelstehenden oder serial gepaarten Blüten. Es zeigte sich, dass eine neue, im folgenden erstmals beschriebene Art vorlag. Sie war freilich schon früher einmal in derselben Gegend gesammelt worden, und zwar 1961 von C. GOULIMIS, der den Wert seines Fundes jedoch nicht erkannte; die betreffenden Belege liegen, mit dem GOULIMIS-Herbarium, ebenfalls im Naturhistorischen Museum GOULANDRIS.

Dem Präsidenten des Stiftungsrates dieses Museums und grosszügigen Förderer der botanischen Erforschung Griechenlands, Herrn ANGELOS GOULANDRIS, sind wir für sein vielfaches Entgegenkommen sehr zu Dank verpflichtet. Frau ELLI STAMATIADHOU verdanken wir zahlreiche wertvolle Hinweise, Frau VASSO ZAMBELI die sorgfältige Ausführung der Zeichnungen.

Verbascum spathulisepalum GREUTER & RECH. FIL., sp. nov.

TYPUS: STAMATIADHOU 15216, herb. Mus. GOULANDRIS; isotypus: W. — Fig. 1.

Perenne, caudice lignoso pluricipiti, rosulas foliorum steriles et caules floriferos e rosulis anni praeteriti orientes edente. Caules 40—70 cm alti, tenues, graciles, in dimidio superiore laxe paniculato-ramosi, in parte inferiore appresse albo-araneoso-tomentosi demum saepe glabrescentes, in regione inflorescentiae subglabri. Indumentum totius plantae e pilis fasciculatis (i.e. stellatis radiis elongatis tenuibus flexuosis intertextis) constans, nusquam glandulosum. Folia rosularum consistentiâ crassiuscula formâ magnitudineque variabilia:

lamina suborbicularis vel elliptico-ovata vel late lanceolata, 3—6×1.5—4 cm, basi late vel anguste cuneata rarius abrupte contracta, apice acuta vel obtusiuscula vel rotundata, indivisa, margine minute regulariter simpliciter crenata, in statu juvenili utrinque dense appresse subsericeo-albo-tomentosa, serius supra griseo-virens subtus saltem secus costam et nervos primarios candida, petiolo 1—8 cm longo suffulta; folia caulina pauca cito decrescentia, infima breviter petiolata basalibus similia sed proportione angustiora, jam media valde diminuta anguste lanceolata subpetiolata vel basi cuneatâ sessilia, valde acuta, minutissime vel indistincte crenulato-subserrulata, summa inflorescentiae ramos fulcrantia anguste lanceolata minuta saepe glabriuscula in bracteas sensim transeuntia. Flores laxe racemosi, in axillis bractearum superiorum singuli inferiorum bini (altero accessorio serialiter disposito) perraro 3—4ni; bracteae inferiores axeos principis simul ramum lateralem et florem singulum accessorium alarem fulcrantia. Bracteae lanceolatae acutae glabrescentes quam pedicelli pluries breviores; bracteolae nullae. Pedicelli calyce sesqui- usque triplo longiores, plurimi c. 10 mm longi, tenues, glabrescentes, erecto-patuli, stricti vel subflexuosi, sub alabastro apice nutantes, fructiferi vix elongati. Calyx florifer 3—5 mm longus, floribus delapsis 5—6 mm longus, per 3/4 vel 4/5 divisus, viridis, tubo glabro vel pilis fasciculatis sparsis obsito, laciniis glabris in tertiâ c. parte superiore spathulato-expansis ibique rite contiguis, basin versus valde attenuatis sinubus saepe perviis, apice acutiusculis vel rotundatis minute apiculatis, margine imprimis apicem versus minutissime papilloso-scabridis, crassiusculis, nervo mediano tenui interdum subindistincto. Corolla 20—25 mm diametro, in vivo flava (fide collectrici) in sicco brunnescens, extus glabra intus basi secus nervos pilis elongatis pistillatis iis filamentorum conformibus obsita, non pellucide punctata, lobis suborbiculatis late rotundatis. Flores isandri, stamina 5, filamentis usque ad antheras pilis pistillatis purpurascentibus obtectis, antheris omnibus reniformibus ± medifixis. Ovarium albovillosum; stylus 7—9 mm longus, glaber, apicem versus leviter incrassatus, stigmate ± hemisphaerico. Capsula seminaque ignota.

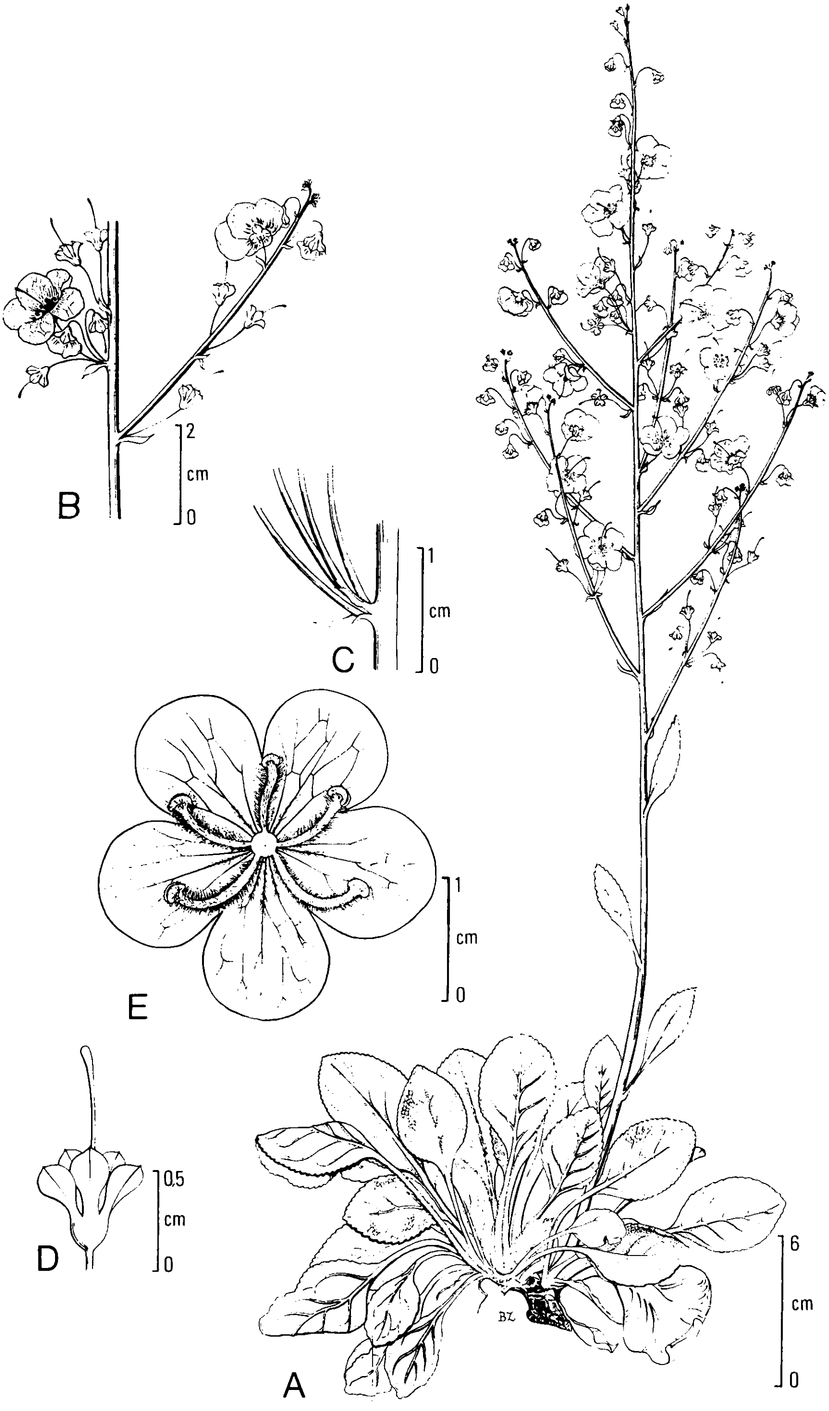
Graecia, Thracia, prov. Evros: in silvis pagi derelicti Pessani, 20.5. 1961, GOULIMIS 21539; a pago Loutros 15—16 km septentriones versus, secus viam forestalem ad pagum derelictum Pessani ducentem, loco „Lofos Taousan“ vocato, alt. 350—400 m, in silvâ *Pini, Querci pubescentis* et *Arbuti Andrachnes* ad fines ditionis mediterraneae et submediterraneae abundans, solo petroso, 19.5. 1972, STAMATIADHOU 15216.

Die neue Art scheint in ihrem Vorkommen auf ein kleines Gebiet des bewaldeten Hügellandes beidseits der Grenze der Verwaltungsbezirke (Eparchien) Alexandhroupolis und Soufli beschränkt, dort aber stellenweise häufig zu sein.

Sie gehört, wie ein Vergleich mit der Monographie MURBECKS (1933—1934) lehrt, in die Nähe von *Verbascum humile* JANKA, das in vielen der besprochenen Merkmale mit *V. spathulisepalum* übereinstimmt und auch arealmässig benachbart ist. *V. humile* wird von MURBECK in die Gruppe Isandra-Ebracteolata-Trichosantha von *Verbascum* subsect. *Fasciculata* gestellt. *V. spathulisepalum* würde nach dieser Gliederung in die Nachbargruppe Isandra-Ebracteolata-Leiantha gehören; doch sind diese Gruppen, auch im Sinne MURBECKS, nicht als natürliche Einheiten aufzufassen, und ein engerer Anschluss von *V. spathulisepalum* an die übrigen Leiantha-Arten scheint nicht zu bestehen.

Ein Vergleich unserer Art mit *V. humile,* bzw. mit den drei von MURBECK unter diesem Namen zusammengefassten Sippen (Unterarten bzw. Varietäten), ergibt folgendes Bild. Bezüglich des Induments ist *V. humile* recht variabel, am ehesten erinnert subsp. *tsar-borisii* DAVIDOV (Nordostbulgarien) an *V. spathulisepalum.* Auffällig ist die grössere Zahl der Blüten pro Brakteenachsel, wobei alle (bis zu 4) radial angeordnet sind, während die Verhältnisse bei *V. spathulisepalum* komplizierter liegen (siehe unten). Der Kelch ist bei *V. humile* kürzer (2—3.5, zur Fruchtzeit 5 mm lang), in der Jugend deutlich flaumig behaart, bis zum Grunde geteilt;

Fig. 1. *Verbascum spathulisepalum* (GOULIMIS 21539). — A. Habitus. — B. Infloreszenzabschnitt mit oberstem Seitenast und Viererbüschel von Blüten. — C. Büschel mit 4 Blüten. — D. Kelch und Griffel nach dem Abfallen der Blütenkrone. — E. Blütenkrone von innen, mit Staubblättern.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seine Abschnitte sind vielgestaltig, bisweilen schmal spatelig oder länglich-elliptisch, nie aber so deutlich spatelig verbreitert wie bei unserer Art. Die aussen, mit Ausnahme von subsp. *tsar-borisii* auch innen sternflaumige Krone liefert, wie schon erwähnt, einen diagnostisch sehr wertvollen Unterschied. Schliesslich ist noch der kürzere (5—7 mm), ± dicht flaumig behaarte Griffel von *V. humile* zu erwähnen.

Zusammengenommen genügen diese Unterschiede zweifellos, um die Aufstellung von *V. spathulisepalum* als gut definierte, selbständige Art zu gewährleisten. Es mag noch zusätzlich erwähnt werden, dass die geographisch nächste *humile*-Sippe, var. *rhodopeum* (STOJ.) MURBECK (in RECHINGER 1939), morphologisch (Indument, Stengelbeblätterung, Form der Kelchabschnitte) am stärksten von *V. spathulisepalum* abweicht, während die in dieser Hinsicht ähnlichere Sippe, subsp. *tsar-borisii,* das entferntere Ende des *humile*-Areals bewohnt.

Die Blütenstandsverhältnisse von *V. spathulisepalum* verdienen eine gesonderte Besprechung, weil die Art in dieser Beziehung zwischen verschiedenen *Verbascum*-Gruppen zu vermitteln scheint. Normalerweise stehen die oberen Blüten jeder Traube einzeln, die unteren gepaart in den Brakteenachseln, wobei die serial äussere, sich später entwickelnde im Sinne MURBECKs als akzessorisch zu bezeichnen wäre. Es kommen nun aber ausnahmsweise auch zu 3—4 gebüschelte Blüten vor, und diese stehen dann nicht alle serial in einer Reihe, wie bei *V. humile* und generell bei den Arten der Gruppe Ebracteolata, sondern sind mit Ausnahme der untersten (akzessorischen) ± unregelmässig angeordnet und können auch Spuren von „Brakteolen“ tragen. Die Stellung solcher Blütengruppen an der Hauptachse unmittelbar über den obersten Auszweigungen (Seitentrauben) zeigt, dass sie (mit Ausnahme der akzessorischen Blüte, die auch in den Achseln der Stützblätter der Seitenzweige entwickelt ist) gesamthaft dem Rudiment einer Seitentraube mit ihren Brakteen (hier „Brakteolen“) entsprechen. Möglicherweise können gerade solche zwar nicht regelmässig, aber doch recht häufig auftretende Bildungen wie die hier beschriebenen vermehrtes Licht auf die Phylogenie der *Verbascum*-Blütenstände werfen.

Jedenfalls dürfte *V. spathulisepalum,* das auch durch seinen ausgeprägt mehrjährigen Wuchs auffällt, eine alte, in mehreren Beziehungen verhältnismässig ursprüngliche Reliktart darstellen.

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Three New Taxa of Iris Subgenus Oncocyclus from Lebanon and Syria

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ABSTRACT

CHAUDHARY, S. A. 1972. Three new taxa of Iris subgenus Oncocyclus from Lebanon and Syria. — Bot. Notiser 125: 497—500.

Iris cedreti DINSMORE ex CHAUDHARY from near Cedars of Lebanon, and *I. kirkwoodii* CHAUDHARY and *I. yebrudii* DINSMORE ex CHAUDHARY subsp. *edgecombii* CHAUDHARY from Syria are described.

Iris cedreti DINSMORE ex CHAUDHARY, sp. nov.

Planta c. 40 cm. alta. Rhizoma fere obliquum, compactum. Folia 8 vel 9, ad 23 cm. longa, 1—2 cm. lata. Flores c. 18 cm. longi, 9 cm. lati. Ovarium triangulare, sexlobatum. Tepala externa ovata, subtiliter crenata, 6.5—8 cm. longa, 4.5—5.5 cm. lata, basi pallida, alba—plumbeoalba; venis tenuissimis, elevatis, densis (10—13 per cm.), atromaroninis—purpureo-maroninis; puncti subtilissimis, basi elevatis. Macula media orbiculata, c. 1.5 cm. diametro. Tepala interna c. 8.5 cm. longa, obovata, interne praecipue plumbeoalba, externe purpureo-atromaronina, venis tenuissimis, purpureo-atromaroninis, elevatis, densis (13—20 per cm.); punctis subtilissimis. Capsula c. 8 cm. longa, inflata, lobata.

Plants rarely exceeding 40 cm in height. Rhizome rather oblique, compact, about 2.5 cm wide, pale yellow. Leaves 8 or 9, up to 23 cm long, 1—2 cm wide from the keel to the margin, narrowed to the tip, the apex acute or narrowly obtuse. Flowers about 18 cm long from the base of the valves and about 9 cm wide. Valves about 10 cm long, reaching to the level of the falls, about 4 cm wide, inflated, green. Ovary stalk 0.5—1 cm long; the ovary about 3.3 cm long, triangular, 6-lobed; the ovary much longer and the lobes more pronounced in flowers that remain unfertilized or fail to open. Perianth tube about 3 cm long. Falls ovate, finely crenate or irregularly finely serrate, 6.5—8 cm long, 4.5—5.5 cm wide, the ground clear, white to lead-white; veins very fine, embossed, densely arranged (10—13 per cm), dark maroon to purplish-maroon; dots very fine, more embossed around the signal patch and the area above this level. In the darker biotype the dots on the falls are larger, anastomosing so closely that the dots form the ground and the ground appears as irregular white spots. Signal patch orbiculate, 1.7 cm long, 1.5 cm wide, dark maroon-purple. Beard of long, pink, purple, rusty-brown or mottled hairs on a pale-green ground. Standard about 8.5 cm long, 6 cm wide, obovate, clawed, the claw channelled; the ground characteristic white to lead-white; veins very fine, purplish dark maroon, prominently embossed, parallel, densely arranged (13—20 per cm); dots very fine, very sparse near the margin, larger and sparse in the central area, finer and denser in the lateral zones;

