

# Drawings of Scandinavian Plants 60–64

## Juncus L.

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Subgen. *Pseudotenageia* V. KREZ. & GONTSCH. in KOMAROV 1935

(Syn. Subgen. *Poiophylli* BUCHENAU 1890 p.p., non 1875)

Perennials, small to moderately tall, caespitose or matforming; rhizome always well developed. Leaves several on each shoot, flat to subterete, with enlarged dorsal epidermis cells and sclerenchyma strands in their margins. Inflorescence apical, flowers single or united in loose clusters, each with normally 2 involucreal bracteoles.  $x=15, 20?, 21, 22$ .

Subgen. *Pseudotenageia* occurs in all temperate regions except S. Africa. In Scandinavia it is represented by 5 species, illustrated as nos. 60–66.

### 60. *Juncus squarrosus* L. 1753

Perennial, laxly caespitose to matforming; rhizome short, suberect. Stems 10–50 cm, rigid, with a usually  $\pm$  horizontally spreading, manyleaved basal rosette and rarely one upper cauline leaf. Leaves subcoriaceous, canaliculate, 7–30 cm long, 1–2 mm broad; auricles of varying length, obtuse. Inflorescence 3–10 cm long, 10–30(–40)-flowered; flowers 4–5 mm. Tepals equally high, outer ones narrowly

<sup>1</sup> NILSSON is responsible for the drawings and SNOGERUP for the text.

ovate, inner ones lanceolate, all obtuse, light to dark brown with whitish scarious margins. Stamens 6, c.  $\frac{1}{2}$  as high as the tepals; anthers 1.5–2 mm, 2.5–6 times as long as the short, broad filaments. Capsule equalling the tepals, ovoidal to ellipsoidal, obtuse, mucronate. Seeds 0.6–0.8 mm,  $\pm$  obliquely ovoidal, with conspicuous longitudinal striae and weaker transverse ones.  $2n=42$ .

*J. squarrosus* is a typical plant of heaths, sometimes also occurring in meadows and on tracks on poor soils. It is common in the humid parts of W. Europe and scattered in heath communities throughout W. and C. Europe. In Scandinavia it occurs mainly in Denmark, S. Sweden and SW. Norway, with scattered localities in the west up to the Lofoten Islands and in the east to N. Uppland. In Finland it is only known as a casual.

### 61. *Juncus compressus* JACQUIN 1762

Perennial, with a creeping rhizome, or laxly caespitose. Stems 10–40 cm, usually slightly compressed, with 0–3 basal sheaths, 1–4 subbasal leaves and 1–2 upper cauline leaves. Leaves 5–25 cm long, 0.8–2 mm broad, flat or rarely canaliculate,  $\pm$  bluish green; auricles short, broad, obtuse. Inflorescence lax or rarely con-

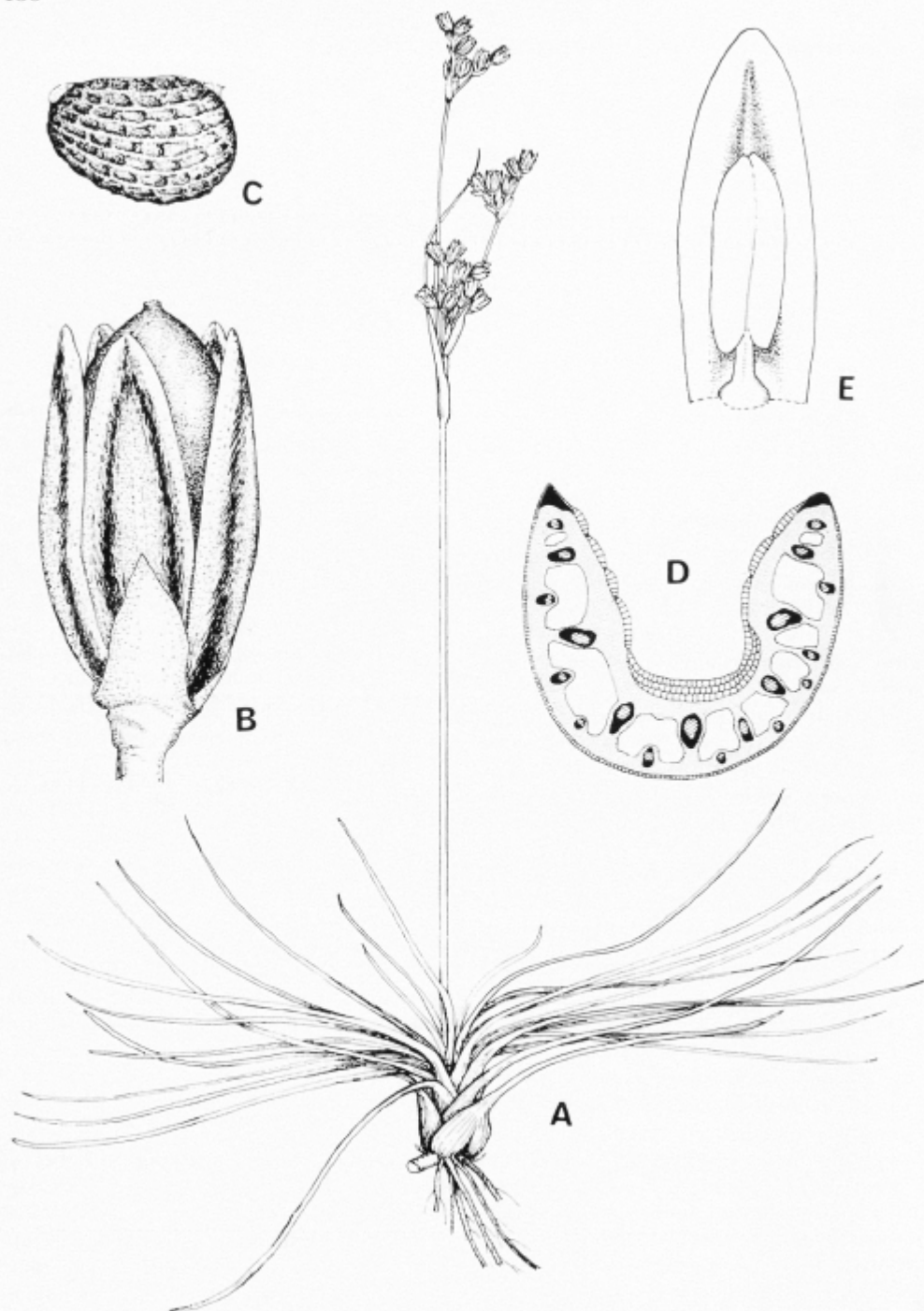


Fig. 60. *Juncus squarrosus* L. — A: Habit,  $\times 0.5$ . — B: Flower with ripe capsule,  $\times 10$ . — C: Seed,  $\times 45$ . — D: Tepal and stamen,  $\times 10$ . — E: Leaf transect,  $\times 40$ .

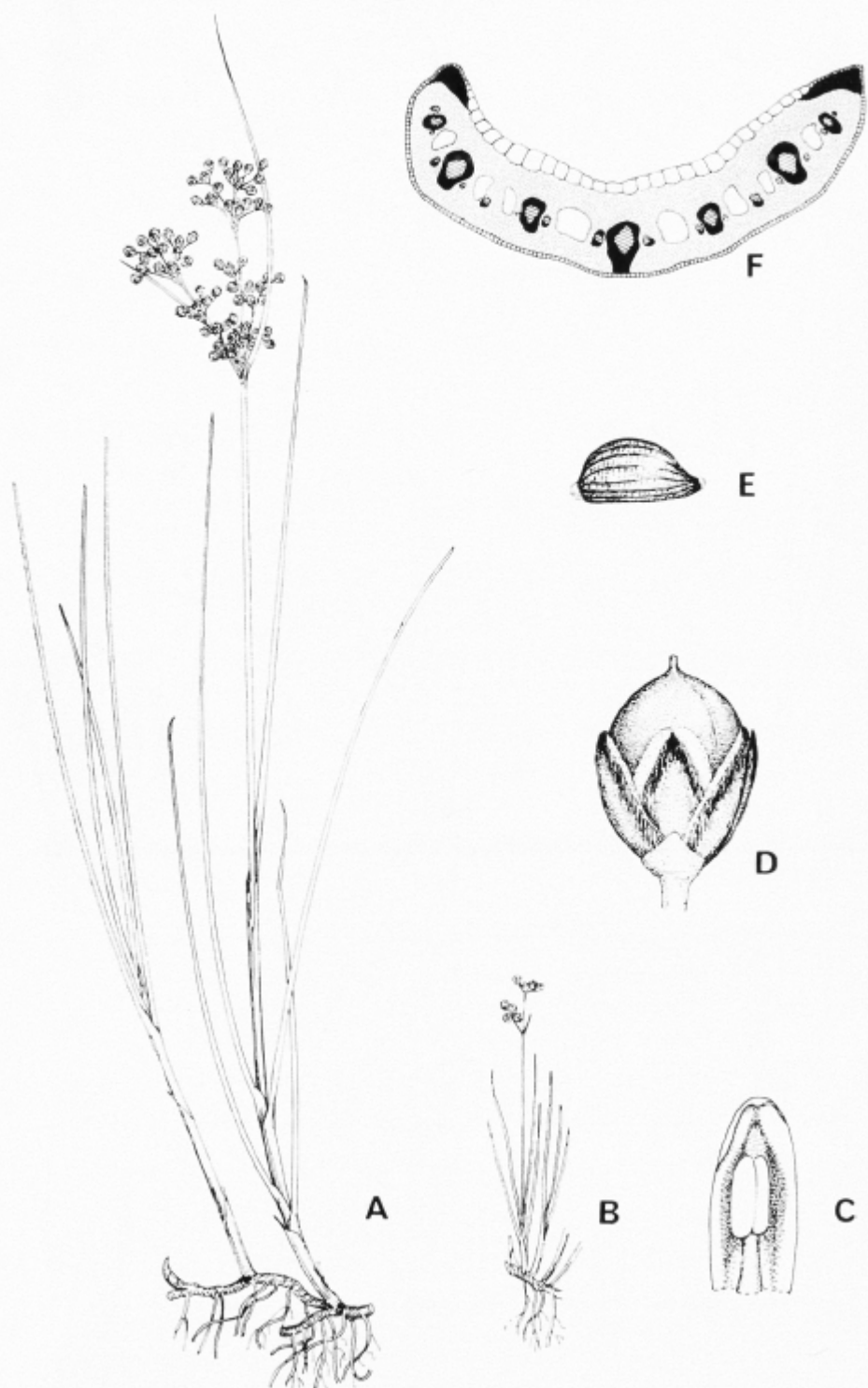


Fig. 61. *Juncus compressus* JACQ. — A—B: Habit,  $\times 0.5$ . — C: Outer tepal and stamen,  $\times 10$ . — D: Flower with ripe capsule,  $\times 10$ . — E: Seed,  $\times 45$ . — F: Leaf transect,  $\times 40$ .





densed, 1.5—8 cm long, 10—60-flowered. Tepals equally high, 2—3 mm, ovate, obtuse, outer ones boatshaped and apically cucullate. Stamens 6,  $\frac{1}{2}$ — $\frac{2}{3}$  as high as the tepals; anthers 0.5—1 mm, 1—2 times as long as the filaments. Style 0.2—0.4 mm; stigmata 1—1.5 mm. Capsule 2.5—3.5 mm, exceeding and up to 1.5 times as high as the tepals, sphaerical to obovoidal, apically often slightly trigonal, obtuse, mucronate. Seeds 0.35—0.5 mm, ovoidal, slightly oblique, conspicuously c. 12-striate with weaker transverse striae.  $2n=44$ .

*J. compressus* occurs on different types of damp ground, preferably in meadows and on open soil, often on tracks and in field margins. It is spontaneous in Europe and W. Asia and in northwestern N America, but has been introduced in other areas. In Scandinavia it is rather common in Denmark, in Sweden up to about 60°N, on Åland and in SW. Finland, with scattered localities up to the northern part of the Bothnian Gulf. It is very rare in Norway except in the area around Oslofjord.

#### ***Juncus gerardi* LOISELEUR 1809**

A widespread and variable species, differentiated into several subspecies. Always differing from *J. compressus* by anthers 1—2.2 mm long and 2—6 times as long as the filaments. The capsule is only equaling or slightly exceeding the tepals. Two subspecies of *J. gerardi* occur in Scandinavia (cf. HÄMET-AHTI 1966, SNOGERUP 1971).

#### **62. *Juncus gerardi* LOIS. ssp. *gerardi***

Perennial, mat-forming or laxly caespitose, with a rhizome of varying internode length. Stems 10—40 cm, with 0—2 basal sheaths, 4—5 subbasal leaves and 1—2 upper cauline leaves. Uppermost cauline leaf usually 3 times or more as long as its sheath. Leaves 2—25 cm long, 0.8—2.5



Fig 63. *Juncus gerardi* LOIS. ssp. *atrofuscus* (RUPR.) PRINTZ. — A: Habit,  $\times 0.5$ . — B: Outer tepal and stamen,  $\times 10$ . — Flower with immature capsule,  $\times 10$ .

Fig. 62. *Juncus gerardi* LOIS. ssp. *gerardi*. — A—C: Habit,  $\times 0.5$ . — D: Outer tepal and stamen,  $\times 10$ . — E: Flower with ripe capsule,  $\times 10$ . — F: Seed,  $\times 45$ . — G—H: Leaf transverse sections,  $\times 40$  (still thinner leaves with smaller epidermis cells are found).

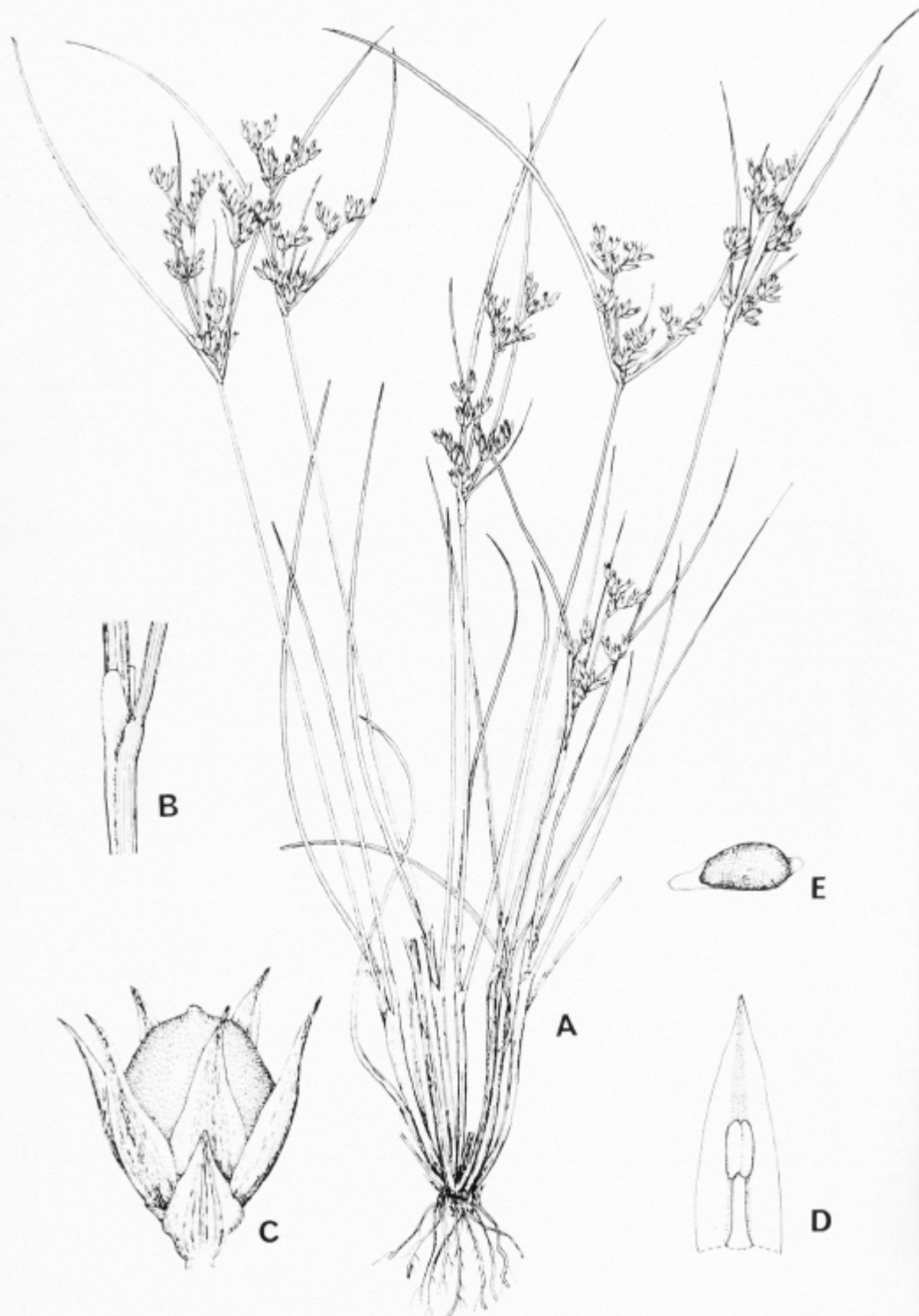


Fig. 64. *Juncus tenuis* WILLD. — A: Habit,  $\times 0.5$ . — B: Leaf base with auricles,  $\times 3$ . — C: Flower with ripe capsule,  $\times 10$ . — D: Tepal and stamen,  $\times 10$ . — E: Seed,  $\times 45$ .

mm broad, usually thick with much enlarged dorsal epidermis cells, but sometimes thin with  $\pm$  convolute margins; auricles short, broad, obtuse. Inflorescence 2—10 cm long, 10—120-flowered, lax or rarely condensed; flowers usually all single. Involucral bracteoles ovate to broadly ovate, obtuse or subacute, scarious and usually partly brown. Tepals 2.5—3 mm, equal in height or almost so, strawcoloured to dark brown, oblong to ovate or broadly lanceolate, outer ones boat-shaped and  $\pm$  cucullate; scarious margin of inner ones broad, of outer ones narrower but apically expanded. Stamens 6, 0.6—0.9 times as high as the tepals; anthers 1.2—1.7 mm, 2—3.5 times as long as the filaments. Capsule equalling or slightly exceeding the tepals, ovoidal to ellipsoidal,  $\pm$  conspicuously trigonal apically, obtuse, mucronate. Seeds 0.5—0.7 mm, ovoidal and usually slightly oblique, conspicuously c. 12-striate with weaker transverse striae.  $2n=84$ .

*J. gerardi* ssp. *gerardi* is almost entirely European. It is mainly a plant of maritime salt marshes, but occurs also in many inland localities. In the east its relations to other subspecies needs further study. In Scandinavia it occurs along the entire coasts of Denmark, Sweden, and Finland, and on the Norwegian west coast up to about 70°N. It is also known from a few inland localities.

63. *Juncus gerardi* LOIS. ssp. *atrofuscus* (RUPR.) PRINTZ 1921

Like ssp. *gerardi*, but basal sheaths usually larger. Stem much exceeding the leaves, uppermost cauline leaf usually less than 3 times as long as its sheath. Leaves flat, 1—2.5 mm broad, with moderately enlarged dorsal epidermis cells. Inflorescence  $\pm$  condensed, usually less than 7 cm long, 5—20-flowered. Involucral bracteoles broad, broadly obtuse or often notched. Tepals dark brown, 3—4 mm long. Anthers 1.5—2.2 mm, 3—4(—5) times as long as the filaments.

Ssp. *atrofuscus* occurs along the Euro-

pean Ice Sea coasts and on the Norwegian west coast down to about 69°N. Transitional forms to ssp. *gerardi* are found in NW. Norway and on inland localities in N. Finland (cf. HÄMET-ATHI 1966).

64. *Juncus tenuis* WILLDENOW 1799

(Syn. *J. macer* S. F. GRAY 1821)

Perennial, densely caespitose. Stems 10—80 cm, with a few basal sheaths and 2—3 subbasal leaves. Leaves flat, often convolute, 1—1.5 mm broad; auricles long, broad, obtuse, very thin and in dried material often incomplete. Inflorescence usually lax, rarely condensed to a few clusters, 5—40-flowered. The two lowest bracts leaflike, usually both exceeding the inflorescence. Tepals narrowly ovate, aristate, the outer ones slightly longer, 3.5—4 mm. Stamens 6, c.  $\frac{1}{2}$  as high as the tepals; anthers 0.7—0.8 mm,  $\frac{1}{2}$ — $\frac{2}{3}$  as long as the filaments. Capsule shorter than the tepals, broadly ovoidal,  $\pm$  trigonal in the upper part, apically abruptly obtuse or truncate, shortly mucronate. Seeds 0.3—0.4 mm, obliquely ovoidal, with very faint ornamentation; seed-coat persistent, forming one short appendage.  $2n=84$ , but also e.g.  $2n=30$  reported in literature.

*J. tenuis* is most probably native only in N America, but introduced by man in all temperate areas. Its seed-coat becomes sticky as wet, and forms a very effective aid in dispersal. In Scandinavia *J. tenuis* was first found in 1843 in Denmark, but has most probably been introduced independently on several places later on. It is now rather common and increasing in frequency in Denmark, S. Sweden, and Norway up to about 60°N, with scattered localities further north. It has not yet reached its maximum distribution in the area, and its advances should be followed.

LITERATURE CITED

- HÄMET-ATHI, L. 1966. Variation of *Juncus gerardi* Lois. in northern Fennoscandia. — Ann. Bot. Fenn. 3: 391—398.  
 SNOGERUP, S. 1971. Juncaceae. — In K. H. RECHINGER (Ed.), Flora Iranica, Lf. 75. — Graz.

# The Disk and its Vasculature in the Flowers of some Dicotyledons

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## ABSTRACT

RAO, V. S. 1971. The disk and its vasculature in the flowers of some dicotyledons. — Bot. Notiser 124: 442—450.

In some dicotyledons, the disk is non-vascular. In others, it is vascularized to varying degrees. There is a great variety in the method of vascular supply to the disk. Its traces may arise from the petal traces or stamen traces or gynoecial traces, or from the receptacular stele directly. The vascular supply to the disk may be from one or more of the above mentioned sources. The view is advocated that the disk may not always be sought to be interpreted as a modification of some of the typical parts of the flower.

## INTRODUCTION

FAHN (1952, 1953, 1967) gave a topographical classification of nectaries and also dealt with some of the histological features of the nectar secreting tissue. FREI (1955) dealt with the nature of the conducting tissue within the nectary — whether it is made up of xylem or phloem or both. The present paper is written from an entirely different angle, and shows the immense variety seen in the *origin* of the vascular supply to the disk. The term "disk" is preferred by the writer as it refers to a morphologically distinguishable entity, without implying anything about its functions.

Floral disks have been interpreted, without sufficient evidence in most cases, as modified staminodes or carpelodes or as receptacular outgrowths. In fact, some workers took it for granted that a disk associated with the androecium must represent staminodes; that one associated with the gynoecium must represent carpelodes; and that one not closely associated with either must be an outgrowth of the receptacle. In a number of dicotyledons with

superior ovaries a disk is present either close to the base of the ovary or close to the bases of the stamens; or it may be present between these two whorls. In many species it is quite prominent and visible to the naked eye. At the other extreme, there are species in which only a microscopical examination would reveal whether a disk is present or not. Usually the disk is annular or cushion-like, and entire or lobed. It may be free from the ovary wall as well as from the outer floral parts. On the other hand, it may be partly or completely adnate to the inner surface of the corolla tube or floral tube, or to the base of the ovary. In many epigynous flowers also a disk is present, but it is at the top of the ovary, surrounding the base of the style. It may be free from the style and corolla; or it may be fused partly or completely with the style or with the inner surface of the corolla tube.

Whether it be in flowers with superior ovaries or with inferior ovaries, the disk differs from the surrounding tissues, being made up of small, compactly arranged, deep-staining cells. DAWSON (1936) distinguished between (a) cushions, glands or

emergences with a secretory function and (b) those which are secretory, vestigial organs. There is an implication in many publications that the former type are without any vascular supply, whereas the latter have a reduced vascular supply of the organs from which they were derived in evolution. A detailed study of the vascular supply to the floral disk has given a large amount of information which leads to a re-orientation of our ideas about this structure. In the following account, the various examples given are mostly from those families which have been personally investigated by the author.

## OBSERVATIONS

The disk is non-vascular in *Neuracanthus sphaerostachys* (NEES) DALZ., *Blepharis maderaspatensis* (L.) ROTH., *Hypophila serphyllum* (NEES) T. ANDERS., *H. polysperma* (ROXB.) T. ANDERS., *Fittonia argyrea* E. COEM., *Hemigraphis colorata* HALLIER FIL., *Crossandra infundibuliformis* (L.) NEES and *Peristrophe bicalyculata* (RETZ.) NEES of Acanthaceae (RAO 1953). MOORE (1936) reported non-vascular disks in *Diosma* and *Feronia elephantum* of Rutaceae as well.

Where the disk is vascularized, the method of vasculature and the extent of vasculature show all possible types of variations, even within one and the same family. In *Dictamnus* (MOORE 1936) the disk supply is from the fused calyx laterals and the corolla traces. ARBER (1936) described the nectary supply in *Ranunculus* as from the median bundle of a petal, often with the addition of components from the main laterals. The vascular traces to the disk are derived from the petal traces and the stamen traces in *Thunbergia alata* BOJ. ex SIMS. (Fig. 1 A), *Lepidagathis trinervis* WALL. ex NEES, *L. cristata* WILLD., *Barleria lupulina* LINDL., *B. prionites* L., *B. strigosa* WILLD., *B. alba* TODD, *B. rosea* Hort., and *Aphelandra pectinata* WILLD. (RAO 1953). In *Haplophragma adenophyl-*

*lum* (WALL. ex G. DON) DOP. of Bignoniaceae also the vascular supply is similar but the disk is adnate to the corolla tube for some distance (Fig. 1 B; RAO 1954). Branches arising from the stamen traces supply the disk in *Asystasia gangetica* (L.) T. ANDERS. (Fig. 1 C), *A. dalzelliana* SANT., *A. chelonoides* NEES, *Eranthemum laxiflorum* GRAY (Fig. 1 D), *Ruellia tuberosa* L., *Dipteracanthus patulus* (JACQ.) NEES, *D. cernuus* (ROXB.) SANT., *Graptophyllum pictum* GRIFF., *Pseuderanthemum bicolor* (SCHRANK) RADLK. ex LINDAU, and *Odon-tonema nitidum* O. KTZE. of Acanthaceae (RAO 1953), *Citrus* (MOORE 1936) and some members of Aurantiaceae (TILLSON & BAMFORD 1938) in Rutaceae and some members of the Polemoniaceae (DAWSON 1936). In *Acacia pennata* WILLD. and *Calliandra haematocephala* HASSK. (Fig. 1 E, F) of Mimosaceae, an annular disk is adnate to the inner surface of the stamen tube, and its vascular supply is by inward branches from the stamen traces (RAO, SIRDESHMUKH & SARDAR 1958). In *Calliandra haematocephala*, as compared with *Acacia pennata*, the disk traces are more and the stamen traces are fewer. The central flower of the inflorescence of *Samanea saman* (JACQ.) MERRILL has a prominent lobed disk and it is supplied by inward branches of the stamen traces (Fig. 2 A). In *Cajanus cajan* (L.) MILLSP. of Papilionaceae, the basal part of the disk is adnate to the inner surface of the "calyx tube". The large, tubular stamen strands bifurcate into the stamen traces and the disk traces. The latter, at their base, are as prominent as the stamen traces (Fig. 2 B—D). A similar adnation of the disk to the calyx tube is seen in *Tephrosia purpurea* of the same family, but the vascular supply to it is as slender inward branches from the stamen traces (RAO et al. 1958). *Thunbergia erecta* (BENTH.) T. ANDERS. (Fig. 2 E), *Asteracantha longifolia* (L.) NEES, *Phlogacanthus thyrsoiflorus* NEES and *Ecbolium linneanum* KURZ have the disk supplied from petal traces, stamen traces, and also by branches from the re-



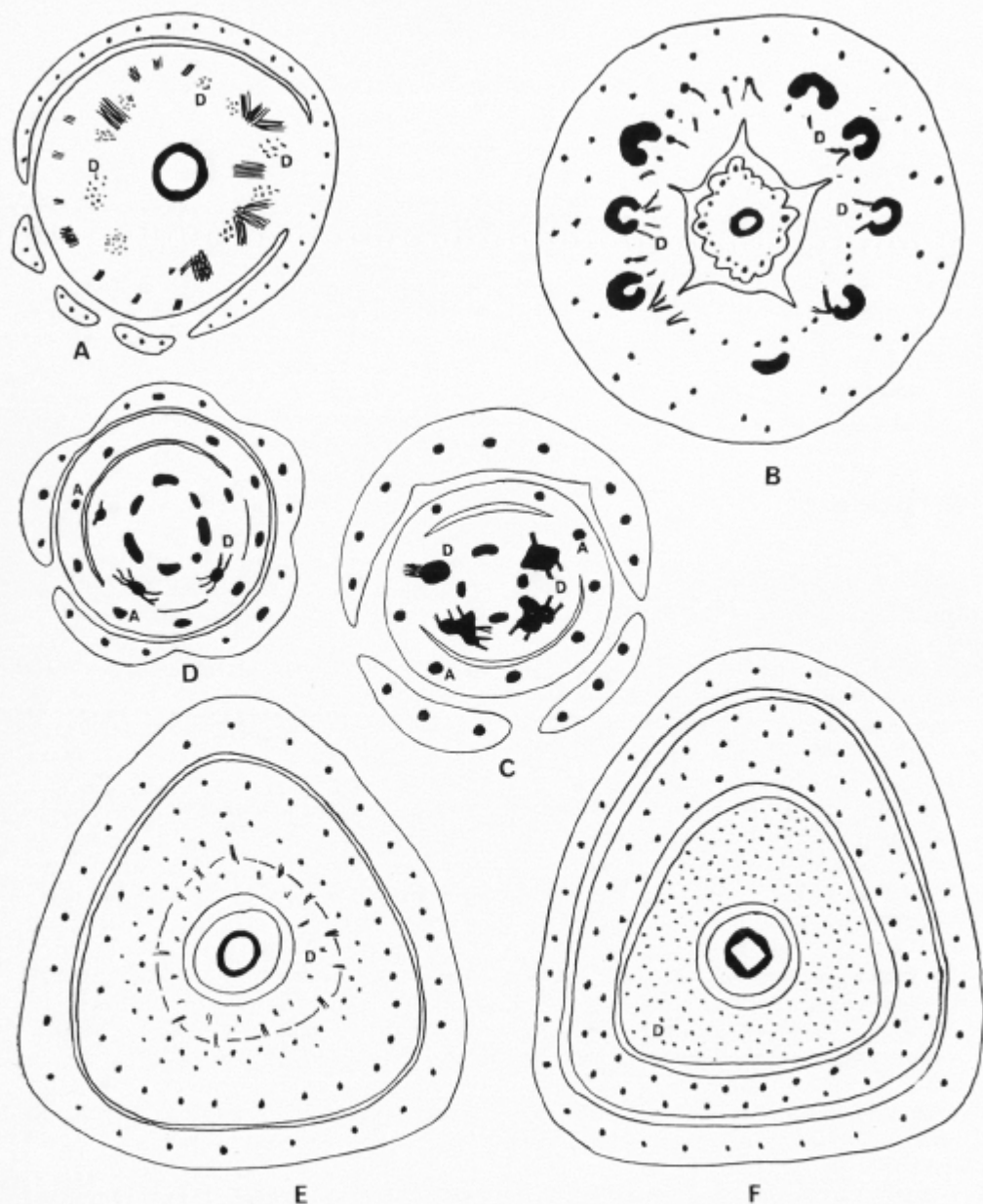


Fig. 1. A: *Thunbergia alata*. Origin of disk traces from the petal traces and stamen traces. — B: *Haplophragma adenophyllum*. Disk seen adnate to corolla tube, and supplied by inward branches from the petal traces and stamen traces. — C: *Asystasia gangetica*. The disk supply is from a branch of the stamen trace, but the branch supplying the disk is much larger than the one supplying the stamen. One of the stamen strands is seen dividing into a small stamen trace and a large disk trace. Three other large disk traces are seen bearing small branches. — D: *Eranthemum laxiflorum*. Almost as in the previous species, but the disk traces are small. — E—F: *Calliandra haematocephala*. — E: Disk adnate to inner surface of the stamen tube, and its vascular supply arises as inward branches from the stamen traces. — F: The disk has become free from the stamen tube. — A and D in the figures stand for stamen traces and disk traces, respectively.



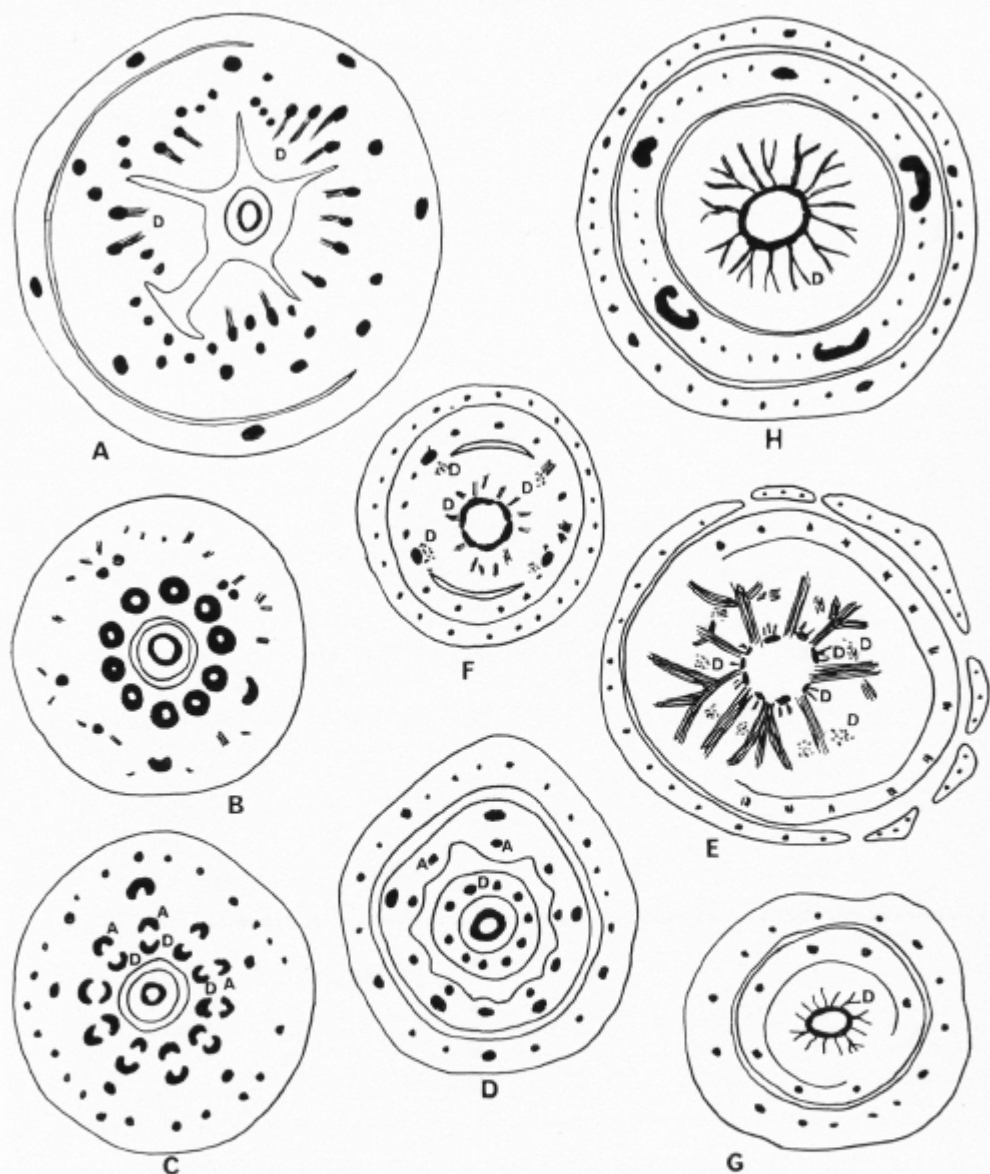


Fig. 2. A: Central flower of the inflorescence of *Samanea saman*, with disk lobed and adnate to the inner surface of the stamen tube, and its vascular supply arising as inward branches of the stamen traces. — B—D: *Cajanus cajan*. — B: Floral tube ("calyx tube") separated from the gynoeical stalk. Forming an innermost ring within the floral tube are ten tubular vascular strands, which higher up divide to supply the stamens and the disk. — C: The tubular strands have bifurcated into the stamen traces and the disk traces. — D: Annular disk, with ten bundles separated from the corolla tube. — E: *Thunbergia erecta*. Disk traces arise from the petal traces, stamen traces, and also from the vascular cylinder. — F: *Thunbergia fragrans*. Disk supply from the stamen traces and from the vascular cylinder. — G: *Andrographis paniculata*. Disk traces arise from the receptacular vascular cylinder. — H: *Spathodea campanulata*. Disk traces from a considerable portion of the length of the vascular cylinder above the origin of the stamen traces.

