Latest developments in Botaniska Notiser

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Changes in printing method, layout and editorial routine are introduced in Volume 129 of Botaniska Notiser to make optimum use of space, and to conform to international practice. Some advice to authors is included and the manuscript routine is described. As an experiment an editorial body serving three of the Swedish journals of plant taxonomy has been appointed in Lund. The advantage of this is pointed out.

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From this issue onwards, Botaniska Notiser will change in many respects – method of printing, layout and editorial routine. The scope, however, is to remain the same: original research of international interest in plant taxonomy, morphology and related branches of botany.

Regarding the length of papers there is an upper limit of 32 printed pages. Articles exceeding this limit will not be accepted but may be considered for publication in the monograph series Opera Botanica.

It has not been considered appropriate to introduce a system permitting a set number of free pages, with additional pages charged for. Even a short article can be wordy and an article may of necessity be long though concisely written (for example a presentation of the results of many years' work on a revision). Instead, rigorous standards of concentration will be imposed for all papers irrespective of length. Authors with a tendency to wordiness will be held in by the Editor and the referees in cooperation.

CHANGES

Printing method. Botaniska Notiser is to be printed in offset at Berlings, Lund, Sweden. The method cuts down expenses considerably in particular for illustrations. Moreover, in some instances corrections of drawings and diagrams can be made without making a new block as would have been necessary in letterpress printing. Some special problems, such as oblique lines in tables, are also easily solved. However, corrections in the text will be more expensive than before, and authors making alterations in the proofs against the final manuscript will be charged.

Typeface and type area. The main text is set in 9/10 pt Times (a typeface allowing more characters per line than that previously used). The column width has been increased from 63 to 68 mm (14 and 15 cic, respectively), and there are two lines more per column. This increase in type area within an (almost) unchanged format of 168×235 mm, together with the change in typeface reduces the number of pages to a given amount of text by almost 20 %. However, since there are also illustrations and blank space we estimate that the actual reduction in the number of pages for a whole volume of Botaniska Notiser will be about 10 %. This will mean that an average volume will now comprise only about 480 pages, which, however, will present as much information as was previously given in 540 pages.

With these changes we shall achieve at least almost maximum economy of space. Within the frame imposed by the printing method it is probably not possible to further lower production costs significantly.

Blank pages. In apparent conflict with the principle of economy of space blank left-hand pages after articles with an odd number of pages are introduced. However, for technical reasons, this reduces the cost of reprints considerably so that we can still offer 100 reprints of each article free of charge. Furthermore, since all papers will thus begin on a right-hand page, reprints will automatically carry the author's name and the title of the paper fully visible without (expensive) printed covers. It is, however, possible to obtain covers at extra cost, but we feel they are somewhat out of date and fill no obvious function.

Cover. We have found it appropriate to mark the revised layout and editorial routine with a new cover. We hope that the majority of our readers will approve of this. In order to preserve a certain continuity we have retained the typography of the name of the journal, and selected a colour similar to that of earlier volumes.

Particulars

Since there are a fair number of less readily noticed changes we ask you to go carefully through Information to contributors on the inside back cover. The most important introductions are the following.

(1) Make the title of your paper as short as possible while still giving maximum information. Avoid starting a series – the function of the serial name is much less important than you may believe. "A new *Euphrasia* species from S Sweden" is much shorter than and just as informative as "Patterns of evolution within the genus *Euphrasia* L. (Scrophulariaceae) in Sweden. 1. A new species from southeastern Skåne".

(2) The headings can be even shorter. A single key word will often do – regard the headings as a sort of "macro punctuation" rather than as "micro abstracts". For preference use at the most two grades of headings since an elaborate hierarchy serves to entangle the reader rather than to guide him. Write all headings in lower case throughout, and do not underline them. The intended hierarchy can be noted by means of numbers in the margin or on a separate sheet of paper.

(3) Avoid making cross references by page number as these necessitate resetting of the line. This will be charged for, and – even worse – errors may also arise on resetting. Refer instead to the headings in question.

(4) *Do not underline names of persons.* From this issue on they will be set in lower case and should thus not be marked in any way. If they are, it may make some re-typing necessary and this may delay publication.

(5) *Study the lists of References in this issue in detail.* We have made considerable changes to conform with international practice. This conformance will minimize editorial corrections and simplify the compilation of reference lists for authors who also publish in other journals.

(6) Supplementary material, such as extensive lists of localities, will not be printed (even if paid for by the author) unless the paper would be incomprehensible without it. It should preferably be deposited at an official institute referred to in the article.

MANUSCRIPT ROUTINE

When a manuscript has been received it will be acknowledged at once. The manuscript will also be immediately sent to a referee for examination. There are at present 38 referees, all from the Scandinavian countries to cut down postal delays. The maximum time set for referee examination is three weeks; as a rule it takes much less time. When there is doubt as to whether the manuscript should be accepted, or when the paper is specialized in more than one respect, more than one referee may be consulted.

When the referee has returned the manuscript the Editor will make a close reading of it. A list of recommended or suggested alterations is set up. This will often be fairly long, and may contain notes on punctuation and missing references as well as suggestions for deletions or additional treatment of data. Constructive criticism will also be given in the case of manuscripts that are not accepted.

If the alterations are few or trivial the manuscript will then be submitted to a linguistic check which is, for English, free of charge to the author; otherwise, the manuscript will first be returned to the author for revision. After the linguistic revision the manuscript will be returned to the author for checking and, if necessary, for re-typing.

In the resulting final version of the manuscript no further alterations will be made by the editorial staff; after technical editing, it will be handed over to the printer.

This routine may appear complicated, but has been worked out to get the best possible results with the least possible delay. The time lapse between receiving a manuscript and its publication is fairly short for Botaniska Notiser. In the case of this issue the average time lapse is estimated at less than five months.

Primarily, however, the time taken for a manuscript to pass through the editorial routine depends on the author himself. A manuscript that is not in good order initially, that is, wordy, inconsistent or illogical, will probably progress slowly. The referee will keep it a long time, and it will be returned to the author for revision at least twice.

On the other hand a concisely and logically written manuscript that conforms to the requirements set out in Information to contributors, may be ready for publication within a short time and may even appear in an earlier issue than a poor manuscript that arrived several weeks earlier.

ORGANIZATION

The reason for taking these steps now is that in September 1975 an editorial staff was appointed to serve the three journals Botaniska Notiser, Opera Botanica and Svensk Botanisk Tidskrift. The staff, consisting of an Editor-in-chief (half time) and an Assistant Editor (three-quarters time) was instructed, for instance, to look for simple and efficient ways of improving layout and manuscript routine for the three journals.

The editorial staff is directed by an Editorial Board with representatives from the botany departments of the Swedish universities, from the Societies owning the journals and from the Swedish Natural Science Research Council which supports the journals economically. (The grants for salaries and material are independent of those to the journals.) The Editorial Board is also responsible for Flora of Ecuador, a series issued in close association with Opera Botanica but with other Editors (see inside front cover). Finally, the Editorial Board is to take further steps to rationalize the structure of Swedish botanical publication.

The Editorial Board decided that the three journals should cater for different groups of readers. Botaniska Notiser will thus be the only international Swedish quarterly journal of taxonomic botany and phytomorphology. Opera Botanica is the companion series for comprehensive treatises issued at irregular intervals. Svensk Botanisk Tidskrift is now to be the national Swedish journal of botany, with articles mainly in Swedish (but made internationally accessible by means of abstracts and legends in English). It will cover plant ecology and floristics of mainly national interest as well as plant taxonomy. A special feature is to be an annual Swedish botanical bibliography that will also cover the vast number of stencils and offset-printed reports nowadays produced by various institutes. The bibliography will appear in Svensk Botanisk Tidskrift but will also be available as a reprint.

This reorganization of the journals would not have been very effective with separate editorial offices for each. As it is, a manuscript submitted to the "wrong" journal can now be redirected simply by a suggestion in the letter acknowledging receipt of the manuscript. In our experience no author has yet objected to a proposed redirection of a manuscript.

Another of the advantages of a common editorial office is that it has been possible to introduce a uniform typography and layout for the three journals. This is a fact not only of importance to the Editors and printers (involving a cut in the production costs) but should greatly facilitate matters for authors. It will no longer be necessary to remember two or three sets of instructions on how to plan figures, how to place the headings and how to write abstracts and compile the references.

The idea of experimenting with a common staff for three journals arose out of an analysis of the structure of botanical publishing in

Sweden (Botanical Publication in Sweden, report from the Swedish Natural Science Research Council, Stockholm 1974). The aim is to procure the optimum channelling of scientific results, through journals of high quality specialized for well-defined groups of readers. The experiment will be on trial for three years (with continuous evaluation) after which developments in the field of scientific publication may well make certain modifications necessary.

ACKNOWLEDGEMENTS

The Publication Board of the Swedish Natural Science Research Council has worked constructively on the rationalization and marketing of the Swedish botanical journals making it possible to continue and develop botanical publishing in Sweden.

The economic support of the Council has made possible the appointment of a professional editorial body. It is in place here to mention previous Editors of Botaniska Notiser and Svensk Botanisk Tidskrift who, in addition to their research and teaching activities have done an admirable job of editing, in effect from motives of idealism. It is largely due to their efforts that the journals have become internationally known.

Drawings of Scandinavian plants 111–112

Epilobium L. sect. Epilobium

Alf Oredsson and Sven Snogerup

Oredsson, A. & Snogerup, S. 1976 05 06. Drawings of Scandinavian plants 111–112. Epilobium L. sect. Epilobium. *Bot. Notiser 129*: 5–9. Stockholm. ISSN 0006-8195.

Drawings and descriptions are given for *E. roseum* Schreb. and *E. obscurum* Schreb.

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111. **Epilobium roseum** Schreber 1771

Perennial herb, (20–)30–60(–90) cm high. Stem usually branched in upper and middle part, rarely from the base, stunted branches usually present in most leaf axils not supporting branches. Middle cauline leaves usually longer than the internodes. Stem producing several or rarely one (5–)10–15(–20)-flowered inflorescences. Stolons lacking or up to 5 mm. Turions formed late in the autumn, sessile or at the end of the stolons, as dense rosettes of usually 10–15 fleshy, orbicular to broadly ovate leaves 8–12 mm long.

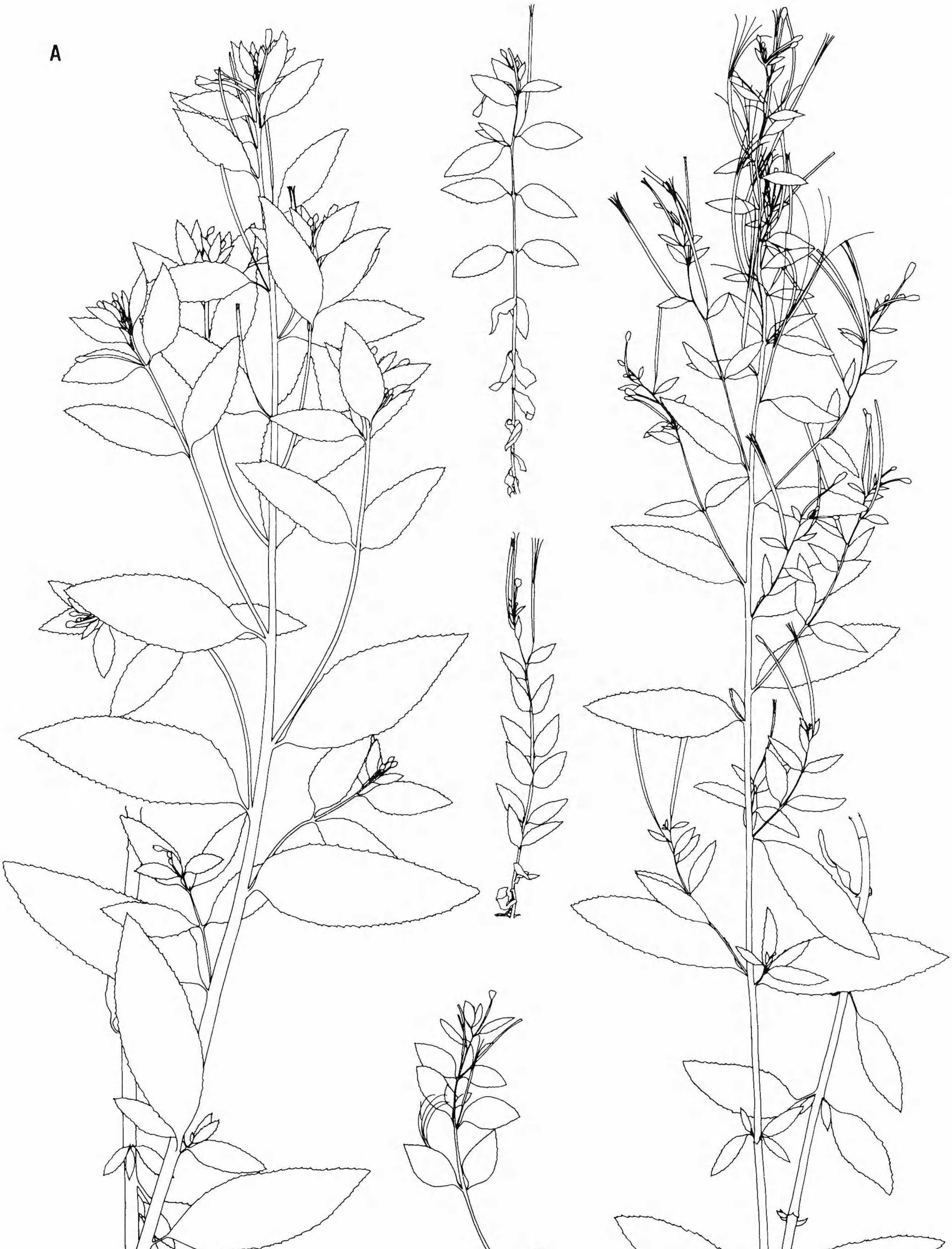
Stem (1–)2–4(–6) mm thick, terete, with two raised lines or low wings below the leaf margins and sometimes also very weak lines below the midribs, subglabrous below, moderately to densely hairy above, hairs 0–0.5 mm, eglandular hairs incurved to adpressed, glandular hairs patent, shorter.

Most leaves opposite, upper ones alternate, or rarely most of them alternate, all petiolate, petioles of middle and upper leaves 3–12 mm, those of basal leaves up to 15 mm, opposite leaves united at base around the stem but not decurrent. Basal leaves smaller, usually lanceolate to narrowly ovate. Middle cauline leaves (25–)35–70(–100) mm long, 10–25(–40) mm broad, lanceolate, narrowly ovate or rarely ovate, acute, irregularly serrate with many small teeth. Upper leaves somewhat smaller, usually narrowly ovate, with shorter petioles. Basal leaves subglabrous, middle leaves sparsely hairy, upper ones moderately hairy, more densely on margins and veins, hairs like those of the stem though usually not more than 0.3 mm.

Pedicels erect to erectopatent in all stages. Buds spindle-shaped, acute and provided with a mucro usually 0.3–0.4 mm long. Sepals 4–5(–6) mm, connate to c. 1 mm, narrowly ovate to lanceolate, apiculate, pure green or reddish, densely hairy. Petals 4.5–7 mm, notched to 1–1.5 mm, rose-pink to pinkish-white or rarely light purplish-pink, usually with darker stripes, lighter when young. Anthers 0.5–0.55(–0.75) mm, long filaments 3–4.5 mm, short filaments 2–3 mm. Style about equalling the short stamens, stigma capitate.

Capsule stalk 5–15(–20) mm. Capsule 40–55 (–65) mm, moderately to densely hairy, hairs like those of the stem. Seeds 1–1.1(–1.15) mm long, 0.45–0.6 mm broad, obovoidal, obtuse at apex, acute at base, without a neck, slightly flattened on one side, surface with many rows of very small but distinct papillae, chalazal hairs usually 30–40, 8–9 mm long. Flowers homogamous.