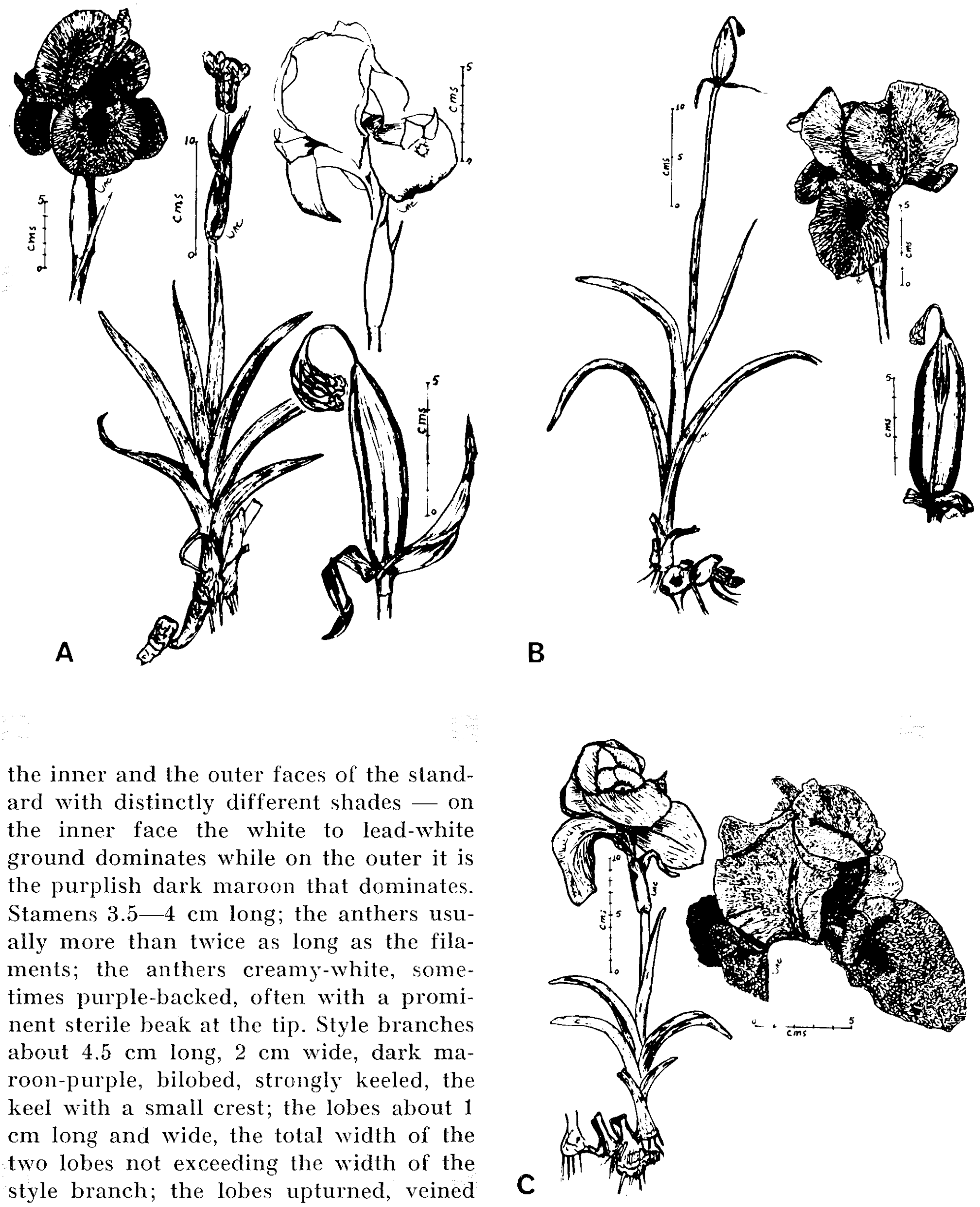

Fig. 1. *Iris* subgenus *Oncocyclus*. — A: *I. cedreti*. — B: *I. kirkwoodii*. — C: *I. yebrudii* subsp. *edgecombii*.

the inner and the outer faces of the standard with distinctly different shades — on the inner face the white to lead-white ground dominates while on the outer it is the purplish dark maroon that dominates. Stamens 3.5—4 cm long; the anthers usually more than twice as long as the filaments; the anthers creamy-white, sometimes purple-backed, often with a prominent sterile beak at the tip. Style branches about 4.5 cm long, 2 cm wide, dark maroon-purple, bilobed, strongly keeled, the keel with a small crest; the lobes about 1 cm long and wide, the total width of the two lobes not exceeding the width of the style branch; the lobes upturned, veined and dotted like the falls. Pods about 8 cm long, inflated, lobed, narrowed towards both ends.

HOLOTYPE. Vicinity of Cedars of Lebanon, May 12, 1972; No. 789; Post Herbarium (BEI). Coll. SHAUKAT and ZAHIDA CHAUDHARY with CAROLYNE WEYMOUTH.

OTHER COLLECTIONS. Vicinity of Cedars of Lebanon; April 15, 1940; No. 20513; Post

Herbarium (BEI). Coll. J. E. DINSMORE. — Cedres du Liban; May 31, 1880; No. 11095 (?); Post Herbarium (BEI). Coll. BLANCHE.

Iris kirkwoodii CHAUDHARY, sp. nov.

Planta ad 75 cm. alta. Rhizoma magnum, c. 3 cm. latum, compactum. Folia 5—7, fere graminea, ad 30 cm. longa, c. 2 cm. lata. Pedunculus super nodum extimum 25—30 cm. longus. Flores c. 14.5 cm. longi, 8 cm. lati. Valvae non inflatae. Ovarium fere teres. Tepala externa 6—8 cm. longa, 4—5 cm. lata, ovata, venis atropurpureis, punctis subtilibus in fundo pallide viride vel albo dense dispersis. Macula media orbicularis, c. 1 cm. diametro. Tepala interna orbicularia—ovata, c. 8.5 cm. longa, 6 cm. lata, venis et punctis tenuibus caesiopurpureis in fundo pallide caeruleo dispersis; venis et punctis non nisi basi elevatis. Capsula c. 9 cm. longa, cylindrica, non lobata.

Plants up to 75 cm tall. Rhizomes large, about 3 cm wide, compact, yellowish brown. Leaves 5—7, rather grassy, up to 30 cm long and about 2 cm wide from the keel to the margin, pale green, the veins slightly raised above the surface; stem-leaves one or two. Peduncle length 25—30 cm above the last node. Flowers about 14.5 cm long and 8 cm wide. Valves rather tight-clasping, not inflated. Ovary about 3 cm long, almost terete. Perianth tube about 3 cm long. Falls 6—8 cm long, 4—5 cm wide, ovate, recurved, clawed, embossed with dark purple veins and fine dots densely scattered over the upper surface on a pale green or white, clear ground; the spots larger and denser below and to the sides of the signal patch. Signal patch orbicular, about 1 cm in diameter. Beard-hairs long, maroon-purple or rusty-brown. Standard orbicular to ovate, about 8.5 cm long, 6 cm wide with fine blue-purple veins and dots on a clear, pale blue ground; the dots and veins embossed only near the base and along the midrib. Anthers purple-backed, 2 to 2.2 cm long, 4 mm wide; the filaments 1.2—1.5 cm long. Style branches 4 cm long, 3 cm wide, maroon in the middle, dark purple to the sides, bilobed; lobes minutely serrate, turned upwards, with fine embossed veins and very fine dots. Pods about 9 cm long, cylindrical, not lobed, the veins thick, prominent, raised above the surface or level with it.

HOLOTYPE. Bishmishly, Syria, April 19, 1972; No. 787; Post Herbarium (BEI). Coll. Mrs. GRACE KIRKWOOD and SHAUKAT A. CHAUDHARY.

Iris yebrudii DINSMORE ex CHAUDHARY ssp. **edgecombii** CHAUDHARY, ssp. nov.

Planta 25—40 cm. alta. Rhizoma parvum, compactum. Folia 6 vel 7, c. 11 cm. longa, 8 cm. lata. Flores c. 15 cm. longi, c. 14 cm. lati. Tepala externa ovata—orbicularia, c. 9 cm. longa, 7 cm. lata, punctis rubropurpureis elevatis et venis atropurpureis subtilibus. Macula media ovata, maronino purpurea, venis obscuris. Tepala interna orbicularia, c. 10 cm. longa, 8.5 cm. lata, venis maronino-purpureis et punctis parvis densis aeque instructa; fundo albo.

Plant 25—40 cm tall. Rhizomes small, compact, about 2 cm wide. Leaves 6 or 7, greyish-green, about 11 cm long, 8 mm wide from the keel to the margin, strongly recurved; the stem leaf erect, reaching or surpassing the valves. Flowers large, about 15 cm long, 14 cm wide. Valves 7—9 cm long, inflated, keeled from near or above the middle, pink-tinged. Ovary broadly trigonal, about 5 cm long. Falls ovate to orbiculate, about 9 cm long, 7 cm wide, covered with red-purple embossed dots and fine dark purple veins, the latter perceptible only at or above the level of the signal patch: in pale biotypes the red-purple dots much smaller and the red-purple veins visible all along the margin: the ground pale green or pale yellow, clear. Signal patch ovate, about 1.5 cm long, 1 cm wide, maroon-purple with dark veins. Beard of dark purple hairs tipped with yellow, the hair covering part of the patch and coming down the sides of the signal patch to about 3/4th its length. Standard about 10 cm long, 8.5 cm wide, the limb orbiculate, gradually tapering to a small claw, uniformly covered with maroon-purple veins more distinct near the margin and small densely arranged spots on a white, clear ground; the margin slightly crenulate; the inner basal area with a few long yellow hairs; in pale biotypes the standard uniformly pale yellow, clear, with very fine purple veins and sparsely scattered fine purple dots or the standard with uniformly densely scattered fine purple dots. Anthers about 3 cm long, 4 mm wide, dotted with minute red-purple dots on the back. Style-branches about 5 cm long, 4 cm wide, with minute dark-purple spots on the maroon median and pale greenish lateral bands, bilobed, individual lobes about 2 cm long, 2.5 cm wide, upturned, dotted and veined with red-purple; the lobes continuing as a prominent double crest over the keel of the style-branch, sometimes the crest folded over near the lobes; the double crest dotted and streaked with red-purple.

HOLOTYPE. Kastel, Syria; April 25, 1972; No. 788; Post Herbarium (BEI). Coll. Mrs. GRACE KIRKWOOD.

ACKNOWLEDGEMENTS

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Origins and Evolution in the Genus Trifolium

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ABSTRACT

ZOHARY, M. 1972. Origins and evolution in the genus Trifolium. — Bot. Notiser 125: 501—511.

A survey of the infrageneric subdivision is given. The geographical distribution of the eight subgenera is related to hypothetical lines of divergence. The affinities of the genus are briefly discussed. Evolutionary trends in the organization of flowers, inflorescences, and habit are outlined. The adaptive significance of some derived characters in dispersal biology are pointed out.

INTRODUCTION

Clovers are widely known and easily recognizable; they have been so since ancient times. Herbalists and pre-Linnean botanists knew already a good number of clover species. LINNAEUS not only recorded about 40 species, but also attempted to group them into natural units some of which have been retained up to date as full or *pro parte* sections.

Yet *Trifolium* is one of the most difficult genera as seen by the fact that for the 238 existing species about 1100 binomials have been published. Attempts to throw light on some difficult group or to revise this genus fully or partly have been made by SAVI (1810), SERINGE (1825), PRESL (1832 pp. 44—50), KOCH (1835), BOISSIER (1872), ČELAKOVSKY (1874), LOJACONO (1883 a, b), GIBELLI & BELLI (1887, 1889, 1890—93), MCDERMOTT (1910), among others. Of all these botanists, LOJACONO (1883 b) should be accredited with having been the first to compile a kind of a key to the over 200 species known at that time, especially so because he was the first to cast light on the American species which previously had only been very dimly known.

All these studies, however, have not lessened the controversies concerning the taxonomical subdivision of the genus, the delimitation of the species and nomenclature, so that much confusion is still to be found in the taxonomy of the genus, hence so many misidentifications in herbaria and misconceptions in floras, especially in regard to American species.

The present author and his collaborator (D. HELLER) have endeavoured to become acquainted with the entire genus with the aim of obtaining a deeper insight into the groups and of preparing a revision of the entire genus, a task which is now approaching completion.

The following account is only a sketch of the evolutionary aspect of this genus, based on a taxonomic study carried out at the Herbarium of the Hebrew University.

SIZE AND DIVERSITY OF THE GENUS

The genus comprises 238 species. It has long been divided into several sections and subsections not always sharply delimited. Only one section is shared by the Eastern and Western Hemispheres: it is the Sect. *Lotoidea* (*Amoria* p.p.). The rest are limited to the Eastern Hemisphere or to the New World alone. While the boundaries between species are in many cases extremely difficult to define, there is in almost all sections a striking grouping of the species into well-definable clusters, which facilitates obtaining a general view on the differentiation of the genus or its sections. We have usually ranked these natural clusters as series or subsections. Within these clusters the delimitation of the individual species is often extremely difficult and open to controversy among students; this especially concerns the American clovers. This difficulty stems from the wide range of diversity met with in very many species. In the majority of cases this diversity is caused by primary polymorphism and not hybridization. However, this polymorphism scarcely obstructs the grouping of the individual species into higher taxa. Accordingly, one is able to trace many evolutionary traits of this genus both as to their vegetative and reproductive structures and behaviour. But before discussing the trends of evolution, let us glance at the genus and its sectional make-up.

The present author has accepted the division of the genus into the following eight sections:

The largest section of the genus is that of *Lotoidea*. It comprises about 90 species and displays the widest range of distribution, extending across the whole N. Hemisphere from the Western to the Eastern Pacific. In this section the author has included a series of subsections such as *Lupinaster, Amoria* (with 5 series), *Platystylium* (with 4 series), *Calycospatha, Ochreata, Loxospermum, Neolagopus* and *Falcatula.* Formerly the group of species equivalent to Sect. *Lotoidea* was very unreasonably divided according to obscure and unreliable characteristics. This applies especially to American members of this section. The misconception of the specific and superspecific taxa has troubled many authors including the present author (and his collaborator D. HELLER) until he decided to free himself from the conventional division of the group and to weigh anew the grouping and ranking of this section.

Sect. *Lotoidea* is not only the largest among the sections of *Trifolium* but also the oldest one. It is in this section that the most ancestral forms of the genus are harboured as will be seen later. Accordingly, one should look on various parts of this section as starting points of the lines of evolution of other sections in this genus. Its wide distribution suggests its existence at a period when the two hemispheres were easily traversable, namely sometime in the Neogene.

On the assumption that several other sections were derived from certain parts of this section, the long span of time needed for this evolutionary process is quite comprehensible.

The main traits that characterize this section are the bracteate and pedicelled flowers, the regular or almost regular calyx with its open or almost open throat and its 2—4(—8)-seeded legume mostly protruding from the calyx tube. This pod has not yet lost the typical leguminous pattern and the ability to dehisce suturally. All these traits are typically leguminous and should therefore be regarded as primitive compared with the extremely derived characteristics dominating in the rest of the sections of this genus. Of course these characteristics when taken as a whole are typical of the *Lotoidea* section, because there are quite a number of individual species or even groups that display only some of these characteristics. Such cases should be looked upon as initial stages of evolutionary trends leading to new patterns that characterize other sections.

The section next in size and nearest in its general features is Sect. *Trifolium* (*Lagopus*). The number of species amounts to 73. It is heterogeneous in appearance and polymorphic in almost all its characters. It appears to fall into a large number of small clusters which were taken as subsections (ZOHARY 1971, 1972).

The diagnostic characters of this section are: sessile, ebracteate flowers, throat of calyx tube provided with a hairy or callous ring or with a bilabiate protrusion, calyx limb often with unequal teeth; pod one-seeded, enclosed in the calyx tube; its pericarp is made of a membranous lower part and a leathery cup-like upper one, rupturing transversely at germination. Some of the above characters are sometimes rudimentary only but the trend towards their development is quite traceable; so for instance is the closure of the calyx tube. The evolutionary links between the sections *Trifolium* and *Lotoidea* are fairly obvious; they will be discussed in a later paragraph.

Section *Vesicaria* with its 7 species (ZOHARY & HELLER 1970) can hardly be linked with any other section of the genus. In its morphological and ontogenetical development of the calyx as a vesicular body serving seed dispersal most efficiently it has no parallel within the genus. But something similar in the structure of the calyx is found in the Subsect. *Calycospatha* of the Sect. *Lotoidea*. This may perhaps be considered a starting point towards the line of Sect. *Vesicaria*.

Section *Mistyllus* comprises 9 species. The unique structure of the calyx and corolla perfectly delimits this section from others. Its close relationship to *Lotoidea* is manifested by the bracteate flowers, the regular calyx limb, the 2—4-seeded pod dehiscing suturally. The section is also unique in its distribution: 6 species in the Mediterranean and 3 in the tropical Eritreo-Arabian subregion.

Section *Paramesus* with its 2 species although considered as a separate section, should in future be placed among the series of *Lotoidea*. It is only the structure of the pod and the occurrence of gland-bearing teeth on the stipules and the calyx that separate it from *Lotoidea*.

The exclusively American Section *Involucrarium* is well delimited from all other sections of the genus, mainly separated on three characters: the fissure of the calyx teeth, the sharply dentate or incised stipules and the presence of an involucrum at the base of the head. The flowers are sessile or slightly pedicelled and ebracteate. The calyx teeth show a clear trend towards excessive fission or dentation, the throat is open. It is not easy to find links between this section and *Lotoidea* as it appears at present. But a thorough search will certainly find within the vast Section *Lotoidea* some points of junction between the two sections.

The Section *Trichocephalum* with its 8 species is a most natural group, sharply isolated from all other sections by the fact that only a small part of the flowers of the head is fertile. All others have been converted to a mass of hairs or bristles serving in the dispersal of the few seeds. Dispersal here is anemochoric, zoidochoric or geocarpic. This section should be considered the most advanced, if only for its highly elaborate and differentiated flower head. Faint links with *Lotoidea* can perhaps be found among those species in which sterilization of the upper flowers of the head is a constant characteristic. Yet, Sect. *Trichocephalum* will always remain isolated.

Section *Chronosemium* is equally clear-cut. It consists of 21 species unique in their floral structure and fruiting calyces. Among its peculiar characteristics are: the two-lipped calyx, the persistent corolla with its spoon- or boat-shaped standard, serving as an anemochorous device to the small, mostly stipitate, one-seeded pod hidden in the short calyx tube. This section like the last one has reached the highest level of organization and functional efficacy of the fruiting and floral organs in the trend towards anemochoric dispersal.

RANGE OF DISTRIBUTION AND PHYLOGENY

The area of the genus is today divided into a few disconnected territories. The largest of them is the Mediterranean with about 150 species representing 7 of the 8 sections of the genus. Among them 6 sections have their predominant number of species here. It is the Section *Trifolium* which has its centre of differentiation here, especially in the East Mediterranean. Other predominantly Mediterranean sections are *Mistyllus, Trichocephalum, Vesicaria,* and *Paramesus.* In the Euro-Siberian and Irano-Turanian regions, *Trifolium* is rather poor and scattered and no country in these regions harbours more than 20 species, most of them having no more than 5 or 10. In these regions the number decreases suddenly towards east and north.