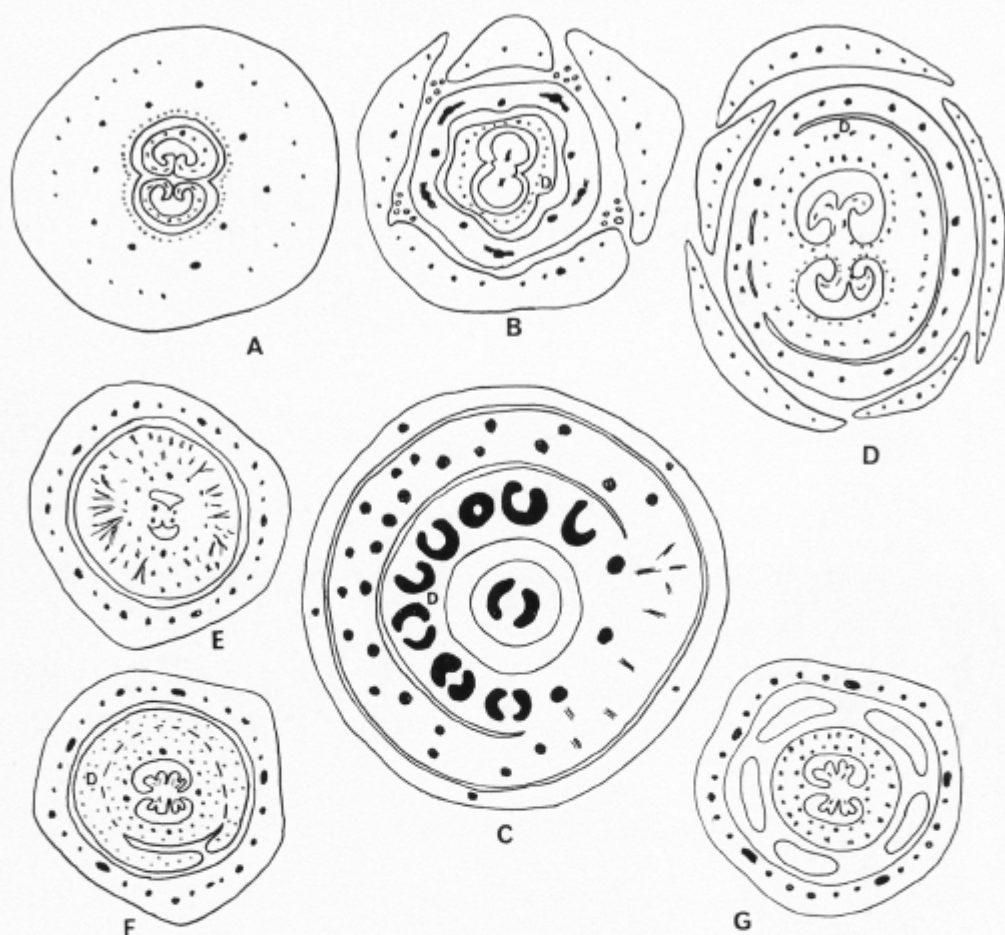


Fig. 3. A—B: *Aganosma cymosa*. — A: Disk at its base adnate to the floral tube. — B: Disk separated from the floral tube. — C: Central flower of the inflorescence of *Albizzia lebbek* shows the annular disk with its prominent vascular supply. — D: *Vallaris solanacea*. Disk seen adnate to ovary. Some of its vascular bundles are derived as branches of the gynoecial strands while others are derived from the vascular cylinder. — E—G: *Cerbera thevetia*. Disk partly adnate to ovary, and its vascular supply also as in *Vallaris solanacea*, but the gynoecium receives extra bundles which appear to be some of the disk traces themselves that run into the ovary wall instead of into the disk.

ceptacular vascular cylinder just above the origin of the stamen traces. In *Thunbergia fragrans* ROXB. (Fig. 2 F) and *Justicia simplex* D. DON of Acanthaceae, *Oroxylum indicum* VENT. of Bignoniaceae and *Sesamum indicum* L. of Pedaliaceae, the disk supply is from the stamen traces and the receptacular stele above them (RAO 1953,

1954, 1955). The vascular traces for the disk arise only from the stele above the origin of the stamen traces in *Andrographis paniculata* (BURM.) WALL. ex NEES (Fig. 2 G), *Sanchezia nobilis* HOOK. FIL., *Eranthemum capense* L., *E. roseum* (VAHL.) R. BR., *E. nervosum* (VAHL.) R. BR., *Odon-tonema bracteolatum* O. Ktze., *Rungia*

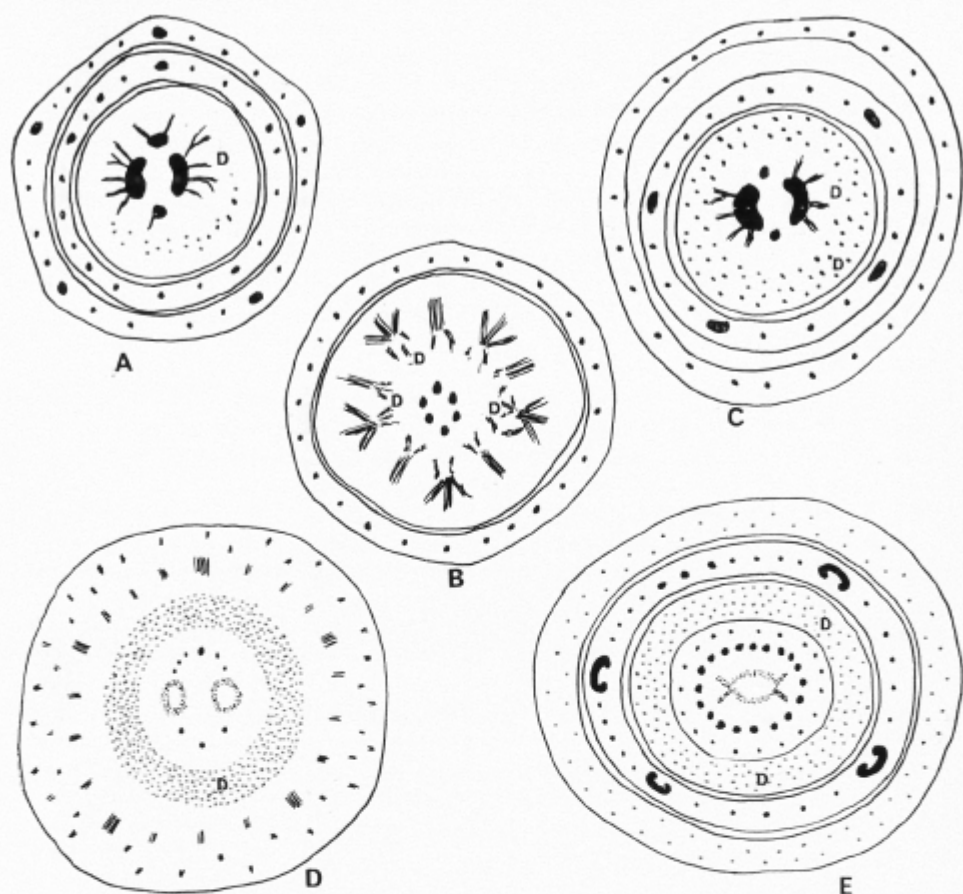


Fig. 4. A: *Tecomaria capensis*. Disk traces from the basal parts of the gynoecial traces. — B—C: *Doxantha unguis-cati*. Origin of the disk traces from the petal traces, stamen traces, and also from the basal parts of the gynoecial traces. — D—E: *Kigelia pinnata*. — D: Shows many disk traces in the receptacle. — E: The annular disk has become separated from the corolla tube and the base of the ovary. Within the ovary wall can be seen the outer extra ring of bundles which are some of the disk traces that have diverted their course and run into the ovary wall.

*laeta* CL., *R. parviflora* NEES, *Adhatoda vasica* NEES, *Dicliptera micranthus* NEES, *Justicia betonica* L. and *Beloperone oblongata* LINDL. of Acanthaceae (RAO 1953), *Spathodea campanulata* BEAUV. (Fig. 2 H) and *Tebebuia pentaphylla* HEMS. of Bignoniaceae (RAO 1954), *Pedaliium murex* L. of Pedaliaceae (RAO 1955) and in *Ruta* (MOORE 1936).

In *Aganosma cymosa* G. DON of Apocy-

naceae (RAO & GANGULI 1963) the lower part of the disk is adnate to the floral tube and the vascular cylinder divides into large outer disk bundles and small inner gynoecial bundles (Fig. 3 A—B). Only the central flower of the inflorescence of *Albizzia lebbek* has a disk, for supplying which the vascular cylinder splits into prominent disk strands and the bundles for the gynoecium (Fig. 3 C). Out of all the plants

personally studied by the author, *Thunbergia grandiflora* (ROXB. ex ROTTL.) ROXB. is the only one where the disk is supplied by the sepal traces, petal traces, stamen traces and the receptacular stele above them (RAO 1953).

At a variable distance from the level of origin of the staminal traces, the receptacular stele divides to produce the gynoeceal traces. In *Pyrostegia ignea* PRESL and *Stenolobium stans* SEEM. of Bignoniaceae (RAO 1954), *Martynia diandra* GLOX. of Pedaliaceae (RAO 1955) and *Vallisneria spiralis* L. of Apocynaceae, the disk supply arises from the vascular cylinder and also from the basal parts of the carpellary traces. In *Vallisneria spiralis* the disk is partly adnate to the ovary. The disk of *Cerbera thevetia* L. (Fig. 3 E—G) of Apocynaceae is somewhat similar to that of *Vallisneria spiralis* but the gynoeceum receives extra bundles which appear to be some of the disk traces that have diverted from their course and entered the ovary instead of the disk.

*Tecomaria capensis* SPACH. (Fig. 4 A), *Phyllarthron comorense* DC., and *Millingtonia hortensis* L. FIL. have the disk supplied by branches from the gynoeceal traces. However, in *Doxantha unguis-cati* REHD. (Fig. 4 B—C) and *Kigelia pinnata* DC. (Fig. 4 D—E) of the same family, branches from the petal traces, stamen traces, receptacular cylinder and bases of some of the gynoeceal traces supply the disk. In *Kigelia pinnata* (Fig. 4 D—E), *Spathodea campanulata* BEAUV., *Oroxylum indicum* VENT., *Tebebuia pentaphylla* HEMSL., *Phyllarthron comorense* DC. and *Doxantha unguis-cati* REHD., some of the disk traces run into the ovary to form an outer ring of bundles in the ovary wall, the regular carpellary bundles forming an inner ring.

## DISCUSSION

The above examples amply prove that even within one and the same family there

can be certain important variations in the vascular supply to the disk. Each species, however, has a definite, constant method by which traces are sent into the disk. In some of the Mimosaceae there are indications that the disk, which is adnate to the inner surface of the staminal tube and vascularized by branches from the stamen traces, might have been derived from the inner stamens. A sort of an inverse ratio is also seen in them between the amount of vascular supply to the disk and the number of stamens. But there are also a few plants of this family where the disk traces and the gynoeceal traces have a common origin. In some of the Caesalpiniaceae the disk is adnate to the inner surface of the calyx tube. It may be non-vascular or be vascularized by branches from the stamen traces. Similarly in some Papilionaceae also, the inner surface of the calyx tube is disk-like. It may or may not be free in the upper region. The stamen traces may simply run through this disk zone in their upward transit, or may send a few branches into it. MOORE's (1936) observations as well as interpretations on the floral anatomy of Papilionaceae have already been shown to be wrong and untenable (RAO et al. 1958). The structure to which the disk is adnate has no relation to the source of its vascular supply. As mentioned earlier, in a few Bignoniaceae, some of the disk traces run through the disk for some distance, suddenly bend inwards and run into the ovary. Within the ovary wall they form a ring external to that of the normal ring of gynoeceal bundles. This feature itself, however, is not enough evidence for regarding the disk in those plants as of carpelodes. One would have to make unwarranted assumptions in such a case, even to the extent of imagining more than one whorl of carpels in the ancestral state. WOODSON and MOORE (1938) described the occurrence of bundles comparable to dorsal and ventral bundles of carpels within the disk of some members of Apocynaceae, and interpreted the disk in that family as of carpelodes. The

present author and his students studied the floral anatomy of many members of Apocynaceae but failed to find anything comparable to the observations of WOODSON and MOORE, and hence cannot agree to that interpretation.

The very great variety seen in the vascular supply to the disk in such a natural family as Acanthaceae — even closely related species sometimes showing different types of vascular supply — makes one hesitant of interpreting the disk as derived from any of the typical floral whorls. The usual practice has been to interpret the disk in any family as a receptacular outgrowth if it does not show any obvious derivation from the carpels or stamens. An assumption which must have been guiding all interpretations is that the floral whorls must be typically four in number. Why the disk, when present, cannot be regarded as a fifth type of floral organ is not clear, without its being always regarded as a modification of something else. Calling the disk as merely "receptacular" in nature might be just a safe way of putting the matter without committing oneself. Taking into account the fact that (1) many plants have quite well developed disks in their flowers and that (2) there is a great variation in the origin of the vascular supply to them in those cases where they are vascularized, it is best to regard the disk as a "fifth" type of floral organ, independent in origin from the others, and *sui generis*. One can say that where it is vascularized, its traces arise from whatever strands that happen to be conveniently located for that purpose. The calyx is too far away from the normal position of the disk and it is only very rarely that we find any connection between calyx traces and the disk supply. The most convenient are the petal traces, stamen traces and the receptacular stele above them. It is again only in a few cases that the disk traces arise from the bases of the carpellary strands. Much would depend upon the location of the disk and its degree of development. In the case of vascularized disks, what matters

is that they have to receive a vascular supply. It is immaterial whether the disk supply arises from the vascular strands of one or more of the floral whorls or even from the receptacular vascular cylinder. Otherwise, from the examples given from Acanthaceae it would be noticed that it is impossible to interpret the disk in many cases as a modification of any of the typical floral parts. This hypothesis does not completely exclude the possibility that in very few instances the nectary might be obviously a modified floral part. But it is certain that in the majority of cases the disk is an organ *sui generis* getting its vascular supply from whatever traces are conveniently located. This expression of "convenient location" would apply not only for the position of the disk within the flower but also for the relative positions or levels where the traces to the different floral parts arise from the receptacular stele.

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# The Genus *Oftia* Adans. and its Systematic Position

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## ABSTRACT

DAHLGREN, R. and RAO, V. S. 1971. The genus *Oftia* Adans. and its systematic position. — Bot. Notiser 124: 451—472.

The genus *Oftia* ADANS. has usually been regarded as belonging to Myoporaceae. It is investigated with regard to distribution, external morphology, variation, anatomy, pollen structure, etc. It is compared with *Myoporum* with which it has usually been placed in text-books and floras in recent years. Some similarities, but also numerous differences are pointed out. In many features closer agreement is found with the genus *Teedia* RUDOLPHI in Scrophulariaceae. This includes vegetative as well as floral characters, characters of the fruit and seed wall, pollen structure and anatomical details. The fruit of *Oftia* is a drupe, that of *Teedia* is either a berry or a drupe. In *Teedia* the ovules (and seeds) are much more numerous than in *Oftia*, and in connection with this there are some conspicuous differences in the vascular anatomy of the flower. The conclusion arrived at is that it would be more justifiable to place *Oftia* in Scrophulariaceae than in Myoporaceae. The conspicuous intercontinental disjunction of the latter family is thereby also partly done away with.

## INTRODUCTION

In association with families which have highly disjunctive distributions on the southern continents (Restionaceae, Proteaceae, Haemodoraceae, Cunoniaceae etc.) one will also usually find Myoporaceae. In the case of this family, however, doubts have several times been raised on its homogeneity. GOOD (1946 p. 66), for example, regarded Myoporaceae as a "very doubtfully natural group", and TAKHTAJAN (1969 p. 239) remarked that "*Oftia* is very isolated in the family".

The family Myoporaceae as it now stands consists of 5—6 genera in all, the majority of species being found in Australia. Except for *Zombiana*, a monotypic, imperfectly known genus reported from western tropical Africa, *Oftia* is the only genus in this family indigenous to Africa. The distribution of Myoporaceae was

mapped by HUTCHINSON 1946 p. 43 and 1959 p. 504.

The present study was undertaken partly to determine whether *Oftia* is actually most closely related to the other members of Myoporaceae, or whether there is some other group exhibiting a more satisfactory combination of similarities that can better indicate the position of the genus.

## THE GENUS *OFTIA* ADANS.

### Synonymy at the Generic Level

*Oftia* ADANSON 1763 p. 199, given as a substitute for "*Jasminum* . . ." COMMELIN, a pre-Linnéan phrase name, and for *Lantana* LINNAEUS pro parte.

*Lantana* LINNAEUS 1753 p. 628, pro parte, the type excluded.

*Spielmannia* MEDIKUS 1775 p. 196.

*Batindum* RAFINESQUE 1838 p. 81, given as a substitute for *Lantana* L. pro parte without knowledge of *Oftia* or *Spielmannia*.

The genus *Oftia* or its synonyms has been placed in various families. *O. africana* was originally described under *Lantana*. It thus belonged naturally to Verbenaceae, where it was also placed in ENDLICHER 1838 p. 635, SCHAUER 1847 p. 526, LINDLEY 1853 p. 664, and HARVEY 1868 p. 289.<sup>19</sup>

In the works of BOCQUILLON 1861 and BAILLON 1888, *Oftia* was moved from Verbenaceae to Scrophulariaceae because of the structure of its gynoeceum. It was included in Myoporaceae by BENTHAM and HOOKER 1876 p. 1126, by WETTSTEIN 1895 p. 360, by ROLFE 1912 p. 93, by MARLOTH 1925 p. 149, and also by DE VOS 1947, SALTER 1950, PHILLIPS 1951, and many other authorities.

JUNELL (1934 p. 61), who examined the morphology of the ovary and ovule in Verbenaceae, came to the conclusion that *Oftia* should not be placed in that family. DE VOS (1947), who studied the embryology and seed structure of the genus, found some conspicuous differences between *Oftia* and the other members of Myoporaceae examined, but did not consider it necessary to remove *Oftia* from the family on these grounds.

### Morphology of *Oftia*

The genus consists of shrubs and shrublets usually 20—70 cm high, occasionally on steep slopes more than 2 m high. The branching system is monopodial. The ends of the branches, which bear flowers in the leaf axils, continue to grow the following season. The branches are decumbent to ascending.

The leaves (Fig. 1) are closely set, especially in *O. revoluta*, more sparsely in the other two species. They are opposite in *O. glabra*, usually also in the other two species but sometimes alternate, at least in *O.*

*africana*. A distinct petiole is lacking but the leaf-base is somewhat narrowed in at least *O. glabra*. The lamina is lanceolate, ovate, elliptic or sometimes almost circular, acute or acuminate at the apex, the margins variably closely dentate or serrate. The sides of the leaf-base are always more or less decurrent, merging at the base into more or less distinct ridges on the young branches. The margins of the leaves are revolute especially in *O. revoluta*, to a lesser degree in forms of *O. africana*.

In *O. africana* and *O. revoluta* the leaves and branch ends are covered with multicellular hairs of varying length, the shorter of which at least having a globose apical head of few to several cells (Fig. 6 C) separated by cell walls perpendicular to the epidermis. In *O. glabra* these hairs are absent.

The flowers are pedicellate or sessile. Bracteoles are usually wanting but present in forms of *O. glabra* and, very rarely, in *O. africana*. When present, they are narrowly triangular to linear, less than 1.5 mm long, and of the same general texture as the ends of the calyx lobes.

The calyx is deeply and almost regularly lobed, the 5 lobes being broadly or narrowly linear to subulate and acute to acuminate. The lobes are covered with glanduliferous hairs and are not particularly stiff in *O. africana* and *O. revoluta*; firmer, more carnosely and glabrous in *O. glabra*.

The corolla is white and almost actinomorphic. It is made up of a rather narrowly cylindrical tube often slightly dilated towards the top, and of 5 rectangular to obovate, truncate or rounded lobes that overlap in bud as shown in Fig. 2 F. The corolla tube is glabrous or often shortly glandular-puberulous on the outer side, and closely covered with hairs pointing forward on the upper half of the inner side.

The stamens are 4 in number, a gap being present in the upper median position below the sinus between the upper two corolla lobes. The filaments start halfway up the tube. They are relatively short and slender. The anthers are narrowly oblong

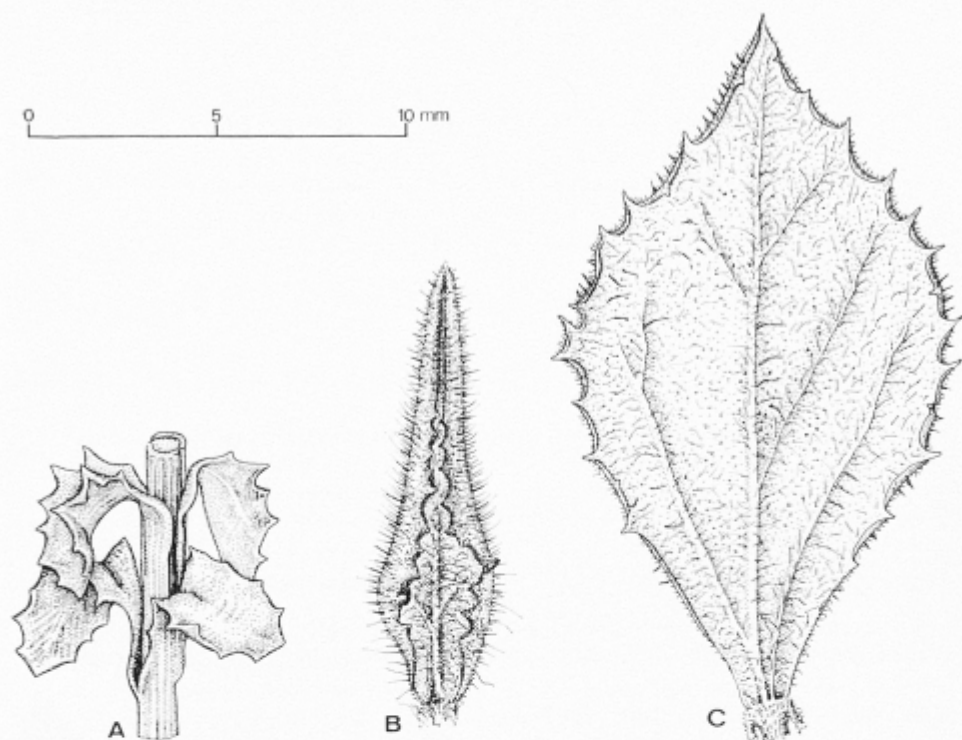


Fig. 1. Leaves of the three species of *Oftia*. — A: *O. glabra*; COMPTON no. 20155. — B: *O. revoluta*; ACOCKS no. 19354. — C: *O. africana*; DAHLGREN & STRID no. 2731. — All  $\times 5$ .

and comparatively large, about 1 mm long or more.

As shown in Fig. 2 F, the hairs of the inner side of the corolla tube probably prevent the pollen from reaching the stigma which comes no higher than the base of the anthers during anthesis. The stigma, which is slightly bipartite and oblique (Fig. 2 A—C), is directed upwards in the flower opposite the gap between the anthers (Fig. 2 F). According to SCOTTELLIOT (1891) the flowers are visited by members of Coleoptera and Diptera but the main pollinators were believed to be night-flying moths. The flowers are also visited by butterflies. It is difficult to explain why the hairs in the floral tube would not prevent the pollen brought by the insect visitors from reaching the stigma.

The pistil is bicarpellary, with a two-

celled, rectangularly ovoid ovary with no additional septa inside. The style is short and the stigma directed upwards and coming no further than to about halfway up the corolla tube. The placenta is central, with 4(—6) (in *O. glabra* sometimes possibly fewer) pendulous ovules in each locule. The ovules are arranged in superposed pairs and emerge from the upper part of the septum.

The fruit is a globose, black drupe with two (or by abortion one) cells with extremely hard, thick inner walls. See Fig. 2 J.

The seeds have a stout, clavate funiculus and a hard, black, somewhat rugous testa due to the lignified walls of large, conical cells (Fig. 6 E—G) which according to DE VOS 1947 (Fig. 61—62) represent a tapetum layer.

**Key to the Species**

- 1 A. Plant entirely glabrous . . . . . *O. glabra*  
 1 B. Plant covered with short to long hairs on leaves and branchlets.  
 2 A. Leaves lanceolate, with strongly revolute margins, usually less than 5 mm broad, and with rather long hairs . . . . . *O. revoluta*  
 2 B. Leaves narrowly ovate to circular, with only slightly (seldom more strongly) revolute margins, usually more than 5 mm broad, with short to moderately long glanduliferous hairs . . . . . *O. africana*

**PRESENTATION OF THE SPECIES*****Oftia glabra* Compt.**

COMPTON 1931 p. 309.  
 Original collection: COMPTON no. 2812, Witteberg, 4000 ft. (NBG).

Shrublet decumbent. Branches ascending, c. 50–80 cm long, glabrous, light greyish-brown, at least on young parts with 4 distinctly demarcated ridges approaching each other in pairs towards basal parts of internodes. — *Leaves* (Fig. 1 A) opposite, 4.5–12 mm long and 2.2–5.2 mm broad, elliptic to obovate, thickly coriaceous, rigid, glabrous, slightly recurved along the mid-vein, sessile (or especially larger leaves narrowing at base into a petiole-like section up to about 1 mm long). Margins on each side with 6–12 deltoid, acute teeth often pointing in diverging directions. Apex with a deltoid, acute or subacute, usually somewhat recurved tooth. Sides more or less incurved, decurrent at base, forming prominent branch ridges each expanded somewhat below the leaf-base into an ear-like lobe (Fig. 1 A). — *Pedicel* usually 1.5–3 mm long, glabrous. — *Bracteoles* present in some of the material studied; when present situated on middle of pedicel, linear, thick and carnos, up to 1.5 mm long, acute to apiculate, glabrous. — *Calyx* divided to about 1 mm from the base; lobes 1.5–2.5 mm long, linear, subterete, acute to apiculate (in one of the collections apically bifid on some flowers), glabrous. — *Corolla* whitish, externally glabrous; tube about 6–7 mm long; lobes about 2.5 mm long, rounded, obovate or almost circular. —

*Anthers* about 1 mm long. — *Ovary* with 7–8 ovules. — *Fruit* a globose drupe, when dry about 3 mm in diameter.

**DISTRIBUTION.** As far as known, restricted to the Witteberg Range, where the species has been collected in the Whitehill region at an altitude of 3500–4000 feet, on slopes which in one collection were given as facing north, implying rather dry conditions.

**COLLECTIONS STUDIED.** COMPTON nos. 8002 and 20155 (NBG).

**REMARKS.** According to COMPTON (1931), bracteoles are lacking in the species. In the collections studied, bracteoles are usually lacking on the flowers in COMPTON no. 8002, usually present but of varying length in COMPTON no. 20155, where the pedicels and calyx lobes are also somewhat longer than in the former collection. The difference between the collections is marked and probably genetically conditioned. Bracteoles are almost constantly lacking in the other two species of the genus, and have not been reported previously in the genus.

According to COMPTON (op. cit.) the ovules of *O. glabra* were only 2 to 3 in each of the locules, but in the material studied by me they were usually 4 as in the other species.

***Oftia revoluta* (E. Mey.) Bocq.**

BOCQUILLON 1861 p. 12; ROLFE 1912 p. 94; KRÄNZLIN 1929 p. 124.

*Spielmannia revoluta* E. MEY.; MEYER 1837 p. 274; SCHAUER 1847 p. 526. — Original col-

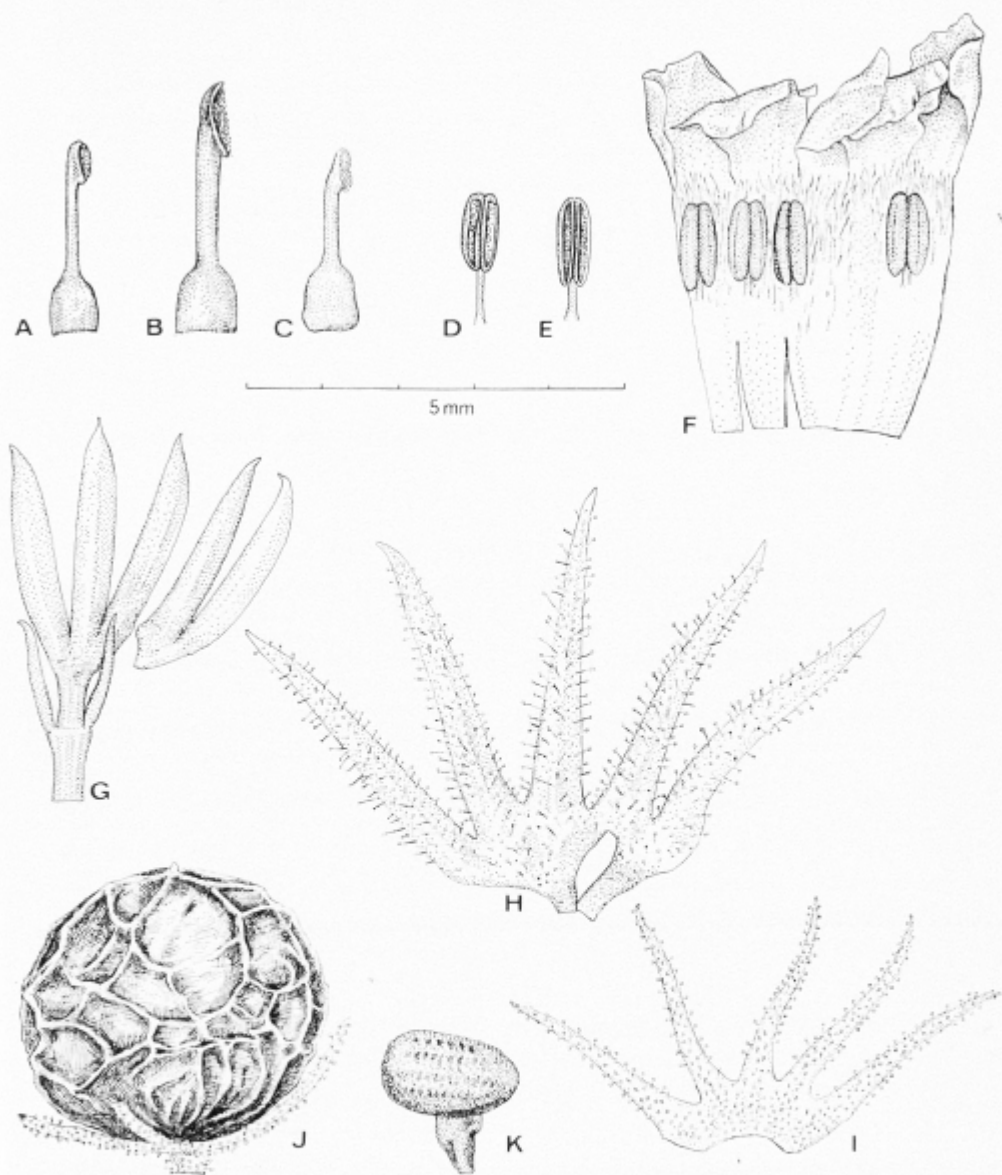


Fig. 2. Details of flowers and fruit in species of *Oftia*. — A, D, and G: *O. glabra*; COMPTON no. 20155. — B, E, and H: *O. revoluta*; ACOCKS no. 19354. — C, F, and I—K: *O. africana*; DAHLGREN & STRID no. 2731. — A—C: Pistils. — D—E: Stamens. — F: Corolla of bud split open to show stamens. — G—I: Calices and pedicels when present. — J: Drupe in dried condition. — K: Seed. — All  $\times 10$ .



lection: DRÈGE, Ellebogsfontein, Little Namaqualand.

(*Spielmannia desertorum* ECKL. & ZEYH. ex SCHAUER in DE CANDOLLE 1847 p. 526, mentioned also in ROLFE 1912 p. 94, was cited as a synonym of *S. revoluta* and thus not validly published.)

A woody shrub up to 1.5 m high. Branches ascending, with light-brown or greyish bark and with prominent leaf scars on the defoliated parts 1 to 3 years old. Young branches closely and imbricately leafy, villous-lanate with shiny, multicellular hairs up to 2 mm long. Sides of leaf bases persistent and continuing into distinct to prominent stem ridges. — *Leaves* opposite or alternate, closely set, erect, in 4 rows (those in the same longitudinal row spaced 3.5–12 mm from each other), 7–12 mm long and 2–5 mm broad, broadly lanceolate but appearing narrowly lanceolate due to the markedly revolute margins. These with 8–15 shortly deltoid, mucronate teeth spreading down- or inwards, occurring more sparsely in apical third of leaf (Fig. 1 B). Apex shortly mucronate. Base laterally decurrent into branch ridges. Leaves covered with short, glanduliferous hairs on the surface and longer hairs, often without apical gland, especially closely on mid-vein of lower side. — *Flowers* similar to those of *Oftia africana*. — *Bracteoles* wanting. — *Pedice* short or very short, up to 0.5 mm long. — *Calyx* deeply divided; lobes linear, 3–4.5 mm long and about 0.4 mm broad, flat, pointed, not particularly stiff, covered with glanduliferous hairs. — *Corolla* tube about 4.5–7 mm long, with glanduliferous hairs on outer side; lobes obovate-rectangular, up to 4 by 2.5 mm, somewhat broader towards the truncate or rounded apex than towards the base. — *Stamens* and *pistil* as in the other species. — *Drupe* globose, in dry condition about 2.5 mm in diameter.

**DISTRIBUTION.** Restricted to the Little Namaqualand Division, where the species occurs on the slopes of the Khamiesberg and on hillsides in the adjacent regions.

According to records of the collection ACOCKS no. 19354, the species occurs in rhenosterbush vegetation, and it is probably also found in the driest types of sclerophyll macchia.

**COLLECTIONS STUDIED.** Little Namaqualand: Between Pedroskloof and Liefontfontein. DRÈGE (LD); Kasparskloof, Ellebogsfontein, etc., DRÈGE (LD); Khamiesberg, ECKLON & ZEYHER (SAM); Wolveton, PHILLIPS (LD); Klipfontein, COMPTON 5516 (NBG); Brakdam, SCHLECHTER (S), BOND 1142 (NBG); Modderfontein, WHITEHEAD (S); Near O'Okiep, BOLUS (SAM).