E. roseum occurs chiefly on bare, wet soil, often in disturbed habitats such as old gravel-pits, embankments, etc. It is fairly common in the lowlands of Denmark and Sweden up to c. 60° N, with some scattered localities near the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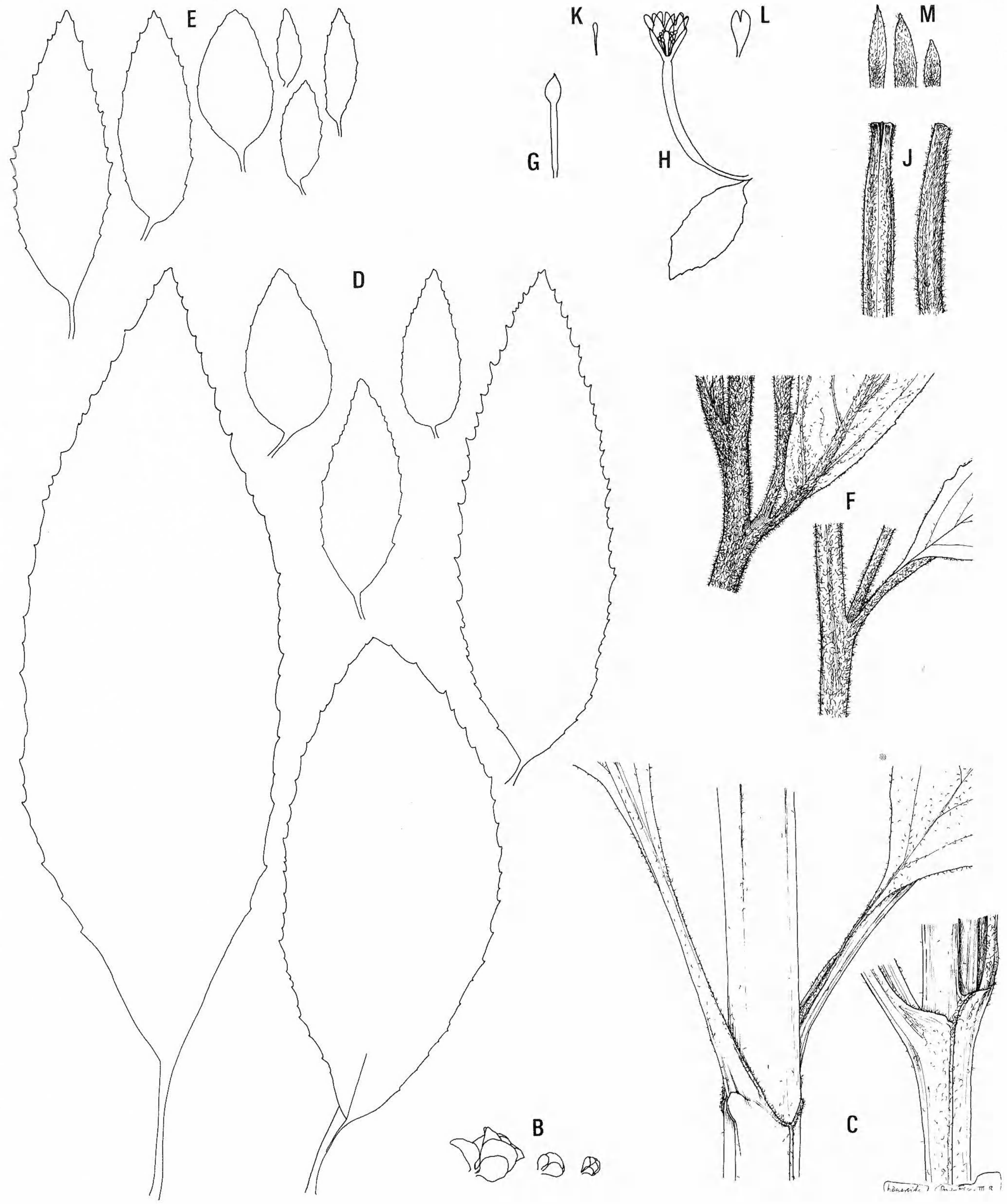

Fig. 111. *Epilobium roseum* Schreb. – A: Habit, × 1/3. – B: Turions, × 1/2. – C: Stem nodes, ×2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem parts and leaves, ×2.5. – G: Bud, × 1. – H: Flower, × 1. – J: Apical part of capsules, ×2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, ×2.5.


K
L
M
G
H
J
E
F
D
C
A
B

Norwegian S and SW coasts, in Sweden up to c. 62° N and in SW Finland. In Scandinavia it has not been recorded north of 62° N.

E. roseum occurs throughout Europe except the extreme south and the arctic and subarctic parts, and in W and N Asia.

Known hybrids: with *E. adenocaulon, collinum, glandulosum, hirsutum, montanum, palustre, parviflorum, obscurum* and *tetragonum*.

112. **Epilobium obscurum** Schreber 1771

Perennial herb, 30–70(–100) cm high. Stem usually at first branched in upper part only, later also at the base, stunted branches present in most leaf axils not supporting branches. Stem producing several or rarely only one (5–)10–20 (–30)-flowered inflorescences. Stolons emerging below as well as above ground, the distal parts always epigean, green, in summer often directly developing into new flowering stems, later up to 15(–25) cm long, creeping, and sometimes rooting at the nodes, with widely spaced pairs of leaves. Stolon leaves with a petiole up to 10 mm long, spatulate to obovate or elliptic, 4–20 mm long. Stolons overwintering without forming specialized turions.

Stems 2–4(–6) mm thick, terete, with raised lines or low wings below the leaf margins and rarely also short and weak lines below the midribs; glabrous or subglabrous below, sparsely hairy above, densely so in the upper part of the inflorescence, especially below denser along the lines, hairs 0–0.25 mm, incurved to adpressed or very short hairs patent, all eglandular or rarely also a few very short glandular hairs. Most leaves usually opposite, upper ones alternate, or rarely most of them alternate, basal leaves often with a winged petiole up to 3 mm long, middle and upper leaves usually quite sessile, leaves usually not united at base around the stem, at least some of them decurrent 0–5 mm on the lines of the stem. Basal leaves smaller except in individuals growing in dry sites, narrowly obovate to lanceolate or narrowly ovate, obtuse. Middle cauline leaves (20–)40–65(–80) mm long, 8–15(–25) mm broad, narrowly to very narrowly ovate or rarely lanceolate, sharply tapering with an acute or obtuse apex, irregularly serrate with few, widely spaced and usually small teeth. Upper leaves smaller, very narrowly ovate. Basal and middle leaves usually subglabrous, upper ones sparsely hairy, denser on margins and veins, hairs like those of the stem.

Pedicels erect to erectopatent in all stages. Buds ovoidal, acute but without a marked mucro. Sepals 3.5–5(–7) mm, connate to 1–1.5 mm, narrowly ovate to lanceolate, acute or narrowly tapering to an obtuse apex, ± reddish especially on margins, densely hairy, with some patent glandular hairs on the basal part. Petals 5.5–7(–9) mm, notched to 1–1.5 mm, rather dark pinkish-purple or rarely lighter purplish-pink. Anthers 0.65–0.75(–0.9) mm, long filaments 3–5 mm, short filaments 1.8–2.5 mm. Style shorter than the long stamens, stigma capitate.

Capsule stalk (5–)10–17(–25) mm. Capsule 40–55(–65) mm, densely hairy, hairs like those of the stem but some patent, glandular hairs present on the apical part. Seeds 0.85–0.95 mm long, 0.4–0.5 mm broad, obovoidal with one flattened side, obtuse at apex, acute at base, without a neck; surface with small papillae arranged in dense, regular, crestlike rows with the bases partially fusing, chalazal hairs usually 40–45, 5–7 mm long. Flowers homogamous.

E. obscurum prefers very wet and often muddy sites, often among dense vegetation. It is fairly common in Denmark and Sweden up to the lakes Mälaren, Hjälmaren and Vänern, with a few localities in SW and S Norway and in SW Finland and Karelia. It has not been recorded N of 62° N in Scandinavia.

E. obscurum occurs in Madeira, N Africa, Europe except the northernmost parts and SW Asia to Caucasus.

Known hybrids: with *E. collinum, montanum, palustre, parviflorum* and *roseum*.

Fig. 112. *Epilobium obscurum* Schreb. – A: Habit, × 1/3. – B: Stolon, × 1/2. – C: Stem nodes, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem parts with leaves, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical part of capsules, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.

The pollination of Ophrys orchids

Bertil Kullenberg and Gunnar Bergström

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The description of the assortative pollination of *Ophrys* species (Orchidaceae) by sexually excited aculeate Hymenoptera males is based on many years of field observations and experimentations. Analytical chemical work on the communication system of this inter-organism relationship started about fifteen years ago. The volatile compounds of the flowers responsible for this specific behaviour release are probably mainly cyclic sesquiterpene alcohols and hydrocarbons. Processes of co-evolution may be assumed to have functioned in the creation of the *Ophrys* pollination groups.

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This paper is a summary of film performance and poster demonstration during the XII International Botanical Congress in Leningrad. The film shown, "The pollination of some *Ophrys* species" (with Swedish text), is kept in the Department of Entomology, University of Uppsala, and is not available for loan.

THE BIOLOGICAL PHENOMENA

Introductory note

The relationship between angiosperm flowers and flower-visiting insects is of the greatest importance for life on earth. This interdependence is in principle based upon the ability of the flowers to supply the carbohydrate-loaded nectar and the protein-rich pollen as food to the insects, and the ability of the insects to transfer pollen to the stigma when feeding or searching for food. The flowers of angiosperms possess the ability to provoke and guide certain instinct-based behaviour in insects. We are fairly well acquainted with the feeding activity of insects on flowers. However, certain flower types have the ability to trigger other instinctive behaviour in insects and among these are the flowers of the orchid genus *Ophrys* L.

This genus has about 30 forms classified as species, the majority growing in the Mediterranean region. Certain forms are difficult to separate morphologically from each other.

In the early 20th century Pouyanne (1917) and Godfery (1925) made observations in the field on the pollination of some *Ophrys* species. On the basis of what they saw, they assumed that the shape of the *Ophrys* labella visually mimicked the female of certain aculeate Hymenoptera. The flower was thought to dupe the male insect, with the result that it became pollinized. In those days, however, thorough studies of the phenomena observed were never performed. Perhaps this state of affairs depended on man's lack of ability to conceive and interpret such behavioural phenomena in living nature before the dawn of modern behavioural physiology. We have studied the behaviour of the male Hymenoptera by ocular observations as well as by electronic flash photography and 16 mm filming.

Film observations

Observation by filming the pollination behaviour may be summarized as follows.

The flowers lack superficially delivered nectar. The flower perfumes attract the males of certain species of Hymenoptera Aculeata and induce them to a high level of preparedness for copulatory behaviour. Tactile stimulation – from the delicately hairy surface of the firmly constructed flower-labellum – under simultaneous chemical, olfactory stimulation – forces the Hymenoptera males to perform movements resembling those performed during the copulatory attempt. During these movements, executed on the flower-labellum, the males will assume such positions and attitudes that the pollinia can be loosened and pollination accomplished. Cf. Kullenberg 1952 and 1961.

Ophrys speculum Link is pollinated by the Scoliid wasp *Campsoscolia ciliata* F. *O. insectifera* L. is pollinated by males of the two Sphecid wasps *Argogorytes mystaceus* L. and *A. fargei* Shuckard (=*campestris* auct.). *O. lutea* Cav. (as *O. fusca* Link*) is pollinated by males of solitary bees, many species of the genus *Andrena* F. (sensu lato). *O. fusca* has been observed to be pollinated by the male *Anthophora acervorum* L.* *O. sphecodes* Mill. (=*araneifera* Huds.) is pollinated by *Andrena* males, at least partly the same species as for *O. lutea* and *O. fusca*. The form-complexes of *O. sphecodes* and *O. arachnitiformis* Gren. & Phil.* are pollinated, at least partly, by the male *Colletes cunicularius* L.* *O. scolopax* Cav., *O. fuciflora* (Crantz) Moench, *O. tenthredinifera* Willd.* and *O. apifera* Huds. and even *O. bombyliflora* Link* are pollinated by males of solitary bees of the genus *Eucera* Scop., and males of the genus *Tetralonia* Spin.* have been seen pollinating *O. fuciflora* (Plate 1 B) and *O. scolopax*. *O. reinholdii* Fl.* has been observed to be pollinated by *Melecta* Latr.* males.

Species not shown in the film, but included in the poster demonstration are marked with an asterisk.

Mr Günter Halx, Worth/Donau, BRD, has most kindly informed us of his observations of *Melecta* males pollinating *O. reinholdii*. In a paper of one of us (Kullenberg 1973) he was incorrectly named G. July and I now take this opportunity to correct the mistake and offer my apologies.

Conclusions from field observations and experiments

It is quite apparent that the flower possesses characteristics which appeal to the supposed inborn male copulatory behaviour of certain species of aculeate Hymenoptera. In all intelligent observation of living nature, experimentation is more or less clearly discernible. Thus, on the basis of field observations and experiments it is possible to state that the *Ophrys* labellum is capable of stimulating the different phases of the male copulatory behaviour from the approach flight to the attempted copulation (Plate 1), although accomplished copulation can never be performed. This type of orchid flower does not secrete nectar, neither is its pollen available to most types of insects. Female aculeate Hymenoptera are never seen visiting *Ophrys* flowers.

Pollination of *O. insectifera* by pollen-feeding Staphylinid beetles, *Anthobium minutum* F., has been observed in a locality in Central Sweden.

The male copulatory instinct is stimulated by the flower-perfume exhaled from the labellum and the approach flight as well as the descent to the flower will not be performed without this chemical stimulation. The movements on the labellum, imitating the introduction of copulation, are indispensable for pollination. They depend on the superficial, epidermal structures of the labellum and on the solid construction of the labellum itself. However, these tactilely guided movements on the labellum cannot be released without the continuation of chemical, olfactory stimulation by the flower perfume. During these movements and shiftings on the flower labellum the males will assume such positions and attitudes that the pollinia can be loosened and pollination accomplished.

The pollination of the different *Ophrys* types carried out by separate Hymenoptera species, or restricted species groups, is in fact assortative. The primary delimiting factor is the scent stimulation or, more correctly, the stimulation by the chemical structure of certain biologically active substances, exhaled by the flowers of the different form groups of *Ophrys*. The secondary form-isolating factor of the *Ophrys* pollination depends on the fact that in one group of *Ophrys* species the pollinia are taken by the Hyme-

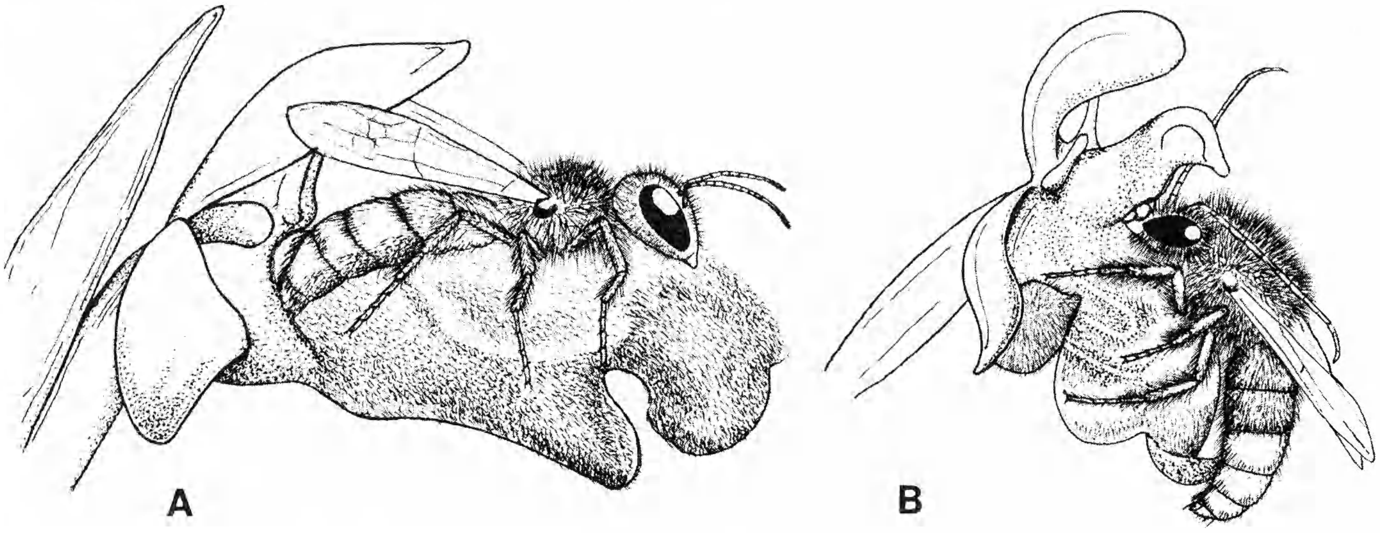

Fig. 1. A: Pollination of *Ophrys fusca* by a male *Andrena*. The pollinia are taken by the tip of the abdomen of the insect. – B: Pollination of *O. scolopax* by a male *Eucera*. The pollinia are taken by the head of the insect.

noptera male with the tip of its abdomen (Fig. 1 A), whereas in the majority of the *Ophrys* forms the pollinia are removed by the insect's head (Fig. 1 B). One species, *O. apifera,* is capable of auto-pollination while still preserving the typical *Ophrys* attraction for Hymenoptera males. A third (virtually form-isolating) factor is the phaenological one. Nevertheless, as regards the flowering-time of *Ophrys* species growing together in a given locality, overlapping seems to occur. Chorologically, on the other hand, the Mediterranean *Ophrys* forms do not seem to be distinctly differentiated. In fact most forms or species seem to have habitats in common. This seems true at least for what may be called "macro-habitats". Sundermann (1975) lists 16 species, but considers numerous forms at the subspecies level. Nelson (1962) lists 21 species with numerous subspecies.