In Africa there is not a single representative of *Trifolium* in the vast Saharo-Arabian region.

The largest centre of *Trifolium* in Africa is the Eritreo-Arabian province (comprising among others Ethiopia, Somalia, Eritrea, S. Arabia, Kenya, Tanzania and Uganda).

Isolated and very poor stations of *Trifolium* are the Cape Province, the western part of the Guineo-Congoan region and some scattered mountain peaks elsewhere.

Among the tropical African representatives the *Lotoidea* with its two Subsections *Ochreata* and *Loxospermum* are exclusive, and this testifies to the independency of this centre as to speciation and formation of peculiar higher taxa of a Lotoidean origin.

On American territory there are a hundred or so species of *Trifolium* belonging to the Sections *Lotoidea* and *Involucrarium.* Of these over half of the species are centred in the Californian region and its eastern borderlands. In South America a great number of them are centred in the Andean (Chile, Peru) and Argentinian regions. There are also some isolated stations with a single or few species outside these centres.

The above brief statement on the distribution of *Trifolium* is well illustrated by MEUSEL et al. (1965). An interpretation of this division into areas needs a lengthy analysis and discussion which can not be given here for lack of space. But even a short glance at the distribution pattern reveals the complicated traits and processes involved in the evolutionary history of *Trifolium.* Quite a detailed discussion on part of the subject has been presented by BOBROV (1947, 1967). Here we shall roughly outline some salient points only deducible from the above geographical pattern. The fact that the Section *Lotoidea* which is the most primitive (in all regards) is the most widespread higher taxon, extending from the western to the eastern Pacific coast is already highly indicative of the part played by this section in the evolution of the genus.

But before dwelling on the relationship of the intrageneric groups and their origin, let us devote some lines to the phyletic position of the genus. The question of whether *Trifolium* is a monophyletic entity, or an assemblage of reduced forms stemming from a whole series of genera which have undergone parallel permutations through reductionary evolution, and which reached "endforms" of similar constitutions such as those characterizing our genus will never be answered with certainty. Questions of this kind could be posed on a whole series of other genera and even families. Is not the monophyletic nature of the Compositae seriously questioned! Also, it is not certain that genera of the Cruciferae with highly reduced fruits (e.g. *Alyssum*) are monophyletic. Looking at the genus from the standpoint of variation and polymorphism, one can not categorically deny the assumption of an ancestral heterophyletic origin of the genus. And yet we ought to treat this genus according to its actual morphological attributes and consider it as a discrete taxonomic entity.

As it is, Sect. *Lotoidea* includes two strikingly distinct subsections at each end. These are Subsect. *Lupinaster* which may be considered an intergeneric link, and Subsect. *Neolagopus* which can be taken as a link joining *Lotoidea* with other sections within the genus and primarily with Sect. *Trifolium*. As to *Lupinaster* with its digitate foliage and other peculiar characteristics this group should, perhaps, link *Trifolium* to an archaic lupinoid, extinct stock.

These extreme groups are, by no means, representative of the section as a whole, which is altogether clover-like and gross-morphologically fairly uniform. BOBROV, who in 1947 discussed the evolution of the genus and looked on it as a rather uniform genus, has radically changed his mind in a later paper (1967) and, without adequate evidence, divided the genus into a series of genera. Moreover, he ranks mainly the American members of this subgenus *Trifoliastrum* (which roughly fits our Sect. *Lotoidea* and which can not be separated from the Eurasian and African members of this section) as an independent genus and transfers it to the tribe Genisteae.

In my opinion, there is no justification for this procedure, if only because the characteristics attributed by BOBROV to his genus *Trifoliastrum* are found only in a small part of this group, while the majority of species in both the Old and the New World do not display protruded pods, bilabiate calyces or bi-coloured corollas, etc., as claimed by BOBROV.

A thorough examination of all 90 species of this section has led the author to the conclusion that *Lotoidea* should remain as it is and where it is and that the other sections should not be raised to the rank of genera as suggested by BOBROV (1967).

As to the position of the genus *Trifolium* within the tribe Trifolieae along with *Medicago, Trigonella, Melilotus* and *Ononis,* it was again BOBROV who questioned this conventional belief and not without justification, not only because there is a hiatus between *Trifolium* and its contribal genera as to the reproductive structures, but also as to their geographical distribution and evolution. None of the genera contribal with *Trifolium* is indigenous in the New World while *Trifolium,* as will be shown in a later paragraph, when taken as a whole, is evidently of North American origin. The fact that *Trifolium* is the most derivative genus of the group rules out any possibility of deriving the genera under consideration from *Trifolium.* It is thus quite reasonable to separate *Trifolium* from the genera mentioned whether as an independent tribe or subtribe. It should, however, not be transferred to the Genisteae as suggested by BOBROV for a variety of reasons and first and foremost because of the remoteness of living Genisteae or *Lupinus* from *Trifolium* in all respects. This does not rule out the possibility of the existence of phyletic relations between a certain part of Sect. *Lotoidea,* namely Subsect. *Lupinaster,* and a hypothetic ancestral lupinoid group.

While we are ignorant as to the origin of the entire group contribal with *Trifolium,* we are in possession of some indirect evidence as to the origin and evolution of *Trifolium* as a genus. From the distributional lay-out of the genus it is obvious that within the temperate latitudes of the Northern Hemisphere, N.W. America constitutes the largest centre of *Trifolium* (about 50 species), especially of Sect. *Lotoidea,* while the eastern states of America almost lack indigenous representatives of this genus. In the Eastern Hemisphere there is no such concentration at or near the eastern Pacific coast but there are still a few species of the *Lotoidea* met with in the Sino-Japanese region. Especially interesting in this respect is *T. pacificum* BOBROV found in the Far East which is very close to *T. lupinaster*. Consequently, *Trifolium* must have migrated across the Pacific one-way, i.e. from N.W. America to E. Asia, probably via the Bering Strait.

Evidence for this assumption is: (1) the diversity of forms crowded in N.W. America which alone could serve as a source of further differentiation and expansion of the genus; (2) the total lack in America of indigenous representatives of other Eurasian *Trifolium* sections; (3) the route concerned was also the main migration route of other taxa (e.g. conifers) shared by both continents.

The species that made their way to E. Asia were exclusively Lotoidean, comprising representatives of all its important subsections and probably also representatives of *Neolagopus,* lacking at present in the Eastern Hemisphere.

This was probably the first step in the tremendous processes of evolution in *Trifolium* that took place in the Eastern Hemisphere. It was a swarm of species of the white clover group or one close to it that gave rise to the formation of other subsections of the *Lotoidea* as well as of the six other sections of *Trifolium* on Eurasian and African ground. The latter, although they differ from one another and from the members of Sect. *Lotoidea* must have had a common ancestor and for this there is within the Eastern Hemisphere no clover-like candidate other than the primitive Old World members of Sect. *Lotoidea.*

Intensive study will be required for supplying detailed evidence of the evolutionary relations between the primitive *Lotoidea* species and the other sections and subsections of *Trifolium,* the bulk of which belong to the six sections with their highly derivative species. They have all been differentiated in the Eastern Hemisphere during the long span of time which elapsed since the Neogene period. Their main concentration in the Mediterranean is no doubt primary, and not a result of being pushed down there through the climatic changes of the Pleistocene. The tropical African centre of clovers with its two *Lotoidea* subsections *Ochreata* and *Loxospermum,* have evidently originated in Africa probably from old members of Subsection *Amoria,* which also occur in Africa. The migratory route from the Mediterranean region to the highlands of tropical E. Africa is the well known Afro-alpine-Mediterranean line. The above assumption is supported by the fact that the Section *Mistyllus* has 6 species in the Mediterranean and 3 in tropical Africa and some representatives of the African *Amoria* Subsection have their nearest relatives in the Mediterranean. That the African stock was in a position to differentiate two Lotoidean subsections (*Ochreata* and *Loxospermum*) of its own suggests that the immigration of clovers into Africa must have taken place in a very remote geological past.

ORGANOPHYLETIC TRENDS WITHIN THE GENUS

Life Forms

There is not a single chamaephyte in the whole genus of *Trifolium.* Life forms are exclusively perennials and annuals in the proportion of about 1 to 2. Most perennials are included in the *Lotoidea* and in some primitive portions of some other sections. Thus for instance the Section *Lotoidea* with its 90 species includes no less than 60 perennials, while the Section *Trifolium* has about 20 perennial species against over 50 annuals.

The Sections *Mistyllus* and *Trichocephalum* have no perennial species. In the *Vesicaria* Section there are 3 perennials and 4 annuals; *Chronosemium* comprises 20 annuals and only one perennial. Similarly the Section *Involucrarium* has 16 annuals and only 1 perennial.

It is not too venturous to conclude that in all cases perenniality is bound to sections or groups with less elaborate morphological and biological devices. On the other hand, annuality here, as elsewhere, is derivative and more progressive at least in regard to the reproductive organization.

It seems that annuality has here a selective value allowing the spread of the species into less mesic habitats, hence the abundance of annuals in the Mediterranean and their scarcity in higher latitudes and altitudes.

The ability of many perennials to reproduce vegetatively by rhizomes, suckers and rooting nodes is perhaps a compensation for the lack of sophisticated devices in the dispersal ecology of the plants.

Evolutionary Trends in the Formation of the Capitulum

A closer examination of the structure of the flowering head in *Trifolium* reveals a striking diversity of form, the main types of which may be mentioned here in a sequence presumably presenting an evolutionary trend:

(1) The racemose type (e.g. *T. brandegei*). Here the inflorescence has preserved its typical ancestral pattern. The head is made of a well-developed rhachis bearing long-pedicellate and bracteate flowers all along. After anthesis the pedicels bend downwards and the open calyx throat allows the release of the seeds or the pods from the calyx. No devices for the dispersal of seeds are met with here.

(2) The "producta" type. Raceme as above, but upper part of rhachis flowerless usually bearing at base some minute sterile flower buds (e.g. *T. kingii*).

(3) The verticillate type. Here the flowers along the rhachis are arranged in more or less regular and fairly distinct whorls. This type of arrangement occurs not only in heads with long-pedicelled flowers, but also in those with sessile or subsessile flowers. Example: *T. albo-purpureum.*

(4) The "alpinum" type is a reduced head with only a few flowers loosely arranged in rows along the conspicuous rhachis. Example: *T. alpinum.*

(5) The "repens" type. This is the most characteristic form in the Subsection *Amoria* of the *Lotoidea*. The flowers are usually long-pedicelled and borne on the extremely abbreviated rhachis, so that the head assumes an umbellate appearance. At post-anthesis the heads are first globular and then become conical due to the bending down of all pedicels.

(6) The "uniflorum" type is derived from the "repens" type. There is no rhachis and the number of flowers is reduced to 1—4.

(7) The "ambiguum" type is of a semi-spicate nature having an elongated rhachis and usually very short-pedicelled flowers in the upper part and long-pedicelled ones in the lower; the latter become reflexed after anthesis while the rest remain erect or patulous. We may term this type semi-spicate to differentiate it from the next type.

(8) The "plumosum" type. This is a true spicate form with sessile, ebracteate flowers all along the elongated rhachis.

(9) The "capituliform" type is the same as (8), but with a shortened rhachis.

These types certainly do not exhaust the entire gamut of head polymorphism in *Trifolium*. Their basically racemose nature is not effaced by any of them. The above examples have been taken from Sect. *Lotoidea* to show the plasticity and the diversity of forms met with in this primitive section. The sequence of the types recorded above does not necessarily present a successive trend in head evolution, but rather one of the possibilities of such a trend.

Organophyletically the heads of all other sections could easily be derived from this rich source of patterns.

Bracteation of the Flowers

Bracteate flowers are, as is well known, a primary state of a racemose inflorescence. There is a trend here and in many other instances to debracteate the spike or the raceme so as to separate the latter from the vegetative parts of the plant. This is fully accomplished in the genus *Trifolium,* but the successive stages of this trend can readily be followed in Section *Lotoidea,* which in its elaborate Subsection *Neolagopus* has achieved rudimentation or total disappearance of the bracts. That the bractless state constitutes the most advanced stage in the evolution of the clover head, is evidenced by the fact that the most elaborated sections of *Trifolium* are bractless, or only rudimentarily bracteate.

Section *Mistyllus* with its well-developed bracts is also in regard to other characteristics the most primitive among the non-Lotoidean sections (regular calyx limb, many-seeded pods with sutural dehiscence, etc.).

The fact that bracts also rarely occur in some non-bracteate sections as in *T. noricum* and *T. longidentatum* of the Sect. *Trifolium* is highly indicative of the evolutionary process leading to the abortion of this organ.

The occurrence of involucral structures at the base of the head, in so far as these involucres are of bracteal and not of stipular origin, should not be looked upon as a trend towards involucration of the head. The distinct or connate bracts that form this involucre are in many cases considered to be vestiges of abortive flowers, even where they are well organized in a cup-like structure as for instance in *T. cinctum*. Rudimentary involucral structures are met with in a series of species of Sect. *Lotoidea,* and also in some species within the sections *Vesicaria* and *Paramesus*.

Different in appearance is the involucre in Sect. *Involucrarium*. Here an anatomical and even a gross-morphological examination is sufficient to consider the involucre as "stipular".[1] The fusion and the whole gamut of forms displayed by this type of involucre are further developments of this organ, the functional meaning of which is not understood. Stipular involucre formation also occurs elsewhere in *Trifolium* (e.g. *T. cherleri*), but it is only in the Sect. *Involucrarium* that it serves as a diagnostic character at sectional level. The section as such though linked in its floral characters with *Lotoidea* from which it has evidently been derived, is quite isolated in the genus and forms a blind alley as to further developments. There is only one Old World section, Sect. *Paramesus,* comprising 2 species which could perhaps join this section because of its rudimentary involucre which is apparently also stipular in origin.

Evolutionary Trends in the Construction of the Calyx

No organ in the realm of the flower has undergone such far-reaching permutation within the evolution of the genus as the calyx. Here again we find the most primitive forms among the species of *Lotoidea.* The prevailing type of calyx in this section is the tubular or campanulate form with an open throat and five more or less equal lobes or teeth. Evolutionary processes that have taken place towards the elaboration of the calyx may be summed up as follows:

(1) Inflation and vesiculation of the tube. Incipient stages of tube inflation are already found in the *Lotoidea,* e.g. Subsections *Loxospermum* and *Pseudostriatum;* it has its perfect continuation in the Section *Mistyllus* where the regularity of the inflated calyx is still well preserved. In only one case in *T. spumosum* of this section, is there real vesiculation but here too the limb is still symmetrical.

Vesiculation of the calyx accompanied by bilabiation, strong asymmetry of the tube, closure of the calyx throat and almost absolute monospermy of the pod, are characteristic of Sect. *Vesicaria.* Here the vesicular fruiting calyx has achieved its highest efficacy in anemochorous dispersal.

(2) Bilabiation of the calyx. Although the functional aspect of bilabiation is not adequately understood, the trend towards bilabiation is here no less obvious than in other genera and families. Section *Vesicaria* has already been mentioned in this regard. Here bilabiation as a process is

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[1] Basically there are no clear-cut differences between "bracteal" and "stipular" bracts. The occurrence in *Trifolium* of bifid or otherwise incised bracts suggest the stipular origin of both kinds of bracts.

still on the march; it is less perfect in the perennial members of this section than in the annuals. Quite well developed is bilabiation of the calyx limb in Sect. *Trifolium* where this process occurs as a striking trend both in the perennial and the annual subsections. In one section, however, in *Chronosemium,* the two-lipped calyx is fully developed.

(3) Calyx closure. There is an obvious trend, in those sections in which monospermy of the pods has been achieved, to close the throat of calyx and to retain the single seed within the tube. The retention of the seed in the calyx has been interpreted elsewhere (KOLLER 1964) as a means of delaying germination until a period of heavy rainfall, sufficient not only to remove the inhibiting matter contained in the calyx and the testa of the seed, but also to ensure further development of the seedling. In arid and semi-arid regions with sporadic rains this is probably an efficient means of ensuring the survival of the flora.

The closure of the calyx is, thus, quite essential in germination biology and a feature of survival value. The successive degrees in the evolution of this characteristic can be clearly followed within the large section of *Trifolium.* Here, in some perennials almost open throats are still met with, while among the annuals, there are all kinds of devices for closing the throat of the calyx. This ranges from hairy or callous rings at the inside of the throat to two-lipped callous outgrowths which shut the calyx very tightly. The type and degree of the closure is a diagnostic characteristic in the section.

The Corolla

Despite the striking diversity of dimension, colour, consistency, persistence, degree of connation and adnation to other organs, no evolutionary trend is traceable in this chaotic variation. Marcescent corollas predominate as a rule in the Section *Lotoidea.* Persisting scarious corollas are characteristic of Sect. *Mistyllus,* early caducous ones prevail in Sect. *Trifolium.* Only in the single Section *Chronosemium* does the persistent corolla play a prominent part in dispersal biology by being converted into a spoon- or boot-shaped wing. Also in the Subsection *Physosemium* of Sect. *Involucrarium* one should accredit the inflated "fruiting corolla" with being a device enhancing the efficacy in anemochorous dispersal.

Carpological Diversity

There is a well-traceable trend in the evolution of the pod from a typical many-seeded and suturally dehiscent legume to an utricle-like, one-seeded body with a non-dehiscent, irregularly breaking pericarp which is often membranous in the lower part and somewhat leathery and cup-shaped in the upper part. The processes connected with this trend are:

(a) reduction of the seed number to one.

(b) corresponding shortening of the pod.

(c) inclusion of the pod within the calyx tube.

(d) membranization of the pericarp.

(e) loss of separation tissue along the sutural zones.

(f) shutting the calyx throat and so converting the fruiting calyx into a diaspore.