#### *Oftia africana* (L.) Bocq.

BOCQUILLON 1861 p. 11; BAILLON 1888 p. 398; SCOTT-ELLIOT 1891 pp. 371–372; ROLFE 1912 p. 94; KRÄNZLIN 1929 p. 125; DE VOS 1947 pp. 176 ff.; HUTCHINSON 1946 pp. 42–43; SALTER 1950 p. 729. — *Lantana africana* L.; LINNAEUS 1753 p. 628; THUNBERG 1800 p. 98; 1823 p. 458. — *Spielmannia africana* (L.) WILLD.; WILLDENOW 1800 p. 321; POIRET 1806 p. 346. — A specimen in CLIFFORD'S herbarium (BM) should probably be selected as the type. In addition, a specimen in LINN bearing the name "*Lantana africana*" in LINNAEUS'S handwriting corresponds well with the conception of *Oftia africana*.

*Spielmannia jasminum* MEDIK.; MEDIKUS 1775 p. 196. — *Batindum jasm(in)e*um (MEDIK.) RAF.; RAFINESQUE 1838 p. 81. — *Oftia jasminum* (MEDIK.) WETTST.; WETTSTEIN 1895 p. 360. — Type not seen.

*Lantana crispa* THUNB.; THUNBERG 1800 p. 98; 1823 p. 458. — Type in THUNBERG'S herbarium (UPS, lectotype). See below.

*Spielmannia decurrens* MOENCH; MOENCH 1794 p. 479, nom. illeg. — The name was given as a substitute for *Lantana africana* L., which was quoted, and thus it is nomenclatorially superfluous by present rules.

Note. *Lantana capensis* THUNB. published in THUNBERG 1800 p. 98, was cited as a synonym of *Spielmannia jasminum* by SCHAUER 1847 p. 526, and of *Oftia africana* by ROLFE 1912 p. 98 and in Index Kewensis. However, it is a synonym of *Tectaria lucida* (SOLAND. in AIT.) RUDOLPHI, which is more closely described below, on p. 458.



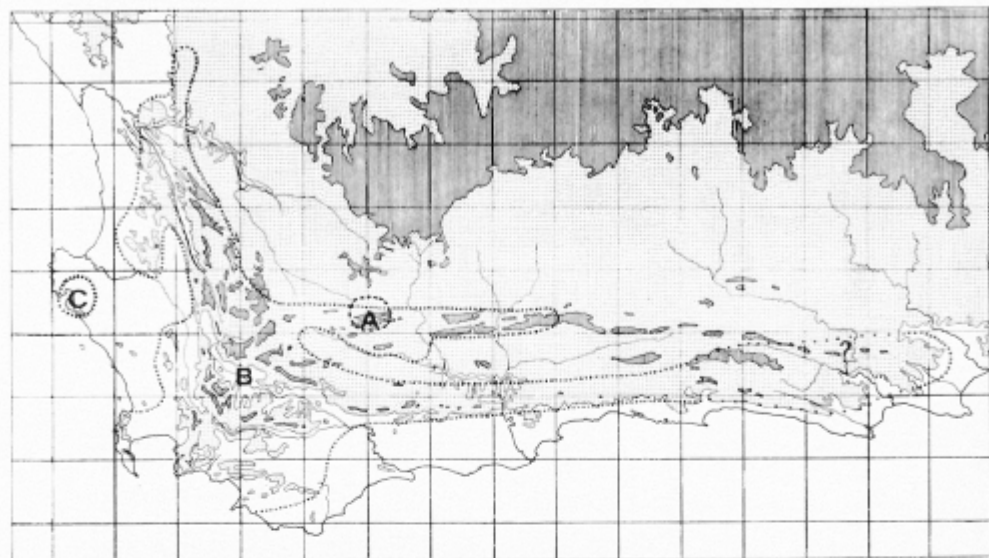


Fig. 3. Approximate distribution of: A: *Oftia glabra* and B: *O. africana* with its western population, C, which has particularly pubescent leaves with revolute margins. *O. revoluta* occurs in Little Namaqualand further to the north-west, and is not included in the map.

A branched shrub up to 1 m high or more, often widely spreading, sometimes (according to SALTER 1950 p. 729) forming thickets several metres across. Branches decumbent, generally 0.5–2 m long, with light-brown bark. Branch ends greenish and somewhat herbaceous, covered with short, glanduliferous and long, multicellular and usually non-glanduliferous hairs, and provided with 4 ridges confluent with the decurrent leaf bases. — *Leaves* (Fig. 1 C) ovate to circular, usually 10 to 40 mm long and 5 to 13 mm broad, sessile, acute to acuminate, rather mesophilous, marginally slightly or rarely conspicuously revolute, serrate or dentate with more or less rigid, sometimes mucronate teeth usually less than 1 mm long. Leaf base cuneate to obtuse, with decurrent margins. Pubescence of closely spaced, glanduliferous hairs 1 mm long or less. — *Bracteoles* usually wanting, seen only in one specimen, then linear-subulate and about 1 mm long. — *Pedicel* short, up to 1 mm long. — *Calyx* (Fig. 2 1) deeply divided, with

the tube about 1–1.5 mm deep; lobes usually 3.5–4 mm long, linear, flat, acuminate, covered with short, glanduliferous hairs. — *Corolla* tube greenish, about 6–8 mm long, glabrous on basal parts, with short, glanduliferous hairs on upper parts of outer side; lobes white, obovate to rounded-rectangular, about 3.2–5 mm long and 2.5–3 mm broad, glabrous or with sparse hairs on basal parts of outer side, with entire or slightly lobate margins. — *Stamens* and *pistil* as in the other species. — *Drupe* when dry about 4 mm in diameter, when fresh black and shiny.

**DISTRIBUTION.** The approximate distribution of *O. africana* can be seen in Fig. 3, which is based on rather limited material. It ranges from the Cape Peninsula along the mountains to the Gifberg and Nieuwoudtville regions (Vanrhynsdorp and Calvinia Divisions) in the northwest, and from the Worcester Division eastwards along the Witteberg and Great Swartberg Mountains at least as far as Sevenweeks-

poort, and along the Langeberg Mountains through the Montagu and Riversdale Divisions as far, perhaps, as the Uitenhage Division (as pointed out by HUTCHINSON 1946 p. 42, who referred to a specimen found by FOURCADE). In the south-western regions especially, *O. africana* is quite common. It occurs on sandstone and sandy soil but has also been recorded from granite outcrops. There are a few deviating records from the hills near Saldanha Bay (see below).

VARIATION. *O. africana* is a very variable species. Part of the variation especially in size, shape and texture of the leaves can be accounted for by seasonal variation and position on the shrub, but some of the conspicuous differences are probably genetically conditioned. To some degree they vary with geographical position. Thus, for example, forms with extremely short pubescence (glanduliferous hairs) occur in the Montagu Division, whereas often relatively small-leaved forms with almost shiny leaves can be found in the northern parts of the Cedarberg Mountains. Forms with relatively large, sometimes almost circular leaves and with relatively long, partly villous pubescence occur, for example, in the Paarl—Wellington region.

One deviating population particularly worth mentioning occurs on the low hills near Saldanha Bay. The stems are villous and the leaves proportionally small with more strongly revolute margins than in other forms of *O. africana*. In the features mentioned it approaches *O. revoluta*. The specimen named *Lantana crispa* by THUNBERG is similar in appearance. In Flora Capensis of 1823 it was reported as coming from Roode Sand below Great Winterhoek Mountain (Tulbagh), but nothing is written on the sheet in UPS and the statement can be queried. Without resort to more extensive material the latter-mentioned forms cannot be adequately judged. It may be that they deserve the rank of subspecies.

#### SYSTEMATIC POSITION OF *OFTIA*, COMPARISON WITH *MYOPORUM* (*MYOPORACEAE*) AND *TEEDIA* (*SCROPHULARIACEAE*)

When discussing the systematic position of *Oftia* there are several possibilities to be taken into account. For a long time *O. africana* was placed in the genus *Lantana* (Verbenaceae) which it resembles in many respects. The occurrence of two locules, each with generally 4 ovules, is one of the chief characters that differ from the characters of Verbenaceae, and besides there is great difficulty in finding obvious connection to any particular genus in that family.

As will be demonstrated below, the same is true of Myoporaceae. In this family *Myoporum* shows the closest similarity to *Oftia*, but the similarity is not always convincing.

As a fresh alternative in discussing the relatives of *Oftia*, the genus *Teedia* RUDOLPHI (Scrophulariaceae) is here presented. The reader will find numerous striking similarities but also differences, such as number of ovules, conventionally regarded as "family characters" in many text-books.

*Teedia* is a small genus of two or three species. It does not seem to have been fully revised. *Teedia lucida* (SOLAND. in AIT.) RUDOLPHI was originally described as *Capraria lucida* by SOLANDER in AITON 1789 p. 353, and has also been named *Borckhausenia lucida* (SOLAND. in AIT.) ROTH (1800 p. 56). It was illustrated with details in Botanical Register 1817, plate 209, and a second species, *Teedia pubescens*, was described from BURCHELL's manuscripts (and illustrated on plate 214) in the same series. Beside these species, there are two species of *Teedia* described by GANDOGER (1919 p. 219), *T. pentheri* from the Knysna region, and *T. obtusifolia* from near Grahamstown. These differ only in details of the leaf shape and are probably conspecific. In addition, they are probably the

same species as *T. pubescens* as pictured in Botanical Register. The types of all the species mentioned have berries, but a specimen (from S) studied by me had typical drupes and fewer and larger seeds (Figs. 4 H—I) although in other respects it agrees to other *Teedia* material from the eastern divisions of Cape Province.

The degree of similarity between the three genera *Oftia*, *Myoporum* and *Teedia* will be presented below as objectively as possible with regard to all principal characters known to the authors. Further studies especially of stem anatomy, cytology and seed and fruit structures would be welcome in the future.

#### DISTRIBUTION

*Teedia* is restricted to southern Africa, but is more widely distributed than *Oftia*, occurring in the Cape Province, Natal, Transvaal and Lesotho. The specific problems in the genus do not seem to be entirely solved. *Myoporum* occurs in Australia and in part of eastern Asia.

#### HABIT

All the genera are woody. *Teedia* and *Oftia* are low shrubs; *Myoporum* is very variable in size and habit; some species are trees and often attain considerable height.

#### PUBESCENCE ON BRANCHES AND LEAVES

In species of *Teedia* and *Oftia* the stems and leaves are covered with hairs consisting of few to several stalk cells and an apical globose gland. The gland is multicellular, being divided by vertical partitions in both genera, but may be unicellular in *Teedia*. In *Oftia* the stalk of the hairs sometimes consists of a row of rather numerous cells, in which case the apical gland may be missing. In the species of *Myoporum* which are not wholly glabrous, the hairs are of an entirely different type.

#### LEAF CHARACTERS

In *Teedia* the leaves are opposite, in *Oftia* they are usually opposite, but may be alternate, in *Myoporum* they are alternate.

The leaves in *Teedia* are sessile or narrowed at the base into a petiole-like stalk, though the base is usually more or less widened or even auriculate (Fig. 4 E) as in forms of *Oftia*. As in this genus the leaves are laterally decurrent, continuing as stem ridges on the internode below the leaf. This similarity is most conspicuous (cf. Figs. 1 A and 4 E). In *Myoporum* the leaf is not decurrent or auriculate at the base, and stem ridges are not present.

The shape of the leaf as a whole varies in each of the three genera. In *Teedia* and *Oftia* the margins always have short teeth. In *Myoporum* the margins are often entire, but sometimes serrate. There are no particular differences in the venation of the leaves.

#### ANATOMY OF STEM AND LEAF

Intraxylary phloem strands have been reported in young stems of *Oftia* (METCALFE & CHALK 1950 p. 1024), but have not been recorded for other members of Myoporaceae nor for Scrophulariaceae. Complementary studies in *Oftia* and *Teedia* are necessary.

According to METCALFE and CHALK (loc. cit.) stomata are confined to the lower side of the leaf in *Oftia* but this has been shown to be not entirely true. In *Oftia*, as in *Teedia*, sparse stomata occur on the upper leaf surface, so that these genera and *Myoporum* do not differ with regard to this character.

The stomata are of Ranunculaceous type in *Oftia* and *Teedia*, but of Cruciferous type in *Myoporum*.

Secretory cavities located in the sub-epidermal layer (see WETTSTEIN 1895 Fig. 142) are present in *Myoporum* and other genera of Myoporaceae in the strict sense, but are absent in *Oftia* and also in *Teedia*. The two latter genera are also alike in that

they have no sclerenchymatous tissue in the leaves.

#### INFLORESCENCE, BRANCHING

In *Teedia lucida* the inflorescence is a thyrse. The flowers are assembled in cymes towards the ends of the branches; some cymes are borne in the axils of the upper foliose leaves and have the appearance of 3- to 7-flowered dichasia (a base of such a dichasium is shown in Fig. 4 E). Towards the apex the leaves gradually become more bract-like and in their axils bear cymes of the same kind though less developed (Fig. 4 B). The branch apex is not capable of continuing growth in the following season, as in *Oftia*, and the branch system accordingly is *sympodial*.

In *Myoporum* the flowers are solitary or a few together in the leaf axils towards the ends of the branches. When several (often 3) in number they presumably represent reduced cymes, although the pedicels all appear to emerge directly from the leaf axil. As in *Oftia* the branches continue apical growth forming a *monopodial* branch system.

#### BRACTS, PEDICEL, BRACTEOLES

In all three genera cymes or solitary flowers are borne in the leaf axils towards the ends of the branches. There seems to be no actual difference in these leaves between the genera except that in *Teedia* they become smaller towards the ends of the branches in connection with the branches inhibiting their growth at the apex of the thyrse.

The long slender pedicels in *Myoporum* represent a deviation from the other two genera. In *Oftia* the pedicel is generally very short.

In *Teedia* bracteoles are always present on the pedicels of well-developed flowers, and floral buds are generally developed in the axils of the bracteoles. In *Myoporum* bracteoles are at least occasionally present (although it is often stated otherwise in

text-books), but small and located near the pedicel base. In *Oftia* well-developed bracteoles occur in forms of *O. glabra* (Fig. 2 G), and small bracteoles may also rarely be found in *O. africana* (seen in one specimen). Lateral flowers are not developed in the axils of the bracteoles, however.

#### CALYX, COROLLA

The calyx is conspicuously similar in *Teedia* and *Oftia*, both having a very short tube and relatively long lobes. The texture and pubescence are also alike. In *Myoporum* the calyx is somewhat different, but very variable.

The corolla of *Teedia* closely resembles that of *Oftia*, including shape and length of the tube as well as size and shape of the lobes. The tube is clothed with the same kind of hairs on the distal parts of the inner side in all three genera. In *Teedia* the corolla is mainly pink, in *Oftia* it is white, in *Myoporum* generally white with variegated patterns.

#### FLORAL ANATOMY

The vascular anatomy of the flower will be treated in detail below. There are certain differences between *Teedia* and the other two genera, but these can probably be largely explained by the more numerous ovules (see p. 471).

#### STAMENS

The stamens are generally 4 in number in all three genera. However, in *Teedia* as well as *Myoporum* there are sometimes 5 functional stamens. In *Teedia* there is variation within the species (and even on the same branch) in this respect (at least in *T. lucida*), in *Myoporum* the number is more constant within species. In *Oftia* the stamens are 4; the upper, median stamen is wanting.

In *Teedia* and *Oftia* the stamens correspond in position in the corolla tube as

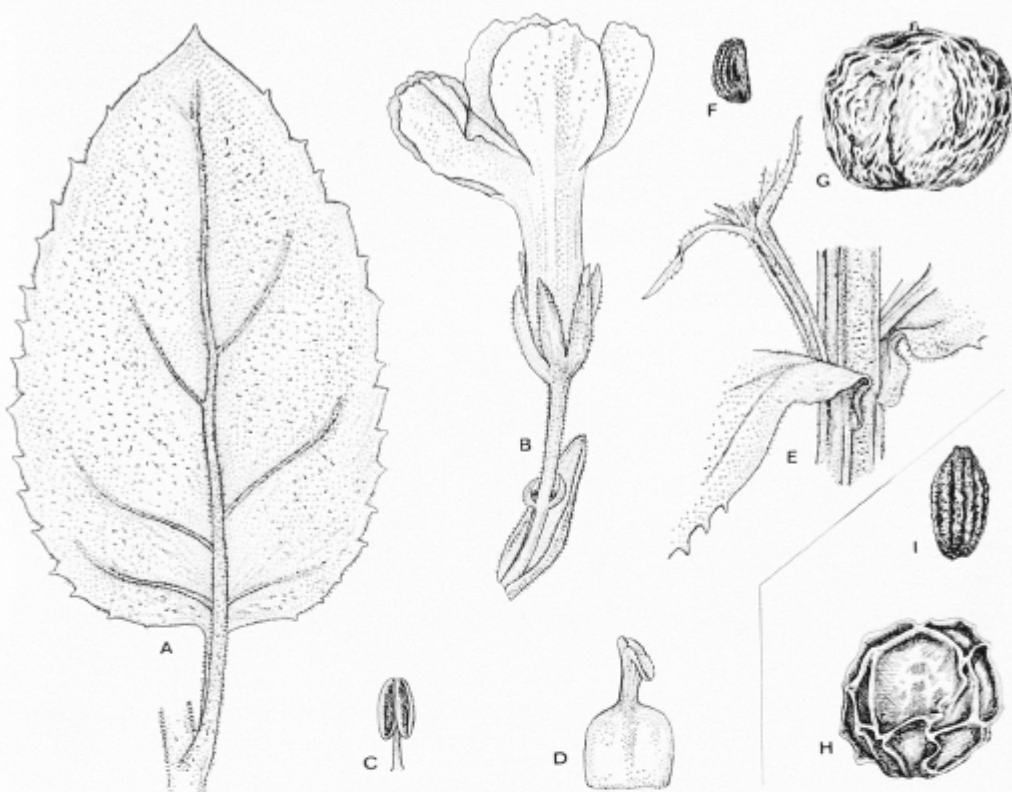


Fig. 4. Details of two species of *Teedia*; A—G: *T. lucida*; H—I: Species of *Teedia* not identified. — A—D: ACOCKS no. 2236; E: WAHLBERG, Table Mt.; F—G: ZEYHER, Tulbagh; H—I: WAHLBERG, Swa(rt)kop River. — A: Leaf,  $\times 4$ . — B: Flower and bract from near top of thyrses,  $\times 4$ . — C: Stamen,  $\times 8$ . — D: Pistil,  $\times 8$ . — E: Base of cyme from lower part of thyrses,  $\times 8$ . — F: Seed,  $\times 8$ . — G: Berry, in dried and somewhat pressed condition,  $\times 4$ . — H: Drupe, dried,  $\times 4$ . — I: Seed,  $\times 8$ .

well as in length of filament and shape of the anthers (Figs. 2 D—F and 4 C). The stamens in *Myoporium* are somewhat different, the thecae, for example, being more distant basally.

#### POLLEN GRAINS

The pollen grains of *Optia* and *Teedia* seem to agree in the main features, being 4-colpor(oid)ate and having a rather smooth, mainly foveolate surface (Fig. 5). In *Optia* the ora are not discernible on the

exterior (Fig. 5 A and C) but they are clearly visible on preparations in optical sections (Fig. 6 A—B). In *Teedia* the mesocolpium surface is more sculptured than in *Optia*, tending towards an ornate-convolute pattern (with small perforations) especially next to the colpi (Fig. 5 G).

In *Myoporium* the pollen grains are entirely different (according to ERDTMAN 1952 p. 277), with 3 colpi, each with two ora. The other members of Myoporaceae investigated seem likewise to have exclusively 3 apertures.



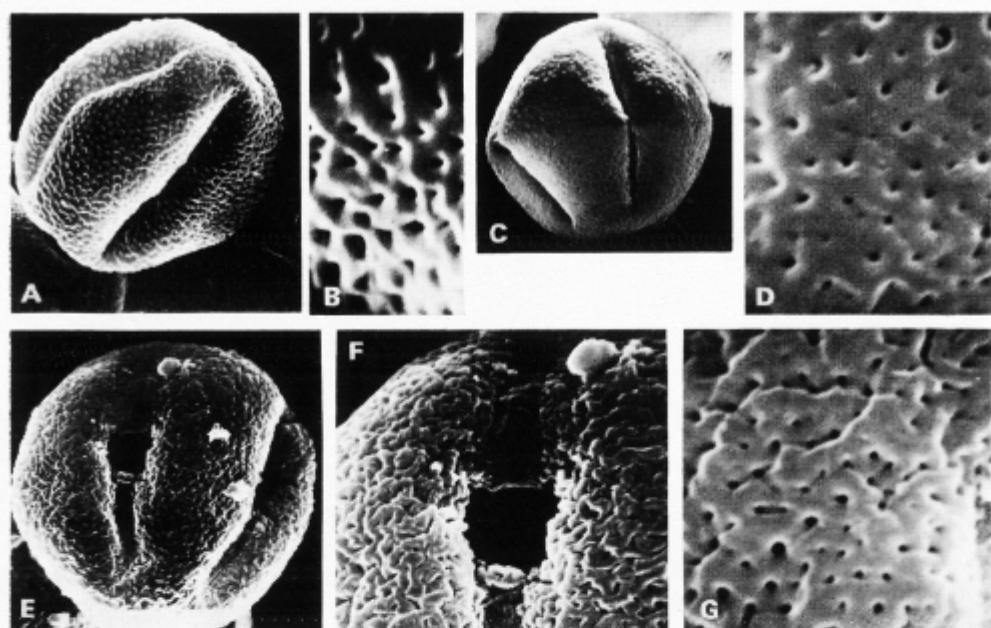


Fig. 5. Scanning electron photo micrographs of pollen grains of *Oftia africana* (A—B). *O. glabra* (C—D) and *Teedia lucida* (E—G). — A—B: DAHLGREN & STRID no. 2236; C—D: COMPTON no. 20155; E—G: ACOCKS no. 2236. — A, C, and E: Entire grains in obliquely equatorial view, all  $\times 2,600$ . — B, D, and G: Detail of mesocolpium, all  $\times 10,500$ . — F: Aperture,  $\times 5,200$ .

## PISTIL

The pistil of *Teedia* (Fig. 4 D) shows conspicuous external similarities to that of *Oftia* (Fig. 2 A—C), but the placenta in each loculus has many ovules and a bilobate appearance (Fig. 8 G, H, L). In *Oftia* the ovules in each loculus are arranged in two superposed pairs and are thus 4 in number. In both genera there are always two locules.

In *Myoporum* the loculi vary from 2 to 10, and the ovules in each loculus are solitary or 2.

Styles and stigmas are very similar, especially in *Oftia* and *Teedia*.

## FRUIT

The fruit in *Teedia lucida* at least, is a berry with a fleshy wall. However, in one

of the *Teedia* collections studied (of *T. pubescens* or an undescribed species) collected by WAHLBERG near Swa(rt)kop River (S), the fruit is a drupe with hard inner walls (Fig. 4 H). At least in the dry condition this is extremely similar to the dry drupes of *Oftia*. The drupe in the *Teedia* collection mentioned is many-seeded, however, like the berries in other collections.

In *Myoporum* the fruit is a drupe which may be very similar to that in *Oftia*. It is commonly globose, but varies greatly within the genus. The locules (and seeds) are frequently more than 2 in number.

## SEED

The seeds of *Teedia* are generally smaller than those of *Oftia* and the funicle is less



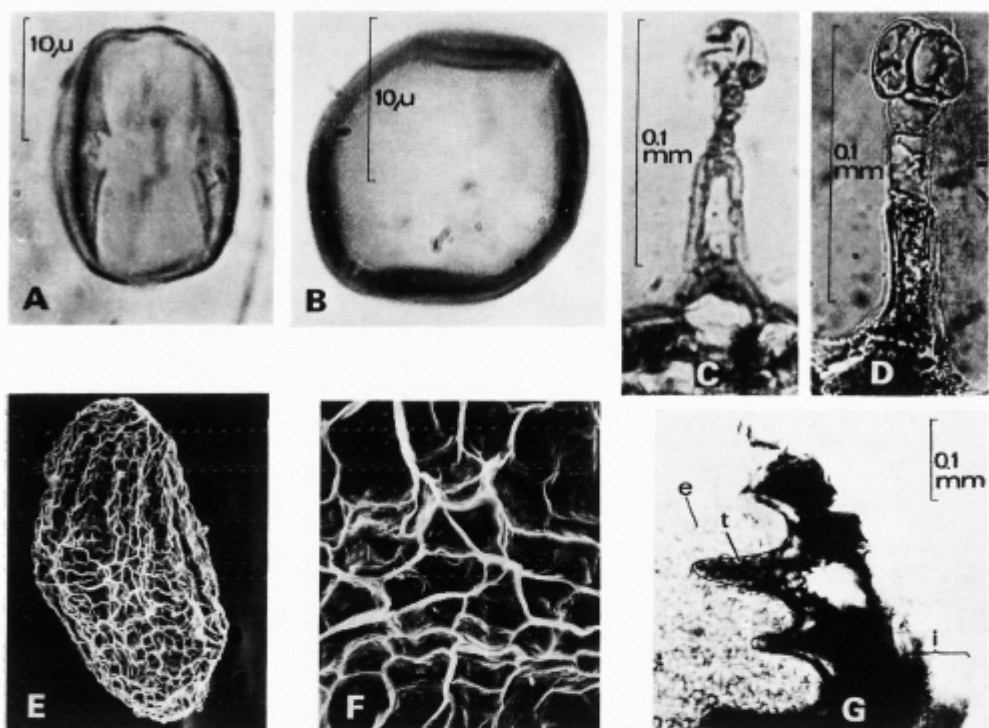


Fig. 6. Pollen, trichome and seed structures in *Oftia* and *Teedia*. — A: *Oftia africana*, pollen grain in equatorial view, optical section in light microscope; DAHLGREN & STRID no. 2236. — B: *O. glabra*, pollen grain in polar view, optical section; COMPTON no. 20155. — C: *O. africana*, glanduliferous hair; WALL, Constantia Nek. — D: *Teedia lucida*, glanduliferous hair; ACOCKS no. 2236. — E: *Oftia africana*, seed,  $\times 90$ , scanning electron micrographs; DAHLGREN & STRID no. 8002; great pressure has caused the outermost thin layers to collapse, so that the walls of the thick lignified cells seen in G (for *Teedia*) stand out as a sharp reticulum. — F: Ditto, detail of wall,  $\times 1750$ . — G: *Teedia* sp., detail of testa in transverse section; WAHLBERG, Swa(r)t(k)ops River; e: endosperm, t: large, conical cells regarded to be the tapetum by DE VOS, i: integumentary layer. See further in the text.

developed. In other respects the seeds show close similarity, however, such as in shape, surface structure, and colour. They are somewhat lunulate, dull black, and have longitudinal rows of rugae along the back (Figs. 2 K, 4 F, I, and 6 E). The seeds of *Myoporum* are different in shape and colour, and the surface is smoother.

Transverse sections of the seed coat in *Teedia* (Fig. 6 G) show the same structure as that in *Oftia* as demonstrated by DE VOS 1947 Figs. 61—62, having large, narrowly conical cells with thick, lignified inner

walls projecting into the endosperm tissue. According to DE VOS these cells represent the tapetum, and are enclosed by thin-walled integumentary tissue. The seed coat of *Myoporum* and *Eremophila* (Myoporaceae) is very different, and the epidermis of the integument makes up the most thick-walled protection.

#### EMBRYOLOGY

According to DE VOS 1947, there are similarities in the main embryological

characters between *Oftia* on the one hand and *Myoporum* and *Eremophila* on the other. However, in *Oftia* the nucellus persists at the base of the embryo-sac until after fertilization, while in the other two genera it disappears at an early stage. In *Oftia* the micropylar haustorium consists of 4 hypertrophied cells, in *Myoporum* and *Eremophila* of a large number of cells.

In addition, DE VOS noted the above-mentioned conspicuous difference in the construction of the testa.

The embryological features of *Teedia* are not known.

### Conclusions

The above evidence, that *Oftia* is more closely related to *Teedia* (Scrophulariaceae) than to *Myoporum* (Myoporaceae), may warrant moving the genus to Scrophulariaceae.

However, there are some doubtful points. Conspicuous differences between *Oftia* and *Teedia* are the fewer ovules of the ovaries and some marked differences in the vascular anatomy of the flower which are probably to a great extent connected with the placentation. Another difference which should not be overlooked, is the apical growth of the inflorescence apex that is wanting in *Teedia*. In addition, the occurrence of intraxylary phloem in the young stems of *Oftia* deserves further attention, and corresponding studies in other genera are needed.

We consider it to be a matter of subjective opinion whether *Oftia* should be treated as belonging to Scrophulariaceae or as a separate family. The differences between *Oftia* and *Myoporum* are in our opinion too conspicuous to justify placing them together in the same family as done at present. The similarity to *Myoporum* that is displayed by flower and fruit may be partly but not entirely due to development along parallel lines.

### DETAILS OF VASCULAR ANATOMY OF THE FLOWER IN MEMBERS OF *OFTIA*, *MYOPORUM* AND *TEEDIA*

#### *Oftia africana*

Material studied: DAHLGREN & STRID no. 2748 from Cape Prov., Cape Peninsula, northerly slopes of hills ESE of Kommetje, 1965.

The pedicel has a rather thick, continuous vascular cylinder (Fig. 7 A) from which arise 10 calyx traces, some of which branch close to the base, others a little higher up (Fig. 7 B), resulting in 16—20 traces. After entering the calyx some of them gradually disappear, so that each of the lobes of the calyx will contain only one median and two lateral bundles (Fig. 7 E, H).

Above the level where the calyx traces arise, the vascular cylinder of the receptacle sends out first 5 petal traces and then 5 stamen traces (Fig. 7 C—E), all of which enter the corolla tube. Within the tube each of the petal traces divide to form a lateral branch on each side. This branching takes place well below the level of the stamen base (Fig. 7 H). The staminal traces do not branch. There are 5 staminal traces, 4 of which supply the stamens, while the fifth trace, posterior in position, proceeds within the corolla tube and gradually disappears near the level of the detachment of the stamens (Fig. 7 J).

Above the point of origin of the staminal traces the vascular cylinder of the thalamus consists of a dorsal trace and a number of lateral traces for each of the two carpels. Transverse sections through the extreme base of the ovary show an outer ring of bundles for the ovary wall and a central ring of small bundles (Fig. 7 E—F). The latter runs along the central region of the septum and in its course contracts into a solid vascular cylinder (Fig. 7 G). Ovular traces emerge from this axile strand near the top of the ovary (Fig. 7 H, K). Above the level of the ovules a short

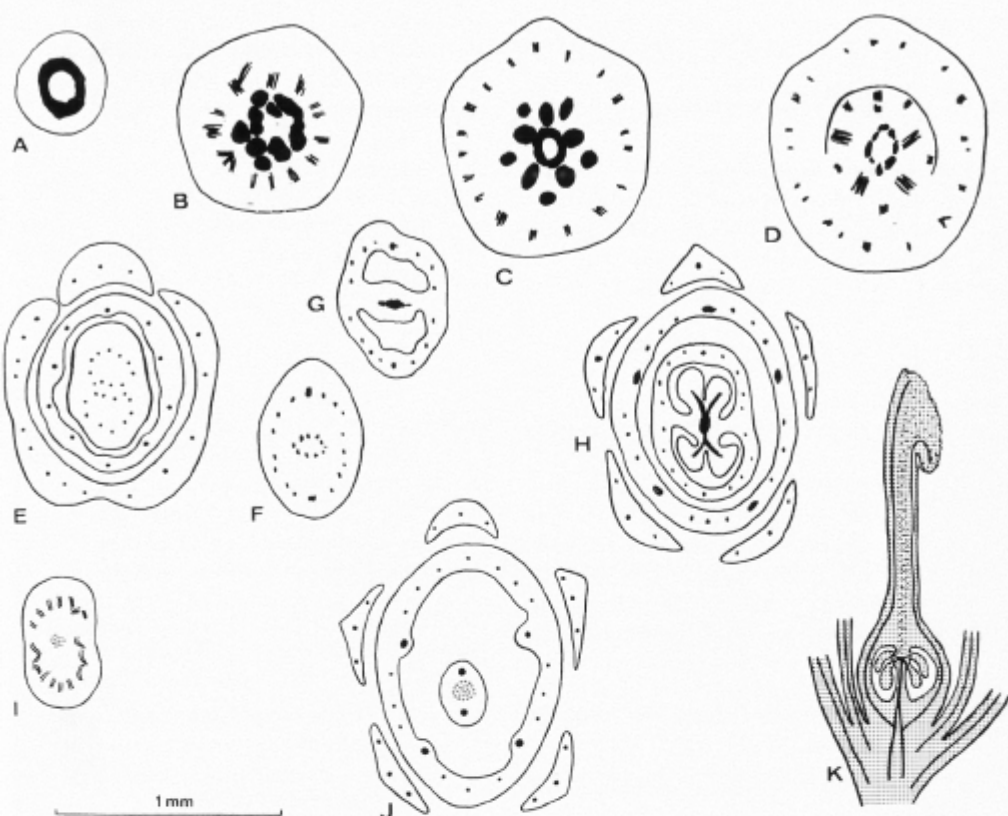


Fig. 7. Vascular anatomy of the flower of *Oftia africana*; DAHLGREN & STRID no. 2748. — A: Transverse section of pedicel showing a complete cylinder of vascular tissue. — B: Origin of calyx traces. — C: Section showing outermost ring of calyx traces, inner ring of petal traces, next inner ring of 5 stamen traces, and the axile cylinder. — D: Section at a slightly higher level, just beneath the detachment of calyx. — E: Section of calyx, corolla (with petal and stamen traces and base of pistil). — F: Section through base of pistil showing an outer ring of bundles for the ovary wall and a central ring of vascular bundles. — G: Section through base of loculi, showing a solid vascular cylinder in centre of septum. — H: Section at placental level showing ovular traces. — I: Section through the ovary above the level of the loculi. The dots in the centre indicate transmitting tissue. — J: Section a little below insertion of stamens. — K: Diagrammatic view of longitudinal section of flower.

channel through the septum links the upper ends of the two loculi. The axile strand, which supplies the ovules, divides into two bundles which run for a short distance in the septum on each side of this channel and disappear without entering the style. A strand of transmitting tissue

runs from the base of the style up to the tip of the stigma. Only the two dorsal bundles of the carpels run throughout the length of the style (Fig. 7 J). The outer bundles of the ovary wall disappear at the top of the ovary after irregular fusions among themselves (Fig. 7 I).

**Myoporum deserti**

Material studied: *Myoporum deserti* A. CUNN. ex BENTH.; BOORMAN sine no. from Australia, New South Wales, Narrabri, 1907 (LD).

The flowers investigated had 5 functional stamens as also in *M. sandwicense*, for example. In most species of the genus, however, there are only 4 stamens, the posterior one being suppressed as in *Offia*.

The pedicel of *M. deserti* has a continuous vascular cylinder (Fig. 8 A) from which arise first 5 median traces to the sepals and then 4 commissural traces for the sepals (Fig. 8 B—C). It is peculiar that although the calyx has 5 lobes and 5 median traces, there were only 4 commissural traces in all the buds sectioned. These branch and supply the margins of adjacent sepals (Fig. 8 C—E). In the region where the commissural bundle is absent, a lateral branch of the median trace of the sepal supplies the margins. Fifteen bundles enter the calyx, 5 of them being the median traces of the sepals and the other 10 the lateral bundles of the sepals derived by the branching of the commissural traces (Fig. 8 C—G).

Above the point where the vascular supply to the calyx begins, 5 petal traces, and a little above them, 5 stamen traces are detached from the vascular cylinder (Fig. 8 D—E). The stamen traces arise at a point above the level of the calyx base.