In order to explain the ecological relationship between the *Ophrys* forms and their specific pollinators, as well as the differentiation of forms within the genus *Ophrys,* it seemed quite clear already at the beginning of the observations that the chemistry of the flower perfumes had to be studied. Cf. Kullenberg 1952 and 1961.

CHEMICAL ANALYSES

Methods

Capillary gas chromatography and mass spectrometry with a splitter-free inlet system is the main method used in these analyses. This technique is complemented by micro-chemical methods and other spectrometric techniques. The volatile compounds have been isolated either by a direct pre-column technique or by adsorption. The methods have been described in earlier publications (Ställberg-Stenhagen 1972, Bergström 1973, Ställberg-Stenhagen, Stenhagen & Bergström 1973, Kullenberg & Bergström 1973).

Volatile compounds from Ophrys labella

The compounds identified can be divided into two classes according to their volatility: (1) Compounds of relatively high volatility. This group is made up of straight-chain fatty acid derivatives with 8 to 14 carbon atoms, viz. hydrocarbons, alcohols, aldehydes, ketones and acetates, as well as some acyclic and cyclic monoterpenes in the form of hydrocarbons, alcohols and aldehydes. (2) Compounds of relatively low volatility. These are mainly cyclic sesquiterpenes, viz. alcohols and hydrocarbons. One cyclic diterpene hydrocarbon has also been found in two species. More diterpenes may be present.

Most of the species and forms of species studied have a characteristic composition of compounds, with representatives of both classes. The second class of compounds has been found to be partially groupwise distributed within groups of closely related *Ophrys* species. These have tentatively been called "cadinene-type", "copaene-type" and "longi-cyclene-type" (Kullenberg & Bergström 1973). Compounds belonging to the first class do not seem to be distributed in such a way. The amount of substances from the first class of compounds varies between species whereas the sesquiterpenes are always present in relatively small amounts.

Volatile compounds from pollinators

Substances which emanate from heads of both females and males (mandibular gland) and from the abdomen (Dufour's gland) of females have been identified in a number of species of solitary bees. Hitherto, only members of the genera *Andrena* and *Colletes* Latr., whose males act as *Ophrys* pollinators, have been studied (Bergström & Tengö 1974, Tengö & Bergström 1975, 1976, Bergström 1974).

The analyses of abdominal secretions have revealed the presence of large amounts of farnesyl hexanoate and geranyl octanoate, and macrocyclic lactones such as 16-hexadecanolide and 18-octadecanolide. These compounds are probably used in nest marking.

In most cases the cephalic secretions have been found to be very similar in males and females of the same species. The secretions are made up of straight-chain fatty acid derivatives of lower chain length, such as alcohols, aldehydes, and acetates. In fact, many of these compounds are identical with some class 1 compounds found in *Ophrys* labella. So far no cyclic sesquiterpenes have been found in the bees studied.

Biological implications of the chemical results

A dispersal model for pollinator stimulants

On the basis of the chemical findings and biological observations in the field we would like to present a model of the dispersal of stimulatory compounds (Fig. 2). We distinguish between 3 different "active volumes", designated A, B and C. These active volumes are characterized on the one hand by the chemical substances present in the volume and on the other hand by the effect on the animal. In Fig. 2 wind direction is indicated and the distance from the odour emitter, in this case an *Ophrys* flower, is given on a logarithmic scale covering 1 cm to 1000 m. It must be emphasized that the model is meant to serve as a working hypothesis.

In the discussion of the dispersal and effect of volatile stimulatory compounds, several intricate questions are posed. One is, at what stage in the stimulation chain is the receiving animal put into a specific "mood" directly related to a certain vital need (e.g. copulation or feeding need). In our model this question means whether the receiving animal in region A is directly coupled into an early phase of a sexual behaviour pattern, or whether a more indeterminate orientation flight, possibly, together with excitation, is triggered. We believe that the relatively long-distance attraction/excitation signal in region A, which is transported by the wind, may be composed of the less volatile sesqui- and diterpenes, i.e. compounds of class 2.

The more spherical region B, which covers the space from a few centimeters to a few meters from the emitter, is less dependent on the wind. In this region the concentration of class 1 compounds is relatively high. Air turbulence in this region together with diffusion can serve to spread and mix the compounds. It is unclear at the moment which particular effect these compounds have, but comparisons with the effect of similar compounds emanated from bees in field observations may lead to the inference that a higher excitation level may be triggered. At the same time the close range orientation, together with visual stimuli, may be effected. The behaviour of the pollinator in this region can perhaps in more detail be successfully compared with the behaviour of a male in the same region towards a female insect, a food plant or an odour marking point.

We have preferred to distinguish a separate region, region C, in the very close vicinity of the emitter, i.e. at a maximum distance of about 1 centimeter. In this region, compounds of very low volatility may operate, either by short distance air transportation or even by contact reception. Candidates for signal compounds are again the class 2 compounds. The behaviour released in this region, together with tactile stimuli, must be late phases in the copulation

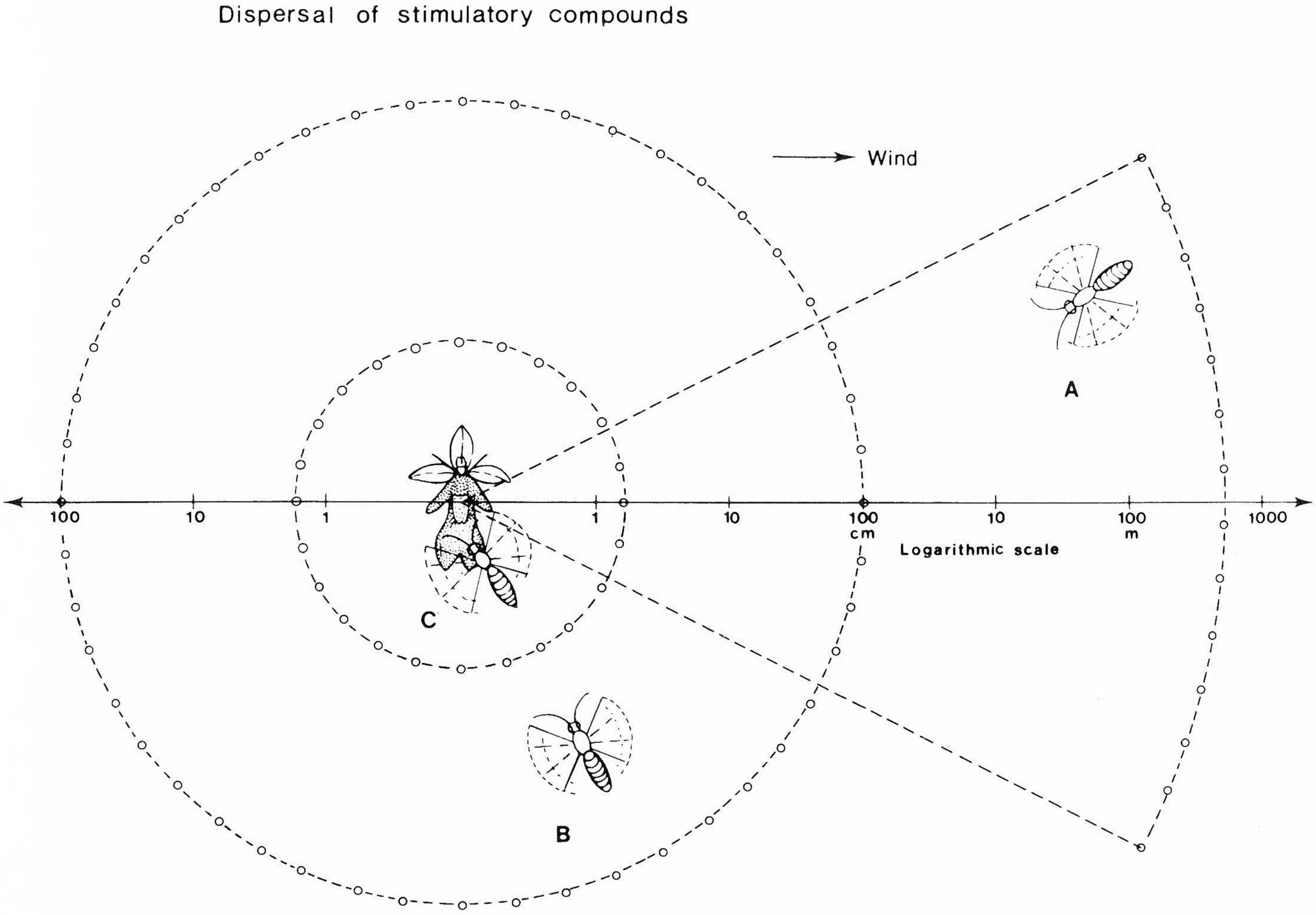

Fig. 2. Dispersal model for pollinator stimulants.

attack; perhaps a further (higher) excitation step manifesting itself in repeated copulation attempts and binding to the flower (Plate 1 C–F).

Species and subgenera specificity of signals

Field experiments and electrophysiological data both point to a high degree of specificity of volatile signals in the *Ophrys* pollinator relationship. A major question is therefore how this specificity is achieved. With regard to the dispersal model and to distinguishing between the two compound classes we can say that the latter partially represent two different ways of obtaining specificity.

In the case of the class 1 compounds, i.e. the simple fatty acid derivatives and the monoterpenes, there is already a base for specificity in the possible structural variants. With these compounds, specificity also seems to originate to a large extent from the multicomponent blends that they form. Thus both the components themselves, and the proportions in which they occur, constitute the specificity.

With the sesqui- and diterpenes the number of different structural variants is very large. So large, in fact, that this phenomenon alone would be enough to explain the high degree of specificity. Often a few of these compounds are present together in the secretion of the plant. This fact further enhances the specificity.

To sum up, specificity is likely to operate in all three regions, A, B and C, but on partially different principles. The different stimulation steps may involve increasing excitation levels. The combination with other stimuli (visual and tactile) may or may not be simultaneous.

THE STIMULI GUIDING THE POLLINATION BEHAVIOUR

As regards the stimuli functioning in the pollination of *Ophrys* flowers by aculeate Hymenoptera males the following conclusions can be drawn.

Olfactory stimulation is doubtless a so-called primary key stimulus. Tactile stimulation is also of primary importance as a key stimulus. The characteristic epidermis structures on the upper side of the *Ophrys* labellum, as well as the labellum's solid construction, are indispensable for the touch-guided movements and shiftings on it. The external morphology of the different types of hair is not of definite importance for these movements, whereas the mechanical properties and the stroking direction of the hairs, as well as their length are essential. Finally, it is the grouping of the hairs with different properties into fairly homogeneous pilose areas that forms the essential tactile-stimulatory basis for how the shiftings on the labellum will take place.

Of the three main types of stimuli – olfactory, tactile and visual – and their effect on the Hymenoptera males, it seems that the olfactory stimulation may be called independent, whilst the tactile and the visual stimuli should be called dependent key stimuli, since they rely on the olfactory preparation for their releasing ability. As regards the visually perceivable habitus, the labella of the *Ophrys* flowers appeal to the basic innate releasing mechanism of a widely definable insect type, whilst, as regards the ability to give tactile and scent stimulation, they appeal to the behaviour releasing mechanism of certain types of aculeate Hymenoptera. Then, in regard to scent stimulation they appeal in a most specialized way. The concept of the specialized releasing mechanism of the scent stimulation, assumes specialization from the physiological as well as from the taxonomical point of view.

Interesting observations on the pollination of certain *Ophrys* types by Scarabaeid, Elaterid and perhaps other Coleoptera types in the male sex, when performing introductory behaviour of copulation on the labella, have to be more thoroughly studied. At least the tactile stimulation from the labella seems to be adequate regarding the male copulatory behaviour of the Coleoptera in question. Observations on this pollination by Coleoptera are made by Mr G. Halx, Worth/Donau, BRD, and Mr J. Forster, Winterthur, Schweiz, who kindly informed us by letters with colour photographs.

A GENERAL CONCLUDING NOTE

The morphological and chemical characters typical of the *Ophrys* flower, can with good reason be assumed to be adaptive, considering the regularity with which they occur within the large orchid group Ophrydoideae alluded to in connection with this specialized entomogamy. The *Ophrys* flower ought to be regarded as an adaptive flower. The *Ophrys* species are adapted for pollination to the male copulatory instinct of certain types of aculeate Hymenoptera. In its characteristic pollination biology the genus *Ophrys* presents a spectrum of increasing rigour with the strictly specialized *O. speculum* at one of the ends, and the least strictly specialized, partly *Eucera* pollinated, partly self-pollinated *O. apifera* (Plate 1 A) at the other; and with the other forms placed in-between. One may venture the metaphor that *O. speculum* has one single, very rigourous, life insurance, *O. apifera* a double one, and the other species, as far as is known, single insurances that nevertheless allow several possibilities.

The description given of the special interactions of the nectarless *Ophrys* flowers with certain aculeate Hymenoptera types of the male sex for the benefit of pollination is based on many years of field observations and experimentations. Analytical chemical work on the communication system involved started about fifteen years ago. The linking of restricted groups of *Ophrys* species and species of certain genera of Hymenoptera Aculeata into delimited pollination groups is based on the ability of the flowers to trigger the male copulatory behaviour via chemical and tactile stimulation. This situation in *Ophrys* pollination ecology can be assumed to have evolved by stepwise evolutionary processes. In other words, processes of so-called co-evolution may be assumed to have been functioning in the creation of the *Ophrys* pollination groups.

ACKNOWLEDGEMENTS

We wish to express our gratitude to Mr Nigel Rollison for the revision of the English text, and Mrs Ivanka Kostova for the translation of the Russian summary.

Plate 1. A: Pollination of *O. apifera* by a male *Eucera longicornis* L. during observations under experimental conditions, Öland, southern Sweden. Note that one of the quasi-spontaneously fallen out pollinia is being pressed by the *Eucera* male against the stigma of the flower. – B: A male *Tetralonia* sp. attempting copulation with the labellum of an *Ophrys fuciflora* flower. Crete. – C: A male *E. longicornis* in "searching behaviour" on the surface of the ground under a dummy or bait of green tulle diffusing scent from hexane extract of five labella of *O. tenthredinifera*. Öland. – D: A male *E. nigrilabris* Lep. in a field experiment closely approaching by direct flight a flower of *O. tenthredinifera* concealed by a piece of green tulle. Notice the head of the *Eucera* male carrying pollinia of *O. tenthredinifera*. Majorca. – E: A male *E. longicornis* in a field experiment attempting to copulate with the green tulle of a dummy diffusing scent from *O. tenthredinifera* labella in hexane solution. Öland. – F: A male *E. longicornis* in a field experiment approaching by direct flight a scent dummy prepared with a hexane solution of (-)-γ-cadinene, concentration 1:100. Öland. Nevertheless, the effect of this substance is varying in field tests. – Length of *Eucera* male about 15 mm.

ОПЫЛЕНИЕ ОРХИДЕЙ ИЗ СЕМЕЙСТВА OPHRYS

Резюме на русском языке

Биологические явления

Орхидеи из семейства *Ophrys* исключительно или почти исключительно опыляются самцами некоторых видов Hymenoptera Aculeata. Цветы не выделяют нектар. Когда привлеченные самцы Hymenoptera садятся на губы цветов *Ophrys* приводится в движение механизм, соответствующий началу копуляции, при этом может освободиться пыльца и происходит опыление.

Пока что установлены следующие виды Hymenoptera Aculeata: *Campsoscolia*, *Argogorytes*, *Colletes*, *Andrena* s. lato, *Eucera*, *Tetralonia*, *Anthophora* и *Melecta*.