Evolutionary Trends in Dispersal Biology

In the foregoing paragraphs we brought into light part of the vast diversity of some organs and habits. We are quite ignorant of the functional aspect of these organs and organizations. We cannot even assess the survival value of certain forms and devices as elements of natural selection. We should not even search for "advantages" in pollination achieved by the diverse patterns of the flowers. In this chaotic mass of traits and forms, one can at most look for some orderly lines along which nature works. So we attempted to direct our attention to evolutionary trends for which no direct evidence could be found, but common sense and homologies from other similar cases.

In the present section on dispersal biology, the assumptions of existing trends are no less venturous than those in the previous paragraphs and the sequence of the phenomena presented here do not necessarily reflect the same line of succession in nature. Here are the various modes of dispersal and their presumable trend deduced from current opinions as to primary and derived structures.

(1) Gymno-monospory (dispersal by solitary, naked seeds) is most common in the section of *Lotoidea* where the protruding polyspermous pod is dehiscing suturally shedding the seeds singly at maturity.

(2) Aestatiphory (ZOHARY 1937). This is the case in which the seeds are released only on the withering of the fruit-bearing axis. This behaviour is again quite common in the vast Subsect. *Amoria* and in some cases of Sect. *Trifolium* where the diaspores are not or only tardily separated from the rhachis of the head.

(3) Anthoboly. Here the mature head disarticulates into one-seeded diaspores which are made up of entire flowers, consisting of a two-lipped calyx, in which the one-seeded pod is hidden and the entire corolla, the standard of which is converted into an anemochorous dispersal-accessory (Sect. *Chronosemium*).

(4) Calycoboly. This is the most common phenomenon in the dispersal biology of the genus. Here the monospermous pods are hidden in the closed calyx, which is detached at maturity from the rhachis and spreads as a telechorous or topochorous diaspore. Examples are Sect. *Mistyllus,* Sect. *Trifolium,* Sect. *Vesicaria* and some cases of Sect. *Lotoidea* (e.g. Subsect. *Neolagopus*).

(5) Synaptospermy. In this case the dispersal unit is an entire head made up of many monospermous calyces attached to the common rhachis. This type is a compound diaspore, which is spread by wind (e.g. some species of Sect. *Trichocephalum* and a single species of Sect. *Vesicaria*) or by animals (*T. chlorotrichum, T. scutatum, T. plebeium,* etc.).

There are some cases which may perhaps be considered as pseudosynaptospermy because their closed monospermous calyces are attached to one another and to the rhachis of the head which does not separate from the stem until the latter is broken or decays.

(6) Amphicarpy. Here the plant produces two kinds of heads — aerial and basal (subterranean) — the first are large, many-flowered, borne on long peduncles, the second are small, one- to few-flowered, borne on the prostrate stolons.

(7) Geocarpy. This is the case with only two species of subterranean clovers in which the upper (inner) sterile flowers are converted into a drilling apparatus enabling the fertile flowers to penetrate into the ground and to produce the few single-seeded pods there.

The above findings and interpretations are only outlines of a study which would be worthwhile giving full attention to because it reveals a vast diversity of features and characters in a single *quasi*-uniform genus. The attempt to arrange this mass of facts and findings along evolutionary lines is based only on the subjective deductions and the experience of the writer, or on conventional procedures of other authors in similar cases.

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The Re-establishment of the Species Asplenium gautieri Hook. and Asplenium efulense Bak.

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ABSTRACT

PICHI SERMOLLI, R. E. G. 1972. The re-establishment of the species Asplenium gautieri Hook. and Asplenium efulense Bak. — Bot. Notiser 125: 512—517.

Asplenium gautieri HOOK. and *A. efulense* BAK. which are regarded as being distinct species, are compared with *A. variabile* HOOK. Types and bibliographic citations are given for these species and for the closely related *A. repandum* and *A. pócsii.*

In my Fragmenta Pteridologiae III I recently described a new species of *Asplenium* from Tanzania (*A. pócsii*) belonging to the group which in Africa is represented by *A. variabile* and related species. In the course of taxonomic research on the new species, I examined the types of all African members of the group. This study led me to ascertain that some species recently treated by some authors as synonyms of *A. variabile* are worthy of specific recognition, and this stimulated me to undertake research on them. My study has not yet been completed but I wish to give the results as far as *A. efulense* BAK. and *A. gautieri* HOOK. are concerned.

The group to which *A. variabile* and related species belong is widely represented in Africa and it consists of several species. Some of them are unanimously regarded as good species; on the other hand others are accepted as independent species by some pteridologists and treated as synonyms by others. Among the latter we find *A. variabile, A. gautieri, A. repandum, A. efulense* and *A. pócsii* which form a group of closely related species, whose bibliographic citations and types are given below in chronological order according to the date of publication.

A. gautieri HOOK., Sp. Fil. 3: 88, t. 184 (1860). — Holotypus: "Nissobé Afr. orient. GAUTIER" Herb. HOOK. (K!). — Nissobé is the same as the island of Nossi-bé near the north-western coast of Madagascar.

A. variabile HOOK., Sp. Fil. 3: 93, t. 185 (1860). — Holotypus: "On trees in gloomy forests. Fernando Po. N.E. 6. 57. BARTER", "& return to F. Po. 1858. Nº 2047. Baikie's 2d. Niger Exped.n". Herb. HOOK. (K!).

A. repandum METT. ex KUHN, Fil. Afr. 114 (1868). — Syntypi: The following specimens are quoted in the protologue: "Ins. Principis (BARTER 1910. MANN). — Ad flumen Niger (BARTER. Ex hb. Kew 505)". — Perhaps the three specimens are kept in the Berlin Herbarium, but I have not seen them. Specimens of BARTER 1910, MANN s. no. and BARTER 505 are preserved in the Kew Herbarium, but none of them bears METTENIUS's or KUHN's identification. I have examined only BARTER 1910 and an isosyntype of BARTER 505 kept in the Paris Herbarium.

A. efulense BAK. in Kew Bull. 1901: 137 (1901). — Holotypus: "Efulen, Kamerun. Sept. or Oct., 1895. G. L. BATES, Esq. 454. Received March 1896" (K!).

A. pócsii PIC. SER. in Webbia 27, Fig. 17 (1972). — Holotypus: "Tanzania. T 6, Morogoro Region: Uluguru Mts. Eastern slope

Fig. 1. *Asplenium variabile* Hook. (holotype, K).

of Bondwa, alt. 1650—2000 m. High altitude wet evergreen forest. Terrestrial or epiphytic; leaves always simple, fleshy. Common. 29. IX. 1970. R. B. FADEN, T. PÓCS, B. J. HARRIS, & K. CSONTOS 70/631" (Herb. PIC. SER. 26151). Paratypi: T. PÓCS 6082/C (EA!) and PÓCS 6297/E (EA!) from Uluguru Mts.

In this paper I take into account only *A. variabile, A. gautieri* and *A. efulense,* since I have not yet examined all the type specimens of *A. repandum,* and I think it superfluous to deal with *A. pócsii,* as I recently pointed out its affinities and differences when I described it.

A. variabile is regarded unanimously as a good species and it can be taken as the basis for this study. The other species do not appear to be related to it, or between each other to the same extent.

A. efulense is most closely related to *A. variabile.* CHRISTENSEN in the Index Filicum considers *A. efulense* to be an independent species; while TARDIEU-BLOT (1953 p. 174) and ALSTON (1959 p. 56) regard it as a synonym of *A. variabile* s. str. The study of the type and several specimens in the herbaria of Paris, Kew and British Museum has convinced me that *A. efulense* represents a species of its own. The main characteristics distinguishing it and *A. variabile* can be established as follows.

A. variabile (Fig. 1) — Rhizome long, creeping, horizontal, tortuous, slender (1—1.5 mm in diam.), yellowish-green, sparsely paleaceous, with paleae lanceolate, 2.0—3.0 mm long and 0.6—1.0 mm wide. Fronds, both fertile and sterile, borne throughout the full length of the rhizome, widely spaced (5—12 mm apart); fertile fronds undivided, irregularly crenate-serrate at the margin, up to 15 cm long and 25 mm wide, yellowish-green, with midrib straw-coloured below; sterile fronds clearly different from the fertile ones, variously divided at the margin, simply serrate to pinnatifid, up to 10 cm long and 15 mm wide; young fronds similar to the sterile ones, but smaller, long persistent, usually present in the adult plant.

A. efulense (Fig. 2) — Rhizome short, creeping, straight or slightly curved, horizontal to suberect, fairly strong (2.5—5 mm in diam.), brown, densely paleaceous with paleae triangular, 3.0—4.0 mm long and 0.7—1.1 mm wide. Fronds, both fertile and sterile, borne on the upper part of the rhizome, near each other, the young ones present on the youngest part of the rhizome only; fertile fronds undivided, irregularly and coarsely crenate-serrate to sinuate, up to 55 cm long and 60 mm wide, deep green with midrib concolorous or brown below; sterile fronds, if present, like the fertile ones in shape and division of the margin, but somewhat smaller; young fronds clearly different from both the fertile and sterile ones, pinnatilobate to pinnatisect, many times smaller than the fertile ones, soon disappearing, usually absent in the adult plants.

A. gautieri is accepted as a distinct species by CHRISTENSEN both in his Index Filicum and in The Pteridophyta of Madagascar (1932 p. 91); on the contrary it is regarded as a synonym of *A. variabile* var. *paucijugum* (BALLARD) ALSTON, by TARDIEU-BLOT (1958 p. 206). On the basis of the examination of the type and other specimens kept in the Paris and Kew Herbaria, I have reached the conclusion that *A. gautieri* is a separate species. In my opinion, although it bears some fronds with 1—2 lateral pinnae, the species is more closely allied to *A. variabile* than to *A. paucijugum* and I list below the main differences between it and the former species.

A. variabile (Fig. 1) — Rhizome long, creeping, horizontal, tortuous, slender, yellowish-green, sparsely paleaceous with paleae lanceolatae, 2.0—3.0 mm long and 0.6—1.0 mm wide, consisting of small cells. Fronds not gemmiferous, borne throughout the full length of the rhizome, widely spaced; fertile and sterile fronds of different shape and size, papery,

75½. **Asplenium (Euasplenium) efulense,** *Baker* [Filices Polypo diaceæ]; ad *A. sinuatum,* P. Beauv., accedit; differt frondibu brevioribus oblongo-lanceolatis, rhizomate gracili repente, soris costa pene ad marginem productis.

Rhizoma gracilis repens, paleis lanceolatis nigrescentibu clathratis dense vestitum. *Stipites* breves, segregati, erecti, nudi. *Lamina* simplex, oblongo-lanceolata 6–8 poll. longa, 1½–2 poll lata, subintegra, acuminata, basi cuneata, modice firma, utrinque viridia, glabra; venæ remotæ, perspicuæ, ascendentes, sæpissime furcatæ. *Sori* graciles e costa pene ad marginem frondis pro ducti. *Indusium* firmum, angustum, persistens.

CAMEROONS. Efulen, *Bates*, 454. Kew Bulletin, 1901, p. 137. Prof.

Asplenium efulense
Baker in Kew Bullet. 1899
p.

Asplenium
n. sp
ver sinuatum,
PB.

454 G. L. Bates, Esq.
Received March 1896

Efulen, Kamerun, Sept. or Oct. 1895

Fig. 2. *Asplenium efulense* Bak. (holotype, K).

yellowish-green; the fertile ones very narrowly oblong-elliptic, long attenuate at the tip, irregularly crenate-serrate at the margin, gradually tapering downwards to a rather short stipe winged to near its base; the sterile and the young fronds clearly different from the fertile ones, variously divided at the margin, simply serrate to pinnatifid. Sori extending from the costa to within a short distance of the margin, rather close to each other.

A. gautieri (Fig. 3) — Rhizome short creeping, suberect to erect, arcuate to straight, relatively strong, brown, with dense ovate-triangular paleae, 3.2—5.0 mm long and 1.0—1.5 mm wide, consisting of large cells. Fronds gemmiferous near the apex, borne on the upper part of the rhizome, near to each other, different in shape and size, membranaceous, deep green; some whether fertile or sterile or young, usually smaller and different in length with blade undivided, narrowly oblong-elliptic, acuminate at the tip, truncate-crenulate at the margin, shortly attenuate at the base; others, larger and longer with blade consisting of one large central pinna like that of the undivided frond, with one or two smaller, more or less distinct pinnae at the base; stipe long, slender, narrowly winged in the uppermost part. Sori fairly distant from both the midrib and the costa, rather remote.

The geographical distribution of the three species is difficult to establish. However, according to the specimens I have examined, *A. variabile* occurs in Fernando Po and the Cameroons, *A. efulense* is widely distributed in West Tropical Africa, but extends eastwards to Congo and Uganda, *A. gautieri* is endemic to the island of Nossi-bé (Madagascar).

As already mentioned, I do not intend to deal with *A. repandum*. However, the isosyntypes I have seen show a species that is clearly distinct from the abovementioned ones in the length and direction of the rhizome, the size and structure of the paleae, in the insertion on the rhizome, shape and length of the stipe, in the shape, size, texture and colour of the blade, and in the length and position of the sori. *A. repandum* appears to be more distinct from the other species than the latter are from one another.

The group contains another species known as *A. dusenii* LUERSS. based on specimens collected by DUSÉN in the Cameroons and kept in the Paris Herbarium (!). As far as I know, the species has not yet been described, and it is not validly published, although its name has been adopted by BONAPARTE (1924 p. 276). It is allied to *A. efulense,* but perhaps it is distinct from the latter.

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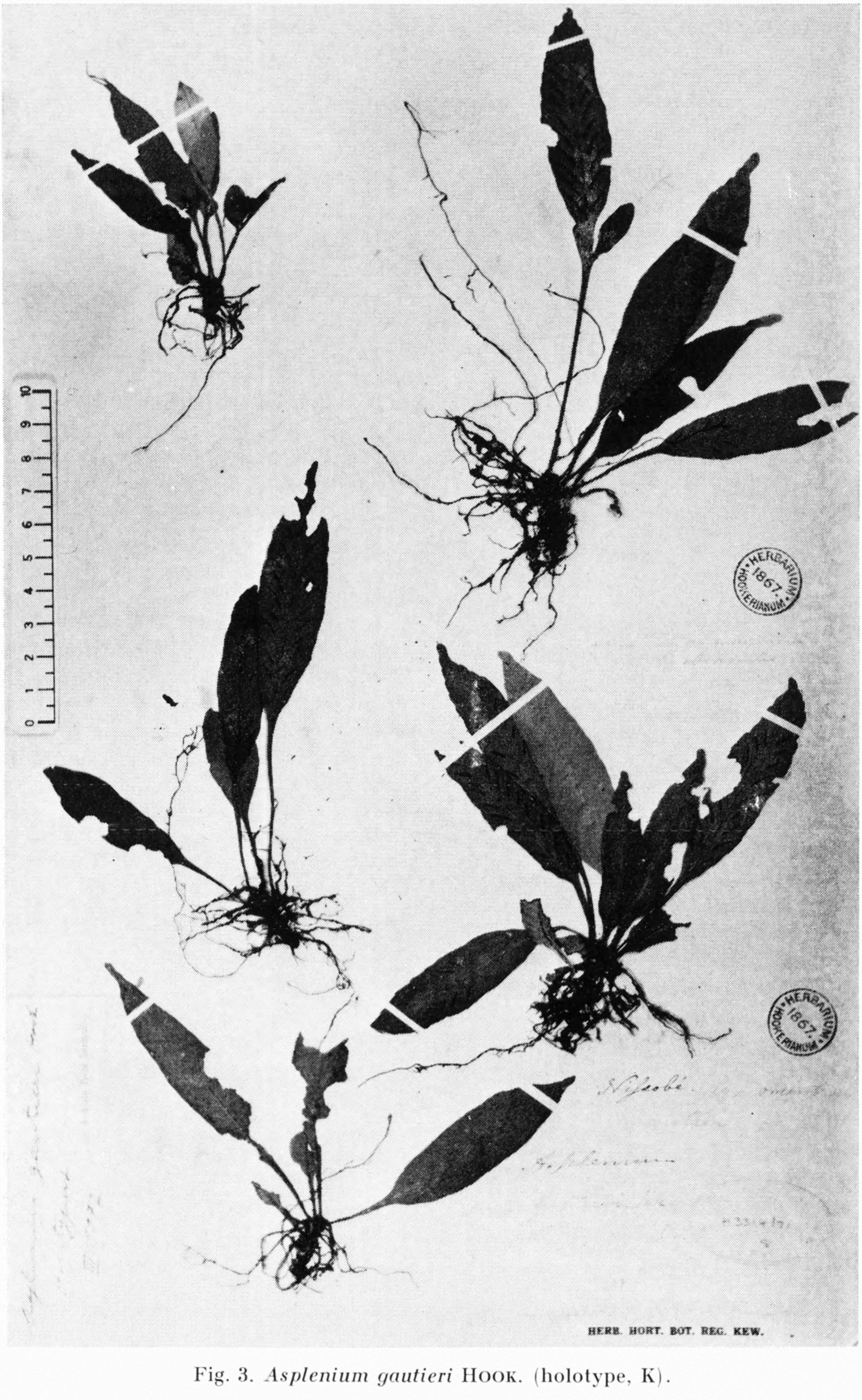

Fig. 3. *Asplenium gautieri* Hook. (holotype, K).

A Contribution to the Moss Flora of Egypt

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ABSTRACT

IMAM, M. & GHABBOUR, S. I. 1972. A contribution to the moss flora of Egypt. — Bot. Notiser 125: 518—522.

A list of 60 species is given with localities. The predominant element in the Egyptian moss flora is Mediterranean with an extension to the Cairo region and Gebl Elba.