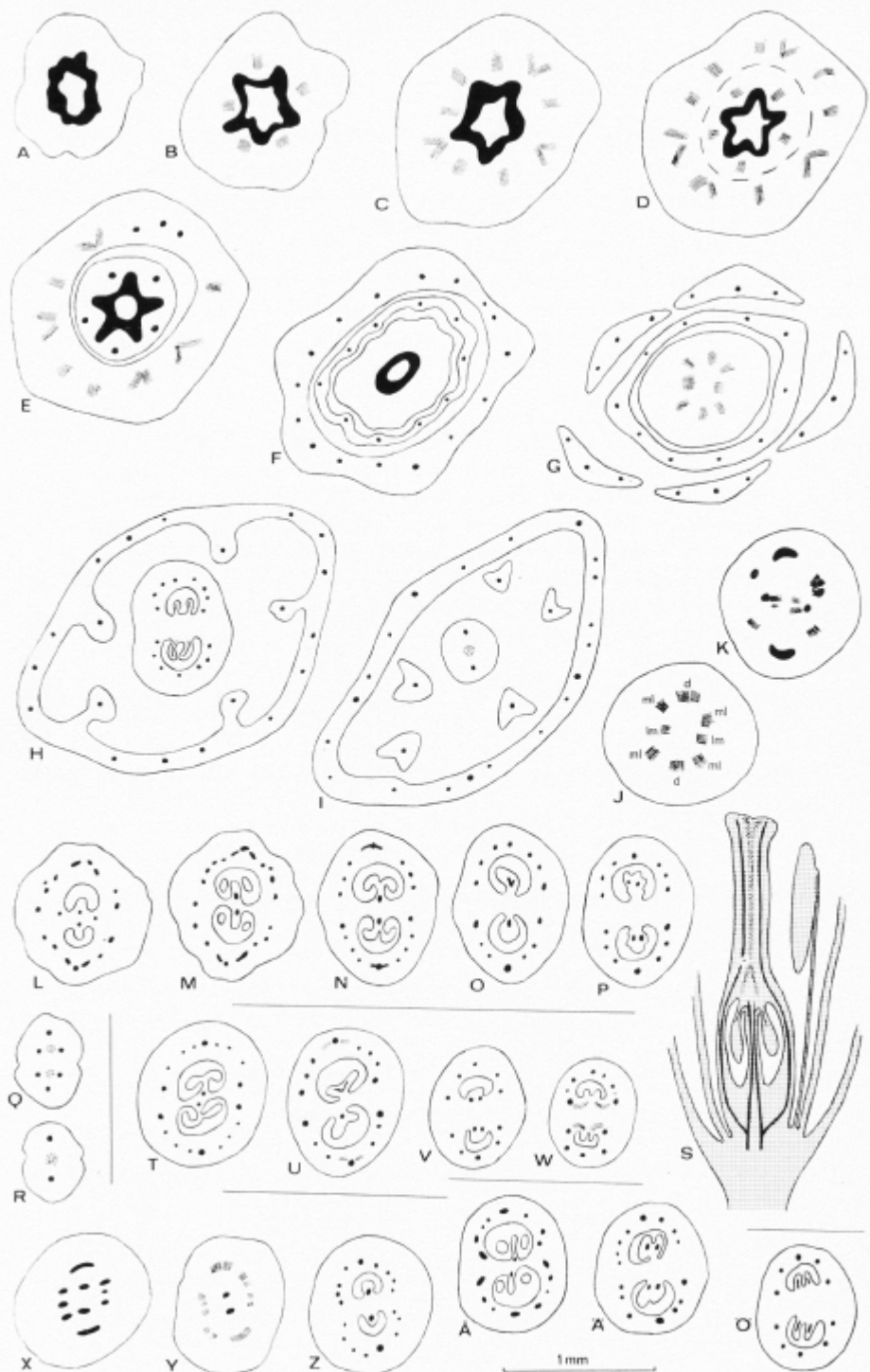
Above this level the corolla tube with the 5 petal traces and the 5 stamen traces is separated from the base of the gynoecium which contains a continuous vascular cylinder (Fig. 8 F). The petal traces divide near the level where the stamens depart (Fig. 8 H—I), while the stamen traces proceed unbranched throughout.

There is considerable variation in some important aspects of the vascular supply to the ovary, especially to the placental areas.

In most flowers the vascular cylinder breaks up into 8 bundles at the base of the ovary, the 2 dorsal bundles of the carpels (d), 2 median lateral bundles (ml), and, in the plane of the septum 2 pairs of latero-marginal bundles (lm) (Fig. 8 J). The latero-marginal bundles divide into carpellary ventral bundles and the lateral bundles of the ovary wall (Fig. 8 K). In some specimens each of them sends out 2 ventral traces (often at slightly different levels), one for each carpel.

Ventral traces coming from opposite sides but belonging to the same carpel fuse to form a placental strand. (In one specimen, however, the placental bundle is a single ventral bundle coming from one side, the corresponding one from the other side being absent.) A longitudinal ridge, single in the basal region, bifid in the upper ovuliferous zone and single again in the short region above this, projects from

Fig. 8. Vascular anatomy of the flower of *Myoporum deserti*; BOORMAN sine no., from Narrabri, Australia. — A: Transverse section of pedicel. — B: Departure of 5 sepal midrib traces. — C: Sepal midrib traces and 4 branching commissural traces. — D: Departure of petal traces. — E: T.s. just above the level of the calyx tube base. — F: T.s. above separation of corolla tube. — G: Slightly higher level, showing the 5 sepal lobes separated. — H: T.s. just below the insertion of the filaments. — I: T.s. above separation of filaments. — J: T.s. of gynoecium base in another flower of *M. deserti*, showing the dorsal bundles of the carpels (d), median lateral bundles (ml) and two latero-marginal bundles (lm). — K: Origin of ventral bundles through division of the latero-marginals. — L: T.s. through basal level of loculi showing ventral bundles in septum at base of the longitudinal ridge. — L—N: T.s. through ovary at successively higher levels. — O: Showing division of one of the ventral (placental) bundles into 2 ovular traces. — P: Showing the 2 ovular traces in the placentas. — Q: T.s. near top of ovary. — R: T.s. through style. — S: Diagrammatic longitudinal section of flower. — T: T.s. of ovary in another flower. — U: Origin of ovular traces as branches of ventral (placental) bundle. — V: Division of the ventral bundles into two. — W: Fusion of the tips of the ventral bundles with a bundle of the ovary wall. — X—Å: T.s. of another flower showing a different origin of the ventral (placental) bundles. — Å—Ö: T.s. of ovary at successively higher levels.





the septum into each loculus. The two placental bundles proceed upwards at the junction of these ridges with the septum (Fig. 8 L—N). Near the ovuliferous level they move into the placentas and divide into two ovular traces (Fig. 8 O—P), which supply the two pendulous ovules in each loculus.

The dorsal bundles, median lateral bundles and the mother strand of the ventral (placental) bundle divide, increasing the number of bundles in the ovary wall (Fig. 8 K—O). In the upper part of the ovary wall the number of bundles is reduced as some fuse and others disappear, leaving only one dorsal bundle and two lateral bundles for each carpel (Fig. 8 Q). Just above each placenta a strand of transmitting tissue is also formed. A little higher up, the two strands of transmitting tissue fuse, and the lateral bundles disappear, so that only the two dorsal bundles of the carpels are left. These proceed throughout the length of the style into the stigma, along with the strand of transmitting tissue (Fig. 8 R).

In one specimen, the bundle in each placenta sends out an ovular branch on each side to the two pendulous ovules in the loculus (Fig. 8 T—U) and bifurcates (Fig. 8 V). These two bundles continue into the septum and then outwards to fuse with a bundle of the ovary wall (Fig. 8 W). Along with the other lateral bundles of the ovary wall it disappears at the top of the ovary, leaving only the dorsal bundles of the two carpels.

In another specimen, the dorsal traces of the two carpels deviate outwards, the rest of the vascular cylinder breaking up into two composite ventral strands, each representing the fusion product of the two ventral bundles of the same carpel, and a few bundles for the

ovary wall (Figs. 8 X—Y), after which the composite ventral bundles proceed as usual.

### *Teedia lucida*

Material studied: *Teedia lucida* (SOLAND. in AIT.) RUDOLPHI; ACOCKS no. 1887 from South Africa, Cape Prov., Ceres Div., cracks in rocks at foot of Ceres Mt., 1933 (S).

Out of 3 flower buds studied, 2 were microtomed transversely and one longitudinally. Of the former, one had 4 stamens while the other had 5, all of which were functional. In the 5-staminate flower the calyx was 5-lobed as usual, while in the latter one of the lobes of the 5-lobed calyx was further split almost up to its base into two lobes. The other features were similar in the flowers.

The vascular cylinder of the pedicel divides into two strands (Fig. 9 A) which divide further and give rise to a ring of bundles and bear traces to the floral organs. In the bud with the normally 5-lobed calyx as well as in that with one of the lobes cleft, there are 6 calyx traces all of which branch as far down as the thalamus region (Fig. 9 B, C, M, N, O). All these 6 traces arise direct from the stele. Due to the branching of these traces in their lower part, each of the calyx lobes receives one median bundle and two or more lateral bundles. In the bud with only 5 calyx lobes, it is the anterior sepal that is supplied by two traces. In the other bud the extra lobe is more or less anterolateral.

Five petal traces and 4 or 5 stamen traces (in the buds with 4 or 5 stamens

Fig. 9. Vascular anatomy of the flower of *Teedia lucida*; ACOCKS no. 1887 from Ceres Mt., South Africa. — A: Transverse section through top of pedicel. — B—C: Departure of calyx traces. — D: Departure of 5 petal traces and 4 stamen traces. — E—F: Showing 5 calyx lobes, corolla tube and the base of the ovary at successively higher levels. — G: T.s. through placental level showing placental and ovular traces. — H: T.s. of ovary at a slightly higher level. — I: T.s. at a level of top of the ovary. — J: T.s. through style, corolla and calyx. — K: T.s. showing corolla and 4 anthers. — L: Longitudinal section of ovary and flower base somewhat diagrammatically. — M—P: T.s. at successively higher levels of a flower with 5 functional stamens and a calyx in which one of the 5 lobes is bifid. Explanation in the text. — Abbreviations: a, stamen trace; c, petal trace; d, dorsal bundle of a carpel; k, calyx trace.

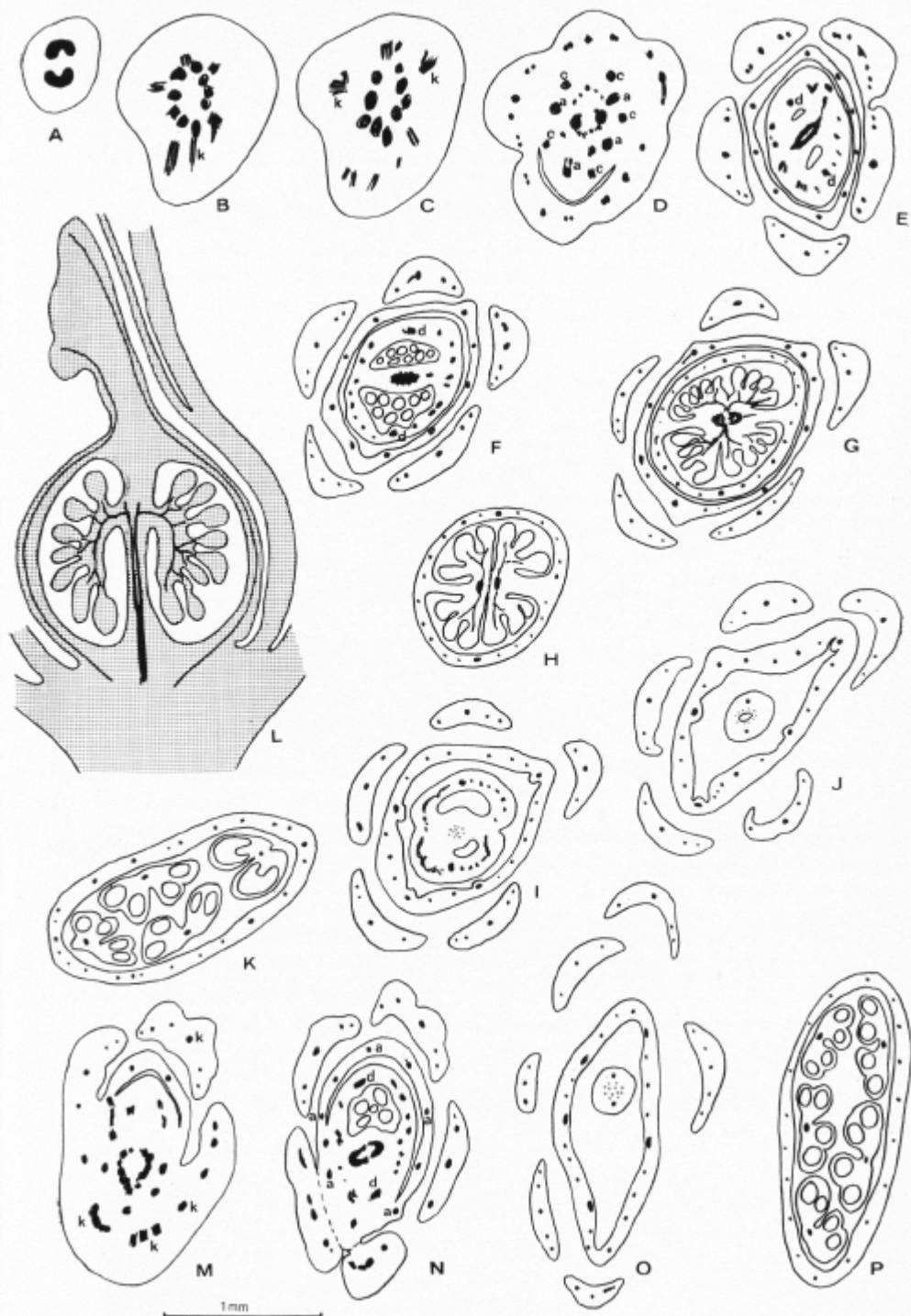


Fig. 9.

respectively) arise at a short distance above the level where the calyx traces arise (Fig. 9 D, E, N, O, P) and enter the corolla tube. Above this point, the dorsal traces of the two carpels and a varying number of traces for the ovary wall depart from the vascular cylinder, which then contracts to an almost solid cylinder. This proceeds upwards in the centre of the septum (Fig. 9 D—F).

The placentas are attached to the septum in its upper half. The placenta of each loculus is bifid, the lobes hanging downwards into the loculus and bearing numerous ovules (Fig. 9 L). At the placental level the central strand splits into two and it is on these that the branching placental traces are borne. They continue downwards into the hanging placentas (Fig. 9 G, H, L). The placental traces divide into ovular traces which supply the ovules.

The two axile strands disappear in the septum a little above the placental level (Fig. 9 L). An extremely narrow channel links up the two loculi (Fig. 9 H) at about this level. In the uppermost region of the ovary this canal closes up and its place is occupied by a strand of transmitting tissue, which continues into the style. For a short length the style has a hollow canal and in this region the transmitting tissue lines the canal. Where the style is solid the transmitting tissue occupies its centre. Only the two dorsal bundles of the carpels continue as far as into the style; the other bundles of the ovary wall disappear at the top of the ovary after irregular fusions (Fig. 9 I—J).

The corolla traces bear lateral branches at some distance below the level of the filament bases. The 4 or 5 staminal traces proceed unbranched throughout their length (Fig. 9 J, K, O, P).

### Discussion

The floral anatomy of all pentamerous, bicarpellary flowers must show certain basic similarities based on similarities in the number and position of floral parts.

In such a case, affinities between taxa may have to be judged by some comparatively minor but significant features of vascular organization. There are certain differences in the floral vasculature in the material of the three genera compared that should be pointed out.

**PEDICEL, SEPALS.** The upper part of the pedicel in *Oftia africana* and *Myoporum deserti* show closed vascular cylinders, while that of *Teedia lucida* has two arc-shaped strands, the gaps probably representing the leaf gaps of the bracteoles, which are better developed in this genus.

The vascular supply to the calyx differs with the genera. In *Oftia africana* 10 traces arise at about the same level, their successive branching later resulting in 16—20 bundles. In *Myoporum deserti* there are median traces and commissural traces for the calyx, the latter being however only 4 instead of the expected 5. In *Teedia lucida*, finally, there are 6 calyx traces arising directly from the stele and branching in the thalamus region.

The differences in the calyx supply mentioned are of limited value for systematic conclusions as long as the material investigated in each genus is not more extensive. A number of commissural traces lower than that of the median traces in the calyx, such as in *Myoporum deserti*, is also known in some genera of Acanthaceae, for example in *Dipteracanthus* (RAO 1953), and in this family the variation in commissural traces is great.

**COROLLA, STAMENS.** The general features of the vascular supply to the corolla and stamens is similar in the three genera, only differing conspicuously with regard to the upper, median stamen trace. In *Oftia capensis*, where the corresponding stamen is lacking, there is still this staminal trace. In *Myoporum deserti* this stamen and its trace are present, but in *Teedia lucida* the trace was present only in the 5-staminate flower, absent in the 4-staminate ones, a difference which is hard to evaluate.

**PISTIL.** There are great differences between the three genera in the details of the vascular system of the pistil base and in the placental supply. Just above the departure of the petal and stamen traces in *Optia africana* and *Teedia lucida* a dorsal trace and a number of lateral traces to the carpels are detached from the vascular axile strand (Fig. 7 G and 9 E). In *Myoporum deserti* the cylinder normally breaks up into 7 strands, some of which divide further as shown in Fig. 8 J—L. The vasculature of the ovary wall and style is similar in principle in the three genera. However, there are great differences between the three species compared with regard to the organization of the central, septal strands and the placental and ovular supply. A similarity found in the material of *Optia africana* and *Teedia lucida* is the presence of a short connecting channel through the upper part of the septum, connecting the upper ends of the loculi. Apart from the much more complex branching of the placental strands to the more numerous ovules in *Teedia*, there does not seem to be greater differences between this genus and *Optia*, than between *Optia* and *Myoporum deserti* (which is very variable in itself).

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# Studies in African Cyperaceae IV

## Lipocarpha R. Br., Hemicarpha Nees, and Isolepis R. Br.

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### ABSTRACT

HAINES, R. W. & LYE, K. A. 1971. Studies in African Cyperaceae IV. *Lipocarpha* R. Br., *Hemicarpha* Nees, and *Isolepis* R. Br. — Bot. Notiser 124: 473—482.

The relationship between the three genera *Lipocarpha* R. Br., *Hemicarpha* NEES and *Isolepis* R. Br. is studied. *Hemicarpha isolepis* NEES, the type species of the genus *Hemicarpha*, is found to have nullets enwrapped by two scales and is therefore a *Lipocarpha*. *Mariscus paradoxus* (CHERM.) CHERM. is very close to *Lipocarpha* in flower-structure, but differs in having a minute third scale carried on a continuation of the spikelet axis above the flower. It is possibly an isolated offshoot of the line leading to *Lipocarpha*. The genera *Lipocarpha*, *Hemicarpha* and *Isolepis* are found to be closely related differing only in minute floral characters.

Four new combinations are made, viz. *Lipocarpha isolepis* (NEES) R. W. HAINES, *Isolepis kernii* (RAYMOND) K. LYE, *I. rehmannii* (RIDLEY) K. LYE and *I. microcephala* (STEUD.) K. LYE.

### GENERIC CIRCUMSCRIPTIONS OF LIPOCARPHA AND HEMICARPHA

The genus *Lipocarpha* was established by ROBERT BROWN (1818), the name "derived from the whole of its squamae being deciduous", "to avoid further confusion" with certain species previously included in *Hypolytrum* RICHARD (1805) and its "probable corruption" *Hypaelyptum* VAHL (1806). Both *Lipocarpha* and *Hypolytrum* have a pair of "hypogynous scales" below the flower, but whereas in *Hypolytrum* they are equal in size, ciliate on the keel and placed laterally and at the same level on the pedicel, in *Lipocarpha* they are unequal, not ciliate and placed dorso-ven-

trally, the larger dorsal below the smaller ventral and enwrapping it. The type species, *L. chinensis* (OSB.) KERN (*Hypolytrum senegalense* RICH., *Hypaelyptum argenteum* VAHL) has the compact involucre head of several sessile cones commonly found in the genus (Fig. 1).

The hypogynous scales of *Lipocarpha* are membranous apart from the white ribs, of which two in the lower scale and one in the upper usually contain vascular tissue, the others only sclerenchyma (BLASER 1944). They enwrap the achene closely and fall with it at the same time as the cone-bract that subtends the flower. It is possible to regard the two scales as a perianth comparable to the six or more setae of a *Scirpus*, the cone-bracts then being glumes and the cone as a whole a spikelet. The genus would then belong to

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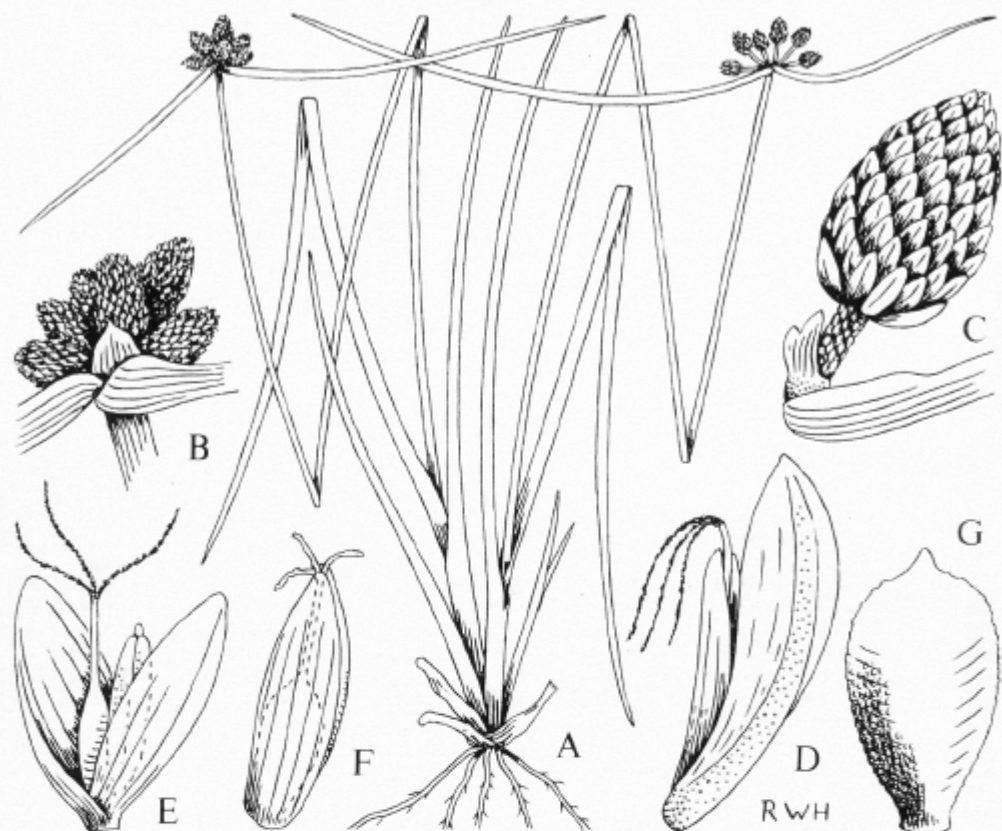


Fig. 1. *Lipocarpa chinensis* (OSB.) KERN, the type species of *Lipocarpa* R. BR. — A: Habit  $\times 1/2$ . — B: Head of cones. — C: Fruiting cone. — D: Flower with bract. — E: Flower with scales. — F: Fruit with scales. — G: Achene. — Drawn from HAINES 4044 (Roadside drain, Kampala, Uganda).

Scirpeae, as in, e.g., BENTHAM'S (1877) account of Australian, CLARKE'S (1901) of South African, and NAPPER'S (1965) of East African Cyperaceae.

ROBERT BROWN (1810), however, suggested that each flower with its scales was a reduced spikelet: "concipe itaque in Kyllingâ squamulam extimam auctam, secundam suppressam, valvulasque floriferas diminutas carinâque orbatas, et habes Hypaelypti speciem". Later (BROWN 1818) on the same "analogy of its structure to that of Kyllinga" found the "spikelet reduced to a single flower as in several other genera of Cyperaceae". A direct derivation

from *Kyllinga* as that genus is now understood is unlikely, for it includes only species with two style-branches while some *Lipocarpa* species have three, but HOLM (1899), PALLA (1905), KOYAMA (1961) and others have followed the reduction of an originally many-flowered spikelet with many distichous glumes characteristic of *Cyperus* to the single-flowered spikelet with only two scales of *Lipocarpa* (Fig. 2).

In *Cyperus* the spikelet clusters are usually pedunculate with a tubular prophyll at the base of the peduncle (Fig. 2). The cluster includes a single terminal spikelet

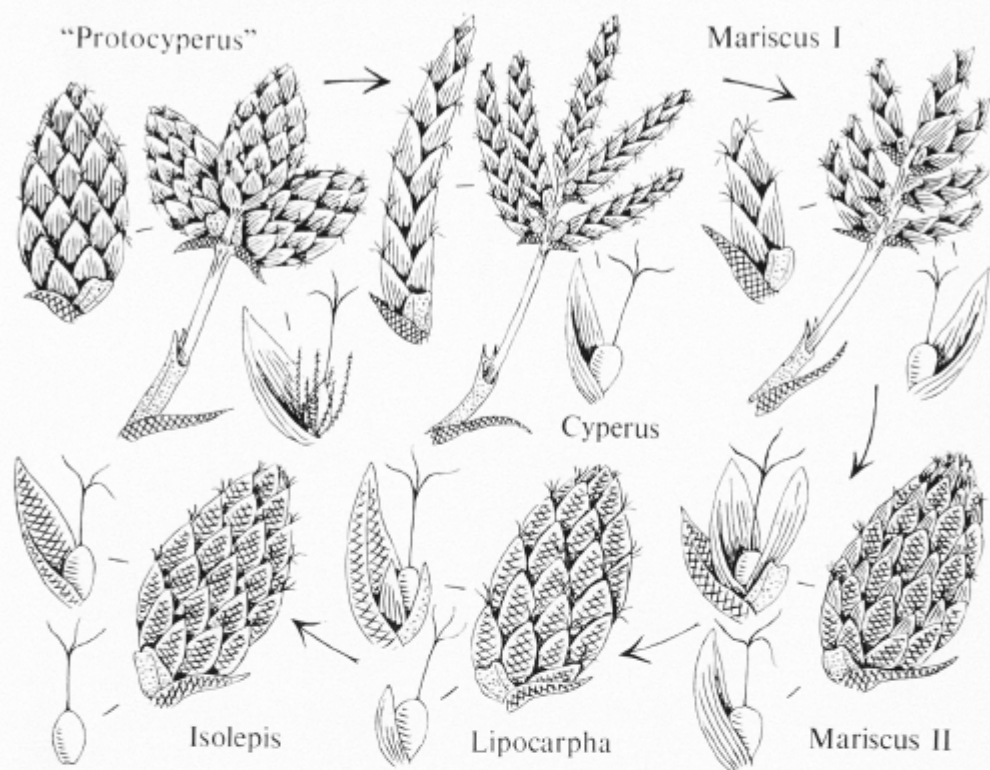


Fig. 2. Diagrams showing equivalent parts in some of the genera discussed, illustrating a possible course of evolution from *Protocyperus* and *Cyperus* to *Isolepis*. Each group of drawing represents a cluster of spikelets, a single spikelet and a single flower with, where they exist, the perianth and subtending bract, but the stamens omitted. Glumes lined longitudinally, subtending bracts of spikelets and spikelet clusters crosshatched, prophylls stippled. *Protocyperus* may have given rise to *Cyperus* by loss of perianth-segments and distichous arrangement of the glumes.

with no prophyll at its base and a number of lateral spikelets each subtended by a bract and bearing a small scale-like prophyll at its base. Such an arrangement is also found in *Scirpeae* and in this respect *Cyperus* may have preserved an arrangement primitive for Cyperaceae as a whole (cf. HAINES 1967).

Paniculate species of *Mariscus* resemble *Cyperus* but often have more spikelets in the cluster and fewer flowers in each spikelet (Fig. 2, *Mariscus* I). Further increase in spikelet number, tighter packing and loss of the peduncle is seen in many *Mariscus* species with capitate inflores-

cences (Fig. 2, *Mariscus* II). There may be but one flower in the spikelet as in *M. macropus* C. B. CLARKE, in which case there are only two glumes above the prophyll, the lower fertile, the upper empty. The terminal spikelet is now lost so that all are lateral and have prophylls at the base.

Loss of the upper glume and reduction of the lower glume and prophyll to membranous scales clasping the achene would give a *Lipocarpha* (Fig. 2). The cone would then be a cone of reduced spikelets subtended by bracts, not equivalent to a spikelet of *Scirpus*, and the genus would

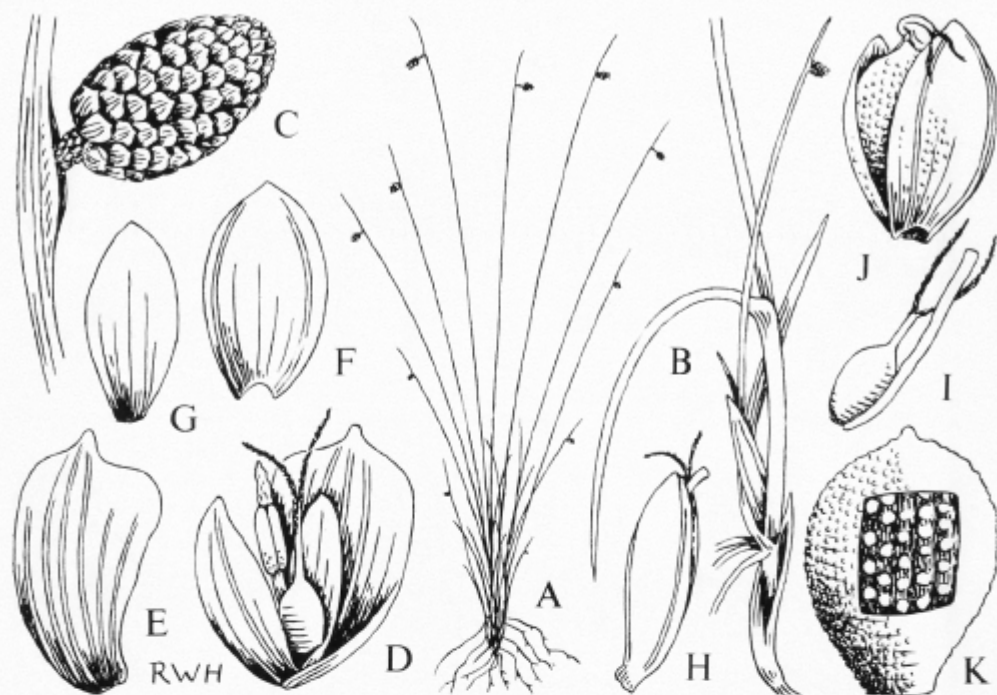


Fig. 3. *Lipocarpus isolepis* (BOECK.) R. HAINES. — A: Habit  $\times 1/2$ . — B: Fragment from plant base. — C: Cone. — D: Flower with associated scales. — E: Cone-bract. — F: Prophyll. — G: Glume. — H: Flower enclosed by prophyll and glume. — I: Isolated flower after fertilization. — J: Fruit with prophyll and glume. — K: Achene. — Drawn from HAINES 4268 (Shallow soil on wet rock, 2000 m, Sebei, Uganda).

belong to Cyperaceae rather than Scirpaceae. RIKLI (1895) reached the same conclusion on purely anatomical grounds. RAYNAL (1967) regarded the proposition as "assez hypothétique" though he later (RAYNAL 1968) accepted its probability. In *Ascolepis* where a similar but independent reduction appears to have occurred, PALLA (1905) clinched his argument by finding occasional two-flowered spikelets with the glumes in distichous arrangement. VAN DER VEKEN (1965) showed that both *Lipocarpus* and *Ascolepis* have a *Cyperus*-type embryo, and there is therefore very strong evidence for placing these genera in Cyperaceae rather than in Scirpaceae (cf. also LYE 1971 a).

Here two species, *Scirpus isolepis* (NEES) BOECK. and *Mariscus paradoxus* (CHERM.)

CHERM. (*Cyperus subparadoxus* KÜK.) are considered. Both have been at one time placed in *Lipocarpus*, the first one as *L. rautanenii* BOECK. and *L. monocephala* TURRILL and the second as *L. paradoxa* CHERM. It is proposed to return the first to that genus as *Lipocarpus isolepis* based on *Hemicarpus isolepis* NEES. Possibly the second also should be so returned, expanding the concept of the genus to include it, but the evidence in support of such a step is not conclusive.

*Lipocarpus isolepis* (NEES) R. W. HAINES comb. nov. [syn. *Hemicarpus isolepis* NEES in Edinb. New Phil. Journ. 7, p. 263 (1834) and *Scirpus isolepis* (NEES) BOECK. in Linnaea 36, p. 498 (1870)] is an annual, widespread in the warmer parts of the Old World (Fig. 3). A solitary cone

projects horizontally, overtopped by a bract continuing the culm. Each cone-scale covers a flower enclosed in a membranous sheath which becomes closely applied to the achene as it ripens, so as to require soaking for its separation. NEES (1834) described the sheath as consisting of a single scale, basing his new genus *Hemicarpha* on this species. CLARKE (1901) described an occasional single scale placed laterally but his drawings (1909) showed it dorsal, while HOLTUM (1945) showed two scales side by side as in *Hypolytrum*. In fact there are two scales, a lower dorsal enwrapping an upper ventral as in *Lipocarpa chinensis*. Even if the observations that one or both scales may sometimes be absent is correct (cf. CLARKE 1901), the two species must be placed in the same genus. Again PALLA's (1908) statement that *Lipocarpa* species all have a clearly terminal inflorescence as opposed to *Hemicarpha* where the inflorescence is apparently lateral cannot be upheld, for *Lipocarpa minima* CHERM. and *L. monostachya* R. GROSS & MATTF. figured by CHERMEZON (1937) and NAPPER (1965) have solitary lateral cones. *L. minima* CHERM. was, however, found by RAYNAL (1967) to be a depauperate form of *L. nana* (A. RICH.) J. RAYNAL, which normally has a terminal inflorescence.

The transfer of the type species leaves the genus *Hemicarpha* ill defined, but it can possibly be conserved (if a very narrow concept of the genera is wanted), with *Hemicarpha micrantha* (VAHL) BRITTON (syn. *Scirpus micranthus* VAHL, *Isolepis micrantha* ROEM. & SCHULTES) as the new type. This plant agrees with NEES's (1834) formal description of the genus and was figured by him as *Hemicarpha subsquarrosa* in 1842 (see FRIEDLAND 1941). The genus now appears homogeneous and predominantly of the Western Hemisphere. The present writers agree with KUNTH's (1837) note, "*Lipocarphae proxima, vix distinguenda*", but rely for its separation on the absence of an upper scale, leaving only one scale below the achene. PALLA

(1908) showed that the missing scale was the glume, BLASER (1944) that the prophyll could lose its ribs and FRIEDLAND (1941) that it could occasionally be absent altogether.

PALLA (1905) found the upper scale in *Lipocarpa sellowiana* KUNTH particularly reduced and suggested that if a species were found with the scale still more rudimentary it would give a transition to *Hemicarpha* and the genera would have to be fused. But the distinction between one genus and another derived from it would always be shadowy if the extinct species were known, though a limit, however arbitrary, could be set. In animals where fossils are available the tendency is to push divisions as far back as specialisation can be followed; thus to include the mammal-like reptiles in Mammalia rather than Reptilia on account of their specialized skull structure (REED 1960, 1967). Applying REED's principle the discovery of a plant such as PALLA postulated would not necessarily sink *Hemicarpha*, though it might lead to the transference of both *Lipocarpa sellowiana* and the new plant to that genus.