Что касается изучения стимулов, действующих при опылении цветов *Ophrys* полово возбужденными самцами Hymenoptera Aculeata, то можно сделать следующие выводы:

Ароматный возбудитель, без сомнения, является так называемым ключевым возбудителем. Тактильный возбудитель имеет тоже большое значение как ключевой возбудитель. Характерная структура эпидермы на верхней стороне губы *Ophrys* также как и плотная /твердая/ её конструкция необходимы для тактильно мотивированных движений и поворотов на губах. Разница во внешней морфологии различных типов волос не имеет существенного значения для данных движений, тогда как механические свойства волос, их направленность и длина очень важны. И, наконец, группировка волос с различными свойствами на определенных гомогенных волосяных поверхностях имеет существенное значение для того, как будут осуществляться движения по губе.

Что касается трех основных типов возбудителей — обонятельных, тактильных и зрительных — и их влияния на самцов Hymenoptera, то мы хотели бы назвать ароматный независимым, в то время как тактильные и зрительные возбудители следует называть зависимыми, так как для своего вызывания они зависят от ароматной подготовки. Что касается зрительно воспринимаемого вида губы *Ophrys*, то он апелирует первичному фактору во врожденно вызывающем механизме у явно определенного типа насекомых. Что касается способности дать тактильное и ароматное возбуждение, то она влияет на вызывающий механизм у некоторых типов Hymenoptera Aculeata. Что касается ароматного возбуждения, то влияние при этом является наиболее специализированным.

Под специализированным вызывающем механизмом посредством ароматного возбуждения, понимается специализирование как с физиологической, так и с таксономической точки зрения.

В последнее время сделаны интересные наблюдения по опылению некоторых типов *Ophrys* самцами Scarabaeidae, Elateridae и, возможно, еще другими типами Coleoptera. По крайней мере, тактильное возбуждение губ кажется адекватным относительно характера копуляции у самца упомянутого Coleoptera. Нужно, однако, изучить более подробно как раз их поведение в начальных попытках копуляции на губах.

Химия летучих продуктов из цветов Ophrys

Мы нашли, что цветы выделяют небольшие количества простых алифатических соединений, а также изопренные соединения, особенно цикличные и сесквитерпен-алкоголи и углеводороды. Установлены и некоторые монотерпены. Пока мы исследовали 28 видов и подвидов. Сравнивая данные, полученные главным образом из газохроматографических и масса- спектрометрических исследований летучих продуктов из цветов *Ophrys* и из стандартных соединений, мы установили некоторые типы сесквитерпенов.

Возможно большое количество изомерных структур. В настоящее время мы заняты установлением абсолютной конфигурации некоторых из естественных соединений. Результаты позволяют уже сделать некоторые выводы относительно таксономических связей между определенными формами *Ophrys*. Эти выводы соответствуют тем, которые можно получить при наблюдении опыления самцами Hymenoptera Aculeata.

Изучая наличие в цветах *Ophrys* некоторых типов сесквитерпенных углеводородов, предварительно названных длинноциклическим типом, типом копаен и типом кадиен, мы нашли, что тип копаен встречался лишь у видов, опыляемых главным образом пчелами *Eucera*. Этот сесквитерпен, который может представлять собой несколько родственных изомеров у различных типов, пока что был найден у *O. scolopax*, *O. apifera*, *O. tenthredinifera*, и *O. bertolonii*. Длинноциклический тип встречается у *O. speculum*, *O. insectifera*, *O. lutea*, *O. fusca*, у многих форм *O. sphecodes* и у *O. bombyliflora*. *O. lutea* содержит сесквитерпенный алкоголь, который по своей структуре кажется прямо связанным с типом кадинен у углеводородов. *O. lutea*, *O. fusca* и отдельные формы *O. sphecodes* опыляются самцами *Andrena*. Тип кадинен имеется у *O. lutea*, *O. fusca* и в относительно меньшем количестве у *O. bombyliflora*.

Химический анализ ароматных веществ показывает очень сходный состав летучих секретов у *O. lutea* и *O. fusca*. Существенная разница была найдена среди ароматных веществ, выделяемых формами комплекса *O. sphecodes*. Изучая эту разницу далее, особенно путем сравнения аналитических результатов для различных форм, нам представляется возможным выяснить некоторые факты в сложной таксономии в данной группе.

Летучие вещества, находящиеся в цветах в небольших количествах были выделены из цветочных губ способом «анфлёраж» /холодное извлечение с помощью кремния/. Дополнительный метод — поместить част губы прямо в не дающую осколков инъекционную систему газохроматографа.

Химия летучих секретов у одиноких пчел

Летучие вещества, выделяемые в мандибулярных железах головы самцов и самок пчел *Andrena* были анализированы химически. Пока было изучено 20 видов. Каждый вид имеет характерный состав относительно небольших количеств совсем простых алифатических и изопренных веществ. Состав летучих веществ у самцов и самок у большинства видов очень однородный. До сих пор не обнаружены циклические сесквитерпены, соответствующие найденным у цветка *Ophrys*. Нами были также изучены ароматные субстанции из железы Дюфур, имеющейся только у самок Эта железа была довольно большая у изучаемых нами пчел. Её секрет функционально связывается с водоотталкивающей облицовкой гнезда и с его ароматным маркированием.

Выводы

Морфологические и химические свойства цветов *Ophrys* отличающие их от других, родственных видов орхидей, можно с основанием считать адаптивными, принимая во внимание регулярность в существовании этих свойств у упомянутой большой группы орхидей Ophrydoideae, тесно связанной с особой энтомогамией. Цветок *Ophrys* следует рассматривать как приспособляемый цветок. Виды *Ophrys* для своего опыления приспособлены к инстинкту копуляции у самцов некоторых типов Hymenoptera Aculeata.

Характерная биология опыления у семейства *Ophrys* предлагает спектр различных по силе связей с чрезвычайно специализированным видом *O. speculum* на одном конце, на другом — наименее специализированный, частью опыляемый *Eucera* частью — самоопыляющийся *O. apifera* а между ними — все остальные виды. Можно осмелиться сказать, что вид *O. speculum* имеет одно единственное, строго регулированное «страхование жизни», *O. apifera* — двойное, и все остальные виды — простие «страхования жизни», основывающиеся на несколько возможностей.

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New taxa of Osmitopsis (Compositae)

Kåre Bremer

Bremer, K. 1976 05 06: New taxa of Osmitopsis (Compositae). *Bot. Notiser 129*: 21–24. Stockholm. ISSN 0006-8195.

One new species and one new subspecies of the genus *Osmitopsis* (Compositae) are described. These are *O. glabra* Bremer and *O. pinnatifida* (DC.) Bremer ssp. *serrata* Bremer.

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A few years ago I revised *Osmitopsis* (Compositae) (Bremer 1972), a genus of eight species, confined to the southern and southwestern districts of the Cape region in South Africa. The study was based on herbarium material. This was insufficient for a definite treatment of the infraspecific variation within *O. pinnatifida* and *O. afra*. From August 1972 to January 1973 I travelled in southern Africa and I then had the opportunity to investigate these species in the field. In search for *O. pinnatifida* during a two-day trip to the Klein Drakenstein and Wemmershoek Mts I was guided by Miss Elsie Esterhuysen of the Bolus Herbarium. The result of my field studies is a new species and a new subspecies of *Osmitopsis* described below. The methods, terminology and taxonomic concepts are in concordance with those in my revision.

Osmitopsis pinnatifida (DC.) Bremer ssp. **serrata** Bremer, ssp. nov.

Orig. coll.: Bremer 634, Paarl Div., Wemmershoek Peak, rock crevices facing SW, 1600 m, 1973 (S holotype).

Illustrations. Fig. 1; Bremer 1972 Fig. 6 O–R, p. 27.

Map. Bremer 1972 Fig. 5, p. 25.

Folia ± basaliter serrata (summa raro integra); dentibus foliorum numero usque ad 18, erecto-patentibus, subulato-triangulatis, ad 3 mm longis, ad 1.8 mm latis, basim foliorum versus gradatim minoribus, acutis–acuminatis.

Pappus squamis brevibus, numerosis, subulato-triangulatis, ± connatis (raro nullis) et squamis ad 2.5 mm longis, numero 2–15, subulatis, filiformibus (raro nullis).

Leaves serrate ± basally (a few upper leaves seldom entire); teeth basally gradually smaller, up to 18, erecto-patent, subulate-triangular, 0.5–3 mm long, 0.1–1.8 mm wide, acute–acuminate.

Pappus of many, short, subulate-triangular, ± connate scales (seldom 0) and 2–15 long scales (seldom 0), up to 2.5 mm long, subulate, hair-like.

Flowering period. Mainly November–January.

Collections. Paarl Div.: Mts S of Wemmershoek, in wet spots among rocks, 4000–4500 ft., 1921, Andreae 757 (STE) – April Peak, Wemmershoek Mts, summit, S side in rock crevices, 5000 ft., 1940, Esterhuysen 4026 (BOL, K, NBG, PRE) – Tierkloof, Wemmershoek Mts, SE slopes, rocks, 2500–3000 ft., 1940, Esterhuysen 4079 (BOL, K) – Wemmershoek Peak, 3000 ft., 1944, Lewis (SAM) – Wemmershoek Peak, gully on W side, 4000–5000 ft., 1944, Esterhuysen 11335 (BOL) – Wemmershoek Peak, rock crevices facing SW, 1600 m, 1973, Bremer 634, 635 (S).

Discussion. *O. pinnatifida* has hitherto been divided into two subspecies, viz. ssp. *pinnatifida* and ssp. *angustifolia* (Bremer 1972 pp. 24–26). The former is characterized by serrate–pinnatifid leaves with 6–18 leaf-lobes, if fewer they are

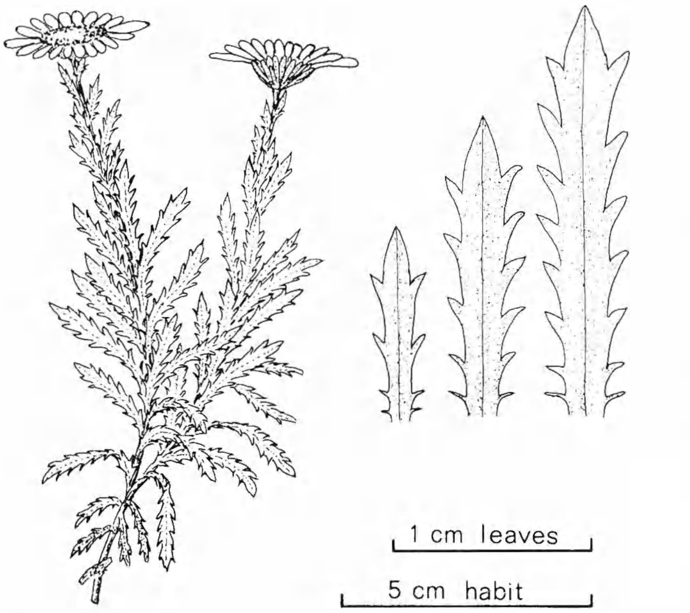

Fig. 1. Habit and leaves of *Osmitopsis pinnatifida* ssp. *serrata*.

distributed below the middle of the leaf. The latter subspecies is known by its entire or pinnatifid leaves with 6 or less leaf-lobes, which are apically or evenly distributed. There are also small differences in pappus structure; the ray-floret pappus of ssp. *angustifolia* generally consists of short scales only, lacking the subulate long scales characteristic of the disc-florets and both kinds of florets in ssp. *pinnatifida*.

Ssp. *pinnatifida* was defined to include plants with either pinnatifid leaves, i.e. with leaf-lobes longer than the width of the central lamina or rachis of the leaf (Bremer 1972 Fig. 6 M–N, p. 27), or serrate leaves, i.e. with teeth shorter than the width of the rachis (Fig. 6 O–R, loc. cit.). The relationship between the plants with these two kinds of leaves was not possible to clarify on the herbarium material available. However, having studied this species in the field I now propose that the plants with serrate leaves should be excluded from ssp. *pinnatifida* and be described as the new subspecies *serrata*. The reasons for this are given below.

Before I saw *O. pinnatifida* growing I knew very little about its habitat requirements. In the Dutoits and Klein Drakenstein Mts I found ssp. *pinnatifida* growing in shadow along water streams and preferably in the sprinkle from small waterfalls. Miss Esterhuysen informed me that there are many suitable localities in these mountains, where ssp. *pinnatifida* is not uncommon. This area corresponds to the three northernmost localities in Fig. 5 in the revision. The inexact locality indicated by a circle near Franschhoek might be wrongly placed, since according to Miss Esterhuysen suitable localities for ssp. *pinnatifida* are rare near Franschhoek and in the Wemmershoek Mts.

O. pinnatifida ssp. *serrata* was also searched for, in the Wemmershoek Mts, where I found it in a habitat quite different from that of ssp. *pinnatifida* in the Dutoits and Klein Drakenstein Mts. It prefers crevices of rather exposed rocks on the higher slopes of the peaks, where for example temperature and water supply must be significantly different. Fig. 2 gives an idea of the environment. The distribution of ssp. *serrata* is in the southern Wemmershoek Mts, which corresponds to the four localities with serrate leaves in Bremer 1972 Fig. 5.

In the Jonkershoek area I studied ssp. *angustifolia*. It occupies the same habitat as ssp. *pinnatifida,* viz. shadowy places along water streams, often near small waterfalls and not necessarily on higher altitudes. The distribution of ssp. *angustifolia* is evident from Bremer 1972 Fig. 5.

Ssp. *angustifolia* seems well established, but are ssp. *pinnatifida* and ssp. *serrata* not only environmental modifications of the same genotype? This is disproved by the fact that all three subspecies have kept their original leaf-shapes during two years of cultivation in greenhouses under identical conditions. Thus the two latter subspecies can be regarded as ecotypes in the classical sense of Turesson. I believe these are formally best treated as subspecies, especially since the two ecotypes here discussed have vicarious distributions, in the Klein Drakenstein–Dutoits Mts and Wemmershoek Mts, respectively. If the dubious record of ssp. *pinnatifida* near Franschhoek should prove to be correct the distribution picture would be less clear. However, I would still recognize ssp. *pinnatifida* and ssp. *serrata* since they occupy different habitats. The concept of subspecies is useful not only for geographically isolated but also for environmentally isolated populations of a species.

Osmitopsis glabra Bremer, sp. nov.

Orig. coll.: Bremer 640, Caledon Div., S slopes of mountain between Heuningklip and Highlands Forest Reserve, burnt section, 400 m, 1973 (S holotype).

Fig. 2. Southern Wemmershoek Mts, the locality for *O. pinnatifida* ssp. *serrata*, photographed from the south with Wemmershoek Peak, 1766 m, to the right.

Illustrations. Fig. 3; Bremer 1972 Fig. 8 N, p. 32.

Map. Bremer 1972 Map 5, p. 21.

Suffrutex glaber, 8–25 cm altus. Caules simplices vel ramosi, erecti vel ascendentes, dense foliati, apicem versus gradatim sparsius sic pedunculoides, capitulo terminali instructi.

Folia inferiora patentia–squarrosa, interdum reflexa, parum coriacea, ± anguste obovata cuneataque, ad 1.5 cm longa, ad 5 mm lata, acuta–obtusa; dentibus foliorum numero usque ad 24, subulato-triangulatis, ad 1 mm longis, ad 0.8 mm latis, acutis–acuminatis. Folia superiora erecto-patentia, anguste elliptico-oblonga, minora; dentibus foliorum paucioribus.

Involucrum late campanulatum, ad 2 cm diametro. Bracteae involucri 20–45, 2–3-seriatae, oblongae vel anguste elliptico-oblongae, exteriores lanceolatae, ad 7 mm longae, apice irregulariter serrulatae et parum purpureae, acutae–acuminatae.

Receptaculum convexum, paleaceum. Paleae obovato-oblongae, ad 5.5 mm longae, apice irregulariter serratae, acutae–acuminatae.

Flores radii 15–30, feminei, steriles. Tubus cylindricus–infundibularis. Lamina anguste elliptico-oblonga, 9–16 mm longa, alba, apice ± profunde 2-lobata. Stylus ad 2.8 mm longus, simplex vel bifidus.

Flores disci numerosi, >75, perfecti. Corolla gradatim sursum ampliata, 3.2–3.8 mm longa; lobi corollae ovato-triangulares, patentes. Stylus corolla paulo brevior; rami styli patentes. Antherae corolla subduplo breviores, appendice apicali ovata, rotundata.