INTRODUCTION

For a long time Egypt was considered to be poor in mosses as her climate is dry and there is a paucity of natural wet habitats. LAURENT-TÄCKHOLM (1932) listed the works concerned with Egyptian mosses and it is apparent that at least 18 species should exist in the Nile region and 27 in Sinai. In 1959 S. RUNGBY (Copenhagen) and later in 1961 S. ARNELL and G. EEN (Stockholm) collected enough material to show that it would be worth while making further investigations and revising the older records. Further collecting was done by V. TÄCKHOLM and M. KASSAS in the Gebl Elba region, by L. BOULOS in Nubia before its inundation (BOULOS 1966), and by M. IMAM and S. I. GHABBOUR in several regions. The following is an alphabetical list of the records kept in CAI as a result of these collections. The mosses were kindly identified by S. RUNGBY, G. EEN, J. FROEHLICH (Wien) and M. BIZOT (Dijon). Species of the genus *Philonotis* are not treated pending a more detailed study.

It is noted that the geographic distribution of mosses in Egypt does not exactly coincide with that of phanerogams. Therefore, the delineation of the phytogeographical regions proposed in TÄCKHOLM, DRAR and FADEEL (1956) had to be modified. Apart from the Cairo region, the largest number of species occurs in desert regions receiving some winter rain, i.e. the Western Mediterranean coast, the Isthmic Desert and Gebl Elba, where the Mediterranean element is predominant. Comparatively fewer species occur in the Nile Delta and the Nile Valley.

It is to be hoped that this preliminary list will be added to through extended studies on this little known group of Egyptian plants.

ABBREVIATIONS OF PHYTOGEOGRAPHICAL REGIONS AND LOCALITIES

Mma: Western Mediterranean coast, including Alexandria but not Rosetta.
- B: Burg El-Arab, Bramley's Grotto, 60 km W. of Alexandria.
- AS: Abu Sir, 25 km W. of Alexandria, on soil in the Roman fort, 17.12. 61.
- RAS: 23 km W. of Alexandria on the road to Abu Sir, from a shallow depression in the ground, 17.12. 61.
- AX1: Alexandria, on limestone in the catacombs, 17.12. 61.
- AX2: Alexandria, on the steps of the Swedish Consul's house, 16.12. 61.

AX3: Greenhouse, Faculty of Science, Moharram Bey, Alexandria, 11.1. 71, leg. M. IMAM.
AX4: S.W. of Alexandria where the desert road from Cairo meets Lake Mariut, on rocks of soft limestone, 16.12. 61.
T1: Tahrir Province, 41 km S. of Alexandria along desert road to Cairo, 16.12. 61.
T2: Tahrir Province, 43 km S. of Alexandria, on soil at the edge of a very shallow puddle, 16.12. 61.

Nd: The Nile Delta, including Rosetta, but not the Cairo region.

Cr: The Cairo region.
BAR: Delta Barrage, on a stone-set river bank, 20.12. 61.
EB: El-Baraguil, on soil in shade of a deep irrigation ditch, 19.12. 61.
MH: Cairo Mental Hospital, 22.12. 61.
MS: Maadi suburb, in shade at the base of a stone wall, 21.12. 61.
MEM: Memphis, 10 km S.W. of Cairo, at the base of a clay wall, 23.12. 61.

Nf: The Nile Fayum.

Nv: The Nile Valley.
SF: El-Saff, Giza Province, 45 km S. of Cairo, in ALFRED BIRCHER's garden.
AG: Abu Ghadir, El-Wasti, Assiut Province, 16.10. 71, leg. M. IMAM.

Nn: The Nile Nubia (now inundated by the waters of Lake Nasser).

Di: The Isthmic Desert, i.e. El-Tih, the Suez Canal Zone and Wadi Tumilat (Ismailia Canal).
ISM: Ismailia, on concrete and mortar at the base of a foundation in the city, 26.12. 61.
SUZ: Eastern Desert, 116 km E. of Cairo (=16 km W. of Suez) along the desert road, on moist soil, 27.12. 61.

S: Sinai proper, i.e. south of El-Tih desert.

Da. sept.: The part of the Arabian Desert from Suez to the Qena-Qosseir road.

GE: Gebl Elba and surrounding mountains in the S.E. corner of Egypt.

O: The oases of the Libyan Desert.

ALPHABETIC LIST

Collections by the authors unless otherwise stated; c. fr.=cum fructificatione.

Aloina ambigua LIMPR. — **Mma,** B, on the ground 17.12 61 (S. ARNELL & G. EEN) — ditto, c. fr. 14.4. 72 — AS (S. ARNELL & G. EEN) — T2 (G. EEN) — ditto (S. ARNELL).

Aloina rigida KINDB. var. *pilifera* LIMPR. — **Mma,** T2 (G. EEN).

Amblystegium varium LINDB. — **Mma,** AX3.

Barbula aaronis HILP. ? — **Di,** ISM (G. EEN).

Barbula acuta BRID. — **Mma,** B, 11.1. 71.

Barbula convoluta HEDW. — **Di,** ISM (G. EEN) — Edge of a ditch under trees, cultivated land by the road from Cairo to Ismailia, near El-Monayir 40 km N.E. of Cairo 6.3. 59 (M. KASSAS & L. BOULOS); — **Nn,** Adendan, on moist ground near the Nile 19.1. 64 (L. BOULOS).

Barbula cylindrica (TAYL.) SCHIMP. — **Mma,** B, on the ground 17.12. 61 (S. ARNELL).

Barbula hornschuchiana SCHULTZ — **Mma,** B, on the ground 17.12. 61 (S. ARNELL).

Barbula tectorum C. MUELLER — **Mma,** AX4 (G. EEN).

Barbula unguiculata HEDW. — **Nd,** El-Qarada, Kafr El-Sheikh Province, on old wall above water on a canal bank 25.9. 70; — **Cr,** MS (G. EEN).

Barbula vinealis BRID. — **Mma,** B, on the ground 17.12. 61 (S. ARNELL & G. EEN) — AS (S. ARNELL & G. EEN) — AX4 (G. EEN) — T1 (S. ARNELL).

Brachythecium rivulare B. S. G. — **S,** Sinai Peninsula, no details (M. HASIB), probably from the southern part of Sinai.

Bryum alpinum WITH. var. *gemmiparum* (DE NOT.) LINDB. — **Mma,** AX1 (S. ARNELL) — T2 (G. EEN); — **Cr,** Gezira aquarium 23.10. 70 — ? MH (G. EEN).

Bryum alpinum WITH. var. *viride* HUSNOT — **Nn,** Adendan, on moist ground near the Nile 19.1. 64 (L. BOULOS).

Bryum argenteum HEDW. — **Cr,** MH (G. EEN).

Bryum argenteum Hedw. var. *lanatum* (Palis.) Br. eur. vergens — **Di,** SUZ (G. Een).

Bryum atrovirens Brid. — **Cr,** Zohria Botanic Garden, inside pot 2.6. 71; — **Nv,** SF, 4.1. 62 (V. Täckholm & I. El-Sayed).

Bryum badium Bruch — ? **Mma,** RAS (G. Een) — AX2 (G. Een); — **Cr,** MS (G. Een); — ? **Di,** ISM (G. Een).

Bryum bicolor Dicks. — ? **Mma,** B, 17.12. 61 (G. Een) — AX4 (S. Arnell) — T1 (S. Arnell); — **Cr,** Ice Factory, Sharia Galaa, Cairo 31.10. 70 (S. Sisi) — Faculty of Science garden, Ain Shams University 30.5. 72 (W. Saadawy); — ? **Di,** SUZ (G. Een); — ? **Nv,** AG.

Bryum caespiticium L. ex Hedw. — **Mma,** ? B, on the ground 17.12. 61 (G. Een) — AS (S. Arnell) — ? RAS (G. Een) — ? T1 (S. Arnell); — **Cr,** MEM (G. Een); — **S,** near the Monastery of St. Catherine 10.5. 56 (M. N. El-Hadidi).

Bryum caespiticium L. ex Hedw. ssp. *comense* (Schpr.) Amann — ? **Mma,** B, 17.12. 61 (S. Arnell) — B, on the ground 17.12. 61 (G. Een).

Bryum caespiticium L. ex Hedw. var. *imbricatum* B. S. G. — ? **Mma,** AX1 (G. Een); — **Cr,** BAR (G. Een) — ? MS (G. Een).

Bryum cellulare Hook. — **Cr,** Mohamed Ali Palace 2.12. 61 (S. Arnell); — **Di,** ISM (G. Een); — **GE,** Gebl Asoteriba, in pothole in the upstream part of Wadi Mawaw 25.1. 62 (M. Kassas).

Bryum funckii Schwaegr. — **Di,** on the road from Cairo to Ismailia, edge of a ditch under trees, cultivated land near El-Monayir, 40 km N.E. of Cairo 6.3. 59 (M. Kassas & L. Boulos).

Bryum gemmiparum de Not. var. *sinaicum* Geh. — **Cr,** MH (G. Een).

Bryum murorum (Schpr.) Berk. — ? **Mma,** B, on the ground 17.12. 61 (S. Arnell) — AX2 (G. Een) — AX4 (G. Een) — T1 (S. Arnell) — T2 (G. Een); — **Cr,** MEM (G. Een).

Bryum syriacum Lor. var. *humile* Schiffn. — **Mma,** T1 (S. Arnell).

Bryum torquescens Br. eur. — **Di,** Inchas, 45 km N.E. of Cairo on the road to Ismailia, on a water tank 10 m above ground 26.12. 61 (G. Een).

Crossidium chloronotus (Brid.) Limpr. — **Mma,** B, on the ground 17.12. 61 (S. Arnell) — T2 (G. Een).

Dichodontium pellucidum (Hedw.) Schimp. var. *fagimontanum* Schimp. — **Cr,** EB (G. Een).

Didymodon tophaceus (Brid.) Lisa — **Mma,** B, 14.4. 72 c. fr. — ditto 20.8. 71 — AX1 (G. Een) — AX2 (G. Een); — **Nd,** El-Qarada, Kafr El-Sheikh Province, on old wall above water on a canal bank 25.9. 70; — **Cr,** BAR (G. Een) — EB (G. Een) — MEM (G. Een); — **Di,** ISM (G. Een) — SUZ (G. Een).

Didymodon tophaceus (Brid.) Lisa var. *humilis* (Schimp.) Warnst. — **GE,** Wadi Aidaib 2.1. 62 (V. Täckholm).

Eucladium verticillatum (Brid.) B. S. G. — **Cr,** Zohria Botanic Garden 2.6. 71; — **Da. sept.,** Ain Gattar, Red Sea coast, near Ghardaqa (Hurghada) 5.9. 60 (M. Kassas).

Fissidens arnoldii Ruthe — **GE,** Gebl Elba 21.1. 62 (M. Kassas).

Fissidens cyprius Jur. — **Cr,** BAR (G. Een) — greenhouse in the garden of Rod El-Farag Secondary School 18.4. 62.

Fissidens impar Mitt. — **Nd,** 5 km S. of Damanhur, Beheira Province 18.9. 70; — **Cr,** Zohria Botanic Garden 2.6. 71.

Funaria calcarea Wahlenb. var. *mediterranea* (Lindb.) C. Jens. & Medel. — **GE,** Wadi Aidaib 21.1. 62 (V. Täckholm) — Gebl Elba 21.1. 62 (M. Kassas).

Funaria fascicularis (Dicks.) Lindb. — **Cr,** BAR (G. Een) — Saqqara, salt marshes 23.12. 61 (G. Een).

Funaria handelii SCHIFFN. — ? **Cr,** MH (G. EEN); — ? **Di,** ISM (G. EEN).

Funaria hygrometrica HEDW. — **Cr,** BAR (G. EEN) — MH (G. EEN) — EG (G. EEN) — Cairo University garden, c. fr. 9.4. 71 and 10.3. 72 (S. SISI) — Rod El-Farag, on a large earthenware water pot (locally called "zir"), c. fr. 20.4. 71 and 21.3. 72; — **Nd,** Benha, 45 km N. of Cairo, on a canal bank, c. fr. 18.2. 71; — **Di,** ISM (G. EEN) — Ismailia, on a stone-set canal bank in the city 26.12. 61 (G. EEN) — SUZ (G. EEN); — **Nn,** Qostul, c. fr. 22.12. 63, 29.12. 63 and 6.2. 64 (L. BOULOS) — Ballana district, Hod Marei, c. fr. 12.12. 63 and 23.4. 64 (L. BOULOS) — Adendan, c. fr. 19.1. 64 (L. BOULOS).

Funaria hygrometrica HEDW. var. *intermedia* WARNST. — **Di,** Ismailia, canal slope 6.3. 59 (L. BOULOS).

Funaria hygrometrica HEDW. var. *patula* Br. eur. — **Di,** Inchas, 45 km N.E. of Cairo, on the road to Ismailia, on a water tank 10 m above ground 26.12. 61 (G. EEN) — ISM (G. EEN) — SUZ (G. EEN).

Funaria mediterranea LINDB. — **GE,** Gebl El-Kassiera 8.2. 62 (M. KASSAS) — Gebl Asoteriba, in Wadi Aak 27.1. 62 (M. KASSAS).

Funaria nilotica BROTH. — **Cr,** MEM (G. EEN); — **Di,** ISM (G. EEN).

Funaria obtusa (HEDW.) LINDB. — **Cr,** EB (G. EEN).

Funaria pallescens BROTH. — **GE,** Gebl Elba 21.2. 62 (M. KASSAS) — Gebl Asoteriba, Wadi Aak 27.1. 62 (M. KASSAS) — Gebl Asoteriba, pothole in the upstream part of Wadi Nawaw 28.1. 62 (M. KASSAS).

Gymnostomiella laevis FROEHLICH — **Cr,** greenhouse in the garden of Rod El-Farag Secondary School 18.4. 62.

Gymnostomum calcareum Br. germ. — **Di,** ISM (G. EEN); — **GE,** Gebl Shandodawi 10.2. 62 (M. KASSAS & V. TÄCKHOLM).

Gymnostomum calcareum NEES & HORNSCH. var. *viridulum* (BRID.) Br. eur. — **Mma,** B, 17.12. 61 (G. EEN); — **Cr,** MS (G. EEN); — **Di,** ISM (G. EEN).

Gyroweisia reflexa (BRID.) SCHIMP. — **Cr,** MEM (G. EEN).

Hydrogonium ehrenbergii (LOR.) JAEG. — **Nd,** El-Hammad, 10 km S. of Rosetta 19.8. 71 — 4 km S. of Edfina, Beheira Province, on a sunken old wall in canal, almost submerged 18.9. 70 — Kafr Beni Helal, 5 km E. of Damanhur, Beheira Province, in the inside wall of a well 4.9. 70 — Bassioum, Gharbia Province, on stone-set canal bank of Bahr Nashart irrigation canal, hidden among grasses 4.9. 70 — Menshat Aghur, Menufia Province, midway between Tanta and Shebin El-Kom 17.9. 70 — **Cr,** Saft El-Laban 28.10. 70 (S. SISI) — Faculty of Agriculture, Cairo University, on a water-wheel (saqia) 26.10. 70 (S. SISI) — Faculty of Science, Ain Shams University 30.5. 72 (W. SAADAWY) — Cairo, early March 72 (S. BATAL) — Zohria Botanic Garden, outside pot 2.6. 71; — **Nf,** El-Siliyyin 25.3. 71 and 17.12. 71 — Qasr Rashwan, Sinnuris 16.10. 70 — Sanhur Qibli 21.8. 70 and 17.12. 71.

Hyophila laxitexta FROEHLICH — **GE,** Gebl Asoteriba, pothole in the upstream part of Wadi Mawaw 28.1. 62 (M. KASSAS).

Leptobryum piriforme WILS. — **Cr,** Zohria Botanic Garden 2.6. 71.

Micropoma niloticum (DEL.) LINDN. — **Cr,** BAR (G. EEN) — Cairo, c. fr. early March 72 (S. BATAL) — 8 km N. of Helwan suburb, on stone-set canal bank 21.12. 61 (G. EEN); — **Nv,** SF 4.1. 62 (V. TÄCKHOLM & I. EL-SAYED); — **GE,** Wadi Aidaib 21.1. 62 (V. TÄCKHOLM et al.).

Philonotis. — The enumeration of Egyptian species of this genus awaits further study. It is distributed, however, in **Nd,** **Cr,** **Nf,** and **O.**

Physcomitrium acuminatum (SCHLEICH.) Br. eur. — **Cr,** MH (G. EEN); — **Di,** ISM (G. EEN).

Physcomitrium pyriforme (HEDW.) HAMP. — **Cr,** Faculty of Agriculture, Dept.

of Ornamentals, Cairo University, c. fr. 8.4. 71 and 10.3. 72 (S. SISI) — Ice Factory, Sharia Galaa 31.10. 70 (S. SISI); — **Nn,** Qostul, Hod Marei, c.fr. 6.1. 64 (L. BOULOS).

Pottia mutica VENT. — **Cr,** BAR (G. EEN) — MS (G. EEN).

Pottia pallida LINDB. var. *longicuspis* WARNST. — **Mma,** RAS (G. EEN) — AX4 (S. ARNELL).

Pottia sarkeana (HEDW.) C. MUELL. — **Mma,** B, c. fr. 14.4. 72 — ditto, on the ground 17.12. 61 (S. ARNELL & G. EEN) — RAS (G. EEN).

Pottia wilsonii (HOOK.) B. S. G. — **Mma,** B, on the ground 17.12. 61 (G. EEN) — AS (S. ARNELL).

Semibarbula orientalis (WEB.) WIJK & MARG. (=*Barbula indica* BRID.) — **Nd,** El-Senil, Kafr Shokr, Qaliubiya Province, 55 km N. of Cairo, on the inside wall of a well 28.8. 70; — **Cr,** MS (G. EEN); — **Nv,** AG.

Timmiella barbula (SCHWAEGR.) LIMPR. — **GE,** Gebl Shandodawi 10.2. 62 (M. KASSAS & V. TÄCKHOLM).