*Mariscus paradoxus* (CHERM.) CHERM. (in CHERMEZON 1925), originally described as *Lipocarpa paradoxa* CHERM. in CHERMEZON 1921 (*Cyperus subparadoxus* KÜK. in KÜENTHAL 1936), figured by CHERMEZON (1937), is a small annual found once in Madagascar and now, as a weed of a rice-field beside a sea inlet in the city of Dar-es-Salaam, on the African mainland. Its minute, closely packed cones resemble those of a *Lipocarpa*, but differ in three respects (Fig. 4). The cones are pedunculate rather than sessile, giving a paniculate inflorescence resembling that of a *Fimbristylis*. Though the two scales below the flower are placed as in *Lipocarpa* there is, in addition, a minute third scale carried on a continuation of the spikelet axis above the flower, "dernier entre noeud de la rachéole (et glume supérieure vide rudimentaire) à peine 3/4 mm. hyaline" (CHERMEZON 1925). The cone-bract and prophyll



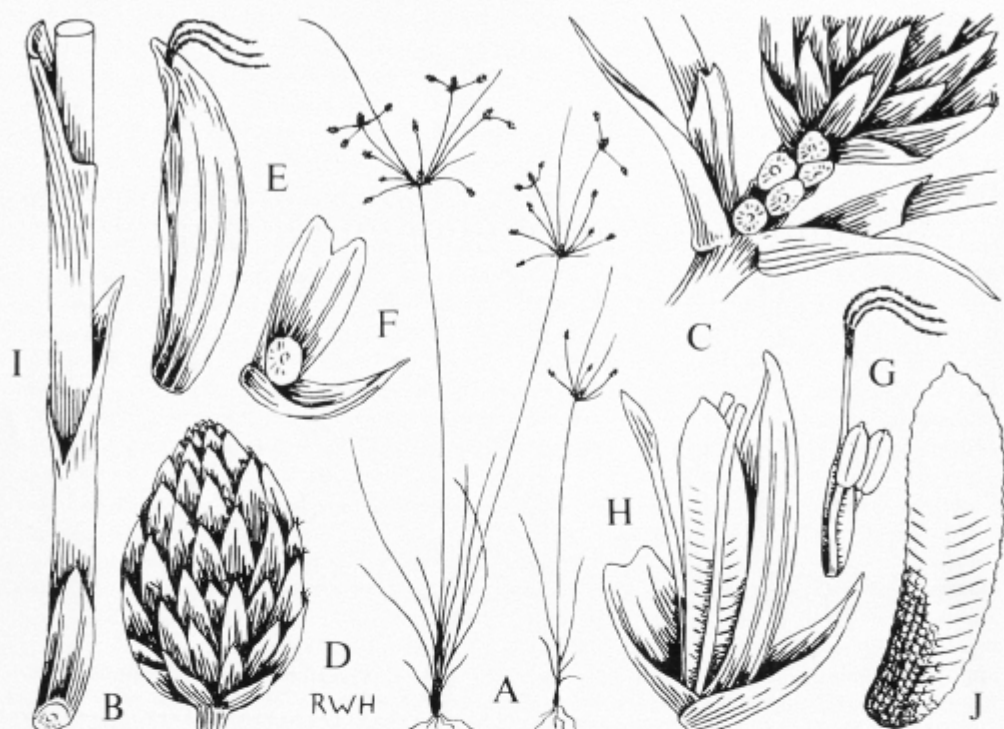


Fig. 4. *Mariscus paradoxus* (CHERM.) CHERM. — A: Habit  $\times 1/2$ . — B: Base of shoot. — C: Inflorescence fragment. — D: Cone. — E: Flower enclosed in scales. — F: Bract and prophyll. — G: Isolated flower. — H: Fruit with associated scales. — I: Achene. — Drawn from HAINES 4138 (Rice-field near sea inlet, Dar es Salaam, Tanzania).

are relatively short and do not cover the much longer glume and fruit, though they fall with it or soon after.

It was the discovery of the third scale that led CHERMEZON to transfer his plant from *Lipocarpa* to *Mariscus*, and KÜKEN-THAL (1936) placed this "planta rarissima critica" in his subsection *Brevistylis*, section *Umbellati*, subgenus *Mariscus* of *Cyperus*. But other species of that group do not have the minute cone and it seems possible that it is an isolated offshoot of the evolutionary line leading to *Lipocarpa*. The presence of the second glume need not preclude its return to *Lipocarpa*, for RAYNAL (1968) has accepted *Ascolepis dipsacoides* (SCHUMACH.) J. RAYNAL as a true *Ascolepis* in spite of the presence of

a small adaxial prophyll not usually found in the genus, basing his action on the relative development of the spikelet elements rather than on their presence or absence. But the uncertainty of the evolutionary pathways precludes the application of REED's principle and the return to *Lipocarpa*. The pedunculate inflorescence could be derived directly from a remote ancestor, but it is equally possible that it is neomorphic in origin.

PALLA (1905) foretold that one day a *Lipocarpa* with two-flowered spikelets would be found, confirming his interpretation of the cone as a cone of one-flowered spikelets. He was expecting an occasional variation with two bisexual flowers, but in *M. paradoxus* the uppermost scale can be

regarded as a second glume emptied of the flower it once subtended. In any case the structure of the cone gives strong support to the placement of *Lipocarpha* in Cyperaceae near *Mariscus*.

### GENERIC CIRCUMSCRIPTION OF ISOLEPIS

The genus *Isolepis* was established by ROBERT BROWN (1810), and the lectotype is *I. setacea* (L.) R. BR. The concept of this genus has changed enormously during the past 160 years, and no less than 435 species combinations are known within the genus (cf. Index Kewensis). Species from the following genera have at one time been included in *Isolepis*: *Abildgaardia*, "*Actinoscirpus*", *Ascolepis*, *Blysmus*, *Bolboschoenus*, *Bulbostylis*, *Carex*, *Desmoschoenus*, *Eleocharis*, *Eleogiton*, *Ficinia*, *Fimbristylis*, *Fuirena*, *Hemicarpha*, *Holoschoenus*, *Kyllinga*, *Phylloscirpus*, *Rhynchospora*, and *Schoenoplectus*. Even at present there is much confusion in the generic concept of *Isolepis* (cf. LYE 1971 b). While CLAPHAM et al. (1962) accept *Isolepis* as separate from *Schoenoplectus*, HESS et al. (1967) include *Isolepis* in the much more recently described genus *Schoenoplectus*. HESS et al. are obviously of the opinion that *Isolepis* R. BR. must be regarded as a *genus confusum*, but with *Isolepis setacea* as the type species there should be no reason for this attitude. Because VAN DER VEKEN (1965) has shown that *Schoenoplectus* and *Isolepis* are not related closely since their embryo-types differ, both genera can be retained.

*Isolepis* R. BR. section *Isolepis* includes such species as *I. setacea* (L.) R. BR., *I. cernua* (VAHL) ROEM. & SCHULTES, and *I. costata* (BOECK.) A. RICH. These are all slender herbs with terete stems and a few filiform leaves or with leaves absent. The inflorescence is apparently lateral with a subterete green bract appearing as a prolongation of the stem. The spikes are lateral, 1—15 together, with scales spirally

arranged. The flowers are bisexual, always without perianth-bristles or hyaline scales, and with 3 stigmas. The nutlet is trigonous, smooth, longitudinally striate or appearing dotted, and the embryo is of *Cyperus*-type.

This is a natural group of species, obviously related to *Eleogiton* on one side and *Hemicarpha* and *Lipocarpha* on the other (all with a *Cyperus*-type embryo). *Eleogiton* differs from *Isolepis* in having a terminal inflorescence usually consisting of a single spike, and an elongated more leafy stem. *Hemicarpha* is also very closely related to *Isolepis* differing only in having a thin hyaline scale within the cone-bract ("glume"). Similarly *Lipocarpha* differs from *Isolepis* and *Hemicarpha* only in having two hyaline scales within the bract.

Since *Isolepis* section *Isolepis* is similar to *Lipocarpha* and *Hemicarpha* in habit, inflorescence-type, achene-structure and embryo-types, and differs only in minute floral characters (i.e., absence of hyaline scales), it is obvious that the genera are closely related and must be placed in the same tribe of Cyperaceae. Fig. 2 shows that *Isolepis* is likely to have evolved from *Lipocarpha* with *Hemicarpha* as the intermediate link.

Two other groups of species with an *Isolepis*-type inflorescence and *Cyperus*-type embryo are more difficult to place on the evolutionary line. Firstly, the four species *Isolepis squarrosa* (L.) H.B.K., *I. kernii* (RAYMOND) K. LYE comb. nov. [syn. *Scirpus kernii* RAYMOND in Natur. Canad. 86, p. 230 (1959)], *I. rehmannii* (RIDLEY) K. LYE comb. nov. [syn. *Scirpus Rehmannii* RIDLEY in Trans. Linn. Soc. Lond. ser. 2, 2, p. 159 (1884)], and *I. hystrix* (THUNB.) NEES, form a distinct group easily recognized on their long mucronate scales (cf. RAYNAL 1968). The flower and inflorescence-structures are, however, as in *Isolepis* s. str. and it is therefore difficult to establish a new genus for these species although they may have evolved from *Cyperus* (or a now extinct "*Protocyperus*") through a different group of ancestors.

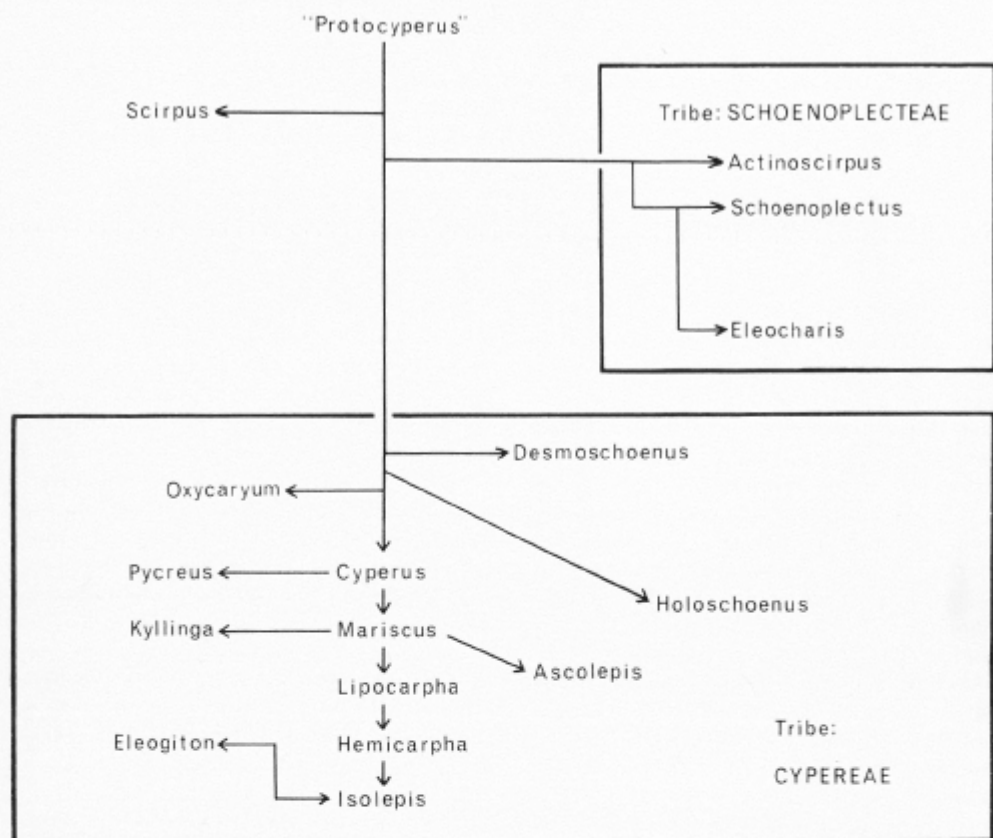


Fig. 5. Evolutionary trends in Cyperaceae tribes Cypereae and Schoenoplecteae. *Protocyperus* is an imaginary extinct genus; it might have been of *Scirpus*-habit, but with *Cyperus*- or *Schoenoplectus*-type embryo. Genera with a *Cyperus*-type embryo and here regarded as belonging to Cypereae inside the lower square. Genera with a *Schoenoplectus*-type embryo are here regarded as belonging to Schoenoplecteae inside the upper square. It is not indicated which genera *Scirpus* may have given rise to.

Another group of species comprises *Isolepis polyphylla* A. RICH. [syn. *Scirpus steudneri* BOECK.], *I. microcephala* (STEUD.) K. LYE comb. nov. [syn. *Kyllinga microcephala* STEUD. in Flora 1842 p. 597], as well as several undescribed species. This group corresponds to *Scirpus* section *Micheliani* in CLARKE 1902 p. 448. This section differs from the *I. squarrosa* group by having a less reduced style and more numerous spikes. There is strong evidence that this group also has developed from a *Cyperus*- or *Mariscus*-type ancestor, but it is not

possible to tell whether the evolution has gone through the same genera as for the two previous groups.

#### EVOLUTIONARY TRENDS IN CYPEREAE

We believe that the genera *Lipocarpha*, *Hemicarpha*, and *Isolepis* are closely related and that they belong to Cypereae and not to Scirpeae (cf. LYE 1971 a). *Lipocarpha* and *Hemicarpha* can either be re-

garded as sections or subgenera of *Isolepis* or as independent genera. A full revision of the genera in question is needed to clarify this matter. Although we agree with KOYAMA (1961) that *Lipocarpha* is more closely related to *Cyperus* than to *Scirpus*, we do not think it can be sunk into that genus. If, however, *Lipocarpha* is sunk into *Cyperus* then even *Isolepis*, which is more closely related to *Lipocarpha* than *Lipocarpha* is to *Cyperus*, has also to be sunk into *Cyperus*.

In Fig. 5 a possible evolution of the genera is indicated. We believe that *Isolepis* s. str. has developed from *Cyperus* through *Mariscus*, *Lipocarpha* and *Hemicarpha*. It is, however, possible that for one or two sections of *Isolepis* the evolution may have gone through *Ascolepis* rather than through *Lipocarpha*—*Hemicarpha*. It is even possible that an *Isolepis*-type plant could have developed directly from *Cyperus* by merely changing from a distichous to a spiral arrangement of its glumes. In *Cyperus michelianus* (L.) LINK [syn. *Isolepis micheliana* (L.) ROEM. & SCHULTES] the glumes are spirally arranged while in another subspecies of the same species, viz. *Cyperus michelianus* subsp. *pygmaeus* (ROTTB.) ASCH. & GRAEBN., the glumes are distichously arranged as typical in *Cyperus* (cf. KÜKENTHAL 1936).

The genus *Actinoscirpus* in Fig. 5 is *Scirpus* section *Actinoscirpus* OHWI in Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, 18, p. 98 (1944). This section can be regarded as a monotypic genus consisting of a single species, viz. *Scirpus grossus* L. FIL. in Suppl. Sp. Pl. p. 104 (1781). We believe this plant to be rather primitive and an earlier member of the genus may have given rise to *Schoenoplectus* through *Bolboschoenus* (cf. also BEETLE 1946).

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# Cytogeography of the Genus *Hedypnois* (Compositae)

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## ABSTRACT

NORDENSTAM, B. 1971. Cytogeography of the genus *Hedypnois* (Compositae). — Bot. Notiser 124: 483—489.

The genus *Hedypnois* SCOP. (Compositae—Cichorieae—Leontodontinae) comprises annual herbs with more or less weedy tendencies. Especially in the East Mediterranean region there is great morphological as well as cytological diversification. In 47 populations studied, the somatic chromosome numbers were  $2n=8, 12, 13, 14,$  and  $16,$  with  $13$  as the most frequent number, and with an almost absolute constancy within each population.

It is suggested, that some type of agamospermy may account for the strict maintenance of odd chromosome numbers like  $2n=13$  in many populations. If  $x=4$  is taken as a basic number in the genus, strains with  $2n=10-14$  may have arisen through occasional hybridization between sexual and normally autogamous diploid and tetraploid stocks. However, the possibility of a step-wise reduction of basic number, viz.  $x=8 \rightarrow 7 \rightarrow 6 \rightarrow 5 \rightarrow 4,$  should also be considered and perhaps favoured. All steps in this chain of descending aneuploidy have now been found in nature. Further investigations have been initiated to test the suggestions put forward and to obtain further data.

## INTRODUCTION

The genus *Hedypnois* SCOP. (Compositae—Cichorieae—Leontodontinae) is notoriously difficult from a taxonomic point of view. This is reflected, e.g., by the fact that about twenty specific names have been applied to what is generally regarded as a single species — to say nothing of the number of infra-specific taxa published. The genus comprises annual herbs of a more or less pronounced weedy character. The distribution range covers much of the Mediterranean region and also includes Madeira and the Canaries. In most current floras only one species is recognized, with or without taxonomic subdivision, but some authors retain a few entities on the species level. The difficulties to define and circumscribe the taxa adopted are obvious in all treatments, except when the whole material is lumped in one heap under the

name of *H. rhagadioloides* (L.) WILLD. or *H. polymorpha* DC.

During excursions in the Mediterranean, particularly in Greece and Egypt, I was struck by the polymorphism exhibited by members of the genus. When plants were studied in cultivation, first on a small scale, some remarkable facts emerged, which called for an extension of the investigation. In the present paper, which has the character of a preliminary report, the variation in chromosome number is presented and discussed.

## ACKNOWLEDGEMENTS

My sincere thanks are due to Prof. H. RUNEMARK and his collaborators in Lund for allowing me to use their herbarium material and seed collections from the Aegean. A special word of thanks is di-

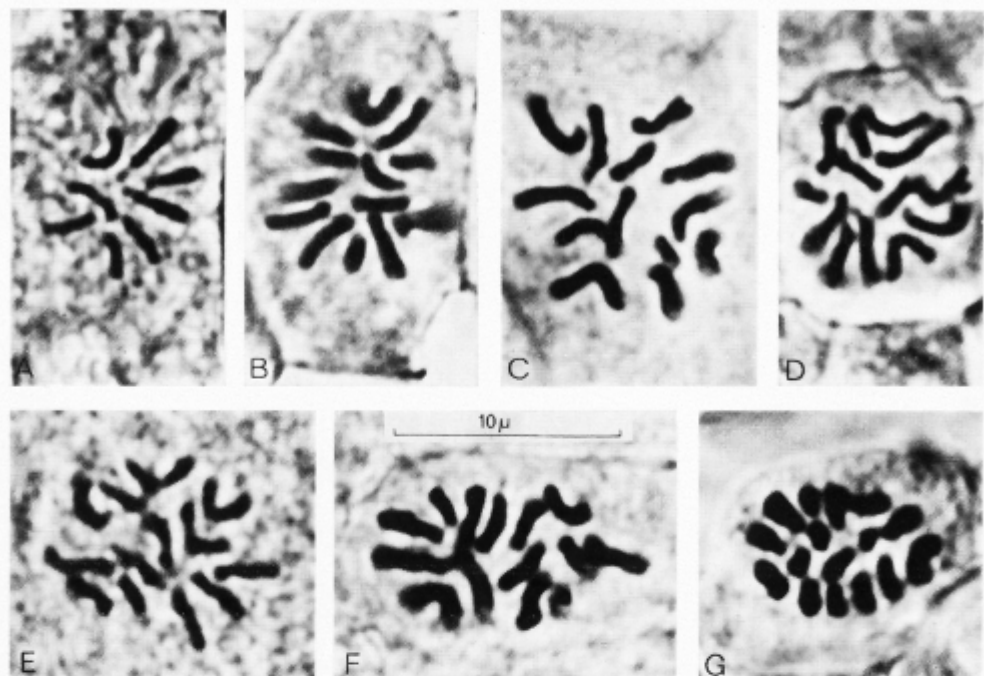


Fig. 1. Metaphase plates from root tip mitoses of *Hedypnois rhagadioloides* (L.) WILLD. s.lat., all  $\times 3000$ . — A:  $2n=8$  (R & Be 29679-1). — B:  $2n=13$  (R & Be 26330-1). — C:  $2n=13$  (R & Be 28622-5). — D:  $2n=13$  (R & Be 27814-1). — E:  $2n=13$  (R & S 7116-6). — F:  $2n=14$  (R & E 35520-10). — G:  $2n=16$  (R & E 36081-5). — Photo K. E. SAMUELSSON, Museum of Natural History, Stockholm.

rected to Dr. A. STRID, who contributed the material from Albania, and to Dr. R. DAHLGREN, Lund, who allowed me to examine his material from the Balearic Islands.

#### MATERIAL AND METHODS

Plants were raised from seeds in the Botanical Garden, Lund, and in Hortus Bergianus, Stockholm. The chromosomes were studied in root tip metaphases, prepared according to the paraffin method. The fixative employed was the Navashin-Karpechenko fluid or its so-called Svalöf modification. After sectioning, the preparations were stained in crystal violet with or without an addition of aniline, and per-

manently mounted. Cytological slides and voucher specimens are deposited in the Botanical Museum, Lund (LD), and in the Museum of Natural History, Stockholm (S).

#### CHROMOSOME NUMBERS IN HEDYPNOIS

The table below lists all counts made by the present author. So far 47 populations from Egypt, Greece, Albania, and the Balearic Islands<sup>1</sup> have been studied, and unequivocal counts have been made on 191 individuals. In most cases many plates

<sup>1</sup> After the preparation of this manuscript the five Balearic counts have been published by DAHLGREN et al. (1971).

from more than one root tip have been examined. A few metaphase plates are shown in Fig. 1. In current taxonomic praxis the entire material would be referable to the complex species *H. rhagadioides* (L.) WILLD. (syn. *H. polymorpha* DC.).

The following abbreviations have been

used in connection with the collection numbers: B=R. VON BOTHMER; Be=B. BENTZER; E=L. ENGSTRAND; Eg=Egyptian material, leg. BJÖRQVIST, DAHLGREN, NORDBORG, NORDENSTAM et al.; N=B. NORDENSTAM; R=H. RUNEMARK; S=S. SNOGERUP; MMF=Balearic material, leg. DAHLGREN et al.

Collection	Locality	2n	No. of individuals studied
MMF 48	Balearic Islands, Mallorca, between San Telmo and S'Arraco, 1969	8	4
MMF 89	Balearic Islands, Mallorca, 2 km S of Andraitx, 1969	8	2
MMF 137	Balearic Islands, Mallorca, a few km SE of Inca (road Palma—Inca), 1969	8	2
MMF 869	Balearic Islands, Minorea, Cabo Dartuch, 1969	8	2
Eg 714	Egypt, NW of Mersa Matruh, village Om el Racham, 1969	8	2
R & Be 29020	Greece, Paros, the island of Glaropounda, 1967	8	5
R & Be 29104	Greece, Paros, the island of Mavronisi, 1967	8	2
R & Be 29228	Greece, Paros, the island of Gaidaronisi, 1967	8	5
R & Be 29679	Greece, Milos, S of Akr. Romma, 1967	8	6
STRUD 0610	Albania, S of the shore at Durrës, 1969	12	3
R & S 7116	Greece, Safora (Safrania), N of the harbour, 1958	13	3
R & S 7159	Greece, Safora (Safrania), N of the harbour, 1958	13	3
R & S 11554	Greece, Petalides, Megalo Nisi, bay on the S. side, 1958	13	2
R & S 17561	Greece, Crete, 1 km S of Ag. Nikolaos, 1962	{ 13 17	3 1
R & S 18802	Greece, Samos, S and W of the harbour at Kalovasi, 1962	13	4
R & Be 26330	Greece, Poliagos, the NW, part, 1967	13	2
R & Be 27814	Greece, Serifos, the island of Serifopoula, 1967	13	1
R & Be 28140	Greece, Kamila, 1967	13	5
R & Be 28413	Greece, Stakida, central part, 1967	13	5
R & Be 28622	Greece, Antiparos, the island of Despotiko, 1967	13	4
S & B 31372	Greece, Andros, the island of Akrama, S of Gavriion, 1968	13	4
S & B 31868	Greece, Andros, 0.5—1 km NW—N of Apoikia, near the road to Vourkoti, 1968	13	2
S & B 32542	Greece, Andros, in the valley 1.5 km S—SSE of the mtn Ag. Saranda, 1968	13	5
MMF 146	Balearic Islands, Mallorca, a few km SE of Inca (road Palma—Inca), 1969	13	3
S & B 33006	Greece, Andros, at the river S of the town of Andros, 1968	13	5
R & E 35091	Greece, Mikonos, N of the town along the shore, 1968	13	10
R & E 36082	Greece, Mikonos, Dilos, the island of Ekati, 1968	13	4
R & E 36300	Greece, Mikonos, Dilos, Fourni, 1968	13	6
R & B 37625	Greece, Siros, Ag. Varvaras, 1968	13	7
Eg 163	Egypt, 21 km W of Alexandria on Mariut road, 1969	13	5
Eg 410	Egypt, 15 km W of Mersa Matruh, road junction to Siwa Oasis, 1969	13	5
Eg 431	Egypt, 15 km W of Mersa Matruh, road junction to Siwa Oasis, 1969	13	1
R & N 15629	Greece, Ano Koufonisi, 1960	14	1
R & Be 29888	Greece, Milos, in the bay NNE of Prof. Elias, 1967	14	2

Collection	Locality	2n	No. of individuals studied
R & E 35520	Greece, Mikonos, Ormos Ornos, 1968	14	10
R & B 37727	Greece, Siros, Ialissas, 1968	14	8
R & S 10774	Greece, Naxos, Panormon Canyon, 1 km N of 'Ancient Acropolis', 1958	15	1
		16	2
R & S 7529	Greece, Saria, Ormos Armiro, 1958	16	4
R & S 11535	Greece, Petalides, Megalo Nisi, bay on the S. side, 1958	16	3
R & S 11582	Greece, Petalides, Prassonisi, 1958	16	5
R & S 11997	Greece, Levita, 'Porto di Levitha', 1958	16	2
R & Be 28456	Greece, Stakida, S. part of the island, 1967	16	4
R & E 35162	Greece, Mikonos, N of Ano Mera, 1968	16	7
R & E 35887	Greece, Mikonos, Rinia, Lazaretto, 1968	16	2
R & E 36081	Greece, Mikonos, Dilos, the island of Ekati, 1968	16	9
R & E 36519	Greece, Tinos, 3 km S of the town, 1968	16	5
R & E 37927	Greece, Kithnos, NE of Ag. Louka, 1968	16	3

### Previous studies

The first chromosome number reported for the genus *Hedypnois* was counted by KUHN (cited in TISCHLER 1931), who stated the gametic number of *H. cretica* WILLD. to be  $n=27$ .

NEGODI (1932) made a serious attempt to analyze the polymorphism of the species complex, which he called *H. globulifera* LAM. He made crossing experiments between two morphologically very different strains, originating from Sardinia and referred to as *tubaeformis* and *monspeliensis*, respectively. The technique employed was simply rubbing of the flower-heads against each other. The achenes obtained were germinated and the progeny analyzed. Of the resulting 150 plants, only two individuals were morphologically intermediate between the parents and supposed to be hybrids. The remainder were all maternal and dismissed as the result of selfing. The offspring ( $F_2$ ) of the two hybrids was studied in more detail by NEGODI, who observed a wide morphological range among the segregates. NEGODI concluded that most natural populations very likely represent pure lines, resulting from strict autogamy. Occasional outbreeding would account for recombination of characters in a random and multifarious fashion.

In a later paper NEGODI (1936) presented chromosome counts of the two parents used in his crossings as well as of the hybrids obtained. All plants were reported to have the somatic number  $2n=16$ , and the same number was found by NEGODI in material from some botanical gardens under the names of *monspeliensis*, *tubaeformis* and cfr. *cretica*, respectively.

STEBBINS et al. (1953) counted the number  $2n=8$  in two collections referred to *H. cretica* and  $2n=16$  in two other collections referred to *H. tubaeformis*. They concluded that the basic number is  $x=4$ , and they characterized the genus as "an extensive polyploid complex".

FAHMY (1951, 1955) reported  $2n=16$  and  $2n=12$  in material from southern France, the latter number being the more rare one. He also studied meiosis and in 16-chromosomal plants observed a high percentage of irregularities (2 or 4 univalents), possibly indicating a hybridogenous origin.

LARSEN (1956) found  $2n=13$  in two strains from southern Italy. He interpreted the smaller, odd chromosome as an accessory, although he remarked that it showed no signs of being heterochromatic. LARSEN suggested that the basic number would be  $x=6$ , and that from the original number of  $2n=12$ , races with different numbers of

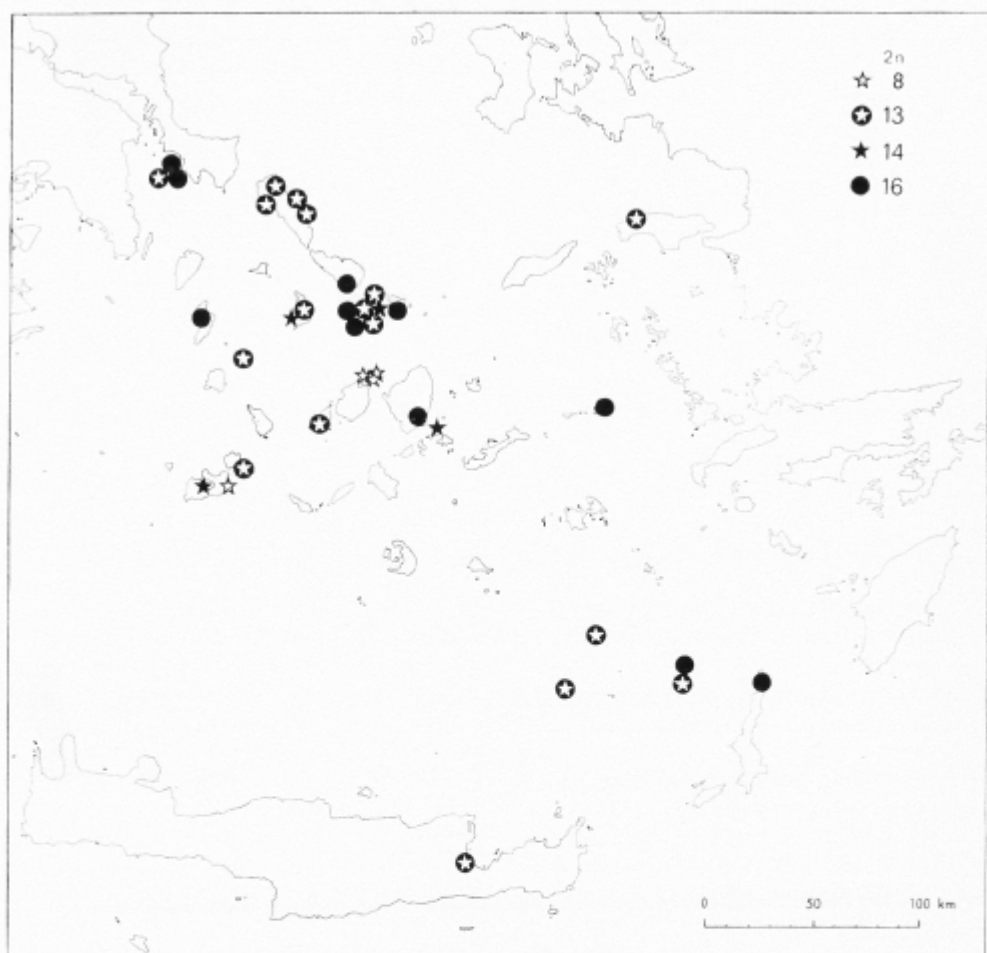


Fig. 2. Distribution in the Aegean of different chromosome numbers in *Hedypnois rhagadioides* (L.) WILLD. s.lat.

accessory chromosomes might have developed (e.g.,  $12+1 B$ ,  $12+4 B$ ).

The number  $2n=10$  was recently reported from the Canary Islands by BORGES (1970).

### Discussion

A morphological analysis will not be presented here, but is deferred to a later treatise. Nor can any taxonomic conclusions be drawn at this stage of the inves-

tigation. It should be noted, however, that there is no immediate and easily observed correlation between external morphology and chromosome number in the material investigated, with the following exception. In all populations with  $2n=16$  the peduncles are apically thickened in a very conspicuous manner, and furthermore, this character is in my material almost confined to plants with this chromosome number. Such plants are usually named *tubaeformis* (as species, subspecies or



variety) in current literature and herbaria. The epithets *monspeliensis* and *cretica*, on the other hand, are widely used for material comparable to some of the populations with chromosome numbers ( $2n$ ) from 8 to 14.

However, the above generalizations are partly contradicted by the papers by NEGODI (1932, 1936) and LARSEN (1956). The former reported the number  $2n=16$  in plants classified as *tubaeformis* as well as in those referred to as *monspeliensis* and cfr. *cretica*. The latter only found  $2n=13$ , and his material was said to represent *tubaeformis*. However, these apparent discrepancies may be due to classificatory difficulties. In this connection it should be mentioned that KUHN's early report of  $n=27$  never has been verified and remains highly doubtful.

The 37 Aegean populations studied could be roughly sorted into 20 morphological groups with various combinations of characters. The most useful characters include those of leaf-shape, peduncle thickness and pubescence, involucre shape and pubescence, achene and pappus morphology, and some more. The morphological diversity is surprisingly great and best studied on plants in cultivation under comparable conditions. E.g., not even the four Aegean populations with  $2n=8$  are morphologically uniform, but represent two morphological types, viz. one from the islets near Paros and one from Milos (cf. Map 1). Similarly, the four populations with  $2n=14$  represent three different character combinations, which in turn appear to be distinct from those encountered in populations with  $2n=13$ . The latter are far from uniform, comprising several morphological types.

Another noteworthy feature is the striking morphological uniformity within the populations. Up to ten individuals have been grown from each population, and the similarity between the individuals is always very strong. Segregation, like in NEGODI's hybrid offspring, has not been observed.

The morphological uniformity of the populations is paralleled by the constancy in chromosome number. In the 22 populations with  $2n=13$ , all individuals but one, i.e. 89 out of 90, proved to have the same somatic number. The single exception was a plant with  $2n=17$  in a population from Crete.

The geographic distribution ranges of the different chromosome numbers are wide and largely sympatric, as can be seen from Map 1, showing the best investigated area, i.e. the Aegean. Possibly the number  $2n=14$  has a more restricted distribution, hitherto being known only from the Kiklades.

In the absence of further data, the facts presented are wide open for speculation. The variation in chromosome number can be interpreted in different ways. The original basic number in the group may be  $x=4$ . The diploid and tetraploid populations are probably sexual and normally autogamous, with a high degree of homozygosity as a result. Occasional outbreeding may maintain gene circulation, resulting in new character combinations and eventually new pure lines. It should be noted in this context, that NEGODI's few successful crossings were on the same chromosomal level ( $2n=16$ ). Hybrids between diploid and tetraploid strains, however, may be expected to show reduced fertility. If the decrease or loss of sexuality is compensated by agamic reproduction, true-breeding segregates with various character combinations and different chromosome numbers ( $2n=10-14$ ) may result.

Another possibility is that of a descending series of aneuploid basic numbers, in analogy with the convincingly demonstrated reduction in *Crepis*, i.e. in this case  $x=8 \rightarrow 7 \rightarrow 6 \rightarrow 5 \rightarrow 4$ . The frequent somatic number  $2n=13$  could with LARSEN be interpreted as  $12+1B$ , but to my mind there are some obstacles to this interpretation. One point is that the number  $2n=12$  appears to be very rare — so far only observed in a single population from Albania and also reported from southern France.

A less serious objection is that the odd chromosome is large and apparently not heterochromatic. But above all, if accessories were present, their number would be expected to oscillate within the populations, due to loss or enrichment during the meiotic process. The present study has demonstrated a high constancy of chromosome number, including  $2n=13$ , within the populations.

The facts at hand thus favour the assumption that agamospermy occurs at least on some chromosomal level in *Hedypnois*, although very likely sexuality may be the rule. Clearly, further investigations are necessary, including a study of breeding systems in the genus, artificial hybridizations, meiotic studies and karyotype analyses. The ultimate object is a secure foundation for a taxonomic treatment of the genus throughout its range. *Hedypnois* is clearly a case, where taxonomic revision, exclusively based on herbarium material, would be a highly precarious undertaking.

### Request

Since it is desirable in the future studies to include a representative material from the whole distribution range, colleagues

are requested to send spontaneous seed collections of *Hedypnois* to the author.

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# Chromosome Numbers in some Albanian Angiosperms

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## ABSTRACT

STRID, A. 1971. Chromosome numbers in some Albanian Angiosperms. — Bot. Notiser 124: 490—496.