Achaenia oblonga–obovata, 1.5–2.8 mm longa, 0.8–

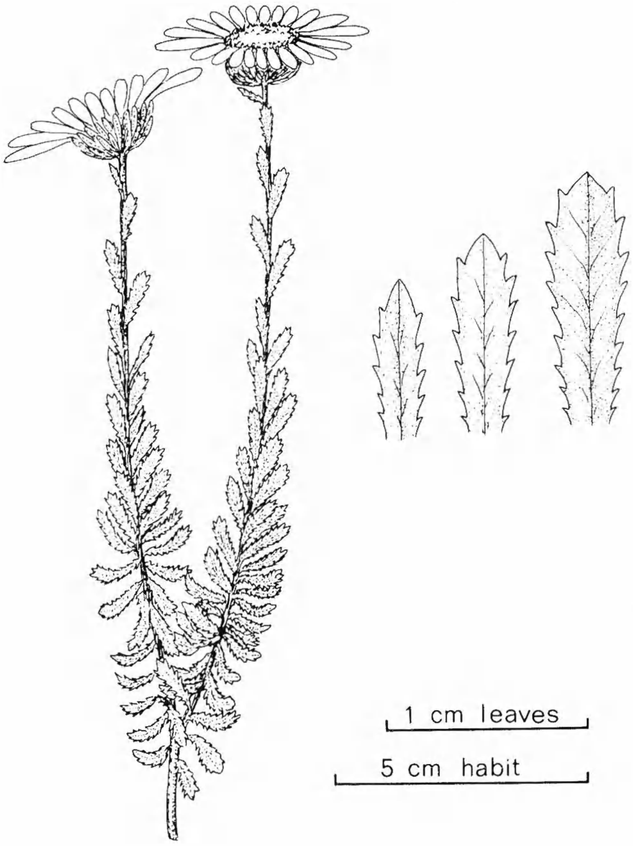

Fig. 3. Habit and leaves of *Osmitopsis glabra*.

1.5 mm lata, parum tetragona; pappus squamis numerosis, basaliter ± connatis, usque ad 1.8 mm longis.

An 8–25 cm high, glabrous suffrutex. Stems simple or ramifying, erect or ascending, somewhat striate, densely leafy below, gradually more sparsely upwards and thus somewhat pedunculoid, terminally bearing a capitulum. Cortex light brown.

Lower leaves spreading–squarrose, sometimes reflexed at the base and ± curved and ascending, somewhat coriaceous, ± narrowly obovate and cuneate, 0.5–1.5 cm long, 2–5 mm wide, acute–obtuse, serrate; teeth 12–24, subulate-triangular, 0.5–1 mm long, 0.2–0.8 mm wide, acute–acuminate. Upper leaves different in being erectopatent, straight, narrowly elliptic-oblong, 0.3–1 cm long, 0.5–4 mm wide, acute, serrate–serrulate; teeth 2–14, subulate-triangular, 0.2–0.7 mm long, 0.1–0.5 mm wide, acute–acuminate.

Involucre widely campanulate, 0.6–2 cm wide. Involucral bracts 20–45, 2–3-seriate, oblong or narrowly elliptic-oblong, outer lanceolate, 3–7 mm long, 0.7–3 mm wide, laterally ± plane and scarious, apically minutely and irregularly denticulate-serrulate and somewhat purplish, acute–acuminate.

Receptacle convex. Paleae glabrous, somewhat scarious, obovate-oblong, 4–5.5 mm long, 1–1.8 mm wide, apically irregularly serrate, acute–acuminate, ± persistent.

Ray-florets 15–30, female, sterile, glabrous. Tube cylindrical–funnel-shaped and gradually widening, 1.5–2 mm long, 0.8–1.1 mm wide. Lamina narrowly elliptic-oblong, 9–16 mm long, 2–4 mm wide, indistinctly 8–15-veined, apically ± deeply 2-lobed. Style 1.5–2.8 mm long, simple or bifid; style-branches up to 1 mm long, coherent or spreading, somewhat acute; stylopodium 0.

Disc-florets numerous, >75, perfect. Corolla gradually widening upwards, 3.2–3.8 mm long, 0.7–1.2 mm wide; corolla lobes ovate-triangular, 0.5–0.8 mm long, somewhat spreading. Style 2.8–3.7 mm long; style-branches 0.6–1 mm long, spreading; stylopodium conical, short. Anthers 1.8–2.5 mm long; apical appendage ovate, rounded.

Achenes oblong–obovate, 1.5–2.8 mm long, 0.8–1.5 mm wide, somewhat four-edged; pappus of many, up to 1.8 mm long, subulate, basally ± connate scales.

Flowering period. Mainly November–January.

Collections. Caledon Div.: Honingklip, Bot River, Taylor 5121 (NBG) – Near Elgin, between Grabouw and the Paardeberg, 1947, Stokoe (SAM) – Palmiet River Mts, 1948, Stokoe (SAM) – Palmiet River Mts, Oudebosch, 1952, Stokoe (SAM) – S slopes of mtn between Heuningklip and Highlands Forest Reserve, burnt section, 400 m, 1973, Bremer 640 (S).

Discussion. O. glabra is closely allied to *O. afra,* from which it differs by its foliage. The leaves are quite glabrous, ± narrowly obovate and distinctly serrate along the entire margin. *O. afra* is always tomentose with usually somewhat longer and narrower leaves; the teeth are fewer and ± concentrated towards the apex. A comparison of the descriptions of both species might suggest further differences of mainly quantitative nature. However, with the limited material available these cannot be shown to be significant. Since the glabrous versus the tomentose leaves is the most obvious difference I have chosen the epithet *glabra,* although there are other glabrous species in the genus.

In my revision (Bremer 1972) I included the material of this new species as deviating collections in *O. afra* (pp. 30–33). With the herbarium material available it was not possible to determine whether it was occasionally glabrous forms or a separate species. Now, having seen the actual plants in the field, I consider it a no doubt good species. *O. glabra* is very constant in foliage and grows in considerable quantities in several localities as seen from the list of collections and Map 5 on p. 21 in Bremer 1972.

Both *O. afra* and *O. glabra* have rhizomes, from which aerial shoots may regenerate after veld fires. Thus they are often seen in abundance in burnt fynbos areas.

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Die Struktur und Taxonomie einiger Stephanodiscus-Arten aus eutrophen Seen Südschwedens

Hannelore Håkansson

Håkansson, H. 1976 05 06: The structure and taxonomy of some species of Stephanodiscus from eutrophic lakes in southern Sweden. [Die Struktur und Taxonomie einiger Stephanodiscus-Arten aus eutrophen Seen Südschwedens.] *Bot. Notiser 129*: 25–34. Stockholm. ISSN 0006-8195.

Light and electron microscopy have been used to study some species of *Stephanodiscus* (Diatomeae) occurring in eutrophic lakes in southern Sweden. The sculpturing, processes, and areolation have been decisive in the determination of species and an attempt has been made to reach a new tentative grouping based on these observations. The discussion is chiefly concerned with *Stephanodiscus astraea* (Ehr.) Grun. var. *astraea*, var. *minutulus* (Kütz.) Grun. and var. *intermedius* Fricke, *S. hantzschii* Grun. var. *hantzschii* and var. *pusilla* Grun., *S. dubius* (Fricke) Hust. and *S. tenuis* Hust.

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Bei den Analysarbeiten mit fossilen Diatomeen verschiedener Seesedimente, sowie einzelner rezenter Planktonproben südschwedischer Seen, befanden sich mehrere *Stephanodiscus*-Arten mit unterschiedlicher Struktur, deren Bestimmung recht schwierig war, da diese Struktur oft ineinander überging. Da die moderne paleoökologische Forschung immer stärker Gebrauch von bestimmten Indikatoren hat, ist es von Bedeutung genaue Bestimmungen der Diatomeen zu machen. *Stephanodiscus hantzschii* Grun. ist zum Beispiel eine Charakterform stark eutropher Gewässer. *S. astraea* var. *minutulus* (Kütz.) Grun. wurde dagegen nur wegen ihres isolierten, massenhaften Auftretens als besondere Form beibehalten (Hustedt 1928).

Mit Hilfe der Bestimmungsschlüssel und der in der Literatur befindlichen Abbildungen ist es oft schwierig die *Stephanodiscus*-Arten zu bestimmen. Die Beschreibungen der meisten Arten sind auf lichtmikroskopischen Untersuchungen basiert, während elektronenmikroskopische Aufnahmen uns noch feinere Details zeigen, die manchmal verwirrend wirken, oft aber unsere Augen beim Sehen im Lichtmikroskop öffnen.

Das Folgende ist ein Versuch die im Licht- und Elektronenmikroskop gemachten Beobachtungen zu kombinieren, um – falls möglich – deutlichere Unterschiede zwischen den einfachen Arten machen zu können. Während das Hauptgewicht früher auf die Areolierung und die Form der Zelle gelegt wurde (z. Beisp. Hustedt 1930), haben die Raster-Elektronenmikroskop-Untersuchungen gezeigt, dass das Vorhandensein von Prozessen wichtige Aufschlüsse der Gattung *Stephanodiscus* geben kann (Round 1970, 1972, Hasle 1972, 1974, Lowe & Crang 1972, Sreenivasa & Duthie 1975).

MATERIAL

Das Material besteht aus Planktonproben des Vombsees, des Bysees, des Sees Vidöstern und Plankton- sowie Gyttjeproben des Södresees, des Sees Trummen und des Växjösees.

Der Vomb- (55°42'N, 13°37'O) sowie der Bysee (55°50'N, 13°41'O) sind eutrophe Seen im Zentralen Schonen. Der Vombsee ist 12,4 km² gross, der Bysee nur 0,14 km². Der Berggrund beider Seen besteht aus Granit und die losen Erdlager aus Sand oder kalkreicher Moräne. Die pH-Werte des Vombsees liegen

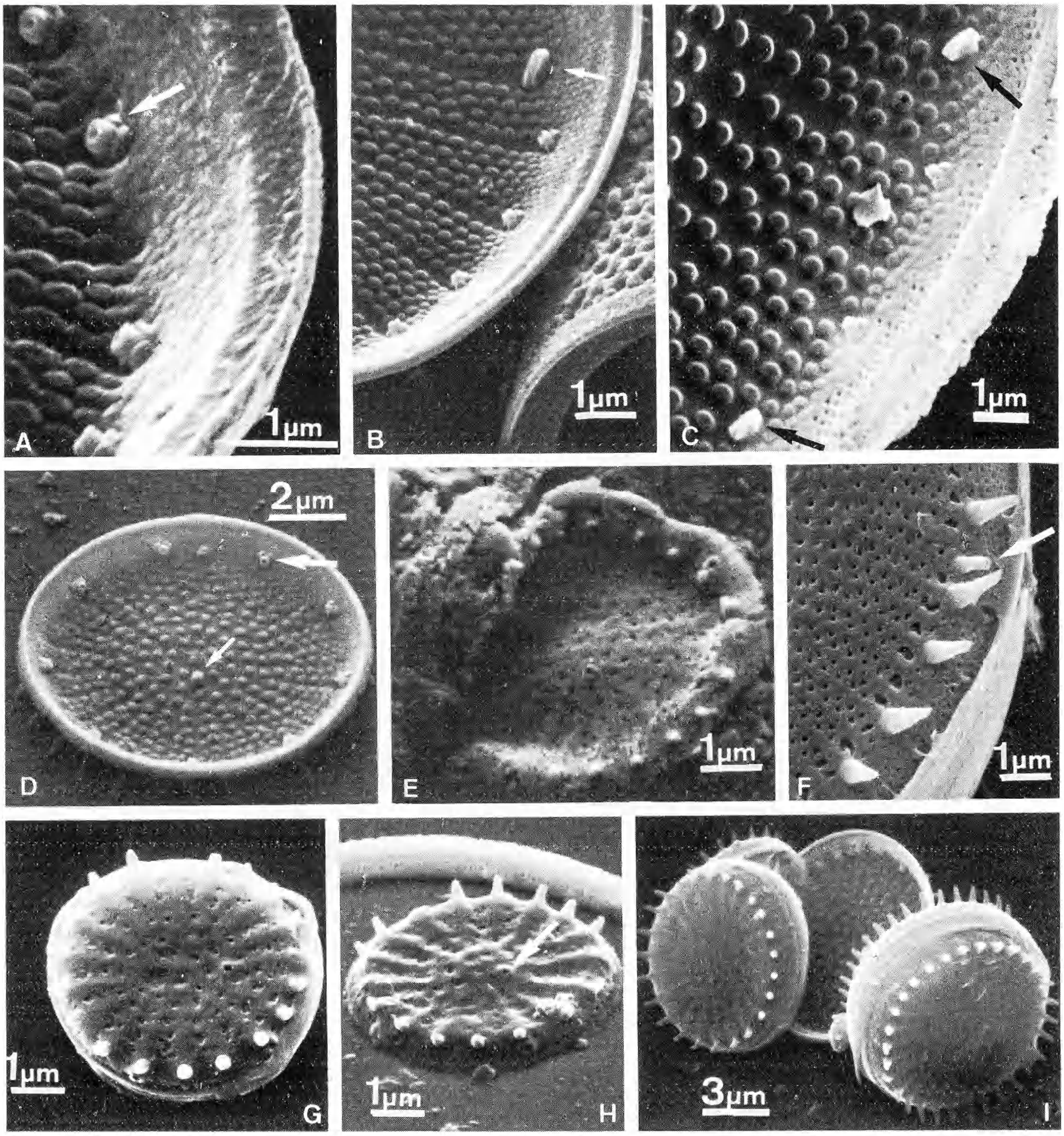

Abb. 1. A: *Stephanodiscus tenuis*. Detailbild einer Schale. Innenansicht mit den Stützenfortsätzen. – B: Dto. mit einem Lippenfortsatz. – C: *S. astraea*. Detailbild einer Schale. Innenansicht mit den Stützenfortsätzen und zwei Lippenfortsätzen. – D: *S. hantzschii*. Innenansicht einer Schale mit den marginalen Stützenfortsätzen, dem Lippenfortsatz und dem zentralen Fortsatz. Sediment des Södresees. – E: *S. hantzschii*. Aussenansicht einer Schale. Sediment des Södresees. – F: *S. astraea*. Aussenansicht einer Schale mit Stacheln und dem Lippenfortsatz, der hier als Fortsatz sichtbar wird. – G: *S. hantzschii*. Aussenansicht einer Schale. Sediment des Södresees. – H: *S. hantzschii*. Aussenansicht einer Schale mit den Stacheln und dem zentralen Fortsatz. Nicht unter jedem Stachel ist ein Fortsatz sichtbar. Rezente Probe des Vombsees. – I: *S. hantzschii*. Frusteln und eine Schale mit Innenansicht. Stacheln und Stützenfortsätze sichtbar. Planktonprobe des Bysees. – Prep.: Hannelore Håkansson; F: G. Cronberg.

Fig. 1. A: *Stephanodiscus tenuis*. Detailed view of interior of valve with strutted processes. – B: Do, with one labiate process. – C: *S. astraea*. Detailed view of interior of valve with strutted processes and two labiate processes. – D: *S. hantzschii*. Interior view of a valve with marginal strutted processes, labiate process and

zwischen 8,7–8,8; während des Winters können diese Werte auf 7,6 sinken (Gelin 1971). Der Bysee hat schwankende pH-Werte zwischen 7 und 10. Interessant ist, dass dies nicht nur jahreszeitliche, sondern auch tiefenmässige Schwankungen sein können; d.h., dass bei Messungen von 0,2 m Tiefe der pH-Wert 9,8; bei 7 m Tiefe dagegen 7,5 sein kann (Enell, unveröffentl.).

Der See Vidöstern (57°5'N, 14°1'O), der Växjösee (56°52'N, 14°50'O) und der Södresee (56°51'N, 14°47'O) liegen alle im zentralen Teil des Südsmåländischen Hochlandes. Der Berggrund besteht aus Granit, die losen Erdlager aus hauptsächlich kalkarmer Moräne. Bis etwa zur Jahrhundertwende waren diese Seen alle oligotroph. Doch in jüngeren Jahren sind durch Verunreinigungen Veränderungen sichtbar. Der pH-Wert des Sees Vidöstern liegt zwischen 6,8–7,4 (Graneli & Leonardson 1974). Im Södresee liegen die pH-Werte während der Vegetationsperiode um 7,8–9,7 (Bengtsson et al. 1972, Bengtsson 1974). Der Växjösee hat pH-Werte, die über 7 liegen, während die pH-Werte im See Trummen unter 7 liegen (Digerfeldt 1972).