Tortella inflexa (BRUCH) BROTH. — **Mma,** B, 17.12. 61 (G. EEN) — ditto 16.3. 62 (V. TÄCKHOLM) — Burg El-Arab, on soil in a garden 17.12. 61 (S. ARNELL).

Tortella nitida (LINDB.) BROTH. — **Mma,** B, on the ground 17.12. 61 (G. EEN) — B, 18.9. 70 and 11.1. 71; — **GE,** Wadi Akaw 27.10. 57 (L. BOULOS).

Tortula muralis HEDW. — **Mma,** Abu Sir, c. fr. 19.5. 58 (V. TÄCKHOLM) — AS (S. ARNELL) — AX1 (G. EEN); — **Cr,** BAR (G. EEN).

Tortula muralis HEDW. var. *incana* Br. eur. — **Mma,** AX1 (S. ARNELL) — T1 (S. ARNELL).

Tortula muralis HEDW. var. *obcordata* SCHIMP. — **Mma,** B, on the ground (G. EEN) — AS (S. ARNELL) — AX1 (G. EEN & S. ARNELL) — AX4 (G. EEN) — T1 (S. ARNELL).

Tortula vahliana (SCHULTZ.) MONT — **Mma,** B, c. fr. 14.4. 72.

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The Family Zygophyllaceae in Egypt

I. Fagonia L. and Seetzenia R. Br.

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ABSTRACT

El Hadidi, M. N. 1972. The family Zygophyllaceae in Egypt. I. Fagonia L. and Seetzenia R. Br. — Bot. Notiser 125: 523—535.

This account is the first part of a revision of Zygophyllaceae in Egypt, based on collections from Egypt and adjacent countries. Thirty-five species belonging to 6 genera are now represented in Egypt; the highest number of Zygophyllaceae in any African country.

The genus *Fagonia* L. includes 18 species grouped in 8 complexes. *F. olivieri* DC. has not been recorded earlier from Egypt, while two varieties, *F. boulosii* var. *crameri* and *F. mollis* var. *densiglandulosa* are newly described.

Seetzenia R. Br. is treated as a monotypic genus and not as containing two species.

INTRODUCTION

During the last two years, the author has had the opportunity to study ample material of the Zygophyllaceae of the Old World in connection with the revision of this family for "Flora Iranica" and the "Adumbratio Florae Aethiopicae". Accordingly, 35 species are now represented in Egypt, the highest number of Zygophyllaceae in any African country.

Engler (1931) subdivided the family into seven sub-families, of which Nitrarioideae and Balanitoideae are treated as distinct families by certain authors.

Six genera are known from Egypt, belonging to three sub-families: Peganoideae Engl., Tetradiclidoideae Engl. and Zygophylloideae.

In Peganoideae, all leaves are alternate, while in the two other subfamilies at least the lower leaves are opposite; in Tetradiclidoideae the capsule is four-valved, while in Zygophylloideae it is five-valved.

Peganoideae and Tetradiclidoideae comprise one tribe each. Peganeae Engl. is represented in Egypt by *Peganum* L., while the monogeneric Tetradiclideae Engl. is represented by *Tetradiclis* Stev.

Zygophylloideae, by far the largest subfamily, is represented in Egypt by four genera belonging to two tribes viz. Zygophylleae and Tribuleae Engl. Zygophylleae includes *Fagonia, Seetzenia* and *Zygophyllum*. The first two genera constitute the subtribe Fagoniinae Engl., while *Zygophyllum* belongs to the other subtribe Zygophyllinae. Tribuleae is represented in Egypt by *Tribulus* which belongs to the subtribe Tribulinae Engl.

KEY TO THE GENERA

1. Leaves simple, lobed 2
   Leaves compound, if unifoliolate, then with a distinct joint between petiole and blade 3
2. Herbs not more than 20 cm high, flowers tetramerous, capsule 3 mm in diameter .... 5. *Tetradiclis*
   Shrublets over 25 cm high, flowers pentamerous, capsule over 10 mm in diameter .... 6. *Peganum*
3. Petals absent .... 2. *Seetzenia*
   Petals present 4
4. Stamens with staminal scales .... 3. *Zygophyllum*
   Stamens without staminal scales 5
5. Leaves pinnate .... 4. *Tribulus*
   Leaves trifoliolate or unifoliolate .... 1. *Fagonia*

1. FAGONIA L.

LINNAEUS 1753 p. 386.

EL HADIDI (1972, in press a and b) distinguishes seven *Fagonia* complexes. All the hitherto-known species from Egypt, with the exception of *F. mollis* DEL., *F. tristis* SICKENB. and *F. taeckholmiana* HADIDI were treated within these complexes. In this revision however, the latter species will be included in the *F. arabica* complex, while *F. mollis* and *F. tristis* will be grouped together in a new complex.

KEY TO THE SPECIES OF FAGONIA

1. All leaves unifoliolate 2
   Lower leaves trifoliolate, upper ones unifoliolate 5
2. Plant spineless .... 2. *F. taeckholmiana*
   Plant spiny 3
3. Internodes quadrangular .... 11. *F. olivieri*
   Internodes terete 4
4. Leaflets oblong-linear, subsessile, calyx deciduous .... 8. *F. paulayana*
   Leaflets ovate-lanceolate, petiolate, calyx persistent .... 7. *F. indica*
5. Leaves long-petioled, petiole at least twice as long as the middle leaflet 6
   Leaves short-petioled, petiole not longer than the middle leaflet 7
6. Plant annual, glabrous .... 12. *F. kassasii*
   Plant perennial, covered with stalked glands with adherent sand .... 18 d. *F. glutinosa* var. *longipetiolata*
7. Spines as long as or longer than the leaves 8
   Spines shorter than the leaves 14
8. Leaves cylindrical 9
   Leaves flat 10
9. Plant glabrous .... 3. *F. thebaica*
   Plant hairy .... 6 a. *F. tristis* var. *tristis*
10. Plant hairy, compound glands present 11
    Plant glabrous or glandular, glands simple 12
11. Branches erect, flowers up to 12 mm in diameter .... 6 b. *F. tristis* var. *boveana*
    Branches prostrate, flowers up to 16 mm in diameter .... 5. *F. mollis*
12. Fruit 4×4 mm with persistent calyx 13
    Fruit over 4×4 mm with deciduous calyx .... 1. *F. arabica*
13. Spines and internodes short, plant glandular .... 9. *F. bruguieri*
    Spines and internodes long, plant glabrous .... 10. *F. schimperi*
14. Flowers about 15 mm in diameter 15
    Flowers less than 10 mm in diameter 19
15. Glands with adherent sand present .... 18 b. *F. glutinosa* var. *grandiflora*
    Glands with adherent sand absent 16
16. Pale green sand plant, leaves coriaceous .... 4. *F. boulosii*
    Dark green rock plant, leaves not coriaceous 17

17. Capsule less than 5 mm in diameter .... 14. *F. sinaica*
Capsule over 5 mm in diameter 18
18. Peduncle shorter than capsule, Mediterranean species .... 13. *F. cretica*
Peduncle longer than capsule, desert plant .... 15. *F. tenuifolia*
19. Glands with adherent sand present .... 18. *F. glutinosa*
Glands with adherent sand absent 20
20. Plant densely hairy .... 16. *F. latifolia*
Plant sparingly hairy 21
21. Leaflets pale green, less than 5 mm long .... 18 c. *F. glutinosa* var. *nuda*
Leaflets dark green, over 10 mm long .... 17. *F. isotricha*

THE FAGONIA ARABICA COMPLEX

In Egypt two species belong to this complex: *F. arabica* L. and *F. taeckholmiana* HADIDI. The latter is characterized by the absence of spiny stipules and the distinctly unifoliolate leaves. The reduction in the structure of stipules and leaves may be regarded as being an advanced character within this complex. The internodes of *F. taeckholmiana* are terete and striate, while the nodes are swollen. In this character and in the presence of unifoliolate leaves, it resembles the species of the *F. indica* complex.

1. **Fagonia arabica** L.

LINNAEUS 1753 p. 386.

Several varieties are described from the North African Sahara. Four of these are known from Egypt.

KEY TO THE VARIETIES

1. Glands sessile, with adherent sand .... 1 b. var. *viscidissima*
Glands stalked, without adherent sand 2
2. All leaves unifoliolate .... 1 c. var. *tilhoana*
Upper leaves unifoliolate, lower trifoliolate 3
3. Flowers 15 mm in diameter, internodes and spines 3 cm long or more .... 1 a. var. *arabica*
Flowers up to 12 mm in diameter, internodes and spines up to 2 cm long .... 1 d. var. *imamii*

1 a. **Fagonia arabica** L. var. **arabica**

Orig. coll.: Arabia, SHAW (BM).

Biennial or perennial shrublet up to 50 cm high; internodes terete and striate. Capsule 5—7 mm in diameter, pubescent; peduncle shorter than capsule, reflexed; calyx deciduous.

DISTRIBUTION: Pakistan, Arabia, Eritrea, Northern Sahara except Algeria and westwards.

1 b. **Fagonia arabica** L. var. **viscidissima** MAIRE

MAIRE 1929 p. 176. — Orig. coll.: Contr. no. 663, MAIRE (P).

Smaller, more coriaceous shrublet; internodes shorter; spines 2—2.5 cm long. The whole plant is covered with glands with adhering sand.

DISTRIBUTION: North and Central Sahara, eastwards in the Libyan Desert in Egypt, particularly in the oases.

1 c. **Fagonia arabica** L. var. **tilhoana** (MAIRE) MAIRE

MAIRE 1937 p. 349. — *F. tilhoana* MAIRE 1932 p. 907. — Orig. coll.: Contr. no. 2240, MAIRE (P).

Robust, less glandular shrublet; internodes and spines longer than in the type; leaves typically unifoliolate.

DISTRIBUTION: Central Sahara eastwards in the Libyan Desert in Egypt.

1 d. **Fagonia arabica** L. var. **imamii** Hadidi

El Hadidi 1966 p. 21. — Orig. coll.: Libyan Desert in Egypt, near the northern entrance of Faiyum, Imam (CAI, holotype).

Annual shrublet up to 25 cm high; internodes and spines short, up to 2 cm long, slender. Flowers and capsules smaller than in the type. Similar to *F. bruguieri,* but fruit calyx deciduous and flowers larger.

DISTRIBUTION: Endemic in the Libyan Desert in Egypt.

2. **Fagonia taeckholmiana** Hadidi

El Hadidi 1966 p. 29. — Orig. coll.: Heliopolis Desert near Cairo 1952, El Hadidi (CAI, holotype).

Perennial pale green, almost glabrous shrublet with terete and striate internodes. Leaves unifoliolate; leaflet short-petioled; spines reduced or absent. Flowers up to 12 mm in diameter. Capsule 5 mm in diameter; peduncle short; calyx deciduous.

DISTRIBUTION: Endemic in the desert plains and wadis near Cairo.

THE FAGONIA THEBAICA COMPLEX

In Egypt two species: *F. thebaica* Boiss. and *F. boulosii* Hadidi, which are closely related to the species of the preceding complex. In fact, *F. boulosii* has characters intermediate between *F. arabica* and *F. thebaica.* This was expressed in an earlier publication (El Hadidi 1966 p. 45). In addition, *F. thebaica* and *F. boulosii* are more widespread than was earlier believed. Most of the records of *F. arabica* from Sinai and eastwards in Palestine were erroneously determined and should be treated as *F. boulosii.* The latter species seems to replace *F. arabica* in these regions. In the meantime, many records from the North African Sahara, determined as *F. arabica* should be referred to *F. thebaica.*

3. **Fagonia thebaica** Boiss.

Boissier 1849 p. 121.

3 a. **Fagonia thebaica** Boiss. var. **thebaica**

Orig. coll.: Aegypto superiore, prope Thebes 1846, Boissier (G, holotype; K, isotype).

Perennial glabrous green shrublet; internodes terete and striate, short, up to 2 cm long. Lower leaves trifoliolate, upper unifoliolate; leaflets distinctly cylindrical; petiole up to 10 mm long; spines as long as internodes. Flowers 15 mm in diameter, petals rose-coloured. Capsule 5 mm in diameter, tomentose; peduncle shorter than capsule; calyx deciduous.

DISTRIBUTION: Southern regions of the Libyan and Arabian deserts in Egypt, rare eastwards along the Gulf of Suez in Sinai.

3 b. **Fagonia thebaica** Boiss. var. **violacea** Boulos

Boulos 1966 p. 20. — Orig. coll.: Southern Libyan Desert, affluent of Wadi Kurkur 1964, Boulos (CAI, holotype).

Flowers intensely violet, capsule larger than in type.

DISTRIBUTION: More wide-spread than the type, known from Southern parts of the Libyan Desert in Egypt, westwards in Libya, Chad and Niger.

4. **Fagonia boulosii** Hadidi

El Hadidi 1966 p. 27.

4 a. **Fagonia boulosii** Hadidi var. **boulosii**

Orig. coll.: Egypt, northern Arabic Desert, Wadi Abu Seyal 1964, Boulos (CAI, holotype).

Perennial, glandular, yellowish-green shrublet; internodes terete, striate, 2.5—3 cm long. Lower leaves trifoliolate, upper unifoliolate; leaflets ovate lanceolate, flat; petiole up to 10 mm long; spines short, not exceeding leaves. Flowers 15 mm in diameter or more, petals rose-coloured.

Capsule 6 mm in diameter, villous; peduncle shorter than capsule; calyx deciduous.

DISTRIBUTION: Arabian Desert of Egypt along the Gulf of Suez, eastwards in Sinai and Palestine (EL HADIDI, in press b).

COLLECTIONS. Egypt. Sinai, Wadi Bedr 1891, KAISER 51 (G) — Sinai, KAISER 710 (G).

4 b. **Fagonia boulosii** HADIDI var. **crameri** HADIDI, var. nov.

Robustior et glandulosior quam typus; glandulae sessiles pulvere adhaerente.

Orig. coll.: Sinai, environs du Convent du Sinai 1.5. 1891, CRAMER (G, holotype).

More robust and more glandular than the type, glands sessile with adhering sand.

DISTRIBUTION: Endemic in Southern Sinai.

COLLECTIONS. Egypt: Entre Tor et Sinai, Juin 1832, BOVÉ 163 (G) — Ad radices montis Sinai, inter lapides, 20.7. 1837, SCHIMPER 251 (G) — Environs du Convent du Sinai 1891, CRAMER (G).

OBSERVATION. The collection SCHIMPER 251 of *Fagonia* from Sinai, determined as *F. arabica* is a heterogeneous collection, where three different taxa can be recognized. The duplicates kept in different herbaria represent specimens of *F. arabica* L., *F. schimperi* PRESL and *F. boulosii* HADIDI. This may explain the confusion concerning this collection and the various interpretations expressed in the literature (BURTT & LEWIS 1954 p. 395, etc.).

THE FAGONIA MOLLIS COMPLEX

Here belong *Fagonia mollis* DEL. and *Fagonia tristis* SICKENB. They approach *F. thebaica,* the leaflets being more or less cylindrical, internodes and spines short. They are characterized however by a certain type of compound gland (EL HADIDI 1966 pp. 41—42) not known in any other *Fagonia* species. In *F. tristis,* the glands consist of a multicellular base, a median elongated cell and a terminal arrow-shaped cell. In *F. mollis* var. *mollis,* the median elongated cell is absent. Specimens of *F. mollis* from Sinai, Negev, and Jordan have the same type of gland as those of *F. tristis.* These specimens agree in habit and size of flowers with those of *F. mollis* and will be described here as *F. mollis* var. *densiglandulosa* HADIDI. This may be regarded as a taxon intermediate between the two species.

5. **Fagonia mollis** DEL.

DELILE 1813 p. 76.

5 a. **Fagonia mollis** DEL. var. **mollis**

Orig. coll.: Egypte, DELILE (MPT, holotype; FI, isotype).
F. grandiflora BOISSIER 1849 p. 121. — Orig. coll.: Prope St Saba 1846, BOISSIER (G, holotype; K, isotype).

Perennial, sparingly hairy shrublet; branches prostrate; internodes quadrangular, sulcate. Leaves mostly trifoliolate; leaflets ovate; petiole 2—4 mm long; spines as the internodes, patent. Flowers 15 mm in diameter or more; petals pink. Capsule 5 mm in diameter, slightly hairy; peduncle as long as capsule; calyx deciduous.

DISTRIBUTION: Arabian Desert in Egypt, wadis along the Gulf of Suez, Sinai, Southern Palestine and Jordan.

COLLECTIONS. Egypt: Egypte 1831, MONTBRET (K, G) — Wadi Ashar 1877, SCHWEINFURTH 100 (K) — South Galala, middle of Wadi Rigba 1944, DAVIS (K). Palestine: Prope St Saba 1846, BOISSIER (G, K) — Jericho 1877, BALL 990 (K) — Jericho 1930, BORNMÜLLER 285 (K). Jordan: Wadi Rum, 1963, GILLETT 16036 (K).

5 b. **Fagonia mollis** DEL. var. **densiglandulosa** HADIDI, var. nov.

Similis typo sed dense glandulosa, glandulae ut in *Fagonia tristi.*

Orig. coll.: Jordan, Wadi Rum, rocky granite slope, 15.4. 1945, DAVIS 9110 (K, holotype).

Similar to the type in habit, but densely glandular, glands as those of *F. tristis*.

DISTRIBUTION: Along the Gulf of Suez in the Arabian Desert in Egypt, Southern Sinai, eastwards in Negev and Jordan.

COLLECTIONS. Egypt: North Galala, Wadi Nooz, 1944, DAVIS (K) — North Galala, Bir Odeib 1944, DAVIS (K) — Sinai, Wadi Gharandal, POST 274 (K).
Negev: Wadi Temina, 28 km from Eilat 1969, STEINBERG & BAVAZANO 4311, 4325 (FI) — Along Bir Sheeba—Eilat street 1969, STEINBERG & BAVAZANO 4252 (FI).
Jordan: Wadi Rum 1945, DAVIS 8996 & 9110 (K) — Wadi Rum, 3 km S. of Rum foot 29°35N×35°25E, alt. 900—1100 m., calc. sandstone resting on ign. basement mainly granite, 1963, GILLETT 16045 (K).