Chromosome numbers are reported for 91 species of Angiosperms from Albania. Nine of these species have not previously been investigated cytologically, viz. *Oenanthe incassans* BORY & CHAUB. ( $2n=66$ ), *Orlaya daucorlaya* MURB. ( $2n=14$ ), *Erigeron crispus* POURR. ( $2n=54$ ), *Oremis mixta* (L.) DC. ( $2n=18$ ), *Trifolium dalmaticum* VIS. ( $2n=10$ ), *Calamintha nepeta* (L.) SAVI ( $2n=40$ ), *Micromeria cremnophila* BOISS. & HELDR. ( $2n=30$ ), *Sideritis romana* L. ssp. *purpurea* (TALBOT) BALL [= *S. purpurea* TALBOT] ( $2n=28$ ), and *Parietaria lusitanica* L. ( $2n=26$ ). In eight cases the counts deviate from previous reports for the same taxon, viz. *Daucus broteri* TEN. ( $2n=22$ ), *Torilis nodosa* (L.) GAERTN. ( $2n=24$ ), *Peltaria alliacea* JACQ. ( $2n=14$ ), *Lepidium graminifolium* L. ssp. *graminifolium* ( $2n=48$ ), *Euphorbia platyphyllos* L. ( $2n=30$ ), *Ononis spinosa* L. ssp. *austriaca* (BECK) GAMS ( $2n=20$ ), *Blackstonia perfoliata* (L.) HUDS. ( $2n=20$ ), and *Marrubium alternidens* RECH. FIL. ( $2n=34$ ). The latter species is new for the Albanian flora.

## INTRODUCTION

During a week's visit to Albania in the late summer of 1969 the author had the opportunity of collecting some plants and seeds. Chromosome numbers have been established for 91 species cultivated in the Lund Botanical Garden.

Seeds were collected from the following localities, all in C. Albania:

1. Tiranë, at the airport. 1.8. 1969.
2. Sandy fields and salt-marshes near the beach at Durrës, 2.8. 1969.
3. Same as 2. 3.8. 1969.
4. State collective farm "Plazh-Sukth" c. 10 km E of Durrës. 3.8. 1969.
5. Sandy fields and salt-marshes between Durrës beach and the town of Durrës. 3.8. 1969.
6. Sandy fields and railway banks just S of Durrës beach. 3.8. 1969.

7. Kruj. Macchia and ruderal ground around the castle, c. 500 m s.m. 4.8. 1969.

8. W. side of the pass E of Prenjas, c. 700 m s.m. Macchia and rocks. 5.8. 1969.

9. Macchia and roadsides in N. outskirts of Progradec (SW. corner of lake Ohrid), c. 600 m s.m. 6.8. 1969.

10. C. 5 km SE of Librash, 250 m s.m. Macchia along a small stream. 6.8. 1969.

11. NW. side of the pass between Elbasan and Mysgetë, c. 720 m s.m. Macchia. 6.8. 1969.

12. Hills just above the town of Durrës. Macchia and pine plantation. 7.8. 1969.

Root tips of young plants were fixed in the Svalöv modification of Navashin-Karpechenko, embedded in paraffin, cut by means of a microtome, and stained with crystal violet. Feulgen staining and squash technique was used in a few cases.

Unless otherwise indicated the nomenclature follows Flora Europaea (TUTIN & al. 1964—) in its present extension and HAYEK (1924—33) for groups not yet treated in Flora Europaea. Voucher specimens and slides have been preserved at the Department of Plant Taxonomy, University

of Lund. Previous counts have in most cases been obtained from "Chromosome Numbers of Flowering Plants" (Ed. FEDOROV 1969) and "Index to Plant Chromosome Numbers" (Regnum Vegetabile vols. 68 and 77), where references to original papers can be found.

## LIST OF CHROMOSOME COUNTS

Taxon	Locality	Voucher	2n	Previous counts
<b>APIACEAE</b>				
1. <i>Ammi visnaga</i> (L.) LAM.	6	0622	20	20, 22 (FEDOROV 1969)
2. <i>Daucus broteri</i> TEN.	6, 7	0612, 0704	22	20 (F 1969)
3. <i>Oenanthe incrassans</i> BORY & CHAUB.	6	0601	66	—
4. <i>Orlaya daucorlaya</i> MURR.	11	1105	14	—
5. <i>Tordylium apulum</i> L.	7	0742	20	20 (Regn. Veg. 68)
6. <i>Tordylium maximum</i> L.	12	1207	20	22 (F 1969); 20 (Regn. Veg. 68)
7. <i>Torilis nodosa</i> (L.) GAERTN.	7	0720	24	22 (F 1969)
<b>ASTERACEAE</b>				
8. <i>Anthemis cotula</i> L.	4	0427	18	18 (F 1969)
9. <i>Crepis foetida</i> L. ssp. <i>rhoadifolia</i> (BIEB.) SCHINZ	7	0703, 0731	10	(8), 10 (F 1969)
10. <i>Crepis pulchra</i> L.	7	0722, 0728	8	8 (F 1969)
11. <i>Crepis setosa</i> HALL. FIL.	9	0918	8	8 (F 1969)
12. <i>Erigeron crispus</i> POURR.	4	0415	54	—
13. <i>Hedypnois rhagadioloides</i> (L.) WILLD. ssp. <i>cretica</i> (L.) HAYEK	6	0610	12	8, 12, 13, 16 (F 1969)
14. <i>Helminthia echioides</i> (L.) GAERTN.	2, 4, 5	0203, 0401, 0508	10	(8), 10 (F 1969)
15. <i>Hypochaeris radicata</i> L.	5	0511	8	8 (F 1969)
16. <i>Leontodon asper</i> POIR.	7	0702	8	8 (F 1969)
17. <i>Oremis mixta</i> (L.) DC.	5	0512	18	—
18. <i>Pulicaria dysenterica</i> (L.) BERNH.	6	0609	18	18, 22 (F 1969)
19. <i>Reichardia picroides</i> (L.) ROTH	12	1203	14	14 (F 1969)
20. <i>Senecio vulgaris</i> L.	7	0754	40	38, 40 (F 1969)
21. <i>Sonchus oleraceus</i> L.	4, 7	0411, 0752	32	32 (F 1969)
22. <i>Xeranthemum annuum</i> L.	9	0921	12	12 (F 1969)
<b>BORAGINACEAE</b>				
23. <i>Cynoglossum creticum</i> MILL.	9	0914	24	24 (F 1969)
24. <i>Echium italicum</i> L.	7	0737	16	16, 32 (F 1969)
25. <i>Echium lycopsis</i> L.	12	1205	16	16 (Fl. Eur. unpubl., F 1969)
26. <i>Echium vulgare</i> L.	7	0717	16	16, 32 (Fl. Eur., F 1969)
27. <i>Onosma tubiflorum</i> VELEN.	9	0908	26	26, 28 (TEPPNER 1971)
<b>BRASSICACEAE</b>				
28. <i>Cakile maritima</i> (L.) SCOP.	5	0506	18	18 (F 1969)
29. <i>Diplotaxis tenuifolia</i> (L.) DC.	12	1204	22	22 (Fl. Eur. 1); 14, 20+2 B, 22 (F 1969)
30. <i>Hirschfeldia incana</i> (L.) LAGRÉZE-FOSSAT	7	0724	14	14 (F 1969)

Taxon	Locality	Voucher	2n	Previous counts
31. <i>Peltaria alliacea</i> JACQ.	7	0727	14	28 (56) (F 1969)
32. <i>Lepidium graminifolium</i> L. ssp. <i>graminifolium</i>	7	0748	48	16 (F 1969)
CARYOPHYLLACEAE				
33. <i>Petrorhagia saxifraga</i> (L.) LINK	9	0917	60	60 (F 1969)
34. <i>Silene alba</i> (MILL.) KRAUSE ssp. <i>divaricata</i> (REICHENB.) WALTERS	7	0714	24	24 (Fl. Eur. 1), 24, 48 (F 1969)
35. <i>Silene conica</i> L. ssp. <i>conica</i>	6	0606	20	20 (Fl. Eur. 1), 20, 24 (F 1969)
36. <i>Silene viridiflora</i> L.	11	1106	24	24 (F 1969)
37. <i>Silene vulgaris</i> (MOENCH) GARCKE ssp. <i>vulgaris</i>	7	0734, 0751	24	24, 48 (Fl. Eur. 1, F 1969)
DIPSACACEAE				
38. <i>Scabiosa atropurpurea</i> L. var. <i>maritima</i> (TORN.) BEGU.	4	0426	16	16 (F 1969)
39. <i>Tremastelma palaestinum</i> (L.) JANCH.	8	0801	16	16 (F 1969)
EUPHORBIACEAE				
40. <i>Euphorbia platyphyllos</i> L.	6	0616	30	28, 36 (F 1969)
FABACEAE				
41. <i>Lotus uliginosus</i> SCHKUHR	3, 5	0305, 0505	24	12, 24 (F 1969)
42. <i>Medicago orbicularis</i> (L.) BARTAL.	7	0709	16	16, 32 (F 1969)
43. <i>Medicago sativa</i> L. ssp. <i>sativa</i>	12	1209	32	16, 32, 64 (F 1969)
44. <i>Ononis spinosa</i> L. ssp. <i>austriaca</i> (BECK) GAMS	6	0615	20	30 (32) (Fl. Eur. 2, F 1969)
45. <i>Trifolium angustifolium</i> L.	4, 6	0402, 0618	16	14, 16 (F 1969)
46. <i>Trifolium arvense</i> L.	6	0617	14	14, 16 (F 1969); 14 (Fl. Eur. 2)
47. <i>Trifolium dalmaticum</i> Vis.	7	0726	10	—
48. <i>Trifolium nigrescens</i> Viv. ssp. <i>nigrescens</i>	7	0732	16	16, 32 (F 1969)
49. <i>Vicia villosa</i> ROTH ssp. <i>varia</i> (HOST) CORB.	4	0405	14	14 (F 1969)
GENTIANACEAE				
50. <i>Blackstonia perfoliata</i> (L.) HUDS.	4	0424	20	40, 44 (F 1969)
GERANIACEAE				
51. <i>Erodium cicutarium</i> (L.) L'HÉR. ssp. <i>cutarium</i>	9	0915	40	40 (60) (Fl. Eur. 2); 20, 36, 30—38, 40, 48, 54 (56) (F 1969)
52. <i>Geranium columbinum</i> L.	5	0509	18	18 (Fl. Eur. 2, F 1969)
53. <i>Geranium rotundifolium</i> L.	7	0733	26	26 (Fl. Eur. 2, F 1969)
LAMIACEAE				
54. <i>Acinos arvensis</i> (LAM.) DANDY	11	1102	18	18 (Fl. Eur. unpubl., F 1969)
55. <i>Ballota nigra</i> L. ssp. <i>uncinata</i> (FIORI & BÉG.) PATZAK	7	0725	22	22 (F 1969)



Taxon	Locality	Voucher	2n	Previous counts
56. <i>Calamintha nepeta</i> (L.) SAVI	7	0745	40	—
57. <i>Clinopodium vulgare</i> L. ssp. <i>orientale</i> BOTHM.	9, 11	0905, 1101	20	20 (F 1969)
58. <i>Lycopus europaeus</i> L.	3	0301	22	22 (F 1969)
59. <i>Marrubium alternidens</i> RECH. FIL.	7	0741	34	54 (Regn. Veg. 77)
60. <i>Micromeria cremnophila</i> BOISS. & HELDR.	7, 8	0743, 0803	30	—
61. <i>Prunella vulgaris</i> L.	4	0404, 0421	28	28 (Fl. Eur., unpubl.) 28, 32 (F 1969)
62. <i>Salvia viridis</i> L.	7	0738	16	16 (F 1969)
63. <i>Sideritis romana</i> L. ssp. <i>purpurea</i> (TALBOT) BALL	1, 12	0101, 1206	28	—
64. <i>Stachys germanica</i> L. ssp. <i>heldreichii</i> (BOISS.) HAYEK	7	0705	30	30 (F 1969)
LYTHRACEAE				
65. <i>Lythrum hyssopifolia</i> L.	6	0620	20	20, 30 (F 1969)
ONAGRACEAE				
66. <i>Oenothera biennis</i> L.	5	0514	14	14 (F 1969)
PLANTAGINACEAE				
67. <i>Plantago lanceolata</i> L.	4, 7	0419, 0701	12	12, 12+1 B, 13, 24, 96 (F 1969)
POACEAE				
68. <i>Agropyron junceum</i> L.	5	0502	42	28, 42, 84 (F 1969)
69. <i>Avena barbata</i> POTT.	6	0604	28	14, 28, 32 (F 1969)
70. <i>Bromus villosus</i> FORSK. var. <i>maximus</i> (DESF.) ASCH. & GRAEBN.	6, 7	0605, 0730	56	28, 42, 56, 70 (F 1969)
71. <i>Hagnaldia villosa</i> (L.) SCHUR	7	0715	14	14 (F 1969)
72. <i>Hordeum murinum</i> L.	4	0414	28	14, 28, 42 (F 1969)
73. <i>Panicum crus-galli</i> L.	5	0501	c. 54	36, 54 (F 1969)
74. <i>Poa bulbosa</i> L.	7	0716	28	Several numbers from 14 to 58 (F 1969)
75. <i>Scleropoa rigida</i> (L.) GRIS.	6	0611	14	14 (F 1969)
76. <i>Setaria verticillata</i> (L.) BEAUV.	4	0412	c. 54	18, 36, 54 (F 1969)
77. <i>Triticum ovatum</i> (L.) GREN. var. <i>triaristatum</i> (WILLD.) ASCH. & GRAEBN.	8	0805	28	28, 42 (F 1969)
POLYGONACEAE				
78. <i>Rumex crispus</i> L.	4	0403, 0408	60	60 (Fl. Eur. 1, F 1969)
79. <i>Rumex pulcher</i> L. ssp. <i>divaricatus</i> (L.) MURB.	6	0613	20	20 (Fl. Eur. 1); 20, 40 (F 1969)
PRIMULACEAE				
80. <i>Anagallis arvensis</i> L. ssp. <i>arvensis</i>	4	0409	40	40 (Fl. Eur. 1, F 1969)
81. <i>Samolus valerandi</i> L.	3	0304	26	24?, 26 (Fl. Eur.) 24, 26, 36 (F 1969)
RANUNCULACEAE				
82. <i>Nigella damascena</i> L.	12	1202	12	12 (F 1969)

Taxon	Locality	Voucher	2n	Previous counts
ROSACEAE				
83. <i>Potentilla recta</i> L.	10	1002	28	21, 28, 42, 84 (F 1969)
84. <i>Sanguisorba minor</i> SCOP. ssp. <i>muricata</i> (GREMLI) BRIQ.	7	0719	28	28 (Regn. Veg. 49)
RUBIACEAE				
85. <i>Galium aparine</i> L.	7	0729	66	Several numbers bwn 22 and 88 (F)
86. <i>Putoria calabrica</i> (L. FIL.) PERS.	11	1109	22	22 (F 1969)
SCROPHULARIACEAE				
87. <i>Linaria vulgaris</i> MILL.	9	0901	12	12 (F 1969)
88. <i>Scrophularia peregrina</i> L.	7	0721	36	36 (F 1969)
89. <i>Verbascum sinuatum</i> L.	6	0602	30	30 (F 1969)
90. <i>Veronica anagallis-aquatica</i> L.	3	0302	36	36 (Fl. Eur., F 1969)
URTICACEAE				
91. <i>Parietaria lusitanica</i> L.	7	0747	26	—

## COMMENTS ON THE CHROMOSOME COUNTS

### 2. *Daucus broteri* TEN., 2n=22

FEDOROV (1969) gives 2n=20 for *D. broteri* TEN., but 2n=22 is recorded for the closely related *D. muricatus* (L.) L. which is sometimes considered to be conspecific with *D. broteri*. The chromosomes are rod-shaped, 1.5–2  $\mu$  long, with indistinct centromeric constrictions.

### 3. *Oenanthe incrassans* BORY & CHAUB., 2n=66

The species was included in *Oe. pimpinelloides* L. in Flora Europaea, but seems to be fairly distinct. FEDOROV gives 2n=22 for *Oe. pimpinelloides*. No hexaploid species is previously known in the genus. The chromosomes are 1–1.5  $\mu$  long, all  $\pm$  equal and rod-shaped.

### 4. *Orlaja daucorlaya* MURB., 2n=14

The number is new for the genus. 2n=16, 18, and 20 have been reported for other species of *Orlaja*. The chromosomes are 3–3.5  $\mu$  long and have median or nearly median centromeres.

### 7. *Torilis nodosa* (L.) GAERTN., 2n=24

The chromosomes are c. 1.5  $\mu$  long, rod-shaped, with indistinct centromeric constrictions.

### 12. *Erigeron crispus* POURR., 2n=54

The closely related *E. canadensis* L. is diploid like the majority of species in this genus. The chromosomes are very small (c. 1  $\mu$ ) and rod-shaped to elliptical in outline.

### 13. *Hedypnois rhagadioloides* (L.) WILLD. ssp. *cretica* (L.) HAYEK, 2n=12

NORDENSTAM (1971) has recently demonstrated that 2n=8, 13, and 16 are the commonest chromosome numbers in *H. rhagadioloides* s. lat., at least in the eastern Mediterranean. 2n=12 has previously been reported from the western Mediterranean, however.

### 17. *Oremsis mixta* (L.) DC., 2n=18

2n=18 has been reported for the closely related *O. nobilis* (L.) GAY. The genus is sometimes included in *Anthemis*. The chromosomes are rather long (5–6  $\mu$ ) with median to submedian centromeres.

27. *Onosma tubiflorum* VELEN.,  $2n=26$ 

This species (as well as several others) was lumped with *O. echioides* L. in Flora Europaea (unpubl.), but regarded as distinct by TEPPNER (1971), who discussed at some length the chromosome numbers and mechanisms in the genus. The *O. echioides* complex is taxonomically very intricate and in need of further revision. The commonest chromosome numbers in the genus are  $2n=12$  and  $2n=14$ , suggesting that *O. tubiflorum* may be an amphidiploid. The chromosomes are all rod-shaped and c.  $3 \mu$  long.

32. *Lepidium graminifolium* L. ssp. *graminifolium*,  $2n=48$ 

This is the highest chromosome number hitherto counted in *Lepidium*. In sect. *Lepidium* (where *L. graminifolium* belongs)  $2n=16$  has been reported for *L. perfoliatum* L. and  $2n=24$  for *L. latifolium* L. The chromosomes are  $3-4 \mu$  long.

40. *Euphorbia platyphyllos* L.,  $2n=30$ 

$2n=28$  and  $2n=36$  have previously been reported. The chromosomes are very small and some of them have very conspicuous centromeric constrictions; one of the latter can thus easily be mistaken for two separate chromosomes.  $2n=20$  and  $2n=40$ , indicating  $x=10$ , are common chromosome numbers in the genus.

44. *Ononis spinosa* L. ssp. *austriaca* (BECK) GAMS,  $2n=20$ 

Previous reports of  $2n=30$  (32) probably refer to ssp. *spinosa*. The chromosomes are small (c.  $1 \mu$  long), but very distinct and rod-shaped to elliptical in outline.

47. *Trifolium dalmaticum* Vis.,  $2n=10$ 

This is the lowest chromosome number in *Trifolium*, previously only reported for the closely related *T. scabrum* L., and for *T. hirtum* ALL. The chromosomes are rod-shaped,  $\pm$  metacentric, and vary in length between c.  $1.5$  and c.  $3 \mu$ .

50. *Blackstonia perfoliata* (L.) HUDS.,  $2n=20$ 

The chromosomes are distinct, stout rods, c.  $1.5-2 \mu$  long, with inconspicuous centromeric constrictions.  $2n=20$  has been reported for two other species of *Blackstonia*.

59. *Marrubium alternidens* RECH. FIL.  $2n=34$ 

$2n=54$  was reported by PODLECH & DIETERLE (1969) in plants from Afghanistan. *M. alternidens* was described from the Flora Iranica area (RECHINGER 1952), but has later been recorded from Asia Minor and Greece. It differs from *M. vulgare* L. chiefly in its calyx teeth (5 large alternating with 5 small). The Albanian plants agree well with the original description. The deviating chromosome number reported in the oriental plants may indicate that further taxonomic revision is needed.

60. *Micromeria cremnophila* BOISS. & HELDR.,  $2n=30$ 

$2n=30$  has been reported for the closely related *M. juliana* (L.) BENTH.

63. *Sideritis romana* L. ssp. *purpurea* (TALBOT) BALL,  $2n=28$ 

$2n=28$  has been reported for ssp. *romana* and ssp. *curvidens*. By most authors *S. purpurea* TALBOT is regarded as a separate species.

64. *Stachys germanica* L. ssp. *heldreichii* (BOISS.) HELDR.,  $2n=30$ 

This collection fairly well matches ssp. *heldreichii* as circumscribed in Flora Europaea. The *St. germanica* complex is taxonomically very difficult and in bad need of further revision, however.  $2n=30$  has been reported for *St. germanica* s. lat.

73. *Panicum crus-galli* L.,  $2n=c. 54$ 

The chromosomes are very small, sticky, and often crowded.  $2n=36$  and  $2n=54$  have been reported previously.

76. *Setaria verticillata* L.,  $2n=54$ 

Chromosomes similar to those in 73.  $2n=18$ , 36, and 54 have previously been reported.

83. *Potentilla recta* L.,  $2n=28$ 

The collection matches *P. recta* s. str. as circumscribed in Flora Europaea.

91. *Parietaria lusitanica* L.,  $2n=26$ 

The chromosomes are very small and rather difficult to count.  $2n=26$  has previously been reported for *P. filamentosa* WEBB & BERTH. and *P. judaica* L.

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# Zur *Taraxacum*-Flora Niedersachsens

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## ABSTRACT

SAHLIN, C. I. 1971. Zur *Taraxacum*-Flora Niedersachsens. — Bot. Notiser 124: 497—504.

In Niedersachsen 93 species of *Taraxacum* are recognized by the author. The flora shows good agreement with the *Taraxacum* floras of the Netherlands and Jütland. Only in the southeastern corner of the province does another element enter, belonging to the mountain or hill flora of central Europe. A new species, *T. baeckii*forme, is described from that area.

Es gibt keine Einzeldarstellung der *Taraxacum*-Flora Niedersachsens nach modernen Gesichtspunkten. Dasselbe gilt auch für ganz Deutschland mit Ausnahme von kleinen Einzelgebieten wie Rügen (HAGLUND 1946). ROTHMALER hat jedoch die *Taraxacum*-Flora Niedersachsens untersucht und einige Arten bekanntgegeben (VAN SOEST 1963). Eine derartige Inventur hat auch J. L. VAN SOEST in seiner Einzeldarstellung über die Sektion *Palustria* gemacht (1965). Das ist z. Z. alles, was von der *Taraxacum*-Flora Niedersachsens bekannt ist. Es ist daher leicht zu verstehen, dass die Artenzahl zu gering ist und dass alle Beiträge dazu willkommen sind. Meiner Erfahrung und Schätzung nach dürfte ein Gebiet von der Grösse Niedersachsens rund 200 *Taraxacum*-Arten haben.

Um die *Taraxacum*-Flora zu erforschen, habe ich vier Exkursionen durch das Land unternommen. Es war meine Absicht möglichst viele Stellen aufzusuchen, um so viele Arten wie möglich zu finden. So besuchte ich 1967 Leer und Oldenburg, 1969 fuhr ich kreuz und quer durch das Land, 1970 ergänzte ich diese Reise durch eine Exkursion entlang der Westgrenze und 1971 suchte ich noch vier neue Stellen auf. Dabei wurden keine *Palustria* von mir gefunden, da ich auf Grund mangelnder Orts-

kenntnis geeignete Standorte nicht beachtete.

Niedersachsen gehört derselben ozeanischen Floraprovinz an wie die Niederlande und Jütland. Die *Taraxacum*-Flora der Niederlande ist durch die Arbeiten von J. L. VAN SOEST und seine Schülern gut bekannt worden. Das gleiche gilt auch für Jütland, wo M. P. CHRISTIANSEN, G. HAGLUND und H. ÖLLGAARD grosse Inventuren gemacht haben. Diese beiden Gebiete haben den grössten Teil ihrer Arten gemeinsam. Es ist deshalb zu erwarten, dass diese auch in dem dazwischenliegenden Gebiet Niedersachsens vorkommen. In dem grossen Flachland ist das auch tatsächlich der Fall, doch gibt es natürlich auch einige Arten, die weder in den Niederlanden noch in Jütland gefunden worden sind:

- T. breviflorum* DT.
- T. britannicum* DT.
- T. brunneum* v. SOEST

*T. brunneum* kommt in Österreich vor. *T. britannicum* kannte man früher nur in England und *T. breviflorum* nur in Schweden und Finnland. Meines Erachtens dürfte es ein blosser Zufall sein, dass diese drei Arten in den Niederlanden nicht angetroffen worden sind.



Die genannten Arten schliesst sich eine Gruppe an, deren nordöstliche Verbreitungsgrenze südlich von Jütland verläuft und deshalb die Halbinsel nicht erreicht:

- T. euryglobum* HAGL.
- T. leucopodum* HAGL.
- T. longifrons* HAGL.
- T. proximiforme* v. SOEST
- T. submucronatum* DT.
- T. tortilobum* FLORSTR.

Diese Arten sind in den Niederlanden gefunden worden und haben eine ausgesprochene westliche Verbreitung. Es besteht Grund anzunehmen, dass einige dieser Arten in Jütland angetroffen werden können.

In Niedersachsen sind auch einige Vertreter der mitteleuropäischen Floraprovinz gefunden worden. Folgende Arten, die weder in den Niederlanden noch in Jütland bekannt sind, hat man nahe der Ostgrenze Niedersachsens angetroffen:

- T. aethiops* HAGL.
- T. glossocentrum* DT.
- T. lagerkantzii* HAGL.

In diesen Fällen handelt es sich wahrscheinlich um Ausstrahlungen der Hauptverbreitungsgebiete im Osten. Die *Taraxacum*-Flora dieses niedersächsischen Gebiets ist doch zu wenig bekannt, um eine eindeutige Feststellung zu treffen. Vermutlich haben einige andere Arten dort ihre Westgrenze, da sie noch nicht mit Sicherheit in den Niederlanden, dagegen aber in Jütland gefunden worden sind:

- T. acutifrons* MARKL.
- T. caloschistum* DT.
- T. hemicyclum* HAGL.
- T. ingens* PALMGR.
- T. lacinosum* DT.
- T. scotiniforme* DT.

Meines Erachtens gehören diese Arten zur mitteleuropäischen Floraprovinz, da ihre skandinavische Verbreitung darauf hindeutet.

In der südöstlichen Ecke Niedersachsens kommen noch andere Vertreter der mittel-

europäischen Floraprovinz vor. Ich habe die Flora in den Räumen von Göttingen und Wolfenbüttel studiert. Doch konnte ich das zwischenliegende Gebiet leider nicht untersuchen, da es zu früh im Frühling war. Drei *Taraxaca* sind in diesem Zusammenhang von Interesse:

1. *T. gibberum* MARKL. aus Wolfenbüttel. Der Schlosspark von Putbus auf Rügen gehört zu den von HYLANDER (1943) untersuchten Parks. Hier wurde *T. gibberum* MARKL. von G. HAGLUND gefunden zusammen mit *T. insigne* EKM., *T. lucidum* DT., *T. pallidulum* LINDB. FIL., *T. pannulatum* DT., *T. piceatum* DT., und *T. sagittipotens* DT. & OHLSEN — eine recht hübsche Gruppe westeuropäischer Herkunft (1947). Allerdings ist die Herkunft von *T. gibberum* fraglich. Diese Art ist früher aus Skandinavien bekannt: Helsinki, Finnland (MARKLUND), Mastrup östlich von Örum in Jütland, Dänemark (HAGLUND 1947), und auf Kjøge auf Seeland, Dänemark (CHRISTIANSEN 1922). Dies deutet darauf hin dass *T. gibberum* in dem Gebiet mit Grassamen eingekommen ist. In Putbus wächst es mit *Poa chaixii* VILL. und *Hieracium grandidens* DT. zusammen. Beheimatet sind letztere daher in den mitteleuropäischen Gebirgs- und Hügelländern. *T. gibberum* ist von mir auch in der belgischen Provinz Luxembourg bei Marche-en-Famenne gefunden (1970).

2. *T. laticordatum* MARKL. aus Göttingen. Diese Art ist von Narva, Estland, beschrieben worden. Man hat sie auch in der Provinz Österbotten, Finnland, gefunden, wo sie zu den von deutschen Truppen eingeführten Polemochoren gehört. J. L. VAN SOEST hat die Art in den Niederlanden angetroffen und selbst habe ich sie in den Ardennen, in Nordrhein-Westfalen und in Hessen gefunden. Ihre Herkunft ist ziemlich klar. Wie *T. violaceipetiolatum* ist sie ein Bestandteil der mitteleuropäischen Flora.

3. *T. violaceipetiolatum* RAIL. aus Göttingen. In Finnland ist eine Menge neuer *Taraxacum*-Arten aus den deutschen Truppenlagern des letzten Krieges beschrieben

worden, die mit den Truppen dorthin gekommen sind. B. SAARSOO und A. RAILON-SALA haben 13 bzw. über 100 Arten derartiger Standorte neu beschrieben. *T. violaceipetiolatum* gehört zu dieser Gruppe. Auch *T. gentile* HAGL. & RAIL., die ich in Hessen und Bayern (Miltenburg/Ufr.) gefunden habe, gehört dazu. Dies deutet darauf hin, dass die deutschen Polemochoren in Finnland hauptsächlich aus Mittel- und Süddeutschland stammen, was auch durch die Funde von *Cardaminopsis halleri*, *Ranunculus montanus* und *Galium cruciata* bestätigt wird. Andere Funde aber, wie *Corispermum hyssopifolium* und *Lagoseris nemausensis* deuten auf die Möglichkeit hin, dass ein kleinerer Teil aus den deutschen Besatzungsgebieten in Ost und West stammen kann (LUTHER 1948).

Die Taraxaca der mitteleuropäischen Flora sind in zwei Wellen ausgewandert: zuerst mit Grassamen in Parke und Gartenanlagen, dann mit Heu nach Häfen und Truppenlagern. Deshalb müssen diese Arten auch im Flachland Niedersachsens an geeigneten Standorten angetroffen werden.

J. L. VAN SOEST hat neuerdings viele Arten aus der Schweizer Ebene und dem Hügelland beschrieben. Einige davon sind in den Ardennen gefunden worden und sind auch in der südöstlichen Ecke Niedersachsens zu erwarten. Ich habe 27 Arten gefunden, die auch in der Schweiz vorkommen. Sie haben aber alle ein grosses Verbreitungsgebiet und sind deshalb nicht interessant.

Das Verzeichnis enthält 93 Arten, von denen eine neubeschrieben wird:

#### **T. baeckiiforme** SAHLIN, sp. nov.

Planta mediocriter alta. Folia erecta, oblongo-lanceolata, subobscure prasinescenti-viridia, canescentia, parce araneosa, 4—5-loba. Lobi laterales in foliis exterioribus approximati — distantes, deltoides — subhamati, integri; in foliis intermediis et interioribus distantes, anguste triangulares — subhamati, patentes — leviter reversi, integri, acuti. Lobus terminalis nunc me-



Abb. 1. *Taraxacum baeckiiforme* sp. nov. — Holotypus.

diocris et hastato- vel sagittato-triangularis, nunc brevis et fere rhomboideus, integer interdum leviter incisus, acutus, in foliis interioribus longior, magnus et oblongo-lanceolatus, hastatus, marginibus  $\pm$  convexulis, incisus. Interlobia ad 2 cm longa et c. 4 mm lata, dentibus tenuibus acutis laciniatisque praedita, piceomaculata. Petioli angusti aequae ac in inferiore parte nervi mediani lucide purpureo-violacei.

Scapi foliis superantes, basi violacei caeterum virescenti-straminei, parce araneosi.

Involucrum latum, ad 20 mm longum, obscure viride, basi truncatum. Squamae exteriores patentes, c. 2 mm latae, 10—12 mm longae, lineares, apicibus  $\pm$  longe filiformes, superne canescenti-virides vel  $\pm$  violascentes, conspicue albidomarginatae;

interiores lineares, c. 2 mm latae, apicibus atroviolaceae.

Calathium sat obscure luteum, densum. Ligulae marginales planae, subtus stria cano-violacea notatae; interiores apicibus non raro purpurascens. Antherae polliniferae. Stigmata virescentia.

Achenium fusco-stramineum, 3.2—3.8 mm longum (pyr. incl.), superne sat brevis spinulis instructum ceterum laevum, in pyramidem subcylindricam 0.5 mm longam abiens.

TYPUS: Deutschland; Wolfenbüttel, Wegrand in Buchenwald bei Neuer Weg. 13.5. 1970. C. I. SAHLIN (S).

Die Blätter dieser Art sind ganz gleich denen der *T. baeckii* RAIL. doch sind die äusseren Hüllschuppen von *T. baeckii*-forme viel schmaler als die des *T. baeckii*.

#### ARTENVERZEICHNIS

##### *Erythrosperma* LINDB. FIL.

*T. brachyglossum* (DT.) DT.

Cuxhafen: Duhnen 12.5. 69. — Lüneburg an der östlichen Zufahrt 1.5. 69.

*T. brunneum* v. SOEST

Lüchow-Dannenberg: Hitzacker 15.5. 70.

*T. lacistophyllum* (DT.) DT.

Stade: Twielenfleth am Deich 11.5. 69.

*T. proximiforme* v. SOEST

Gifhorn: Wesendorf 21.4. 51. — Lüneburg an der östlichen Zufahrt 10.5. 69. — Soltau: Neuenkirchen 10.5. 69.

*T. proximum* (DT.) DT.

Aurich 2.5. 69. — Burgdorf: Grossburgwedel 13.5. 71. — Soltau: Neuenkirchen 10.5. 69. — Verden: Walle 13.5. 71.

Einen Unterschied zwischen *T. proximiforme* und *T. proximum* zu machen, fällt mir schwer, da die Merkmale der beiden Arten sich überlappen. Ich bezweifle dass *T. proximiforme* beibehalten werden kann.

*T. scanicum* DT.

Celle: 3 km westlich von Eschede 10.5. 69. — Burgdorf: Grossburgwedel 13.5. 71. — Cuxhafen: im südlichen Teil des Hafens 12.5. 69. — Gifhorn an der südlichen Ausfahrt nach

Celle 10.5. 69. — Lingen: Rastplatz 2 km östlich von Lohne 4.5. 69; bei den kommunalen Betrieben 4.5. 69. — Lüchow-Dannenberg: Hitzacker 13.5. 70. — Lüneburg an der östlichen Zufahrt 10.5. 69. — Soltau: Neuenkirchen 10.5. 69. — Stade: 8 km westlich Stade im Richtung Elm 11.5. 69.

*T. tortilobum* FLORSTR.

Lingen: Schepsdorf 4.5. 69. — Uelzen: Kirchweyhe 10.5. 69.

##### *Spectabilia* DT.

*T. britannicum* DT.

Leer: 2 km nördlich von Folmhusen 3.5. 69.

##### *Vulgaria* DT.

*T. acutifidum* M. P. CHR.

Grfsch. Diepholz: Lembruch 5.5. 70. — Norden: Norddeich am Deich 2.5. 69.

*T. acutifrons* MARKL.

Stade an der westlichen Zufahrt 11.5. 69.

*T. adami* CLAIRE

Cuxhafen: Duhnen 12.5. 69. — Leer: 2 km nördlich von Folmhusen 3.5. 69. — Meppen: an der Sudradde 2 km nördlich von Herzlake 3.5. 69. — Norden: Tjüche bei Marienhaf 2.5. 69.

*T. aethiops* HAGL.

Lüchow-Dannenberg: Hitzacker 13.5. 70.

*T. alatum* LINDB. FIL.

Leer: 2 km nördlich von Folmhusen 3.5. 69. — Norden: Tjüche bei Marienhaf 2.5. 69.