METHODEN

Die Sedimentproben wurden erst mit 10% HCl behandelt, mit destilliertem Wasser ausgewaschen, sodann mit 30% H_2O_2 gekocht. Die Planktonproben wurden teilweise unbehandelt analysiert, dann aber auch mit 30% H_2O_2 gereinigt. Alles Material ist in Clophenharz (Clophen W+Clophen A 60=5:1) d_n= 1,66 eingebettet. Die Raster-Elektronenmikroskop (SEM)- und Transmissions-Elektronenmikroskop (TEM)-Bilder wurden am Cambridge-Mikroskop am Zoologischen Institut der Universität Lund gemacht.

In der Beschreibung ist die von Anonymous (1975) vorgeschlagene Terminologie angewandt worden.

BESCHREIBUNG

Auf Grund der morphologischen Charaktere, wie Form und Areolierung der Schale und Art und Anzahl der Prozesse (Abb. 1 A–D, F) kann eine vorläufige Gruppierung der *Stephanodiscus*-Arten der südschwedischen Seen aufgestellt werden:

1. Arten mit flacher Schale 2
   Arten mit gewölbter Schale 3
2. Mehrere, regelmässige marginale Stützenfortsätze, ein zentraler Fortsatz, ein Lippenfortsatz, 2–3 Areolenreihen in jedem Streifen, vor jeder Rippe ein Stachel .... *S. hantzschii*
   Mehrere – scheinbar ohne Regelmässigkeit – marginale Stützenfortsätze, kein zentraler Fortsatz, ein Lippenfortsatz, 2–5 Areolenreihen in jedem Streifen, vor jeder Rippe ein Stachel .... *S. tenuis*
3. Mehrere, regelmässige marginale Stützenfortsätze, kein zentraler Fortsatz, ein Lippenfortsatz, 2 Areolenreihen in jedem Streifen – manchmal nur als kurze, marginale Rippen sichtbar – vor jeder 2. oder 3. Rippe ein Stachel .... *S. dubius*
   Mehrere, unregelmässig geordnete marginale Stützenfortsätze, kein zentraler Fortsatz, ein bis zwei Lippenfortsätze, 2–4 Areolenreihen in jedem Streifen, nicht vor jeder Rippe ein Stachel .... *S. astraea*

Stephanodiscus hantzschii Grun.

Hustedt 1928, S. 373, Fig. 194; Cleve-Euler 1952, I. S. 54, Fig. 71.

Abbildungen: 1 D, E, G–I, 2 B, 4.

Die Areolierung ist sehr undeutlich, man kann jedoch – auch bei kaum verkieselten Schalen – radiale Rippen erkennen (Abb. 1 I). Bei starker Auflösung im LM erkennt man ebenfalls Areolenreihen, die büschelartig zur Mitte geordnet sind (Abb. 1 G). Hustedt (1928) gibt eine Grösse von 8–20 μm. Cleve-Euler (1952) hat beim Typus keine Grössenordnung, jedoch hat sie bei der Varietät *delicatulus* A. Cl. eine Grössenordnung von 12–29 μm gefunden, die Varietät *pusillus* Grun. hat den Durchmesser von 4,5–12 μm. In den Planktonproben des Vombsees (1968–1974) hat *S. hantzschii* var. *hantzschii* eine Grösse von 4,5–8 μm.

Vorkommen. In jedem Frühjahr hat *S. hantzschii* ein Maximum (im März oder April, je nach der Eisschmelze), geht zurück, verschwindet aber nie ganz während des Jahres. Im Plankton des Södresees, sowie des Bysees hat auch *S. hantz-*

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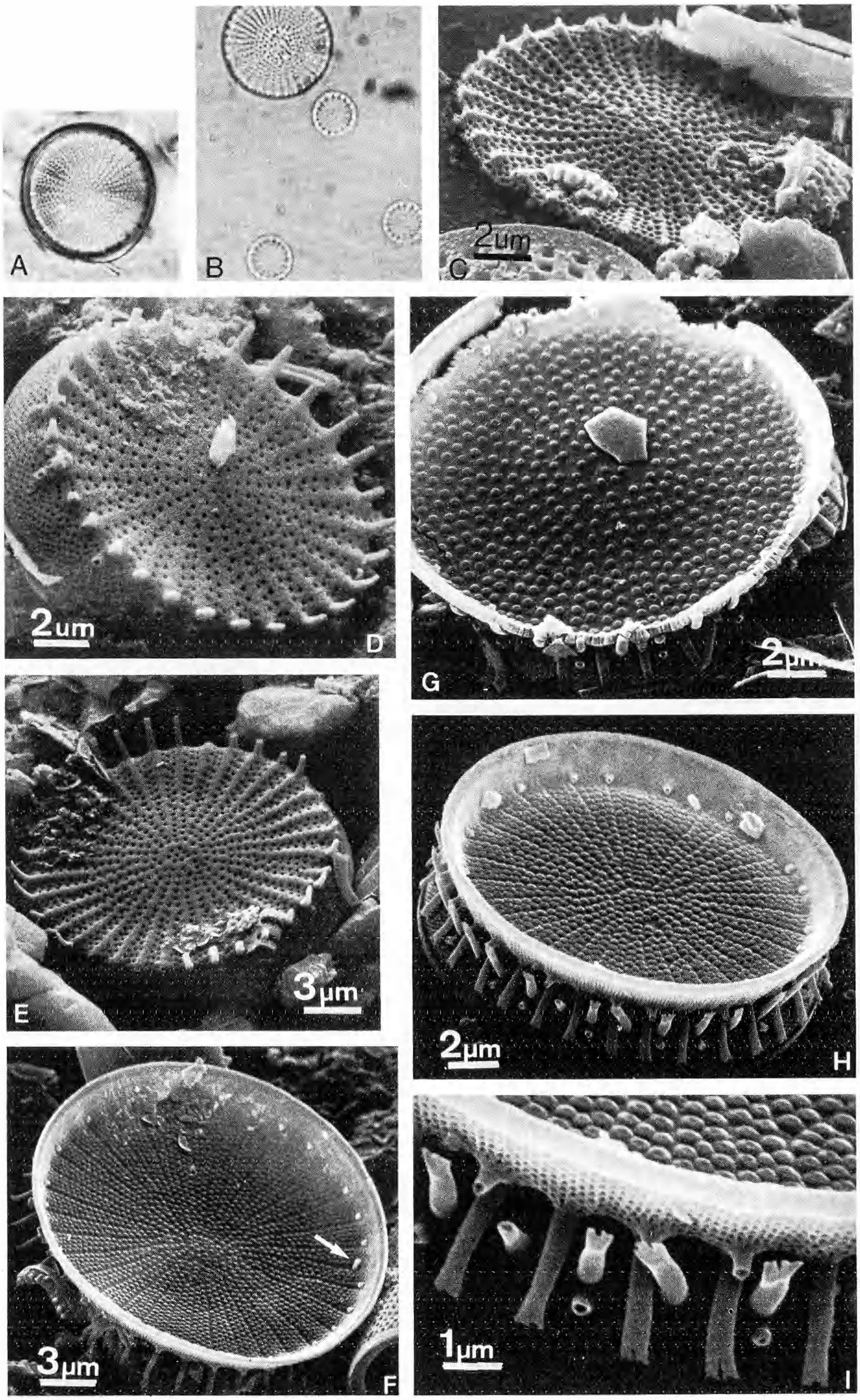
central process. Sediment from the lake Södresjö. – E: *S. hantzschii.* Exterior view of a valve. Sediment from the lake Södresjö. – F: *S. astraea.* Exterior view of valve with spines and external tube. – G: *S. hantzschii.* Exterior view of a valve. Sediment from the lake Södresjö. – H: *S. hantzschii.* Exterior view of valve with spines and central process. Processes not found beneath all spines. Recent sample from the lake Vombsjön. – I: *S. hantzschii.* Frustels and a valve, interior view. Spines and strutted processes. Plankton sample from the lake Bysjön.


A
B
C
2µm
2um
D
G
2µm
E
3µm
H
2µm
F
3µm
I
1µm

schii ihr Maximum im April. Hier ist sie etwas grösser (5–12 μm) und hat eine etwas engere, mehr hyaline Struktur. Im See Trummen findet man in dem obersten Sediment (Fe-Gyttja) – dem verunreinigten Teil – dieselbe kleine *S. hantzschii* wie im Vombsee.

Bemerkung. In dem Material Grunow's aus der Rabenhorst-Sammlung (Rabh.-Alg. Eur. N. 1104) sind wie aus Abb. 4 C und D hervorgeht, trotz der schwachen Verkieselung 2–3 Areolenreihen zwischen den Rippen zu erkennen. Auch die Stacheln, die vor jeder Rippe stehen sind deutlich zu sehen.

In einem Preparat (Ah 8, 3.4.33) vom Untersee nennt Hustedt die dort vorkommende *Stephanodiscus*-Art: eine kleine *S. hantzschii*. Diese ähnelt der im Vombsee und dem See Trummen gefundenen.

Meister fand 1910 im Zürichsee *S. hantzschii* var. *hantzschii* und var. *pusilla*. In seinem Preparat vom 28.4. 1910 haben beide das gleiche Aussehen: flache Schalen, deutliche Stacheln vor jedem Rippenende, grösstenteils nur 2 areolierte Reihen zwischen den Rippen, die oft sehr undeutlich zu sehen sind. Var. *hantzschii* und var. *pusilla* unterscheiden sich nur grössenmässig.

Auf Grund seines schweizerischen Materials – wo beide Grössen nie getrennt vorkommen – meint Meister (1912), dass eine Abtrennung der var. *pusilla* von var. *hantzschii* nicht gerechtfertigt sei.

In Proben aus Lappland (II/§m; 26.3. 1965; Pyhäjärvi), die Dr. Tynni freundlicher Weise zur Verfügung stellte, findet sich die etwas grössere var. *hantzschii* (Abb. 4 B).

Stephanodiscus tenuis Hust.

Hustedt 1939, S. 583–584, Fig. 3.

Abbildungen: 1 A, B, 2 A, C–I.

Hustedt (1939) gibt eine Grösse von 8–28 μm und 4–5 Areolenreihen.

Vorkommen. Diese Art kommt in allen Planktonproben und Sedimenten der untersuchten Seen vor. Ein genaues Maximum ist eigentlich nicht erkennbar – sie tritt mehr oder weniger regelmässig in allen monatlichen Proben (Vombsee 1968–1973, Södresee 1974) auf.

Bemerkung. Bei dem Vergleich mit Hustedts Material aus der Ochtum bei Bremen (Hust. Koll. Prep. Ah 49) ist eine deutliche Übereinstimmung mit der im Södresee gefundenen *S. tenuis* zu sehen.

Stephanodiscus dubius (Fricke) Hust.

Hustedt 1928, S. 367–368, Fig. 192; Cleve-Euler 1952: I, S. 52–53, Fig. 69.

Abbildungen: 3 E–G, 5.

Hustedt (1928) gibt für *S. dubius* eine Grösse von 10–25 μm an, Cleve-Euler (1952) 10–30 μm.

Vorkommen. Im Plankton des Sees Vidöstern ist *S. dubius* im Mai vertreten. Bei den monatlichen Planktonproben des Vombsees findet man sie in allen Proben – im Herbst werden zwar die Formen kleiner.

Abb. 2. A: Aus einer Sedimentprobe des Södresees. *S. tenuis*. LM. – B: Planktonprobe vom April 1970 aus dem Vombsee. *S. hantzschii*. LM. – C: *S. tenuis*. Aussenansicht einer Schale mit 3–4 Areolenreihen. Sediment aus dem Södresee. – D: *S. tenuis*. Aussenansicht einer Schale mit langen und kurzen Stacheln und 2 Areolenreihen zwischen jeder Rippe. Sediment aus dem Södresee. – E: Dto., aber mit 3 Areolenreihen zwischen jeder Rippe. – F: *S. tenuis*. Innenansicht einer Schale mit 4–5 Areolenreihen, den Stützenfortsätzen und dem Lippenfortsatz. Sediment aus dem Södresee. – G: Dto., mit 2–3 Areolenreihen. Sediment des Sees Trummen. – H: *S. tenuis*. Zwei benachbarte Schalen, die mit Hilfe der Stacheln aneinanderhäften. Plankton des Södresees. – I: Dto. Detailbild. – A–B: Schale 20 μm. – LM-Photo und Prep.: Hannelore Håkansson.

Fig. 2. A: Sediment sample from the lake Södresjön. *S. tenuis*. LM. – B: Plankton sample from the lake Vombsjön, April 1970. *S. hantzschii*. LM. – C: *S. tenuis*. Exterior view of a valve with 3–4 rows of areolae. Sediment from the lake Södresjön. – D: *S. tenuis*. Exterior view of a valve with long and short spines and 2 rows of areolae between every costa. Sediment from the lake Södresjön. – E: Do, but with 3 rows of areolae between every costa. – F: *S. tenuis*. Interior view of a valve with 4–5 rows of areolae, strutted processes and labiate process. Sediment sample from the lake Södresjön. – G: Do, but with only 2–3 rows of areolae. Sediment sample from the lake Trummen. – H: *S. tenuis*. Two adjacent valves kept together with the help of spines. Plankton sample from the lake Södresjön. – I: Do, in detail. – A–B: Scale 20 μm.

Stephanodiscus astraea (Ehr.) Grun.

Hustedt 1928, S. 368–370, Fig. 193; Cleve-Euler 1952: I, S. 53, Fig. 70; van der Werff & Hulst 1961, C.A I c. 13.

Abbildungen: 1 C, F, 3 A–D, 5.

Hustedt schreibt (1928), dass sie 30–70 μm gross sind, Cleve-Euler (1952) nennt die Grössenordnung 8–70 μm. Hustedt möchte die kleinere Diatomé (8–30 μm) gern als var. *minutulus* („*minutula*") bestehen lassen, da sie zuweilen isoliert und massenhaft vorkommt. Cleve-Euler hat als Unterschied zwischen *S. astraea* var. *astraea* und var. *minutulus* den unterschiedlichen Verlauf der Areolenreihen angegeben. Bei der Varietät *astraea* gehen die Areolenreihen gegen das Zentrum in Einzelreihen über und bei var. *minutulus* bleiben sie unsortiert. Van der Werff & Hulst (1961) geben in ihren Abbildungen eine genaue Abbildung von *S. astraea* var. *astraea* – nur eben kleiner.

Nach Hendey (1964) müsste diese Art *S.*

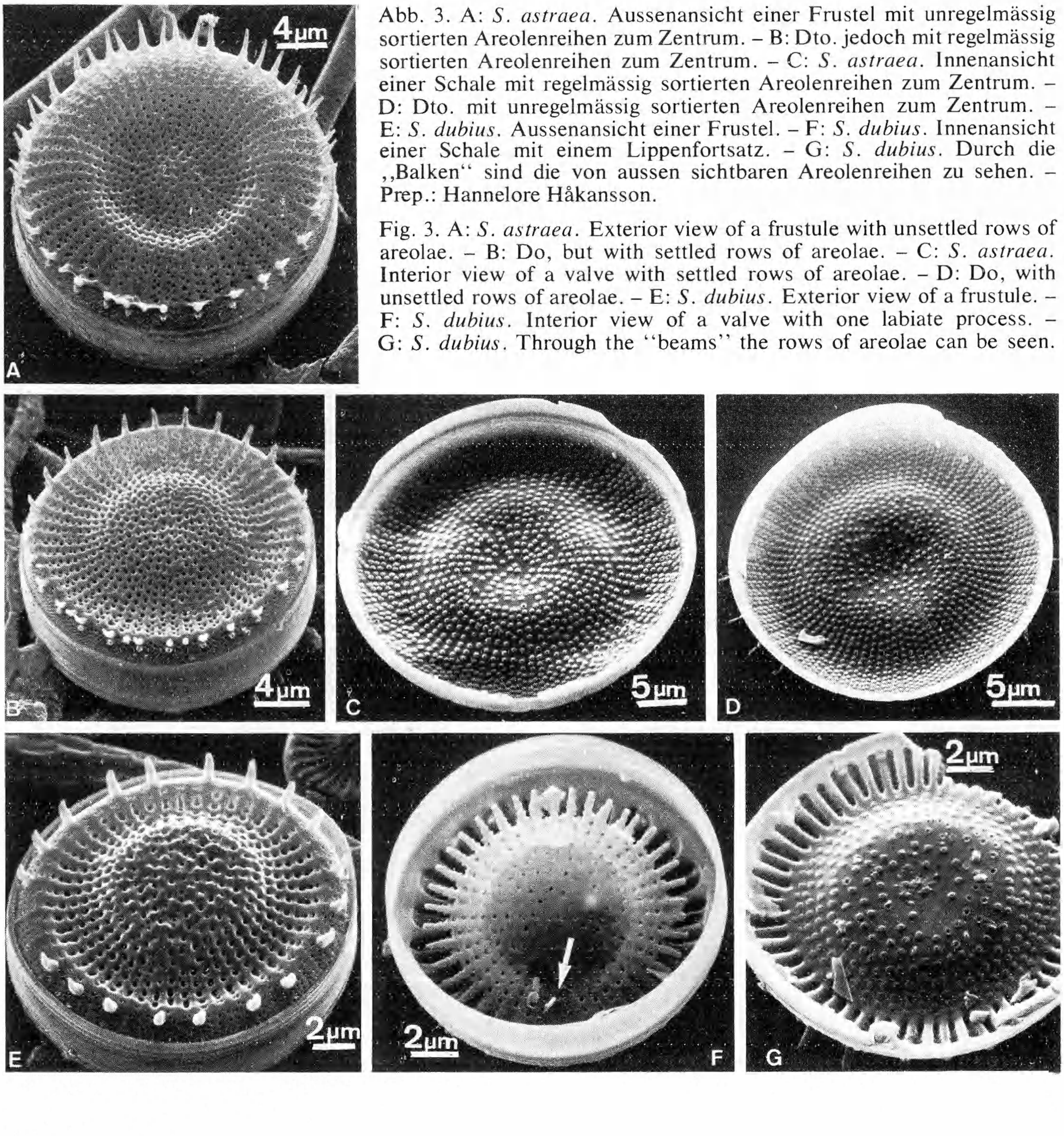


Abb. 3. A: *S. astraea*. Aussenansicht einer Frustel mit unregelmässig sortierten Areolenreihen zum Zentrum. – B: Dto. jedoch mit regelmässig sortierten Areolenreihen zum Zentrum. – C: *S. astraea*. Innenansicht einer Schale mit regelmässig sortierten Areolenreihen zum Zentrum. – D: Dto. mit unregelmässig sortierten Areolenreihen zum Zentrum. – E: *S. dubius*. Aussenansicht einer Frustel. – F: *S. dubius*. Innenansicht einer Schale mit einem Lippenfortsatz. – G: *S. dubius*. Durch die „Balken" sind die von aussen sichtbaren Areolenreihen zu sehen. – Prep.: Hannelore Håkansson.