6. **Fagonia tristis** SICKENB.

SICKENBERGER 1901 p. 201.

6 a. **Fagonia tristis** SICKENB. var. **tristis**

Orig. coll.: Between Moqattam and Gebel Ahmar near Cairo 1880, SICKENBERGER (CAI, isotype).

Perennial pubescent shrublet; branches erect; internodes quadrangular, sulcate, 1—1.5 cm long. Leaves typically trifoliolate; leaflets cylindrical; petiole 2—4 mm long; spines as long as the internodes, densely crowded. Flowers ± 12 mm in diameter; petals pink. Capsule 5 mm in diameter, pubescent; peduncle shorter than capsule; calyx deciduous.

DISTRIBUTION: Endemic, Egypt: Northern Arabian and Isthmic Deserts.

6 b. **Fagonia tristis** SICKENB. var. **boveana** HADIDI

EL HADIDI 1966 p. 33. Orig. coll.: Desert du Sinai, Juin 1832, BOVÉ 162 (P, holotype; K, FI, isotypes).
F. cistoides DEL. in BOVÉ, Pl. exs.; nom. nudum.
F. glandulosa MONTB. in BOVÉ, Pl. exs.; nom. nudum.
F. mollis auct., non DEL.: BOISSIER 1867 p. 907.

Perennial, semispherical shrublet, entirely covered with yellowish glandular hairs; internodes longer than in the type, up to 2 cm long. Leaflets flat, ovate; spines as long as the internodes.

DISTRIBUTION: Along the Gulf of Suez in the Arabian Desert in Egypt, Southern Sinai, Negev and Jordan.

COLLECTIONS. Egypt: Isthme de Suez 1833, AUCHER (FI) — Suez, AUCHER 769 (K, FI) — Between Nekhl and Mittla Hills 1945, DAVIS 10459 (K) — Mittla Pass, foot of hills, 1945, DAVIS 10463 (K) — Desert du Sinai 1832, BOVÉ 162 & 167 (K) — Sinai, ELOY 799 (FI) — Sinai, KAISER 367 (K).
Negev: Eilat 1969, STEINBERG & BAVAZANO 4429, 4453 & 4547 (FI).
Jordan: Rum 1963, GILLETT 15924, 16045 (K) — Arabia petrea, MCDONALD 849 (K) — Arabia petrea, PICARD (G, K, FI) — Wadi Ishim 1945, DAVIS 9272 (K).

THE FAGONIA INDICA COMPLEX

In Egypt two species are known: *Fagonia indica* BURM. FIL. and *Fagonia paulayana* WAGNER & VIERH. They are characterized by their terete internodes, swollen whitish nodes, unifoliolate leaves, well-developed spiny stipules, small flowers and small fruits.

7. **Fagonia indica** BURM. FIL.

BURMAN 1768 p. 102.

A polymorphic, wide-spread species (EL HADIDI 1972 pp. 85—88; in press a), represented in Egypt by var. *indica*.

Earlier (EL HADIDI 1966 p. 27), I was of the opinion that the typical *F. indica* (=*F. parviflora*) is lacking in Egypt. I regarded the taxon occurring in Egypt, being short-spined, to be conspecific with *F. parviflora* var. *brevispina* SCHWEINF. The latter is a South Arabian taxon and is apparently different from the typical var. *indica*. This seems to be replaced westwards through the African Sahara by the closely allied *F. jolyi* BATT. The latter taxon was regarded by OZENDA & QUÉZEL (1956 pp. 41—43) to be conspecific with *F. indica*. The collections of *F. jolyi* which I have examined are different.

Fagonia indica BURM. FIL. var. **indica**

Orig. coll.: Iran, GARCIN (K, holotype; G, isotype).
F. mysorensis ROTH 1821 p. 215.
F. persica DE CANDOLLE 1824 p. 704.
F. parviflora BOISSIER 1849 p. 124.

Perennial, pale green, frequently pruinose and glandular shrublet. Leaves unifoliolate, short-petioled, with a distinct joint between petiole and blade; leaflet ovate-lanceolate, 12—16 mm long. Capsule 4×4 mm; peduncle longer than capsule, reflexed; calyx persistent.

DISTRIBUTION: South-west Libya eastwards to the Nubian Desert in Egypt, North and Central Sudan, Ethiopia, Somalia, Tihama of Saudi Arabia, Iraq, Southern Iran, Afghanistan and Pakistan.

8. **Fagonia paulayana** WAGNER & VIERH.

WAGNER & VIERHAPPER 1904 p. 34. — Orig. coll.: Socotra, ST. PAULAY (WU, lectotype).
F. armata R. BROWN 1814 p. 36, nom. nudum — Orig. coll.: Eritrea, G. MENAH (BM, holotype).
F. elba HADIDI; EL HADIDI 1966 p. 29. — Orig. coll.: Gebel Elba, TÄCKHOLM et al. (CAI, holotype).
F. indica BURM. FIL. var. *elba* (HADIDI) HADIDI; EL HADIDI 1972 p. 88.

Annual, biennial or perennial, glabrous, pale green plant. Leaves unifoliolate; leaflet linear, up to 40 mm long, 3 mm broad, subsessile. Capsule 5×5 mm; peduncle twice as long as capsule, reflexed; calyx deciduous.

DISTRIBUTION: Gebel Elba of Egypt, southwards along the Red Sea coast of Sudan, Ethiopia, Somalia and Socotra.

OBSERVATION. *F. paulayana* (=*F. elba*) was regarded (EL HADIDI 1972 p. 88) as *F. indica* var. *elba*. Further studies (EL HADIDI, in press a) showed that *F. paulayana* differs from *F. indica* in several respects which favours keeping them as two distinct species.

THE FAGONIA BRUGUIERI COMPLEX

In Egypt, *F. bruguieri* DC., *F. olivieri* DC., *F. schimperi* PRESL and *F. kassasii* HADIDI belong to this complex. These species are characterized by their quadrangular, sulcate internodes, small flowers and small capsules with persistent calyx.

9. **Fagonia bruguieri** DC.

DE CANDOLLE 1824 p. 704.

This species was considered to be represented in the Northern Sahara by var. *bruguieri* and var. *laxa* (EL HADIDI 1966 pp. 21—22). Further studies (EL HADIDI 1972 p. 91) showed that the latter taxon is restricted to the Persian Gulf in Iran, Bahrein and in Afghanistan. However, the specimens from Egypt which were earlier considered to belong to this var. *laxa* seem to be an intermediate form between *F. bruguieri* var. *bruguieri* and *F. schimperi*.

Fagonia bruguieri DC. var. **bruguieri**

Orig. coll.: Inter Aleppo et Bagdad, BRUGUIÈRE & OLIVIER 1522 (G-DC, lectotype).
F. echinella BOISSIER 1849 p. 123. — Orig. coll.: inter Kahiram et Suez 1846, BOISSIER (G, lectotype).

Biennial or perennial glandular yellowish-green shrublet; internodes quadrangular, sulcate, up to 2.5 cm long. Lower leaves trifoliolate, upper unifoliolate; petiole short, 0.5—1 cm long; spines patent, slightly recurved, as long as internodes. Flowers small, 8 mm in diameter. Capsule 3—4 mm in diameter, sparingly hairy; peduncle shorter than capsule; calyx persistent.

DISTRIBUTION: Northern Sahara, eastwards to Jordan, Syria, Iraq, Iran, Afghanistan, Pakistan, Arabia and Somalia.

10. **Fagonia schimperi** PRESL

PRESL 1844 p. 30. — Orig. coll.: Sinai 1835, SCHIMPER 251 (M, lectotype).
F. myriacantha BOISSIER 1849 p. 123. — Orig. coll.: Arabia petrea et Sinai 1846, BOISSIER (G, lectotype).

Pale green, glabrous, robust shrublet; internodes quadrangular, up to 4 cm long. Lower leaves trifoliolate, upper unifoliolate; petiole 5—10 mm long; spines patent, over 4 cm long. Flowers ± 12 mm in diameter. Capsule 3—4 mm in diameter, glabrous; calyx persistent.

DISTRIBUTION: Arabian Desert in Egypt, eastwards to Sinai and adjacent regions of Negev; also in Iran.

COLLECTIONS. Egypt: Cairo—Suez Road 1958, KASSAS (CAI) — Suez Road 1958, GHABBOUR (CAI) — Suez, Gebel Ataqa, Wadi Aber 1956, V. TÄCKHOLM et al. (CAI) — Sinai, SCHIMPER 251 partially (K, BM, G, M) — Entre Tor et Sinai, Juin 1832, BOVÉ 164 (K) — Arabia petrea et Sinai 1846, BOISSIER (K, G) — Wadi Sheik 1884, HART (K) — Wadi Sheik, NAIYAL (CAI) — Sinai mountain region 1940, HASSIB (CAI) — Gebel El Deir near St. Catherine Monastery 1956, V. TÄCKHOLM (CAI) — Wadi El Raha 1961, EL HADIDI (CAI) — Vicinity of St. Catherine Monastery 1963, BOULOS (CAI) — Gebel Musa 1965, EID (CAI).

Iran: Bushire 1926, HORNER 37 (K) — Inter Khurasan et Dalaki 1868, HAUSSKNECHT (K, BM) — In deserto persico, ELOY 802 (K).

OBSERVATION. The occurrence of a form intermediate between *F. bruguieri* and *F. schimperi* has caused confusion concerning *F. schimperi*. Some of the duplicates of SCHIMPER 251, BOVÉ 164 and ELOY 798 represent a robust form of *F. bruguieri*. The latter is typically glandular while *F. schimperi* is distinctly glabrous.

11. **Fagonia olivieri** DC.

DE CANDOLLE 1824 p. 704. — Orig. coll.: Inter Aleppo et Bagdad, OLIVIER & BRUGUIÈRE (G-DC, holotype).

Biennial almost glabrous, bright green shrublet; internodes quadrangular sulcate, 2.5—4 cm long. Leaves unifoliolate, almost sessile; spines patent, not longer than internodes. Flowers up to 15 mm in diameter. Capsule 4—6 mm in diameter, glabrous; peduncle as long as or longer than capsule; calyx persistent.

DISTRIBUTION: Sinai, eastwards to Jordan, Syria, Iraq, Northern Saudi Arabia, Kuwait, Iran, Afghanistan and Pakistan.

COLLECTIONS. Egypt: Sinai, Jebel Katarina 6000—8000 ft. Sept. 1945, Lord KINROSS (K) — Desert entre Suez et Tor, Juin 1832, BOVÉ 163 (BM).

OBSERVATION. The occurrence of *F. olivieri* in Sinai was expected (EL HADIDI 1972 p. 89). The origin of the two robust Asiatic species *F. schimperi* PRESL and *F. olivieri* DC. is the smaller North African *F. bruguieri* var. *bruguieri*. A form intermediate between *F. schimperi* and *F. bruguieri* var. *bruguieri* exists. This is especially abundant in the Arabian Desert of Egypt, particularly along the borders of Sinai, where both species occur.

12. **Fagonia kassasii** HADIDI

EL HADIDI 1966 p. 23. — Orig. coll.: Red Sea coast at Gebel El Faraied, 12.2. 1961, KASSAS et al. 775 (CAI, holotype).

Annual, pale green, glabrous plant; internodes quadrangular, up to 5 cm long. Leaves trifoliolate; petiole 3—4 cm long; spines spreading, shorter than internodes. Flowers small, up to 10 mm in diameter. Capsule 3—4 mm in diameter, covered with short hairs; calyx persistent.

DISTRIBUTION: Southern Sinai, Red Sea coast and Gebel Elba.

COLLECTIONS. Egypt. Sinai: Feiran Oasis, March 1928, MEINERTZHAGEN (BM).

Red Sea coast: Wadi El Faraied 1961, V. TÄCKHOLM et al. 802, 832, 871 (CAI) — Gebel El Faraied 1961, KASSAS et al. 775 (CAI) — Wadi Hankalia 1961, V. TÄCKHOLM et al. 67 (CAI).

Gebel Elba: Wadi Oolak 1962, V. TÄCKHOLM et al. 701 (CAI) — Wadi Haiteem 1962, V. TÄCKHOLM et al. 773 (CAI) — Wadi Aak 1962, V. TÄCKHOLM et al. 791 (CAI) — NE. & W. slopes of Gebel Asotriba 1962, V. TÄCKHOLM et al. 110 (CAI).

THE FAGONIA SINAICA COMPLEX

All the species of this complex are represented in Egypt: *F. cretica* L., *F. sinaica* Boiss. and *F. tenuifolia* Steud. & Hochst.

They are sparsely glandular, prostrate shrublets with quadrangular sulcate internodes. The leaves are generally trifoliolate and the spines are shorter than the leaflets. Flowers usually large, up to 20 mm in diameter.

13. **Fagonia cretica** L.

Linnaeus 1753 p. 386. — Orig. coll.: Cultivated in Uppsala Botanical Gardens, no. 5461/1 (LINN, holotype).

Perennial, dark green, glabrous, prostrate shrublet. Leaves trifoliolate; leaflets lanceolate; spines shorter than leaflets. Flowers up to 20 mm in diameter; petals purple. Capsule up to 10 mm in diameter, glabrous; peduncle shorter than capsule; calyx deciduous.

DISTRIBUTION: On the calcareous slopes along the Mediterranean coast of Africa, from Morocco to Egypt; and in Europe, from Spain to Greece and the Mediterranean islands.

14. **Fagonia sinaica** Boiss.

Boissier 1843 p. 61.

A polymorphic species, wide-spread all over Africa (El Hadidi, in press b). It is represented in Egypt by three varieties. Apart from var. *kahirina*, the other two varieties represent forms intermediate between *F. sinaica* and other species. *F. sinaica* var. *longipes* which is especially abundant in the southern parts of the Arabian Desert in Egypt approaches in some of its characters *F. tenuifolia*. The latter species is restricted to the mountainous blocks of the southern Egyptian deserts. On the other hand, *F. sinaica* var. *sinaica*, which is endemic in Sinai and the adjacent deserts of Negev, approaches *F. glutinosa*, particularly var. *nuda* which is exceptionally non-adherent of sand as well as all the varieties of *F. sinaica*.

KEY TO THE VARIETIES

1. Flowers small, not exceeding 8 mm in diameter .... 14 a. var. *sinaica*
   Flowers up to 15 mm in diameter 2
2. Petiole not more than 5 mm long .... 14 b. var. *kahirina*
   Petiole at least 10 mm long .... 14 c. var. *longipes*

14 a. **Fagonia sinaica** Boiss. var. **sinaica**

Orig. coll.: In jugi Sinaitico, Aucher 800 (G, holotype; K, FI, isotypes).
F. kahirina var. *sinaica* (Boiss.) Boiss.; Boissier 1867 p. 905.

Perennial, greyish-green, densely glandular shrublet with quadrangular sulcate internodes. Leaves trifoliolate; petiole up to 10 mm long; spines not more than 5 mm long. Flowers up to 8 mm in diameter. Capsule 4 mm in diameter, covered with spreading hairs; peduncle up to 10 mm long; calyx deciduous.

DISTRIBUTION: Endemic in Sinai and the Negev Desert.

COLLECTIONS. Egypt. Sinai: Aucher 800 (G, K, FI) — Desert du Suez et Tor, Juin 1832, Bové 165 (FI). — Negev: Along the street between Bir Sheeba and Eilat 1969, Steinberg & Bavazano 4162 & 4244 (FI).

14 b. **Fagonia sinaica** Boiss. var. **kahirina** (Boiss.) Hadidi, comb. nov.

Basionym: *F. kahirina* Boissier 1849 p. 122. — Orig. coll.: In deserto Kahirino 1846, Boissier 1843 p. 61.

Perennial, dark green, sparingly glandular shrublet. Leaves trifoliolate; petiole short, up to 5 mm long; spines less than 10 mm long. Flowers up to 15 mm in diameter. Capsule 4 mm in diameter, covered with spreading hairs; peduncle up to 5 mm long; calyx deciduous.

DISTRIBUTION: Sahara north of 27°N; eastwards in Sinai, Palestine, Jordan and Syria.

14 c. **Fagonia sinaica** BOISS. var. **longipes** MAIRE

MAIRE 1934 p. 297. — Orig. coll.: Algerie, Oranis, Brezina. POMEL (MPU, holotype).

Perennial, olive-green, almost glabrous shrublet. Leaves trifoliolate; petiole over 10 mm long; spines 2—5 mm long. Flowers about 12 mm in diameter. Capsule 4 mm in diameter, covered with short hairs; peduncle about 10 mm long; calyx deciduous.

DISTRIBUTION: Sahara, south of 27°N except Morocco; eastwards in Sinai and Negev.

COLLECTIONS. Egypt. Mediterranean region, Sollum plateau 1963, BOULOS (CAI) — Suez, Gebel Ataqa, Wadi Aber 1956, EL HADIDI (CAI) — Helwan, Wadi Hof 1952, IMAM (CAI).

15. **Fagonia tenuifolia** STEUD. & HOCHST. ex BOISS.

BOISSIER 1867 p. 909. — Orig. coll.: In cacumine montis Gesser, Arabia desertae 1837, SCHIMPER 917 (G, holotype).
F. bishararum SCHWEINFURTH 1899 p. 276.
F. flamandi BATTANDIER 1900 p. 284.

Perennial olive-green glabrous shrublet. Leaves trifoliolate; leaflets linear, 10—15 mm long, 2 mm in diameter; petiole 10—15 mm long. Capsule 5×5 mm, covered with short hairs; peduncle longer than capsule, up to 20 mm; calyx deciduous.

DISTRIBUTION: mountainous blocks of the southern Arabian Desert in Egypt, those deserts on the same latitude in Arabia and Central Sahara (Ahagar, Tibesti).