*T. amplum* MARKL.

Hameln-Pyrmont: Schloss Arensburg 2.5. 71. — Leer: 2 km nördlich von Folmhusen 3.5. 69. — Oldenburg: Steinkimmen 3.5. 67. — Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. ancistrolobum* DT.

Oldenburg: Steinkimmen 3.5. 67.

*T. atactum* SAHLIN & v. SOEST

Bremervörde: Walkmühle 11.5. 69. — Grfsch. Diepholz: Barnstorf 4.5. 70; Lembruch an der nördlichen Zufahrt und am Dümmer See 5.5. 70; Hüder am Dümmer See 5.5. 70. — Gifhorn an der südlichen Ausfahrt nach Celle 10.5. 69. — Lingen: Talge-Wilsten bei Beesten 4.5. 69; Rastplatz 2 km östlich von Lohne 4.5. 69; Lohne 4.5. 69. — Meppen: an der Sudradde 2 km nördlich von Herzlake 3.5. 69. — Rotenburg: Waffensen 2.5. 69.

*T. atrovirens* DT.

Lingen: Schepsdorff 4.5. 69.

*T. aurosulum* LINDB. FIL.

Aurich an einem Strassenrand 2.5. 69. — Lingen: Talge-Wilsten 4.5. 69. — Oldenburg: Steinkimmen 3.5. 67.

*T. baeckii* SAHLIN

Göttingen: Eddigehausen 12.5. 70. — Wolfenbüttel, Neuer Weg 13.5. 70.

*T. borgvallii* DT.

Lüchow-Dannenberg: Hitzacker 13.5. 70.

*T. bracteatum* DT.

Cuxhafen: Duhnen 11.5. 69.

*T. breviflorum* DT.

Leer, am Bahnhof 3.5. 67.

*T. caloschistum* DT.

Cuxhafen, Duhnen 11.5. 69.

*T. caudatum* DT.

Grfsch. Diepholz: Barnstorf 4.5. 70.

*T. cordatum* PALMGR.

Burgdorf: Grossburgwedel 13.5. 71. — Göttingen: Eddigehausen 12.5. 70. — Oldenburg: Steinkimmen 3.5. 67. — Rotenburg: Waffensen 11.5. 69. — Uelzen: Kirchweyhe 10.5. 69. — Verden: Walle 13.5. 71.

*T. corynodes* HAGL.

Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. crispifolium* LINDB. FIL.

Leer: 2 km nördlich von Folmhusen 3.5. 69. — Verden: Walle 13.5. 71.

*T. crociflorum* DT.

Lingen: Rastplatz 2 km östlich von Lohne 4.5. 69. — Uelzen: Kirchweyhe 10.5. 69. — Wolfenbüttel: Neuer Weg 13.5. 70.

*T. cyanolepis* DT.

Bremervörde: Walkmühle 11.5. 69. — Rotenburg: Waffensen 11.5. 69.

*T. dilaceratum* M. P. CHR.

Leer: 2 km nördlich von Folmhusen 3.5. 69.

*T. duplidentifrons* DT.

Aschendorf-Hümmling: Lathen 3.5. 69; Rheder-Emsbrücke 3.5. 69. — Bremervörde: Walkmühle 11.5. 69. — Meppen: an der Südradde 2 km nördlich von Herzlake 3.5. 69. — Rotenburg: Waffensen 11.5. 69. — Stade: 8 km westlich von Stade in Richtung Elm 11.5. 69.

*T. ekmanii* DT.

Bremervörde: Walkmühle 11.5. 69. — Leer: 2 km nördlich von Folmhusen 3.5. 69. — Lingen: Schepsdorff 4.5. 69; Talge-Wilsten 4.5. 69. — Oldenburg: Steinkimmen 3.5. 69. — Schaumburg-Lippe: Steinhude am Meer 9.5. 69. — Stade: 8 km westlich von Stade in Richtung Elm 11.5. 69; an der westlichen Zufahrt 11.5. 69.

*T. eurylobum* HAGL.

Stade: 8 km westlich von Stade in Richtung Elm 11.5. 69.

*T. expallidum* DT.

Oldenburg: Steinkimmen 3.5. 69.

*T. falciferum* MARCK.

Grfsch. Diepholz: Barnstorf 4.5. 70; Lehmbruch, bei Dümmer See 5.5. 70.

*T. fasciatum* DT.

Göttingen: Eddigehausen 12.5. 70.

*T. gibberum* MARCK.

Wolfenbüttel, Neuer Weg 13.5. 70.

*T. glossocentrum* DT.

Uelzen: Kirchweyhe 10.5. 69.

*T. haematicum* HAGL.

Norden: Norddeich am Meer 2.5. 69.

*T. hamatiforme* DT.

Aurich, am Strassenrand in der Stadt 2.5. 69. — Aschendorf-Hümmling: Rheder-Emsbrücke 3.5. 69. — Cuxhafen: Duhnen 12.5. 69. — Grfsch. Diepholz: Barnstorf 4.5. 70. — Leer: 2 km nördlich von Folmhusen 3.5. 70. — Lingen: Talge-Wilsten 4.5. 69. — Lüchow-Dannenberg: Hitzacker 13.5. 70. — Norden: Norddeich 2.5. 69. — Rotenburg: Waffensen 2.5. und 11.5. 69. — Verden: Walle 13.5. 71.

*T. hamatum* RAUNK.

Bremervörde: Walkmühle 11.5. 69. — Celle: Altencelle 10.5. 69. — Göttingen: Eddigehausen 12.5. 70. — Leer: 2 km nördlich von Folmhusen 3.5. 69. — Schaumburg-Lippe: Steinhude am Meer 9.5. 69. — Soltau: Brunautal bei Bispingen 2.5. 71.

*T. hemicyclum* HAGL.

Oldenburg: Steinkimmen 3.5. 67. — Stade: 8 km westlich von Stade in Richtung Elm 11.5. 69.

*T. huelpersianum* DT.

Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. ingens* PALMGR.

Leer: 2 km nördlich von Folmhusen 3.5. 69.

*T. insuetum* M. P. CHR.

Burgdorf: Grossburgwedel 13.5. 71.

*T. kernianum* H., v. S. & Z.

Gfsh. Diepholz: Barnstorf 4.5. 70. — Soltau: Brunautal bei Bisingen 2.5. 71.

*T. lacinosifrons* WINST.

Leer, am Bahnhof 3.5. 67. — Lingen: Schepsdorf 4.5. 69.

*T. lacinosum* DT.

Cuxhafen: Duhnen 15.5. 69.

*T. lagerkranzii* HAGL.

Uelzen: Kirchweyhe 10.5. 69.

*T. lamprophyllum* M. P. CHR.

Lingen: Schepsdorf 4.5. 69; Talge-Wilsten 4.5. 69.

*T. laticordatum* MARKL.

Göttingen: Eddigehausen 12.5. 70.

*T. leptodon* MARKL.

Lüchow-Dannenberg: Hitzacker 15.5. 70.

*T. leucopodium* HAGL.

Norden: Norddeich am Meer 2.5. 69.

*T. linguatum* DT.

Celle: Altencelle 10.5. 69.

*T. longifrons* HAGL.

Lüchow-Dannenberg: Hitzacker 13.5. 70. — Rotenburg: Waffensen 2.5. 69.

*T. lucidum* DT.

Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. marklundii* PALMGR.

Bremervörde: Walkmühle 11.5. 69. — Gifhorn: südliche Ausfahrt nach Celle 10.5. 69. — Leer, am Deich 4.5. 67. — Lingen: Lohne 4.5. 69.

*T. melanthoides* DT.

Leer: 2 km nördlich von Folmhusen 3.5. 70.

*T. mimulum* DT.

Lüchow-Dannenberg: Hitzacker 13.5. 70. — Stade: Twielenfleth, am Deich 11.5. 69.

*T. obliquilobum* DT.

Cuxhafen: Duhnen 12.5. 69.

*T. oblongatum* DT. (*T. perhamatum* DT.)

Lingen: Lohne 4.5. 69; Talge-Wilsten 4.5. 69. — Wolfenbüttel, Neuer Weg 13.5. 70.

*T. obtusifrons* MARKL.

Hameln-Pyrmont: Schloss Arensburg 2.5. 71.

*T. ostefeldii* RAUNK.

Burgdorf: Grossburgwedel 13.5. 71. — Celle: Altencelle 10.5. 69. — Lingen: Schepsdorf 4.5. 69. — Lüchow-Dannenberg: Hitzacker 13.5. 70. — Stade: 8 km südwestlich von Stade in Richtung Elm 11.5. 69.

*Taraxacum ostefeldii* RAUNK. ist von Pollenmangel und hellen Blüten gekennzeichnet. Die Art ist später von DAHLSTEDT als Kollektiv aufgefasst worden als er die ganze Sektion *Septentrionalia* DT. mit dem ursprünglichen *T. ostefeldii* zusammenführte. Aus diesem Komplex sind später sechs gut getrennte Formen ausgeschieden, u.a. *T. duplidens* LINDB. FIL. und *T. ostefeldii* sensu DAHLSTEDT. Diese letztere Form wurde nie mehr aufgefunden. Die Beschreibung von *T. ostefeldii* ist ganz unvollständig, doch können in Dänemark nur zwei Arten in Frage kommen: *T. duplidens* LINDB. FIL. und *T. laceratum* (BRENN.) BRENN. Die Blattabbildungen von RAUNKIAER gehören nicht zu der letzteren Art, sondern zu der Form, die DAHLSTEDT als *T. duplidens* bezeichnet. Für mich steht es fest, dass *T. ostefeldii* RAUNK. und *T. duplidens* LINDB. FIL. identisch sind. Der ältere Name sollte erhalten bleiben.

*T. pallescens* DT.

Hameln-Pyrmont: Schloss Arensburg 2.5. 71.

*T. pallidipes* MARKL.

Burgdorf: Grossburgwedel 13.5. 71. — Hameln-Pyrmont: Schloss Arensburg 2.5. 71.

*T. pannucium* DT.

Gifhorn: an der südlichen Ausfahrt nach Celle 10.5. 69. — Lingen: Lohne 4.5. 69; Schepsdorf 4.5. 69.

*T. pannulatiforme* DT.

Oldenburg: Steinkimmen 3.5. 67.

*T. pectinatiforme* LINDB. FIL.

Cuxhafen: Duhnen 12.5. 69. — Rotenburg: Waffensen 11.5. 69.



*T. piceatum* DT.

Wolfenbüttel, Neuer Weg 13.5. 70. — Göttingen, Eddigehausen 12.5. 70.

*T. polychroum* EKM.

Leer, am Bahnhof 3.5. 67. — Norden: Norddeich 2.5. 69.

*T. polyodon* DT.

Aurich, Strassenrand in der Stadt 2.5. 69. — Celle: Altencelle 10.5. 69. — Cuxhafen: Duhnen 12.5. 69. — Leer, am Bahnhof 3.5. 67; 2 km nördlich von Folmhusen 3.5. 69. — Lingen: Lohne 4.5. 69. — Norden: Norddeich 2.5. 69; Tjüche 2.5. 69. — Rotenburg: Waffensen 2.5. und 11.5. 69.

*T. privum* DT.

Norden: Norddeich 2.5. 69.

*T. pulchrifolium* MARKL.

Hameln-Pyrmont: Schloss Arensburg 3.5. 71.

*T. pycnolobum* DT.

Norden: Tjüche 2.5. 69.

*T. retroflexum* LINDB. FIL.

Leer: 2 km nördlich von Folmhusen 3.5. 69. — Verden: Walle 13.5. 71.

*T. sagittipotens* DT. & OHLSEN

Burgdorf: Grossburgwedel 13.5. 71. — Leer, am Bahnhof 3.5. 67. — Norden: Norddeich, am Deich 2.5. 69. — Rotenburg: Waffensen 11.5. 69.

*T. scotiniforme* DT.

Grfsch. Diepholz: Lehmbruch, am Dümmer See 5.5. 70.

*T. scotinum* DT.

Grfsch. Diepholz: Barnstorf 4.5. 70.

*T. sinuatum* DT.

Oldenburg: Steinkimmen 3.5. 67. Rotenburg: Waffensen 11.5. 69.

*T. speciosiflorum* M. P. CHR.

Hameln-Pyrmont: Schloss Arensburg 2.5. 71.

*T. stereodes* EKM.

Aurich, Strassenrand in der Stadt 2.5. 69.

*T. subhamatum* M. P. CHR.

Aschendorf-Hümmling: Rheder-Emsbrücke 3.5. 69.

*T. sublaeticolor* DT.

Leer: 2 km nördlich von Folmhusen 3.5. 69.

*T. submucronatum* DT.

Leer, am Deich 4.5. 67.

*T. subpratensis* HAGL.

Oldenburg: Steinkimmen 4.5. 67. — Lingen: Lohne 4.5. 69.

*T. subundulatum* DT.

Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. tenebricans* (DT.) DT.

Norden: Tjüche 2.5. 69.

*T. trilobatum* PALMGR.

Aschendorf-Hümmling: Lathen 3.5. 69; Rheder-Emsbrücke 3.5. 69. — Bremervörde: Walkmühle 11.5. 69. — Leer, am Bahnhof 3.5. 67. — Lingen: Rasplatz 2 km östlich von Lohne 4.5. 69; Schepsdorf 4.5. 69. — Norden: Norddeich, am Deich und an der südlichen Zufahrt 2.5. 69. — Stade: 8 km westlich von Stade in Richtung Elm 11.5. 69.

*T. trigonum* M. P. CHR.

Bremervörde: Walkmühle 11.5. 69. — Schaumburg-Lippe: Steinhude am Meer 9.5. 69.

*T. tumensilobum* MARKL.

Celle: Altencelle 10.5. 69. — Lingen: Lohne 4.5. 69. — Rotenburg: Waffensen 11.5. 69.

*T. vastisectum* MARKL.

Leer: 2 km nördlich von Folmhusen 3.5. 69. — Norden: Norddeich, am Deich 2.5. 69.

*T. violaceipetiolatum* RAIL.

Göttingen: Eddigehausen 12.5. 70.

*T. xanthostigma* LINDB. FIL.

Göttingen: Eddigehausen 12.5. 70. — Leer, am Deich 4.5. 67. — Lüchow-Dannenberg: Hitzacker 13.5. 70. — Wolfenbüttel, Neuer Weg 13.5. 70.

Die korrekte Bestimmung der *Taraxacum*-Arten ist ein grosses Problem. Wenn die Fehler weniger als 1—5 % sein sollen, muss das Material ein- oder zweimal von Spezialisten revidiert werden. Ich habe den grossen Vorteil gehabt, mit den Herren R. BÄCK (Helsinki), C.-F. LUNDEVALL (Stockholm), S. NORDENSTAM (Rönninge), H. ÖLLGAARD (Filskov), H. SÄLTIN (Somero) und J. L. VAN SOEST (Den Haag) in dieser Angelegenheit zusammenarbeiten. Ich nehme die Gelegenheit wahr, diesen meinen guten Freunden meinen herzlichsten Dank auszusprechen.

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# Clonal Variation in Populations of *Anemone nemorosa* L.

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## ABSTRACT

BOTHMER, R. VON & al. 1971. Clonal variation in populations of *Anemone nemorosa* L. — Bot. Notiser 124: 505—519.

20 stems from each of 58 clones from altogether 11 localities were studied. From each clone were investigated 10 numerical characters, 2 form characters, pollen fertility, and area and density of the clone. The clones are moderately large in this material and the populations merge into extensive population clusters. A wide variation was found between the clones of each locality, but also a difference in width of variation between localities. A disruptive variation was found between ecologically different parts of the same population cluster. Reduced fertility was found in a large proportion of the clones, and its consequences in relation to vegetative propagation are discussed. Only the chromosome number  $2n=30$  was found. The special features and evolutionary possibilities of a sexual clonal material in stable and in slowly changing habitats are discussed.

## INTRODUCTION

This paper is a preliminary report on the effects of vegetative propagation on variation patterns and evolutionary possibilities. The material studied was *Anemone nemorosa* L. in southernmost Sweden. This species forms local clones of limited extension but with large numbers of clones in each locality. This implies the frequent occurrence of reproduction by means of seeds. Thus the results will be applicable to other materials where both vegetative propagation and sexual reproduction occur. Our aim was to collect information on the amount of morphological variation within and between clones, populations and biotopes. We also attempted to study the fertility of the clones and its relation to the area covered and to the degree of variation in morphology. A future control of the spreading or decline of the clones is also planned.

*Anemone nemorosa* usually occurs in more or less confluent patches over areas often extending up to several square kilometers. In most places the actual breeding population comprised a large number of clones, but pollination will be predominantly vicinistic (cf. GRANT 1971 p. 16). The species has a wide ecological tolerance, and consequently variation patterns under different environmental conditions could also be studied.

## METHODS

Eleven localities were selected as to represent different ecological conditions. They are all situated in the Swedish province of Skåne, within a distance of 85 km between the extremes. Ecological conditions vary from very rich woods on calcareous soil to heaths and poor meadows on silicious soil.

In each locality we tried to identify a suitable number of clones in as small and ecologically uniform an area as possible. Only clones that could be clearly recognized and circumscribed were taken into consideration; the number studied in each locality varied from two to seven. None of the localities represent an isolated population, but all form parts of large, irregular population clusters typical of the species.

The localities are listed below. A map was made for each locality, giving the exact position and size of the clones. The area covered by each clone was noted, and the density of flowering and sterile shoots was determined within an area of 0.04 m<sup>2</sup>. Quantitative characters were measured in the field. Twenty flowering stems from each clone were measured, having been selected as evenly as possible over the clone area. The specimens were then dried for reference and further study and will be deposited in the Lund Botanical Museum (LD). Means, standard deviations, correlations, etc., were calculated by the computer at the Institute of Mathematical Statistics, University of Lund, with kind assistance of Mr. H. ANDERSSON.

#### LIST OF LOCALITIES

- I. Dalby hage, the eastern part. Meadow-forest with *Ulmus*, *Fagus* and *Carpinus*. Dense field layer of herbs.
- II. Dalby hage, the western part. Meadow-forest with *Ulmus*, *Fagus* and *Quercus*. Dense field layer of herbs.
- III. Dalby: Dalby Norreskog. Old, grazed meadow with dense field layer dominated by grasses.
- IV. S. Sandby: Linnebjär. Oak woodland. Dense field layer dominated by grasses.
- V. S. Sandby: Linnebjär. Meadow-forest with dominating oak and hazels. Rather dense field layer of herbs.
- VI. Hällestad: Knivsås. Grazed heath. Dense field layer of grasses, rushes, sedges and heather.
- VII. S. Sandby: Linnebjär. Heath-forest dominated by *Fagus*. Sparse field layer of herbs.

- VIII. Hörby: 5 km NE of Hörby. Poor meadow with scattered trees and shrubs. Dense field layer dominated by grasses.
- IX. Linderöd: 3 km NE of Linderöd. Alder-swamp. Rather dense field layer dominated by herbs.
- X. Hjärsås: Bosagårdarna. Poor meadow with scattered birches. Dense field layer dominated by grasses.
- XI. Hjärsås: Hylta, Fjäreboda. Poor meadow, formerly cultivated, with scattered trees. Dense field layer dominated by grasses.

#### THE CHARACTERS STUDIED

In the following discussion the numbers given within brackets after a character are the character numbers used in tables and diagrams. The variation ranges indicated refer to mean values for clones, not to single flowering stems.

The stem height (1) was measured from the rhizome up to the leaf whorl. The measurements are somewhat inexact as all stems were not broken equally close to the rhizome and some were curved. But the character is such a typical feature of many clones, that we considered it had to be included. The variation range is great, from 84 to 163 mm.

The pedicel length (2), from leaf whorl to flower, is not fully correlated with the stem height, and must thus be measured separately. Mean values vary from 23 to 74 mm (Fig. 5).

The leaves are three in number, arranged in a whorl, and always ternate with approximately equal leaflets. The length of the petiole (3) varies from 9 to 18 mm (Fig. 7 E), the length of the middle leaf lobe (4) from 22 to 47 mm (Fig. 7 D), and the breadth (5) from 9 to 24 mm. The leaf margin varies from almost entire to deeply serrate, as partly illustrated by the number of teeth on the middle leaf lobe (6), varying from 6 to 20 (cf. Fig. 7 A).

The shape of the leaf lobes is very variable, the variability being of about the same magnitude in most localities. Varia-

Fig. 1. Variation in the shape of middle leaf lobes. Variation within the clones IX: 1, VII: 4 and between clones in the localities IV, XI and I. Half natural size.

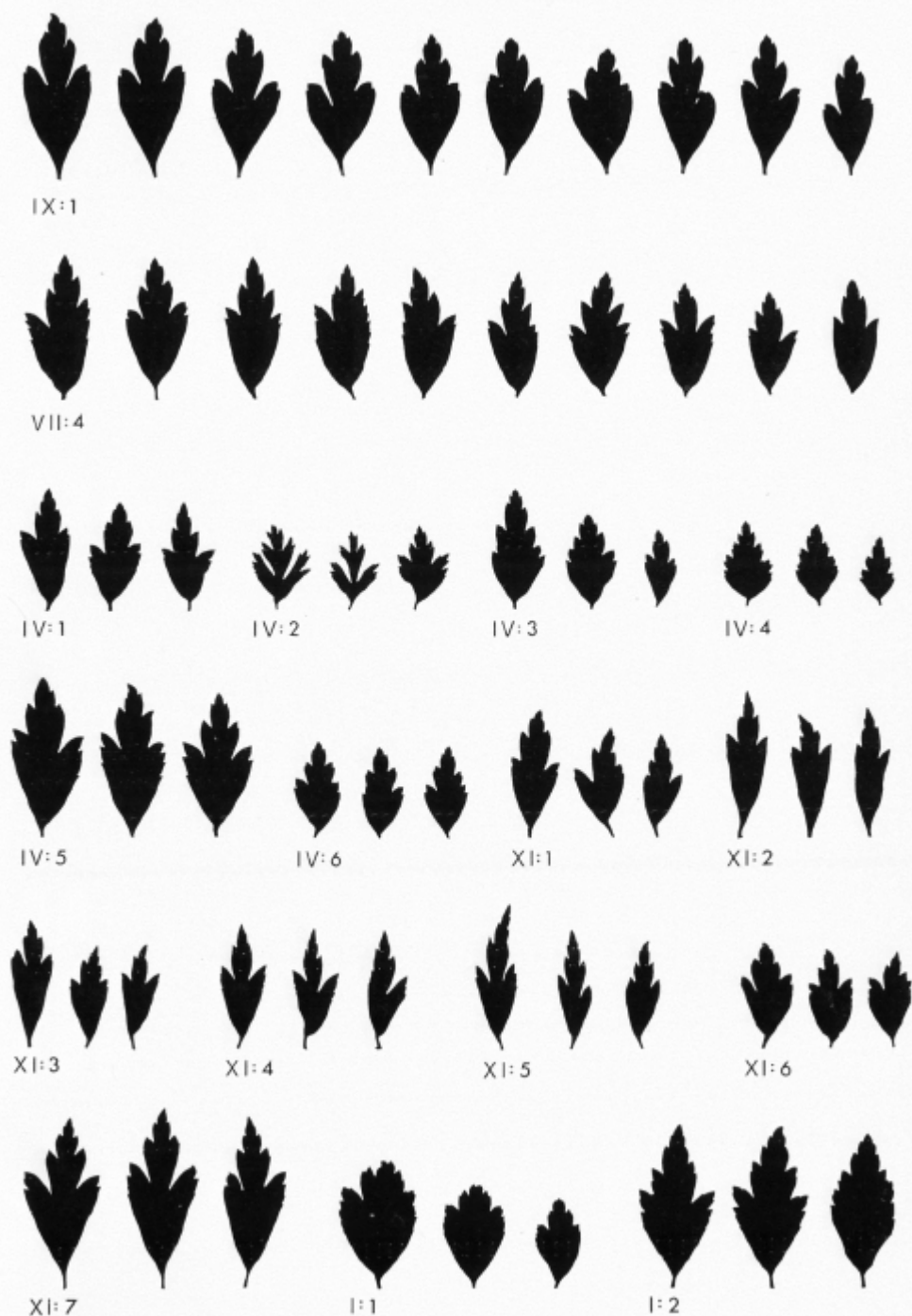


Fig. 1.



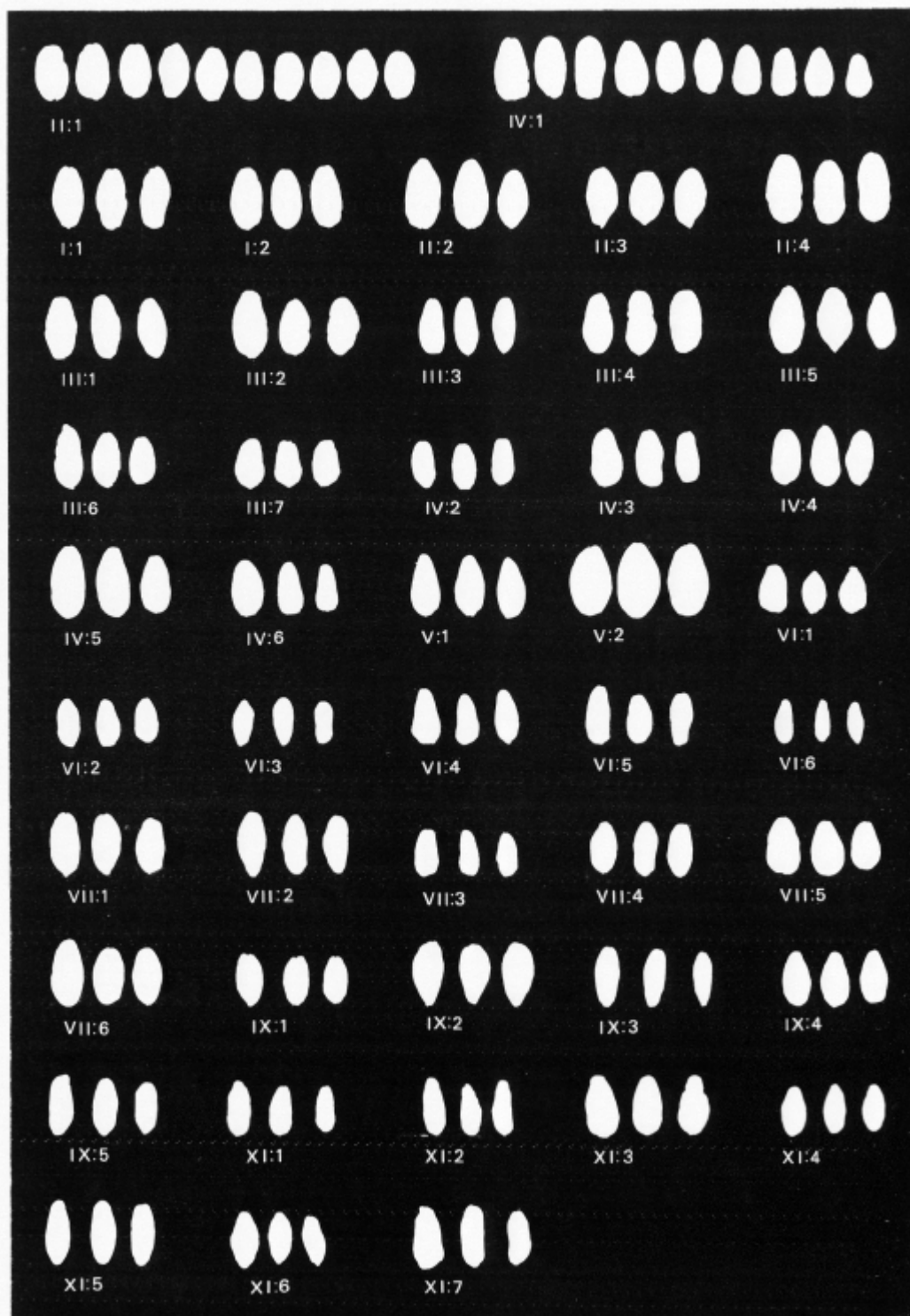


Fig. 2.

tion in this character is illustrated in Fig. 1. It is often one of the best marker traits to identify clones.

The leaf colour is apparently to some extent modified by the environment, being generally darker in open habitats than in shadow. There are many clones characterized by more or less intense anthocyanic or greyish colour of the leaves. In a few cases variegated leaves have also been observed.

The number and shape of the floral parts show great variation. Some of these characters are also easily modified.

The number of petals (7) is usually six (Fig. 7 B), arranged in two more or less distinct whorls of three. There is often a slight difference between the petals of the lower and upper whorl; all studies of petals have been confined to the lower ones. Reductions in number are rare, but extra petals are often found, their frequency varying in different clones. The highest mean noted in our material is 9.6. The extra petals are produced in a more or less definite spiral arrangement above the first six, and often the whorl arrangement of the latter breaks down when there are several extra ones.

The length of the petals (8) varies from 11.6 to 20.3 mm, their breadth (9) from 5.3 to 12.4 mm. The shape of the petals is illustrated in Fig. 2.

The petals are usually white, though often with a greenish or reddish basal spot or faint striation. Pale purplish, or less often reddish to pink petals are found in some clones in most populations. In clone I:1 the colour was even bluish violet.

The number of carpels (10) varies from 7 to 32 in clone means (Fig. 7 C), but there is also a large variation between flowers of the same clone.

The indumentum is differently developed in different clones. It varies more or less independently on the different parts,

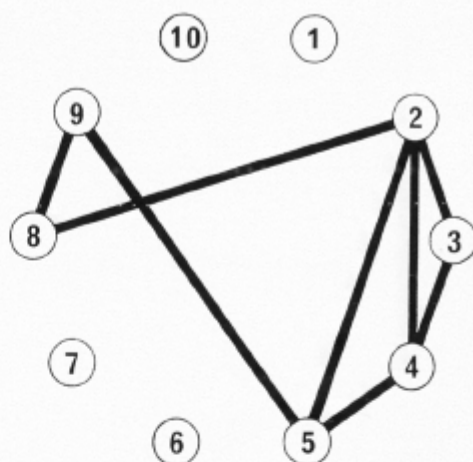


Fig. 3. Correlation between characters, lines indicating correlation coefficients ( $r$ ) higher than 0.5. Legend to character numbers on pp. 506 and 509.

such as leaves and pedicels. Thus many clones may be recognized by the specific combinations of hairiness.

#### DIFFICULTIES AND SOURCES OF ERROR

It is often impossible to define and map all the clones in a given area. This is due to the similarity of certain clones and to their tendency to mix vegetatively. These difficulties are most noticeable in densely populated localities, where the clones are in direct contact and new individuals may be established only within already existing clones. In such localities it was necessary to define each clone measured by means of some marker traits. As marker traits it was often possible to use petal colour, colour and shape of leaflets, hairiness and size relations. We consider it unlikely that the clones we were able to identify deviated from the normal with respect to other characters.

Fig. 2. Variation in the shape of petals. Variation within the clones II:1, IV:1 and between clones in some localities. Approx. half natural size.

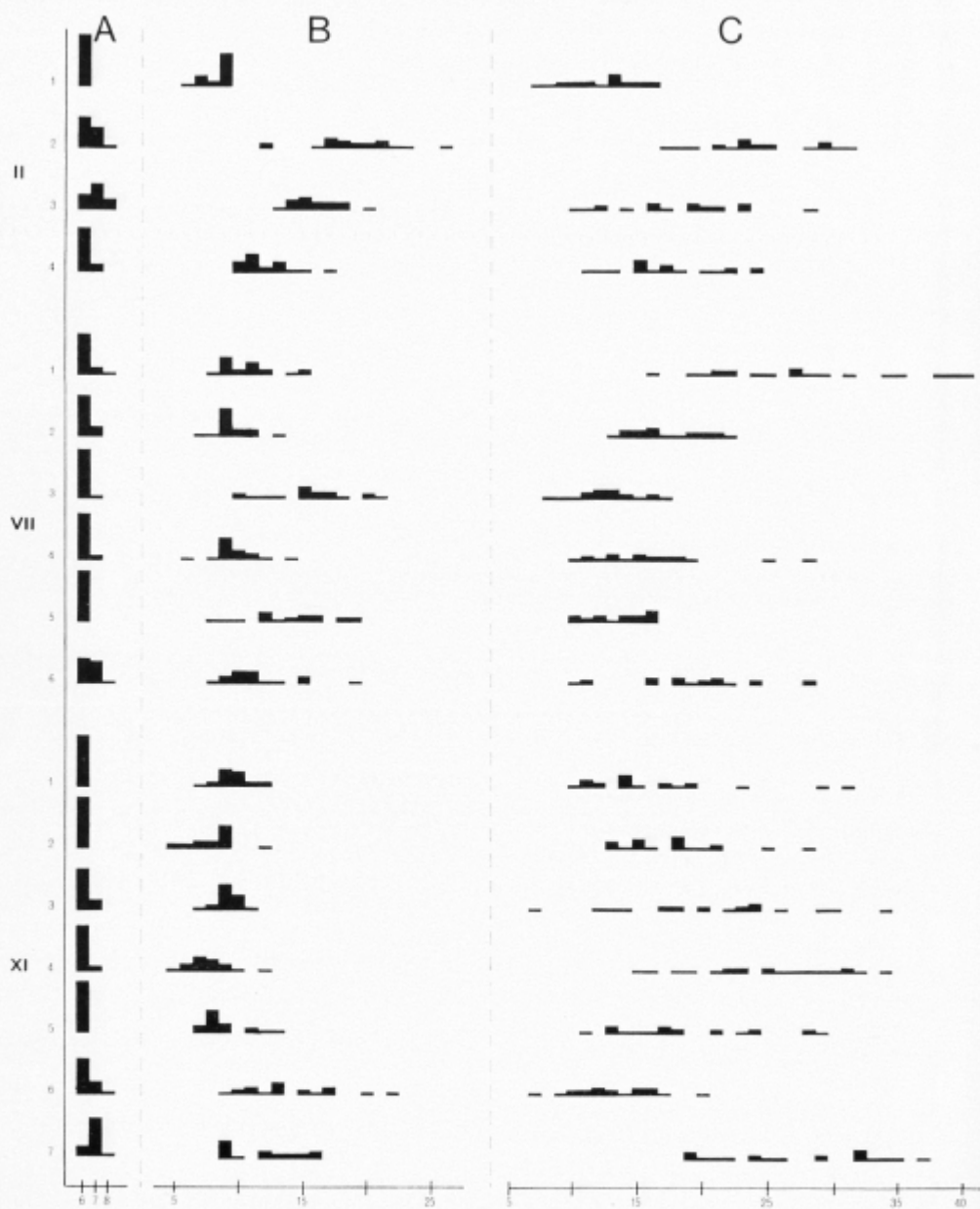


Fig. 4.

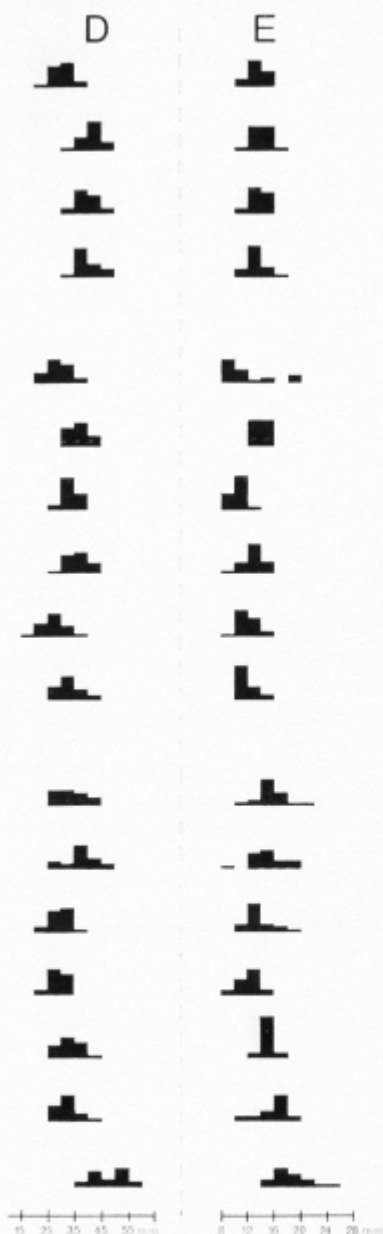


Fig. 4. Variation in some characters within clones of the localities II, VII and XI. — A: Number of petals. — B: Number of teeth on the middle leaf lobe. — C: Number of carpels. — D: Length of middle leaf lobe. — E: Length of petioles. — Every histogram represents 20 specimens.