Fig. 3. A: *S. astraea*. Exterior view of a frustule with unsettled rows of areolae. – B: Do, but with settled rows of areolae. – C: *S. astraea*. Interior view of a valve with settled rows of areolae. – D: Do, with unsettled rows of areolae. – E: *S. dubius*. Exterior view of a frustule. – F: *S. dubius*. Interior view of a valve with one labiate process. – G: *S. dubius*. Through the "beams" the rows of areolae can be seen.

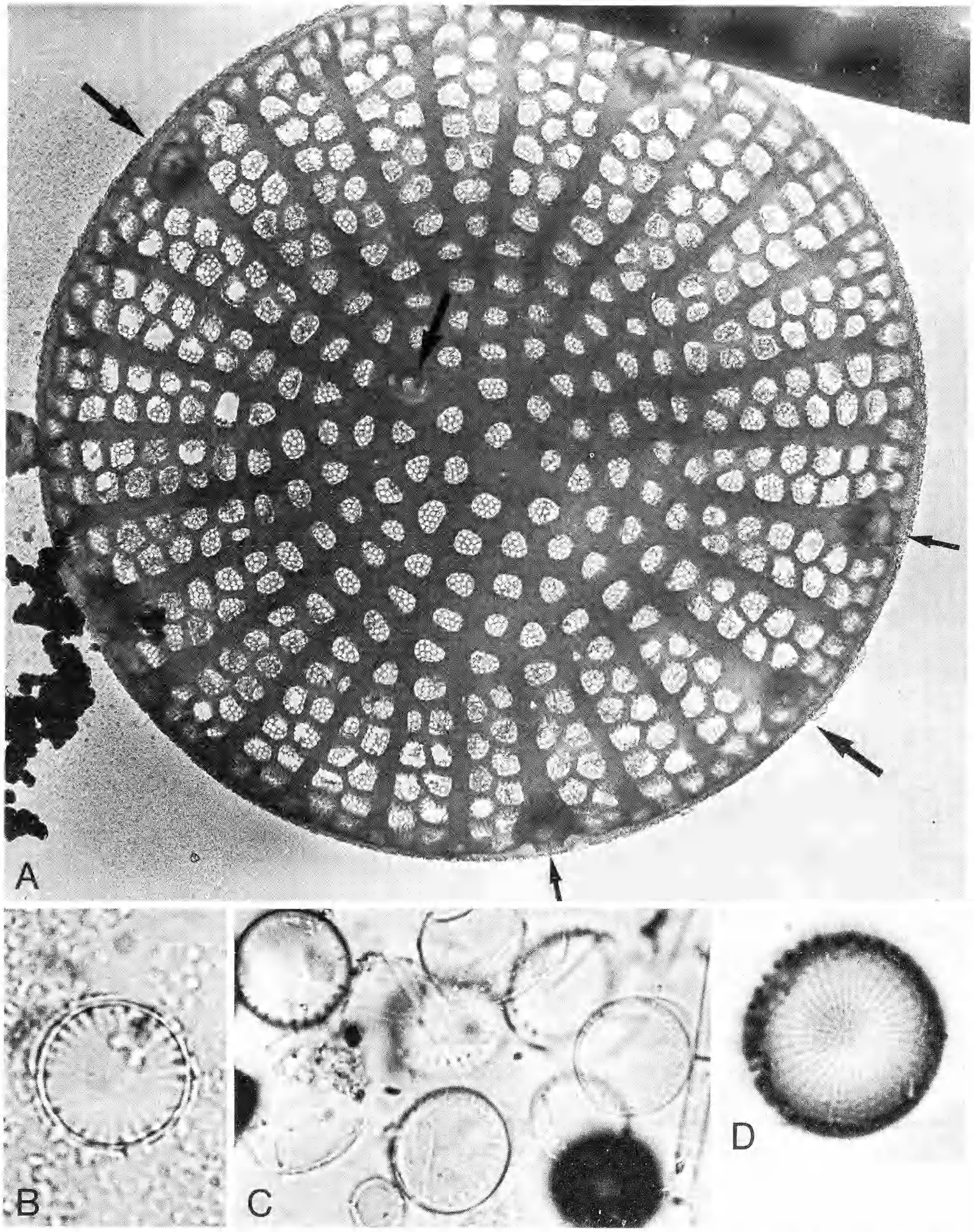


Abb. 4. *Stephanodiscus hantzschii.* A: TEM 22300 x. – B: Dr. Tynnis Material. LM. – C–D: Material aus der Rabenhorst Sammlung. Material from the Rabenhorst Collection. LM. – B–D: Schale 20 µm. Scale 20 µm. – LM-Photo und Prep.: Hannelore Håkansson.

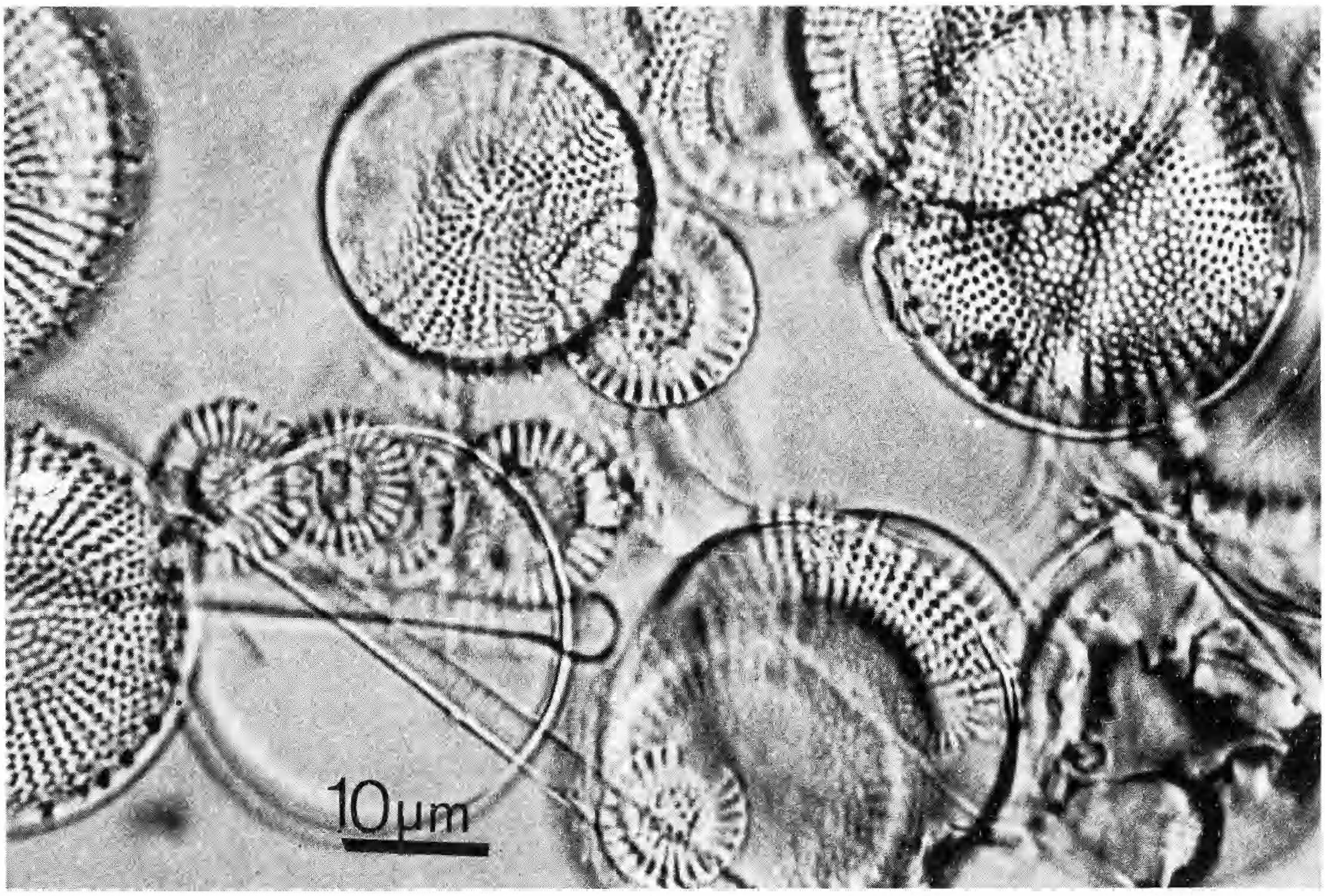


Abb. 5. Eine Planktonprobe aus dem Vombsee mit *Stephanodiscus astraea* und *S. dubius*. LM. – Plankton sample from the lake Vombsjön with *S. astraea* and *S. dubius*. LM.

rotula (Kütz.) Hendey heissen. Wie aus der Beschreibung (op.cit.) hervorgeht, hat *S. rotula* vor jeder Rippe einen Stachel, was *S. astraea* jedoch nicht hat.

Vorkommen. Vereinzelt kommt *S. astraea* var. *astraea* in allen Proben vor – oft handelt es sich dabei um die kleineren Formen (um etwa 20–25 μm). Im Plankton des Vombsees sind die grösseren Formen – etwa 35–63 μm – während des ganzen Jahres zu verzeichnen.

Bemerkung. Da bei dem untersuchten Material *S. astraea* mit Grössen zwischen 8 und 70 μm mit sortierten und unsortierten Areolenreihen zum Zentrum (Abb. 3 A–D) mehr oder weniger regelmässig in allen Proben gefunden wurden, scheint eine Abtrennung der var. *minutulus* von var. *astraea* nicht gerechtfertigt zu sein.

Das Original-Material von *S. astraea* var. *intermedius* Fricke (A. S. Atlas Taf. 225, Fig. 37–39, 1901) konnte leider nicht zum Vergleich erhalten werden. In Helmcke & Krieger (1964) Taf. 421, wird eine *S. astraea* var. *intermedius* abgebildet, die sich – wie aus der Beschreibung hervorgeht – nur durch Grösse und dichtere Struktur von *S. astraea* unterscheiden soll. Sie hat ausserdem vor jeder Rippe einen Stachel.

DISKUSSION

Nach den hier gemachten Beobachtungen, ist es trotz allem nicht einfach eine sichere Artbestimmung zu machen. Viele Dinge scheinen noch weiteren Untersuchungen zu bedürfen; so z. Beisp.:

Sind die Fortsätze und Lippenfortsätze nur an einer Schale oder an beiden? Diese Frage wird gerechtfertigt, wenn man die Taf. 21 und 22 und Taf. 116 in Helmcke & Krieger (1953–54) mit den Taf. 751 und 752 (1974) vergleicht. Ersteren fehlt der mittlere Prozess.

In wieweit ist eine Variation dieser Fortsätze und Lippenfortsätze betr. Anzahl und Aussehen möglich? In Helmcke & Krieger (1974), Taf. 751, 752, und 753 sind flache und gewellte Frusteln von *S. hantzschii* abgebildet. Die flachen – und auch kleineren Formen – haben einen zentralen Prozess, die gewellten – und grösseren Formen – haben mehrere zentrale Prozesse. (Taf. 751 und 752 zeigen eine deutliche Übereinstimmung mit Abb. 4 A).

Die mehr oder weniger starke Verkieselung (vgl. Abb. 1 E, G, I) und damit die Deutlichkeit der Areolierung zu kennzeichnen, ist von anderen Faktoren abhängig und kann nicht das Kennzeichen einer Art sein. Im Bysee verändert sich gerade die Deutlichkeit der Areolierung innerhalb kurzer Zeit. Hustedt (1957) meint zwar, dass gerade die Zartheit der Struktur das unterscheidende Merkmal zwischen *S. hantzschii* und *S. subtilis* (van Goor) A. Cleve-Euler sei. Leider war es nicht möglich das Material von van Goor zum Vergleich zu erhalten.

Die Länge oder Dicke der Stacheln kann auch als ausschlaggebendes Merkmal nicht verwandt werden, da kürzere oder längere Stacheln an ein und derselben Schale vorkommen können. Dieses scheint von chemischen oder mechanischen Abnutzungen anhängig zu sein (Abb. 2D–E).

Dass 6 Jahre hintereinander im Plankton des Vombsees nur die kleine *S. hantzschii* massenhaft im Frühjahr auftritt, dafür hat Nipkow bei seiner Untersuchung im Zürichsee (1921) eine Erklärung gegeben. Nach ihm vollzieht sich im Zürichsee alle 2–8 Jahre ein Verjüngerungsprozess. Dabei kann der Schalendurchmesser bis zu 28 μm ansteigen. Leicht wäre es, wenn *S. tenuis* mit 2–3 Areolenreihen als Verjüngerungsschalen dieser kleinen Art angesehen werden könnte. Hier fehlt jedoch der mittlere Fortsatz.

Nicht weniger wichtig ist wohl die Frage, welchen Einfluss die verschiedenartigen Gewässer auf die Entwicklung und das Aussehen der einzelnen Diatomeen haben. Beruht z. Beisp. der geringe Unterschied zwischen *S. hantzschii* des Vombsees und des Bysees darin dass der Bysee einen grösseren Phosphorgehalt hat (Cronberg und Enell unveröffentl.)?

Von grosser Bedeutung ist daher das Studium des Aussehens der einzelnen Diatomeen unter verschiedenen Milieuverhältnissen, damit sie als Indikator z. Beisp. in der Geologie angewandt werden können.

DANK

Das Material wurde zum grössten Teil freundlicher Weise vom Limnologischen Institut zur Verfügung gestellt. Hier möchte ich besonders L. Bengtsson, J. Berthilsson, M. Enell und nicht zuletzt G. Cronberg nennen. Letztere hat mir mit Bildern und vielseitigem Vergleichsmaterial geholfen. Allen möchte ich herzlich danken. Prof. B. Berglund, Doc. G. Digerfeldt, Doc. M.-B. Florin, Lektor N. Foged, Dr. U. Miller und dem verstorbenen Apotheker M. Møller möchte ich für die gebenden Diskussionen und Hilfe danken. Dr. G. Hasle sage ich besonders Dank für die kritische Durchsicht des Manuskriptes und ihre wertvollen Ratschläge. Die Elektronenmikroskopbilder wurden am Zoologischen Institut aufgenommen, wo ich für die gute Zusammenarbeit mit Folke Larsson und Birgitta Sandström danken möchte. Herrn Prof. Thomas und Prof. Müller, Zürich, möchte ich meinen Dank sagen für die Freundlichkeit Meister's Sammlung einsehen zu dürfen. Ganz besonderen Dank möchte ich auch Herrn Dr. R. Simonsen am Amt für Meeresforschung in Bremerhaven sagen, der mir die Möglichkeit gab einige Typen einzusehen und zu photographieren.