COLLECTIONS. Egypt. Aegyptus 1831, FISCHER (M) — Südl. Wadi Ashar 1877, SCHWEINFURTH 223 (K) — Red Sea coast, Gebel Hamata 1961, V. TÄCKHOLM et al. 444 (CAI).

THE FAGONIA ISOTRICHA COMPLEX

Fagonia latifolia DEL. and *F. isotricha* MURB. are the species represented in Egypt. They are characterized by the presence of a special type of gland (EL HADIDI 1966 pp. 41—42); internodes quadrangular sulcate; leaves trifoliolate, median leaflet rhombic, broader than side leaflets.

16. **Fagonia latifolia** DEL.

DELILE 1813 p. 86. — Orig. coll.: Egypte, DELILE (MPT, holotype; FI, isotype).

Annual slender herb, entirely covered with brownish glandular hairs of two types: one simple capitate and the other compound consisting of a basal, a median and a terminal capitate cell. Leaves broad, rosetted at the base; median leaflet broader than the lateral ones, up to 15 mm long. Flowers up to 8 mm in diameter. Capsule 4 mm in diameter, spreadingly hairy; calyx deciduous.

DISTRIBUTION: Egypt, particularly around Cairo and in the wadis of the northern Arabian Desert.

17. **Fagonia isotricha** MURB.

MURBECK 1897 p. 54.

Fagonia isotricha MURB. var. **isotricha**

Orig. coll.: Algerie, Biskra 1853, BALANSA (LD, holotype).
F. lahovarii VOLKENS & SCHWEINFURTH 1897 p. 6.
F. soturbensis SCHWEINFURTH 1899 p. 276.

Perennial robust shrublet, sparsely covered with viscid glandular hairs of one type only, each hair consisting of a basal and a terminal capitate cell. Leaves trifoliolate; median leaflet up to 20 mm long, broader than the lateral ones. Flowers about 10 mm in diameter. Capsule 5 mm in diameter, tomentose; calyx deciduous.

DISTRIBUTION: Widely spread through the Northern Sahara, westwards to the

Cape Verde Islands. Along the Red Sea coast in the southern parts of Egypt and Sudan. Along the Gulf of Eden in southern Yemen and Somalia, also along the coasts of South West Africa.

THE FAGONIA GLUTINOSA COMPLEX

This complex is represented in Egypt by *F. glutinosa* DEL., a polymorphic species with viscid, simple glands with adhering sand.

It was believed that *F. microphylla* POMEL is known from Egypt (EL HADIDI 1966 p. 33). The specimens which were earlier treated as *F. microphylla* should be related to *F. glutinosa* var. *longipetiolata* HADIDI (EL HADIDI, in press b); *F. microphylla* is endemic in the deserts of Algeria and Morocco.

18. **Fagonia glutinosa** DEL.

DELILE 1813 p. 86.

KEY TO THE VARIETIES

1. Plant sparsely glandular, without adhering sand .... 18 c. var. *nuda*
   Plant densely glandular, with adhering sand 2
2. Petiole 10 mm long or more .... 18 d. var. *longipetiolata*
   Petiole up to 5 mm long 3
3. Flowers small, 8 mm in diameter .... 18 a. var. *glutinosa*
   Flowers large, 15 mm in diameter .... 18 b. var. *grandiflora*

18 a. **Fagonia glutinosa** DEL. var. **glutinosa**

Orig. coll.: Egypte, DELILE (FI, isotype).
F. viscida PRESL 1844 p. 30.
F. getula POMEL 1875 p. 338.

Annual or perennial prostrate herb, entirely covered with viscid glands with adherent sand; internodes terete and striate. Leaves trifoliolate; median leaflets usually twice as long as the lateral ones; petiole up to 5 mm long; spines short, not exceeding the petiole in length. Flowers small, 8 mm in diameter. Capsule 5×5 mm, densely covered with hairs; calyx persistent.

DISTRIBUTION: Northern Sahara, eastwards in Palestine, Jordan, Iraq, Northern Arabia and Kuwait.

18 b. **Fagonia glutinosa** DEL. var. **grandiflora** BOISS.

BOISSIER 1867 p. 905. — Orig. coll.: Arabia petrea 1846, BOISSIER (G, holotype).

Densely woolly, glands less viscid, only a few, fine sand particles adhering. Flowers 15 mm in diameter. Capsule 6×6 mm, densely covered with hairs.

DISTRIBUTION: Endemic in Sinai.

18 c. **Fagonia glutinosa** DEL. var. **nuda** HADIDI

EL HADIDI 1966 p. 33. — Orig. coll.: Wadi Liblab near Cairo 1952, M. IMAM (CAI, holotype).

Bright green, less glandular, without adherent sand. Flowers and capsules smaller than in the type.

18 d. **Fagonia glutinosa** DEL. var. **longipetiolata** HADIDI

EL HADIDI, in press b. — Orig. coll.: Egypt, North Sinai, Mittla Pass 13.4. 1945, DAVIS 10473 (K, holotype).

Similar to the type, but internodes longer, petioles at least 10 mm long.

DISTRIBUTION: Endemic in Northern Sinai, probably wide-spread.

COLLECTIONS. Egypt. North Sinai, Mittla Pass, DAVIS 10473 (K) — Isthmic Desert, Sadd Rawafa 1951, V. TÄCKHOLM et al. 123 (CAI).

2. SEETZENIA R. BR.

BROWN 1826 p. 231.

BULLOCK (1965 p. 204) recognizes two *Seetzenia* species: a North African, *S.*

orientalis DCNE and a South African, *S. lanata* (WILLD.) BULLOCK. The latter has pubescent leaves beneath, while *S. orientalis* is glabrescent. The geographical isolation of these two forms and the difference led to the recognition of two distinct taxa. However, the two forms grow together in North Africa and Sinai which favours considering the one as a synonym of the other.

1. **Seetzenia lanata** (WILLD.) BULLOCK

BULLOCK 1965 p. 204. — Basionym: *Zygophyllum lanatum* WILLDENOW 1799 p. 564. — Orig. coll.: Sierra Leone (B, Herb. Willd. 8098, holotype).

Seetzenia africana R. BROWN 1826 p. 231 nom. nud. — Orig. coll.: Africa Orientalis, prope Olifant's River, Mr. MASSON (BM, holotype).

Seetzenia orientalis DECAISNE 1834 p. 281. — Orig. coll.: Desert du Sinai, Juin 1832, BOVÉ 168 (P, holotype; G, K, isotypes).

Seetzenia prostrata (THUNB.) ECKLON & ZEYHER 1835 p. 98. — Basionym: *Zygophyllum prostratum* THUNBERG 1800 p. 189. — Orig. coll.: Thunb. Herb. 10129 (UPS, holotype).

Pubescent shrublet with jointed prostrate branches. Leaves opposite trifoliolate short-petioled; stipules membranaceous. Flowers axillary, solitary, pentamerous; petals absent; stamens 5, opposite to the sepals; ovary 5-loculed, each 1-ovuled; styles 5, free; stigma capitate. Capsule ovoid, 5-lobed, 5-carpelled, each with one pendulous seed. Seed oblong, compressed; testa crustaceous.

DISTRIBUTION: African Sahara, Sinai, Palestine, Jordan, Kuwait, Afghanistan, Pakistan, along Persian Gulf, Somalia and South Africa.

ACKNOWLEDGEMENTS

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I am also much obliged to the Directors and the staff of the herbaria B, BM, CAI, FI, G, K, M, MPU, P, W, and WU, where I have been working or from which I have received material on loan.

Thanks are also due to Professor Dr. L. BOULOS, Cairo University for reading the manuscript.

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Brief Articles and Reports

Chromosome Counts of some Egyptian Plants

The importance of recording chromosome counts of taxa from natural habitats has led us to undertake this study on some plants from the western Mediterranean coast of Egypt. Specimens were collected (March, 1972) and identified by Professor VIVI TÄCKHOLM of Cairo University. Flower buds were fixed on the spot in Carnoy's solution by Dr. A. AMIN of the Desert Institute, Cairo. To both of them we wish to express our thanks. The buds were then stained in hydrochloric carmine for 4 days and stored in 70 % ethanol.

The chromosome numbers listed below are mostly meiotic counts. However, in two instances mitotic counts of anther wall cells or pollen grain mitosis are given. Those instances are marked with [1] and [2] on the numbers, respectively. To our knowledge, the following counts have not been reported previously.

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MANTON, I. 1932. Introduction to the general cytology of the Cruciferae. — Ann. Bot. 46: 509—556.

Taxon	n	2n	Locality
BORAGINACEAE			
Echium setosum VAHL (big flowers)	8		Abu Sir, 48 km W. Alexandria
COMPOSITAE			
Anthemis microsperma BOISS. & KY.	9		Vicinity of Mersa Matruh
Centaurea pallescens DEL.	10	20 [1]	El-Garawla, 25 km E. Mersa Matruh
Onopordon alexandrinum BOISS.	16		Vicinity of Mersa Matruh
CRUCIFERAE			
Diplotaxis viminea (L.) DC. (2n=c. 20 by MANTON 1932)	8 [2]		El-Garawla, 25 km E. Mersa Matruh
DIPSACACEAE			
Scabiosa arenaria FORSSK.		18 [1]	Maktala, 105 km W. Mersa Matruh, in *Urginea* stand.
LABIATAE			
Marrubium alysson L.	13		El-Garawla, 25 km E. Mersa Matruh
LILIACEAE			
Asparagus stipularis FORSSK.	8		Vicinity of Mersa Matruh
SCROPHULARIACEAE			
Kickxia aegyptiaca (DUM.) NÁBĚLEK	9		El-Garawla, 25 km E. Mersa Matruh

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Seven Chromosome Numbers of Egyptian Plants

Fig. 1. Somatic chromosomes. — A. *Iphiona mucronata.* — B. *Lygeum spartum.* — C. *Salvia verbenaca* var. *serotina.* — D. *Asteriscus graveolens.* Scale 10 μ.

The author is preparing a study on the chromosome numbers of Egyptian plants (AMIN in press). The present note comprises seven more chromosome counts. Root tips or flower buds were fixed in Carnoy's solution, stained in hydrochloric carmine and smeared in 45 % acetic acid (SNOW 1963). Pretreatment of root tips in parachlorobenzene (MEYER 1945) was found to be useful in spreading the chromosomes.

In the case of *Lygeum spartum* LOEFL. ex L., 2n=40 was recorded by RAMANUJAM (1938). For *Iphiona mucronata* (FORSSK.) ASCHERS. & SCHWEINF. 2n=18 is recorded for the first time, and for *Salvia verbenaca* L. var. *serotina* BOISS. 2n=44. The rest of the numbers confirm previous investigations by other workers.

Professor VIVI TÄCKHOLM kindly determined the plants and offered facilities to carry out this work in the Herbarium, Faculty of Science, Cairo University.

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Taxon	n	2n	Locality
ASCLEPIADACEAE			
Pergularia tomentosa L.		22	Wadi Hof, near Helwan, S. Cairo, September 1972.
CAPPARACEAE			
Capparis spinosa L.	19		Same locality and date
CARYOPHYLLACEAE			
Spergula fallax (LOWE) E. H. L. KRAUSE		18	180 km from Cairo along the desert road to Alexandria, August 1967.
COMPOSITAE			
Asteriscus graveolens LESS.		14	Wadi Hof, near Helwan, S. Cairo, September 1972.
Iphiona mucronata (FORSSK.) ASCHERS. & SCHWEINF.		18	Same locality and date
GRAMINEAE			
Lygeum spartum LOEFL. ex L.		46	C. 90 km E. Mersa Matruh, western Mediterranean coast, March 1972.
LABIATAE			
Salvia verbenaca L. var. *serotina* BOISS.		44	Same locality and date

AMAL AMIN

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The Flower-buds of the Linden

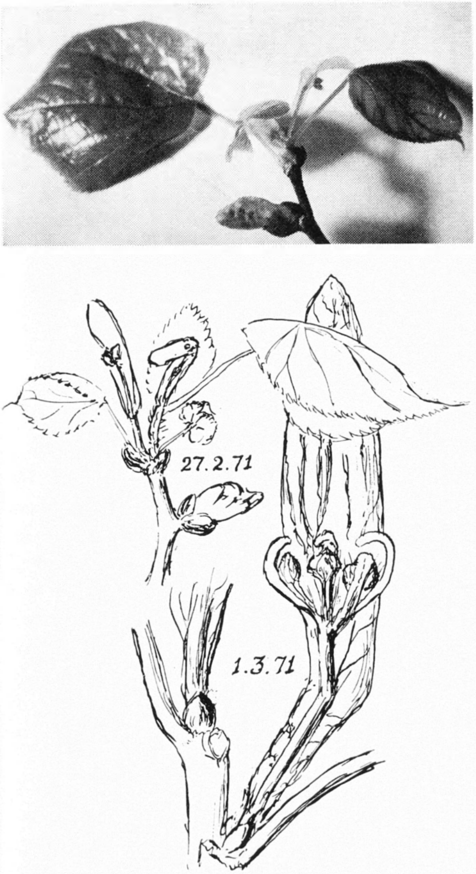

Fig. 1. Development of flower buds on forced twigs of the linden. The photograph is from 27.2. 1971.

The linden flowers (in Sweden) in July, and people have probably not thought much about what happens to the buds before that time. Upsala is full of linden-trees, and twigs from the pruning in early spring are welcome objects for those who want to enjoy some of the greenness of the spring in advance. And on such forced twigs the writer, some years ago, saw something not expected, namely clusters of small flower-buds with their bracts. This was not accidental as such buds appeared on forced twigs year after year together with leaves. At the bursting of the leaves in May twigs taken from the trees were examined, and on them the flower-buds were preformed, but hardly come as far as on the drawing from 27.2. (Fig. 1) — tender bract with buds as tiny little grains. And so the "natural" buds evidently remain during the time when the developing leaves take all the nourishment. Then the flower-buds will have their turn. On forced twigs the natural mechanism fails, and the buds go on increasing in size. They never open, but they reach, however, at least such size that one has to notice them. The phenomenon might be worth mentioning as not one of the really great botanists to whom it was demonstrated seems to have pondered over from where the flowering in July has its origin.

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Botanical Literature

HULTÉN, E.: Flora of Alaska and Neighboring Territories. A manual of the Vascular Plants. — Stanford University Press, Stanford, California 1968. XXII+1008 pp. $35.

As ERIC HULTÉN's Flora of Alaska appeared four years ago, this review can be considered somewhat over-due. Four years is, however, a short period compared with the long span of time during which this flora will be an indispensable aid to botanists studying the Alaskan flora.

HULTÉN has an eminent talent for obtaining skilful co-workers. He succeeds in finding those who can contribute with illustrations to make the reading a still more pleasant task. Mrs. DAGNY TANDE-LID, Oslo, has done the drawings of the habit of each plant. The composition of the whole volume is very beautiful. One could possibly have wished that the illustrations had been completed with some drawings of essential details.

HULTÉN has in this work, as in previous ones, a very broad species concept. This is surely a necessity in a study comprising a survey of such a vast area. It has been necessary for him to negligate much concerning the splitting of taxa into smaller entities during the last decades. His method is the only possible one in a region like Alaska. Detailed research can be carried out only after his Flora has been used for a long time. The problem is different in Northern Europe, for example, where we have long had the broad view and are now studying the details.

The author has inevitably a heterogeneous species concept. What is known, for example, about *Potentilla*? Or about the reproduction of *P. egedii* having four sub-species? Such stimulating questions are initiated many times and with necessity.

HULTÉN's many grand floras are of the utmost interest for the future taxonomic research in the circumpolar region. The disjunct areas of distribution found for many taxa imply problems of great interest. How is taxonomic differentiation, evolution, related to phytogeographic disjunction? We know little about that. Many new research projects can be initiated and stimulated.

HENNING WEIMARCK

SAVILE, D. B. O.: Arctic Adaptations in Plants. — Monograph No. 6. Canada Department of Agriculture 1972. 81 pp.

The booklet gives an account of the modes of adaptation to Arctic environment in plants. The characteristics of especially the Arctic climate are reviewed. Besides angiosperms, fungi are also discussed in some detail, whilst other cryptogams are more briefly discussed. Physical, physiological, morphological and genetic adaptations are accounted for in connection with the problem of survival and dispersal.

A great number of valuable references are given although an encyclopedic review is explicitly said to be beyond the scope of the paper. The reader meets a very stimulating multitude of ideas, suggestions and new problems.

Typographically, the little volume does not at all attain the high standard of the text. Especially unfortunate is the positions of a heading at the very bottom of p. 14. The proof-reading of some pages could have been better. In some contexts (pp. 38, 42) the author uses the term "modification" as if it were a synonym of adaptation.

The volume can be obtained (free) from Information Division, Canada Department of Agriculture, Ottawa, Canada K1A OC7, and can be highly recommended.

GUNNAR WEIMARCK

IN MEMORIAM

Carl Blom 1888—1972

CARL BLOM passed away on November 1st, 1972, at the age of eighty-four. He has been an honorary member of the Lund Botanical Society since 1958.

Botaniska Notiser has been printed at his printing-house since 1922, Botaniska Notiser Supplement and Opera Botanica since their inception. CARL BLOM, together with his family, has personally supervised the production of each issue during these more than fifty years.

To those young scientists preparing their doctor's theses for publication, and they were many in number, he was not only the manager of a printing-house. He was like a wise father advising and encouraging them, and they felt like devoted sons and daughters.

The editors of the journals remember CARL BLOM for his ambition to meet the demands on his printing-press. He often more than fulfilled his promises. In a critical situation when a volume needed to be published in less than no time the impossible was sometimes made possible by his efforts, but the standard was always the same. The personal contribution he has made to Swedish scientific publication during half a century cannot be over-estimated.

The Lund Botanical Society owes CARL BLOM a great debt of gratitude for his work to the benefit of botanical research. He will long be remembered both for his personality and his craftsmanship.

THE EDITOR