In some very dense populations in rich meadow-forests only a few clones could be used which limits the value of the data from these localities. They must, however, be included so that the morphological variation in the area will be fully represented. In more open localities the clones often form distinct patches and can easily be identified.

One source of error lies in the possibility of two or more seeds germinating and establishing clones on the same spot. If they are also sibling plants, as might easily be the case, they might give rise to clones so similar that they will appear as a single clone. Clone IV:4 might be an example of this, as it shows abnormal variation in leaflet form, but is otherwise rather homogeneous. The same situation might, however, also be caused by somatic mutation.

#### CORRELATIONS BETWEEN CHARACTERS

The degree of correlation for each combination of two characters in all the material was calculated. The result is shown in Fig. 3 where correlation coefficients greater than 0.5 are illustrated by lines. Obviously, one group of size characters are loosely correlated and partly represent an expression of general vigour. It must be stressed, however, that the correlation is not equally strong in all clones and in all localities. For example, in locality no. III there is great variation in leaflet length between the clones, and this is not correlated to the other size characters. We interpret the result as showing that there is probably separate genetic control of each of the characters, but that there are also some pleiotropic factors affecting several characters through control of the overall size of the plant. Modification, acting in a similar manner on different size characters, may also contribute to give higher correlation values between them.

## VARIATION WITHIN CLONES

There is a certain amount of variation between the individual stems of each clone in every character. This variation is always of minor importance compared with the total variation in the locality. It is always possible to refer every ramete to a certain clone by the use of one or a few numerical characters. The existing intracolonial variation stresses the necessity of measuring a sufficient number of individuals from each clone and not only selected representatives.

The greatest intracolonial variability was found in stem length, in the number of carpels and in the length and breadth of petals. The most constant characters were the form of leaf lobes and petals and the number of petals, but the length and breadth of the leaf lobes also showed little intracolonial variation (Figs. 1, 4, and 7 D).

The intracolonial variation must be interpreted as a result of modification by local ecological factors. The stem length, for instance, is easily modified by the presence of taller grass in part of the clone area. Nutrition may also be different within the distances of metres or tenths of metres covered by the clone. In the further course of the investigation the ability for modification will be controlled by comparative cultivation and transplantations. On the whole it may be stated that shape characters are less easily modified than quantitative characters.

## VARIATION BETWEEN CLONES AND LOCALITIES

One important question is, whether the variation between localities is greater than the variation between clones in each locality. There is no general trend that holds for all characters. As regards size and number of petals there is so much variation between the individual clones that it obscures the differences between localities. The same is usually true of shape of leaf-

lets and petals. As regards other characters, only part of the total variation is found in each locality, so that differences between localities are greater than between clones. This variation is not geographically determined within the area investigated. The general impression received is that each of the localities has its own characteristic variation amplitude in one or several characters (Figs. 5 and 6). There is a slight similarity between the rich localities nos. I, II, III, and IX on one hand and the heath and poor meadow localities nos. IV, VI, VII, and X on the other, though mainly in the correlated size characters (Fig. 6). When considering the predominant lack of similarity between localities, it must be kept in mind that they were selected to represent as diverse habitats as possible.

The facts mentioned indicate that the amount of variation developed in a certain locality is to a great extent determined by local ecological factors. A particularly clearcut case is represented by the localities IV, V, and VII, which belong to the same population cluster with at least indirect possibilities for gene exchange. The differences found must thus be considered to be caused by local selection, which acts here as disruptive selection resulting in localisation of certain genes and gene combinations to different parts of the cluster. By this process the different populations of the cluster become also morphologically dissimilar when adapting to different ecological conditions. *Anemone nemorosa* is in fact dominant in plant communities on very different types of soils and under very different moisture conditions. This means that it would be of little significance in any sociological study, and the same would presumably apply to many other species with a similar genetic system.

## FERTILITY

The pollen fertility of all clones was determined as the percentage of grains



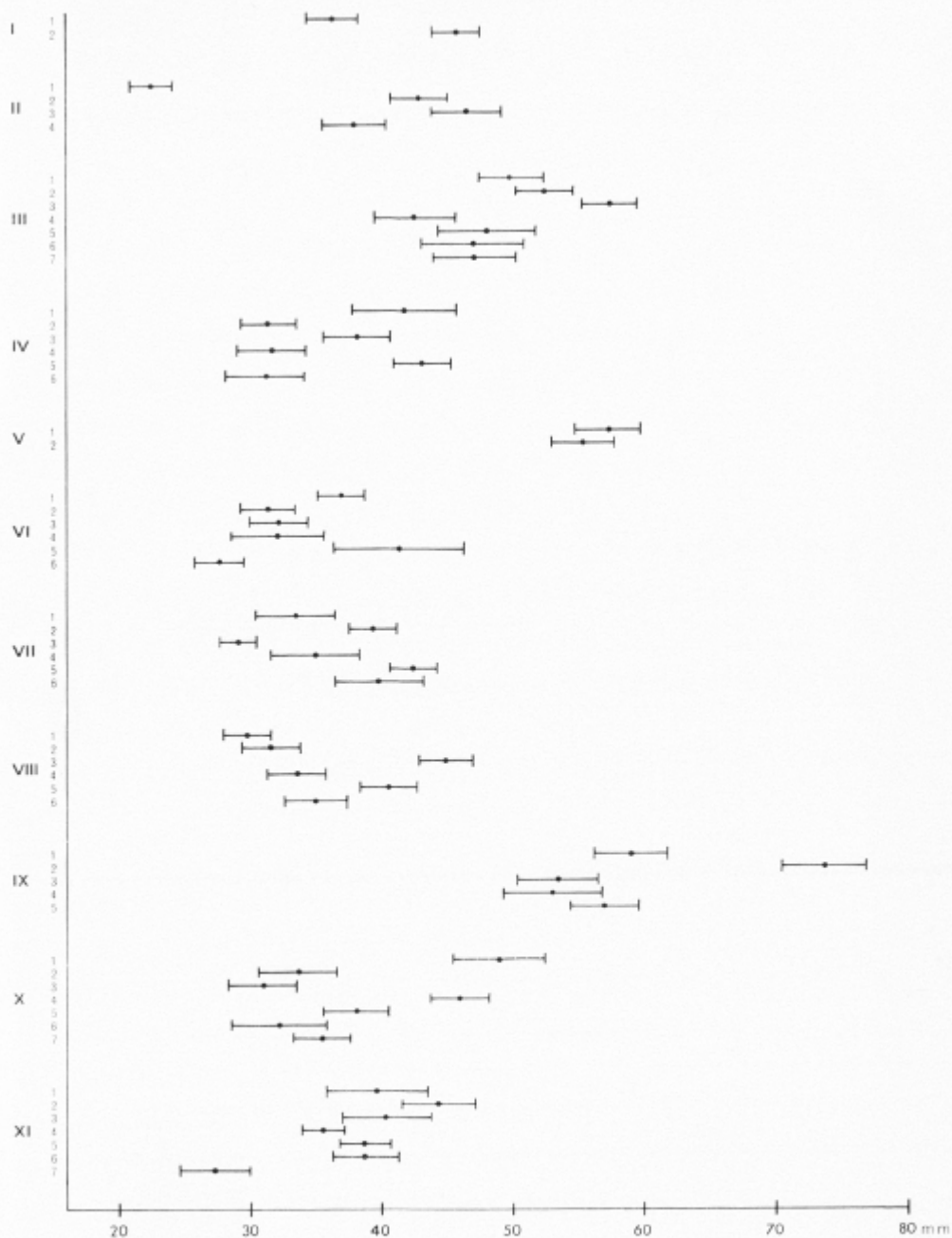


Fig. 5. Variation in the length of pedicels in the 58 clones studied. Mean values  $\pm 2sE$ ; if two lines do not overlap, the differences between the mean values are significant at approximately the 1% level.

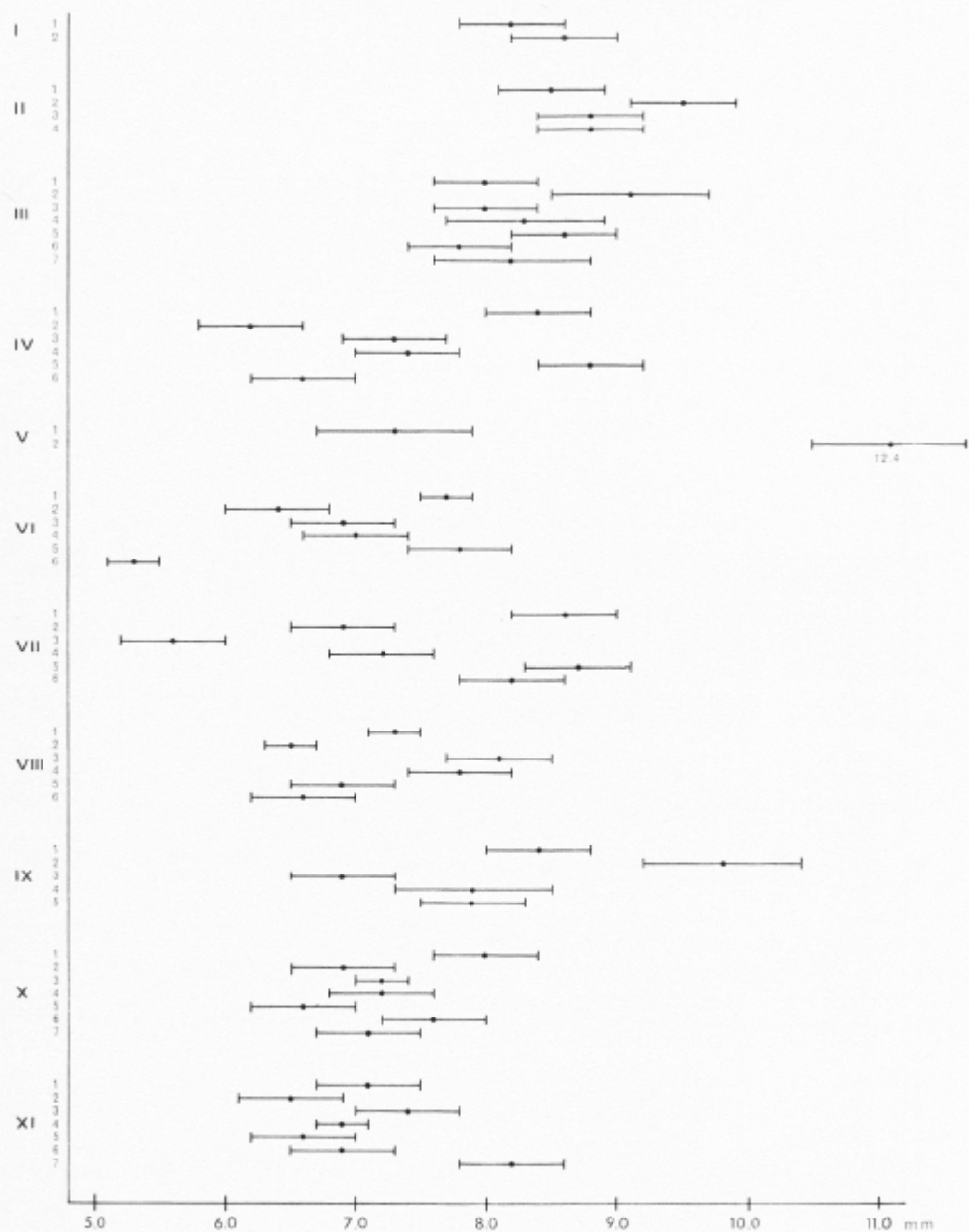


Fig. 6. Variation in the width of petals in the 58 clones studied. Explanation see Fig. 5.  
 Bot. Notiser, vol. 124, 1971

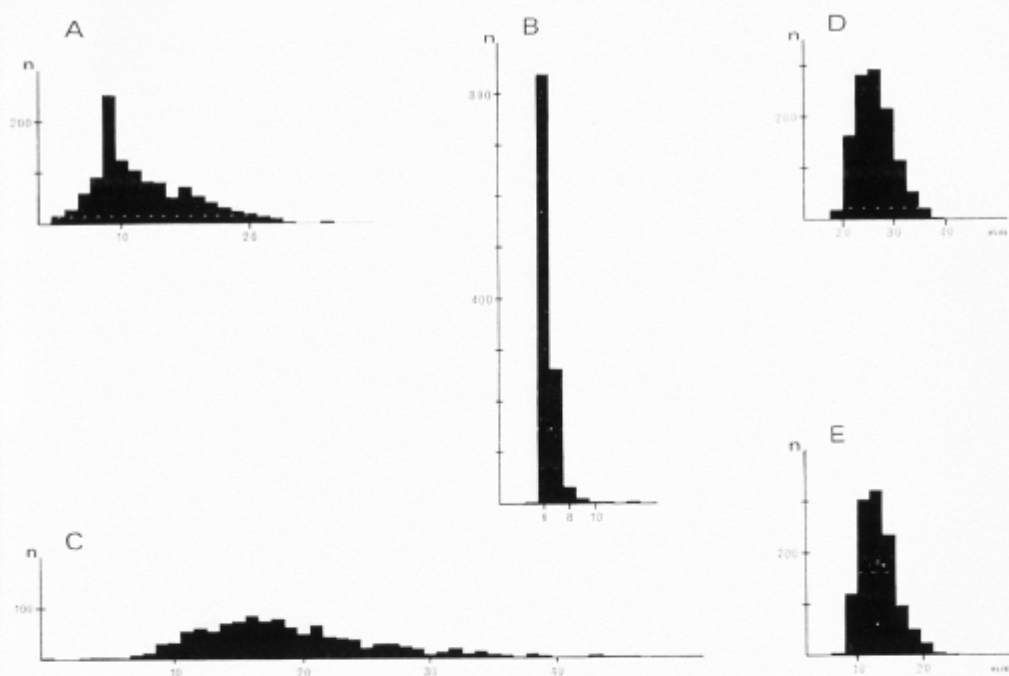


Fig. 7. Total variation in some characters in the entire material studied (1160 specimens). — A: Number of teeth on the middle leaf lobe. — B: Number of petals. — C: Number of carpels. — D: Length of middle leaf lobe. — E: Length of petiole.

stainable in cotton blue. The determinations were based on 500 grains counted from different flowers in each clone. In Fig. 8 the clones have been sorted into fertility classes with a width of 5 %. There is great variation in pollen fertility. In several localities the majority of the clones have fertility values as low as 50–80 %, in locality XI even as low as 15–40 %. This must mean that they contain a rather heavy "genetic load" of fertility-reducing genes and/or cytological disturbances. The degree of seed setting has not yet been sufficiently investigated, but the results available indicate differences of about the same magnitude as for pollen fertility. A few clones are also characterized by a low number of carpels, which will decrease their seed production efficiency.

The possibility for clonal species and other long-lived perennials to tolerate a

heavy "genetic load" has been stressed by STEBBINS (1950). The relation between vegetative propagation and various sterility phenomena was also discussed by GUSTAFSSON (1947). The present results are in agreement with theoretical expectations.

## CYTOLOGY

Various chromosome numbers have been reported for *Anemone nemorosa* in earlier investigations, e.g. by BÖCHER 1932 ( $2n=28-32$ ), BERNSTRÖM 1946 ( $2n=29-31, 37, 45, 46$ ) and GUINOCHET 1935 ( $2n=16$ ). For further information see FEDEROV (1969).

Chromosome numbers have been determined from six clones only (II: 6, III: 6, VI: 1, VII: 2, VII: 4 and VII: 6). They all have  $2n=30$ , which is in agreement with most previous reports.

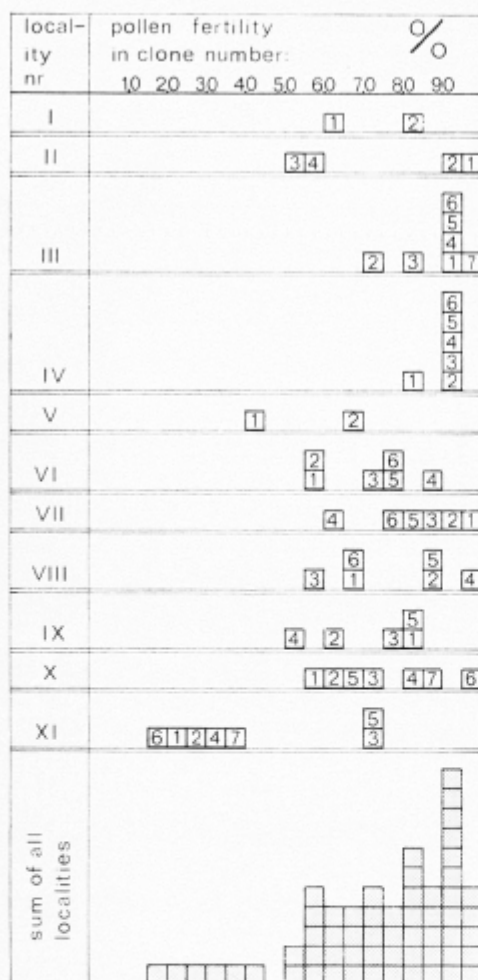


Fig. 8. Pollen fertility in all the clones studied. Further explanation in the text.

Detailed studies of chromosome numbers and chromosome structure will be carried out later, with special attention to the clones with low pollen fertility (cf. Fig. 8).

It has been observed that when using the squash technique the chromosomes often break in the centromere. This may have given rise to some of the earlier reports of deviating numbers.

Bot. Notiser, vol. 124, 1971

**Table 1.** Fertility relationships in some of the populations and clones studied. Male reproductive capacity is defined as the product of per cent stainable pollen and number of flowering shoots per clone. Note that high pollen fertility does not necessarily indicate high male reproductive capacity.

Clone no.	Pollen fertility (%)	Number of flowering shoots per clone	Male reproductive capacity
VII: 1	96	63	5,048
VII: 2	93	375	34,875
VII: 3	85	105	8,925
VII: 4	61	200	12,200
VII: 5	84	94	7,896
VII: 6	79	100	7,900
VIII: 1	67	100	6,700
VIII: 2	89	56	4,984
VIII: 3	59	81	4,779
VIII: 4	95	60	5,700
VIII: 5	89	40	3,560
VIII: 6	66	45	2,970
IX: 1	83	45	3,735
IX: 2	64	90	5,760
IX: 3	78	42	3,276
IX: 4	51	34	1,734
IX: 5	84	47	3,948
X: 1	58	146	8,468
X: 2	62	108	6,696
X: 3	73	150	10,950
X: 4	82	70	5,740
X: 5	67	206	13,802
X: 6	97	23	2,231
X: 7	89	173	15,397
XI: 1	20	84	1,680
XI: 2	28	120	3,360
XI: 3	72	106	7,632
XI: 4	34	193	6,562
XI: 5	73	65	4,745
XI: 6	18	90	1,620
XI: 7	38	190	7,220

## THE REPRODUCTIVE CAPACITY OF THE CLONES

A clone may reproduce in three ways: By means of vegetative propagation, as male parent by the production of functional pollen, and as female parent by the production of functional ovules.

The capacity for vegetative propagation may be measured as the increase in number of shoots per length unit of the clone margin each year. A study extending over several years will be necessary to obtain

**Table 2.** Numbers of sterile and flowering shoots in 0.04 m<sup>2</sup> sample areas. Note large variation in the ratio of sterile to flowering shoots.

Clone no.	Number of sterile shoots	Number of flowering shoots	Ratio sterile/flowering shoots	Clone no.	Number of sterile shoots	Number of flowering shoots	Ratio sterile/flowering shoots
I: 1	45	4	11.3	VII: 3	32	7	4.6
I: 2	37	4	12.3	VII: 4	6	8	0.8
II: 1	52	3	17.3	VII: 5	22	15	1.5
II: 2	27	5	5.4	VII: 6	31	5	6.2
II: 3	23	5	4.6	VIII: 1	18	10	1.8
II: 4	39	4	8.5	VIII: 2	53	8	6.6
III: 1	60	15	4.0	VIII: 3	23	14	1.6
III: 2	29	15	1.9	VIII: 4	44	8	5.5
III: 3	117	15	7.8	VIII: 5	30	8	3.8
III: 4	66	33	2.0	VIII: 6	19	6	3.2
III: 5	63	10	6.3	IX: 1	79	5	15.8
III: 6	91	29	3.1	IX: 2	5	6	0.8
III: 7	80	22	3.6	IX: 3	93	7	13.3
IV: 1	34	17	2.0	IX: 4	52	5	10.4
IV: 2	98	24	4.1	IX: 5	52	7	7.4
IV: 3	69	27	2.6	X: 1	8	13	0.6
IV: 4	74	25	3.0	X: 2	9	9	1.0
IV: 5	46	3	15.3	X: 3	23	24	1.0
IV: 6	22	27	0.8	X: 4	13	14	0.9
V: 1	104	18	5.8	X: 5	1	11	0.1
V: 2	55	9	6.1	X: 6	6	6	1.0
VI: 1	57	13	4.4	X: 7	20	15	1.3
VI: 2	30	17	1.8	XI: 1	70	21	3.3
VI: 3	85	9	9.4	XI: 2	20	16	1.3
VI: 4	26	18	1.4	XI: 3	28	17	1.6
VI: 5	51	12	4.3	XI: 4	46	27	1.7
VI: 6	41	19	2.2	XI: 5	43	20	2.2
VII: 1	8	5	1.6	XI: 6	34	10	3.4
VII: 2	29	10	2.9	XI: 7	21	19	1.1

sufficient data on this property. Some conclusions, however, concerning the correlation of vegetative propagation to low pollen fertility, for example, may be drawn from the proportions of large and small clones displaying that property. As will be further discussed below, the proportions of sterile and fertile shoots produced will also have a great effect, and in this character large differences have been found (Table 2).

The capacity for a clone to function as male parent is approximately proportional to the number of functioning pollen grains produced. This number will depend on the percentage of good pollen, but also on the number of flowers produced. This latter factor is a function of vegetative re-

production and the age of the clone. To what extent it may compensate for low percentages of functioning pollen in a natural population may be concluded from the figures for clone area and flowering shoot density. The localities VII—XI were selected for illustration in Table 1, where the number of flowering shoots is given together with pollen fertility. The products of percentage stainable pollen and number of flowers give rough estimates of the relative amounts of functioning pollen grains produced by the different clones. The results show that low pollen fertility may be fully compensated by a high vegetative propagation, so that partly pollen sterile clones may still have a high production of functioning pollen.



For instance in locality X the highly fertile clone 6 has at present the lowest production of functionable pollen of all the clones investigated. Clone 1, on the other hand, has a high capacity for male reproduction in spite of its much reduced fertility, because of its extension and high proportion of flowering stems.

What has been said above about pollen production also applies to the production of functionable ovules, though there are no figures available for illustration. The number of offspring produced by a given clone compared with the total number of offspring of a population will to a great extent be determined by its competitive capacity and its capacity for vegetative propagation under the prevailing conditions. Other properties, even fertility, may be of minor importance in this respect. This also means that there is no particularly strong selection favouring full fertility. Only if combined with a high capacity for vegetative propagation will it lead to a higher number of offspring by sexual reproduction. On the other hand, selection will favour prolific flowering and a high capacity for vegetative propagation. This means that the genetic system favouring clonal propagation will tend to be conserved irrespective of other evolutionary changes. Our data indicate that a wide range of morphological variation is retained in such a system, especially when combined with a population structure such as that of *Anemone nemorosa*. This will be favourable for the species especially with regards to response to environmental changes and invasion into other habitats at the margins of the established populations.

The number of flowering shoots varies tendentially between different localities. In the rich localities I, II and IX there is a low number of flowers, from 3 to 7, per 0.04 m<sup>2</sup>. In the poor localities VI, X, and XI the number varies from 6 to 33 (cf. Table 2).

In order to eliminate the density factor in a clone the relation between non-flow-

ering and flowering shoots was calculated. In this ratio there are great differences between certain localities, while others are intermediate or show a greater variation between the clones. Generally the rich localities have high values compared with the poor ones. In the localities I and II this ratio varies between 4.6 and 17.3, in X and XI between 0.1 and 3.4.

This factor varies so strongly and tendentially that it is supposed to be under genetic control. It is an important factor when discussing the relationship between vegetative and sexual reproduction. A low value of the ratio between non-flowering and flowering shoots indicates a comparatively high capacity for sexual reproduction. This should be a great advantage when invading new habitats or increasing in frequency on old localities. In fact this is the case in the localities X and XI.

#### THE LOCAL EVOLUTIONARY PATTERN

The clonal material, as tested by the present analysis, shows an unusually large amount of variation. At a given time and place, the individuals best adapted to the environment form extensive clones and dominate the picture of variation. If conditions remain unchanged for long periods of time, they will also dominate the sexual as well as vegetative reproduction and slowly outnumber the other types. In a stable environment one might thus expect more restricted local variation, although the process of relative homozygotization will all the time be counteracted by crossings with individuals in neighbouring parts of the population cluster inhabiting more or less dissimilar habitats.

Due to the great variation, individuals with new combinations of traits will continuously be presented for selection. If the environment changes, some of them will prove to be better adapted. Thus the morphological properties of the population can be rapidly changed. The possibility of

rapid vegetative propagation of suitable biotypes gives the clonal material a better chance in this situation. It has this advantage in common with apomicts and self-fertilizers, but at the same time it has retained the recombination ability (cf. STEBBINS 1950, MATHER 1966, GRANT 1971). By sexual reproduction it gives rise to a large number of different variants, but because of environmental selection only some of them will develop clones in each locality. The magnitude of the "variational reserve" will only be possible to estimate from controlled cultivation with seeds collected in the natural populations.

The above remarks on the changing environment also apply to invasion by seed dispersal into a more or less different neighbouring biotope. This will be attacked by a continuous supply of seeds, some of which will prove suitable for establishing clones in the new habitat. *Anemone nemorosa* occurs from eutrophic meadow-forests with a rich herb flora to poor heath communities. It also occurs in damp alder

swamps as well as on dry esker slopes. Much of this variation in ecological adaptation is often found in a limited area and even within the same population cluster.

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## Botanical Literature

FOTT, BOHUSLAV: *Algenkunde*, 2nd completely revised edition. — Gustav Fischer Verlag, Jena 1971. 581 pp., 303 figures and 1 frontispiece. M. 58.

The first edition of FOTT's *Algenkunde* appeared in Czechish in 1956. It was translated into German in 1959. Since then FOTT has revised the text twice, first in a Czech edition in 1966 and then before publishing the second edition in German.

The layout of the new edition is as good as the old one. Though the number of pictures (mostly drawings) has increased from 258 to 303, the drawings and photographs are on the whole well chosen and well made. Exceptions are CYRUS' drawings of diatoms and some of TRUNCOVÁ's drawings of the Rhodophyta, for example *Rhodymenia palmata* on p. 248 and *Rhodomela subfusca* on p. 252.

In the very interesting first chapter "Die Algen im natürlichen Pflanzensystem", Professor FOTT includes a discussion on different ways of defining the species. In the new edition a change can be noted in the author's opinion of the definition proposed by LYSENKO in 1950. This has now been completely omitted.

The nomenclature used is in most cases up to date, but a few exceptions can be mentioned. FOTT uses Nemalionales instead of Nemaliales (CHRISTENSEN 1967), *Rhodomela subfusca* instead of *Rh. confervoides* (SILVA). In the gross systematics there are some differences between the two editions. In the first edition FOTT uses the division Chrysophyta, including Chrysophyceae, Bacillariophyceae and Xanthophyceae. In the second edition, however, he uses the old taxon Chromophyta established by LAMOUROUX in 1813. In this division he includes five classes: Chrysophyceae, Xanthophyceae, Bacillariophyceae, Phaeophyceae and Dinophyceae. It is a

little doubtful if this is to be recommended; it will make the division Chromophyta too large and too heterogeneous.

In Phaeophyceae FOTT uses the system proposed by KYLIN, with Isogeneratae, Heterogeneratae and Cyclospora. It would be more convenient to use the more modern concept proposed by SCAGEL.

The treatment of Chlorophyta is excellent, with one exception — the siphonous groups. FOTT mentions only two orders, Bryopsidales and Siphonocladales. In Bryopsidales he includes the suborders Bryopsidinae and Dasycladinae. Caulerpaceae is placed in Bryopsidinae and Cladophoraceae is included in Siphonocladales.

The two genera *Acrosiphonia* and *Spongomorpha* are not even mentioned. Even if the author does not agree with JONSSON's Acrosiphoniales, the two genera are too important to be neglected.

The chapters about the ecology of algae and algae in technology are brought up to date. Especially the part on algae in air (Aerophyten) should be noted; it is one of the few to be found in the literature.

The criticisms above, however, are of no great importance. Some details are of course matters of personal opinion. The *Algenkunde* is an excellent textbook for graduate students of phycology and for the phycologist it is a good encyclopedia, especially the references which include many Russian works.

TORGNY VON WACHENFELDT

PANKOW, HELMUT: *Algenflora der Ostsee. I. Benthos (Blau-, Grün-, Braun- und Rotalgen)*. — VEB Gustav Fischer, Jena 1971. 419 pp., 416 drawings, 100 photos (black-and-white). Price M. 53, cloth.

The Baltic is one of the largest brackish-water seas in the world. However, since

the reviews by SVEDELIUS 1901 (Studier öfver Östersjöns hafsalgflora), SKUJA 1928 (Vorarbeiten zu einer Algenflora von Lettland), and LAKOWITZ 1929 (Die Algenflora der gesamten Ostsee) there have been no works dealing with the overall distribution of the bentic algae in the Baltic. Some local investigations have been carried out in parts of the area, for example: LEVRING 1940, Studien über die Algenvegetation von Blekinge, Südschweden; WAERN 1952, Rocky-shore algae in the Öregrund archipelago; RAVANKO 1968, Macroscopic green, brown and red algae in the southwestern archipelago of Finland; and SCHWENKE 1969, Meeresbotanische Untersuchungen in der westlichen Ostsee als Beitrag zu einer marinen Vegetationskunde. Apart from these investigations there have been numerous small communications dealing with baltic algae in different periodicals.

To summarize the present knowledge of the vegetation of the Baltic, Prof. PANKOW from the University of Rostock has published *Die Algenflora der Ostsee I*.

This first part deals with the bentic Cyanophyta, Chlorophyta, Phaeophyta and Rhodophyta. Each division begins with a key to the different genera. For each species, information is given on synonyms, morphology, reproduction and distribution. To most descriptions there are also drawings, mostly well-known from earlier works. In many cases, both the distribution in the Baltic and the total known distribution are given. In some cases algae which are not known from the Baltic are included in the flora.

For some of the species the distributions given seem to be a little dubious, for example *Pelvetia*, *Asperococcus*, *Laminaria hyperborea*, *Platoma*, and *Ceramium echi-onotum*.

In most cases the nomenclature is up to date, for example *Rhodomela confervoides*, but on the other hand the old name is retained for *Phyllophora membranifolia*. The book ends with 100 photos in black-and-white, which in most cases are of such poor quality that they do not provide any

aid to determination. The overall impression is that the flora is an ambitious attempt to fill a notorious gap in our knowledge of the bentic algal flora of the Baltic, and it can be recommended to scientists interested in the Baltic.

BERTIL HÄGERHÄLL

TORGNY VON WACHENFELDT

POELT, J.: *Bestimmungsschlüssel europäischer Flechten*. — J. Cramer (Lehre), 1969. 71 + 757 pp. 68 illustrations in 9 tables. Price DM. 48 (paper-bound).

Since the publication of E. FRIES, *Lichenographia Europaea Reformata* (1831) few efforts have been made to comprehend the lichen flora of the whole Continent. Compilations like OLIVIER, "Lichens d'Europe" (1907—1909) and "Prodromus lichenum Europeorum" (1921) by the same author have not been very useful for the identification of European lichens. As most lichen floras dealing with a special country or another restricted area are either incomplete or out of date there is considerable need for a "Flora Europaea" surveying all lichens of this Continent.

The present volume by Professor J. POELT (Institut für Systematische Botanik der freien Universität Berlin) is an enlarged and revised edition of his "Bestimmungsschlüssel der höheren Flechten von Europa" (1962; cf. review in Bot. Notiser 1963 p. 536). The latter work treated the macrolichens in a wide sense including certain groups of crustose genera with effigurate or squamulose thallus. The present treatise has included also the major part of the entirely crustose genera. It should be emphasized, however, that the scope of this work is not a complete European Lichen Flora. Some genera, whose taxonomy is extremely complicated, have been wholly omitted (e.g. *Verrucaria*) or partially omitted (e.g., *Leptogium*; only sect. *Mallotium* treated). In other cases, e.g. the large genera *Lecanora* and *Lecidea*, the author has mentioned only a limited

number of species. Hence a beginner in lichenology will look in vain in this work for some very characteristic lichens with a wide distribution in Europe, e.g. *Arthopyrenia punctiformis*, *Lecanora atra*, *Leprogium lichenoides*, *Usnea barbata* and *Verrucaria maura*.

Two introductory chapters give a brief account of lichenological literature (mainly from the last few decades) and a glossary including a useful survey of lichen morphology illustrated with drawings by the author. These are the only illustrations in this work. We also find keys to the phycobionts of the lichens, to some major groups (like "Strauch- und Bartflechten") and to all genera recorded from Europe (also to those where no species have been treated).

The bulk of the work contains keys to 226 genera (arranged in alphabetical order) treating some 2600 species or subspecific units. The descriptions have been compiled in a very concise style, often in 4—6 lines including short notes on ecology and distribution in Europe. The author has often used symbols before the generic or specific names in order to indicate that a group is insufficiently known or contains more species than those recorded. These reservations reflect the well-known fact that a good deal of lichen taxonomy urgently needs further research.

Some genera, especially those compiled from RABENHORST's *Kryptogamen-Flora* (1930's), have been treated in a somewhat oldfashioned manner (e.g., *Pertusaria*, founded on ERICHSEN's rather superficial taxonomy), whereas others, where recent sources have been quoted, are quite up-to-date. The most elaborate genera are those which have been revised by Dr. POELT in the 1950's and -60's, e.g., *Caloplaca*, *Lecanora*, subgen. *Placodium*, *Physcia* s. lat. and *Squamarina*.

In spite of these minor remarks, the reviewer would strongly emphasize that Dr.

POELT's treatise is an outstanding work by one of the leading lichen taxonomists of to-day. It is indispensable to any serious worker in this field. For many years it will serve as a stimulus to continued or new researches in many neglected groups of lichens.

OVE ALMBORN

FREY, E.: *Flechten. Unbekannte Pflanzenwelt*. Hallweg-Taschenbücher Bd 89. — Verlag Hallweg (Bern), 1969. 64 pp. incl. 25 coloured plates and 4 black-and-white illustrations in the text. Price S.Fr. 4.80.

Dr. E. FREY, (Münchenbuchsee, Bern, Switzerland), the grand old man of European lichenology, has published a small lichen flora which has proved to be very useful to the beginner as well as to the somewhat advanced lichenologist. It is quite incredible how much information has been condensed in this pocket-book.

Nine introductory pages (including good illustrations) give a brief survey of morphology, reproduction and chemistry of lichens. The principal part of the book contains very short descriptions (often 2—3 lines) of 293 species (including some lower taxa), each illustrated with a colour photo. It is well-known that lichens are difficult to photograph. It is a pleasure for the reviewer to state that he has seldom or never seen such clear and distinct illustrations of lichens as in this booklet.

The choice of the species treated is well-made. There is a predominance of macrolichens, but quite a few common and characteristic crustose lichens have also been included.

This is an ideal book in the hands of a beginner in lichen taxonomy and a welcome complement to Dr. POELT's major treatise.

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