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Ipomoea indica taxonomy: a tangle of Morning Glories

F. R. Fosberg

Fosberg, F. R. 1976 05 06: Ipomoea indica taxonomy: a tangle of Morning Glories. *Bot. Notiser 129*: 35–38. Stockholm. ISSN 0006-8195.

The correct name of one of the widespread tropical wild and cultivated Morning Glories is determined to be *Ipomoea indica* (Burm.) Merrill, based on *Convolvulus coeruleus* Rumphius. This is lectotypified by *Convolvulus indicus flore violaceo* Besler, Hort. Eyst. Or. 13 Fol. 8 figure 2, 1613. Three varieties of this species are distinguished and the combination, *Ipomoea indica* var. *acuminata* (Vahl) Fosberg, made.

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Two of the common large-flowered, often cultivated tropical *Ipomoea* species are characterized by lanceolate or lance-acuminate sepals about 1.5 to 2.5 cm long. They are readily distinguished, though most of the characters that separate them are really not very constant.

One of them is *Ipomoea nil* (L.) Roth, with, as constant features, lanceolate but not or only slightly acuminate sepals with stiff straight patent hairs on the basal parts of the sepals. It usually but not always, has prominently trilobate leaves. There have been rather few difficulties with the nomenclature of *I. nil* except for occasional confusion with the other species under discussion.

The second species is commonly called *Ipomoea indica* (Burm.) Merrill, *Ipomoea congesta* R. Br., *Ipomoea insularis* (Choisy) Steud., or, if interpreted very broadly, *Ipomoea acuminata* (Vahl) R. & S. or *I. cathartica* (Poir.) Steud.

I first learned, in Hawaii, to call this plant *Ipomoea insularis*. Then, mainly on the basis of Merrill's authority but also on a very cursory examination of the plate that it seemed ultimately to rest on, that of *Convolvulus indicus flore violaceo* Besler, Hortus Eystettensis Classis Aestivalis Ordo 13 Fol. 8, II, 1613, I took up *I. indica* (Burm.) Merr.

In all of my Micronesian work I have used *I. indica* without serious question, in the face of more general use of *Ipomoea congesta* R. Br. on the strength of van Ooststroom's authority. He rejected *I. indica* as of doubtful typification, but without a detailed discussion.

In recent years van Ooststroom has taken up *Ipomoea acuminata* (Vahl) R. & S. 1819 (non R. & P. 1799) for this species, advising E. H. Walker (in litt.) that this was the correct and older name, acceptable since the earlier *I. acuminata* R. & P. is illegitimate. I strongly questioned this, since an earlier homonym prevents the use of a later one even though the earlier one is illegitimate (ICBN Art. 64). However, on the basis of this I have taken occasion to re-examine the entire matter before publication of the Convolvulaceae for the Flora of Micronesia, especially since all of the recent and current principal experts on Convolvulaceae reject *Ipomoea indica*. They do not question the priority of the epithet *indica,* but do question its application to the plant in question and whether it can be satisfactorily typified (van Ooststroom 1940 pp. 500–503, O'Donell 1959 pp. 134–139, Verdcourt 1957 p. 231, Austin 1975 a p. 192, Powell 1975, Austin 1975 b).

Merrill, in taking up *Convolvulus indicus* Burman and transferring it to *Ipomoea* merely said that Rumphius' *Convolvulus coeruleus* is the entire basis of the Burman species and that its description fits the plant in question better than it does the other possibility, *Ipomoea nil.*

Examination of the Rumphian treatment shows that Rumphius did not prepare a plate of this species, saying that it is already well enough known. His brief description is not at all diagnostic and does not provide any basis for applying the name to any particular species. However, the protologue also includes five abbreviated references to earlier publications:

"H. Eyst. Aest. Or. 13 F 2.
Boerh. Ind. part. I p. 246.
Weinmannus in opera sua Botanico ... Tab. 414, 415.
Dillenius, Hort. Eltham. 96, T. 80, f. 91, T 82, 83, 84.
Hortus Cliffortianus p. 67."

Of these, the Boerhaave Index altera part. I p. 246 gives only a polynomial and citations, no plate. Linnaeus, in Hortus Cliffortianus, likewise gives no plate of this species but gives a long list of citations of earlier works.

The Weinmannus plates portray a Morning Glory with solitary flowers on long pedicels which suggests precisely no plant familiar to me.

The four Dillenius plates cited by Rumphius have been considered by Verdcourt (1957 pp. 232–233) and, according to him, also by van Ooststroom, in the typification of several *Ipomoea* species of this relationship. Of these plates, the first cited, 80 fig. 91, could be the species under consideration so far as the vegetative parts and the calyx are concerned. However, its corolla is not at all that of this species, being deeply 5-lobate with dentate lobes. Moreover, it has been suggested by van Ooststroom (according to Verdcourt, loc. cit.) as a lectotype for *Convolvulus nil* L., which it resembles perhaps as much. It is clearly not a good choice as lectotype for the Rumphian or Burman species.

Plate 82 fig. 94 looks like what is usually called *Ipomoea hederacea* Jacq. Plate 83 fig. 95 is a reasonable likeness of *Ipomoea obscura* Ker-Gawler. Verdcourt suggests the selection of Plate 84 fig. 97 as lectotype of *Convolvulus purpureus* L. and it does look much like what is cultivated under that name.

None of the Dillenius plates seems suitable as lectotype for *Convolvulus coeruleus* Rumphius and they need not be considered further.

Finally, in the Besler, Hortus Eystettensis plate, rather imperfectly cited, figure 2 is Besler's *Convolvulus indicus flore violaceo* which is our widespread Indo-Pacific plant with little doubt, contrasted on the same plate with an excellent figure of *Ipomoea nil,* with the terminal parts of the two somewhat intertwined. The plant under discussion is well portrayed, with entire leaves, large corollas, the only discrepancy being in the looser, fewer-flowered inflorescence. The sepals are precisely those of our plant. The stigmas are two, globose. The description, also, fits except for the violet color, and the color, as seen on various Pacific Islands, does become violet to pink in the afternoon. The pubescence is described as "tenuiter hirsuta," the seeds as "terno vel quaterno semino nigro subrotundo parum anguloso." It is also stated "A nullo ad huc descriptus."

As no-one seems to have chosen a lectotype for *Convolvulus indicus* Burm. out of the elements available in the protologue of *Convolvulus coeruleus* Rumph., I hereby designate *Convolvulus indicus flore violaceo* Besler, Hort. Eyst. Aest. Or. 13 Fol. 8 figure 2, 1613. This will preserve Merrill's use of *Ipomoea indica* (Burm.) Merr. for the widespread Indo-Pacific species, and end the confusion in the identity of this species.

The names *Ipomoea congesta* R. Br. and *Ipomoea insularis* (Choisy) Steud. seem also to apply to this same plant, but are later taxonomic synonyms.

The name *Ipomoea acuminata* (Vahl) R. & S. remains to be considered. Two questions arise. Is its basionym illegitimate as a later homonym of *Convolvulus acuminatus* R. & P.? If not, is its type conspecific with the Indo-Pacific plant discussed above?

(1) Ruiz and Pavon, Fl. Per. et Chil. 2: p. 11, Ic. CXX, fig. b, 1799, describe their plant in great detail and illustrate it very well, with analyses. In the text on page 11 it is called *Ipomoea angulata* Ortega, with the note under the reference to the plate "acuminatae nomine." The title of the figure, Ic. CXX fig. b, is *Ipomoea acuminata*. The figure is of a small-flowered plant with a rather salverform corolla that according to the description has a scarlet limb, "limbus coccineus."

It seems clear that when the plate was drawn Ruiz and Pavon intended to call their plant *Ipomoea acuminata,* but that by the time the text was prepared they decided that it had already been named *Ipomoea angulata* by Ortega. Hence they did not accept their *Ipomoea acuminata,* though they did not remove it from the plate. A name not accepted by its authors is not validly published (Art. 34 (1)), so for nomenclatural purposes does not exist. Hence it is, technically, not an earlier homonym of *Ipomoea acuminata* (Vahl) Steud.

(2) *Convolvulus acuminatus* Vahl was based on a plant collected by West on St. Croix, Virgin Islands, West Indies. Its description calls for a plant with trilobed glabrous leaves, the stems and inflorescences glabrous or almost so. Fortunately, though I have not seen the West specimen, there are in the U.S. National Herbarium two specimens from St. Croix, Ricksecker 103 and 220, that precisely fit the Vahl description. There are also a large series of West Indian specimens that are the same except that there is considerable variability in the lobing of the leaves. Most are lobed, but to varying degrees, some entire or nearly so. The plant does resemble very strongly the Indo-Pacific *I. indica* except that the latter is almost always notably appressed pilose. A local population, var. *hosakae* Fosb. on Truk in the Caroline Islands, is almost glabrous with hastate-trilobate leaves and a more than usually open inflorescence. The lobing of the leaves of *Ipomoea acuminata* (Vahl) R. & S. is almost exactly as in *Ipomoea nil* (L.) Choisy, with no tendency to a hastate base.

It would be convenient to maintain the American population as a separate species, but the separation is weak, and none of the differences are really constant. So the best course seems to be to treat this and *I. indica* s. str. as varieties of one species. Neither is complex enough to justify setting up subspecies (Fosberg 1942 pp. 154–157).

Therefore the taxonomy and essential synonymy of *Ipomoea indica* are as follows. Specimens, except the types, are not cited as this paper is essentially on nomenclature.

Ipomoea indica (Burm.) Merr.

Merrill, Int. Rumph. Herb. Amboinense 445, 1917; Fosberg, Micronesica 2: 151, 1967.

Convolvulus indicus flore violaceo Besler, Hort. Eystett. Aest. Ord. 13, Fol. 8, II, 1613.

Convolvulus coeruleus Rumphius, Herb. Amb. 5: 432, 1747.

Convolvulus indicus Burm., in Rumph. Herb. Amboinense, Index Universalis 7: (6), 1755.

Convolvulus roseus Mill., Gard. Dict. ed. 8, no: 18, 1768 (non *Ipomoea rosea* Choisy, 1845).

Convolvulus acuminatus Vahl, Symb. Bot. 3: 26, 1794.

Ipomoea congesta R. Br., Prodr. 485, 1810; van Ooststroom, Blumea 3: 500–503, 1940; O'Donell, Lilloa 29: 134–139, 1959.

Ipomoea cathartica Poir. in Lam., Encycl. Suppl. 4: 633, 1816; Britt. & Wils., Sci. Surv. P. R. & Virgin Is. 6: 112, 1925.

Ipomoea acuminata (Vahl) R. & S., Syst. Veg. 4: 228, 1819.

Pharbitis insularis Choisy, Mém. Soc. Phys. Genève 6: 439, 1833.

Ipomoea insularis (Choisy) Steud., Nom. Bot. ed. 2, 1: 817, 1840.

Ipomoea leari Knight ex Paxton, Mag. Bot. 6: pl. 267, 1839.

Twiner, leaves cordate, entire to prominently trilobate, peduncles axillary, exceeding leaves, with a small dichasial cluster of subsessile to pedicellate flowers at summit; bracts linear to lanceolate or ovate-lanceolate; flowers diurnal; sepals lanceolate, caudate acuminate, to 2.5 cm long; corolla narrowly campanulate, limb flaring, about 8 cm long; stamens unequal, included in throat; stigmas 2, globose; capsule globose, seeds black, glabrous.

Pantropical, usually a coastal plant, less frequently inland and then up to some elevation especially on limestone.

Ipomoea indica (Burm.) Merr. var. **indica**

Type: Besler, Hort. Eyst. Aest. Ord. 13, Fol. 8, II, 1613.

Ipomoea congesta R. Br. loc. cit. – Type: Endeavour River, Banks & Solander in 1770 (BM).

Ipomoea insularis (Choisy) Steud., loc. cit. – Type: syntypes from various Pacific islands, including Marianas and Sandwich Is, coll. Gaudichaud, not lectotypified.

Plant generally notably appressed pilose, leaves mostly entire, cordate at base, flowers blue, turning violet and pink in afternoon.

A white form is known from Guam and the Ryukyus, f. *albiflora* Stone, Micronesica 2: 139, 1967. Type: Marianas Is: Guam: Harmon Village, Stone 4729 (GUAM).

Indo-Pacific, from at least as far west as Ceylon to Tahiti and Hawaii, north to Ryukyu Is and Marianas. A practically indistinguishable form occurs from Mexico to Brazil and Argentina, differing principally in the more commonly lobed leaves. There seems no satisfactory way to distinguish it and it is here considered to belong to var. *indica*.

Ipomoea indica var. **hosakae** Fosberg

Fosberg, Micronesica 2: 151, 1967. – Type: Caroline Is, Truk: Moen Island, Mt Takeum, 700 ft, Hosaka 2713 (US).

Leaves essentially glabrous, strongly hastate, trilobate; inflorescence rather open, pedicels 1–1.5 cm long.

So far as known, a local population endemic to the Truk group of islands in the central Carolines.

Ipomoea indica var. **acuminata** (Vahl) Fosberg, comb. nov.

Convolvulus acuminatus Vahl, Symb. Bot. 3: 26, 1794. – Type: Coll. West, St. Croix, not seen.

Ipomoea cathartica Poir. in Lam., Encycl. Suppl. 4: 633, 1816. – Type: Coll. Poiteau, Santo Domingo, not seen.

Ipomoea acuminata (Vahl) R. & S., Syst. Veg. 4: 288, 1819.

Plant nearly or essentially glabrous; leaves cordate at base, blade usually deeply trilobed, lobes acuminate; sepals glabrous.

Throughout the West Indies, Mexico and Central America, northern South America, not sharply separable from var. *indica*.

There seems to be no varietal epithet available that clearly applies to this population. *Ipomoea jamaicensis* var. *glabrata* Griseb. (1862 p. 474) is cited by Britton and Wilson (1925 p. 112), in the synonymy of *I. cathartica* Poir. (=*I. acuminata* (Vahl) R. & S.). Grisebach based this on Descourtilz (1822 t. 137). Examination of this plate, courtesy of C. R. Long, librarian of the New York Botanical Garden, shows that it is an entirely different plant, probably actually a glabrate variety of *I. jamaicensis* with a swollen corolla tube.

Ipomoea indica var. *variabilis* (Schlecht. & Cham.) L. Wms. (*Convolvulus variabilis* Schlecht. & Cham. 1830 p. 116) is said to belong to this species, but all but one of the sheets so determined by Williams in the U.S. National Herbarium seem to be *Ipomoea nil* (L.) Roth, the other being probably a form of var. *acuminata* with somewhat hastate leaves. Study of the original description of *C. variabilis* shows it not to have the characteristic large lanceolate sepals of the species under discussion. This says in part, "Sepala elliptica, breviter mucronato-acuminata, subglabra; exterio ad marginem ciliis longis patentibus instructa." With this kind of calyx it probably belongs to neither *Ipomoea indica* nor *I. nil*.

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The synflorescence of the Marantaceae

Organization and descriptive terminology

Lennart Andersson

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Using Troll's terminology the flowering shoot system of the Marantaceae is described as a polytelic synflorescence. The different structural units are pointed out and a descriptive terminology is proposed on a topographical basis. The florescence component is interpreted as a more or less complex aggregate of monochasial cymes with the support mainly of comparative morphology. Some earlier interpretations of the structure of the florescence component are briefly reviewed.

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Using the term in its widest sense the inflorescences of the Marantaceae have mostly been termed panicles or panicles composed of racemes. In revising the genus *Ischnosiphon* Koern., I have found that these terms do not serve to adequately express the variation in habit which is often of great taxonomic importance.

While inflorescences of the Marantaceae are fundamentally quite uniform almost every structural element is subject to major or minor variation at different taxonomic levels. This variation has already been used a great deal in the taxonomic treatment of the family (see e.g. Schumann 1902, Loesener 1930), but a precise terminology based on a distinction of the structural elements and their homologies would greatly extend the possibilities.

The aim of this paper is to outline the fundamental features of the marantaceous inflorescence and to propose a descriptive terminology. I have found the terminology of Troll (1964 pp. 145 et seq.) suitable for this purpose (for a summary in English see Weberling 1965) but have tried to change the terminology used in earlier taxonomic literature as little as possible. I have included a brief discussion of terms used by previous authors.

MATERIAL AND METHODS

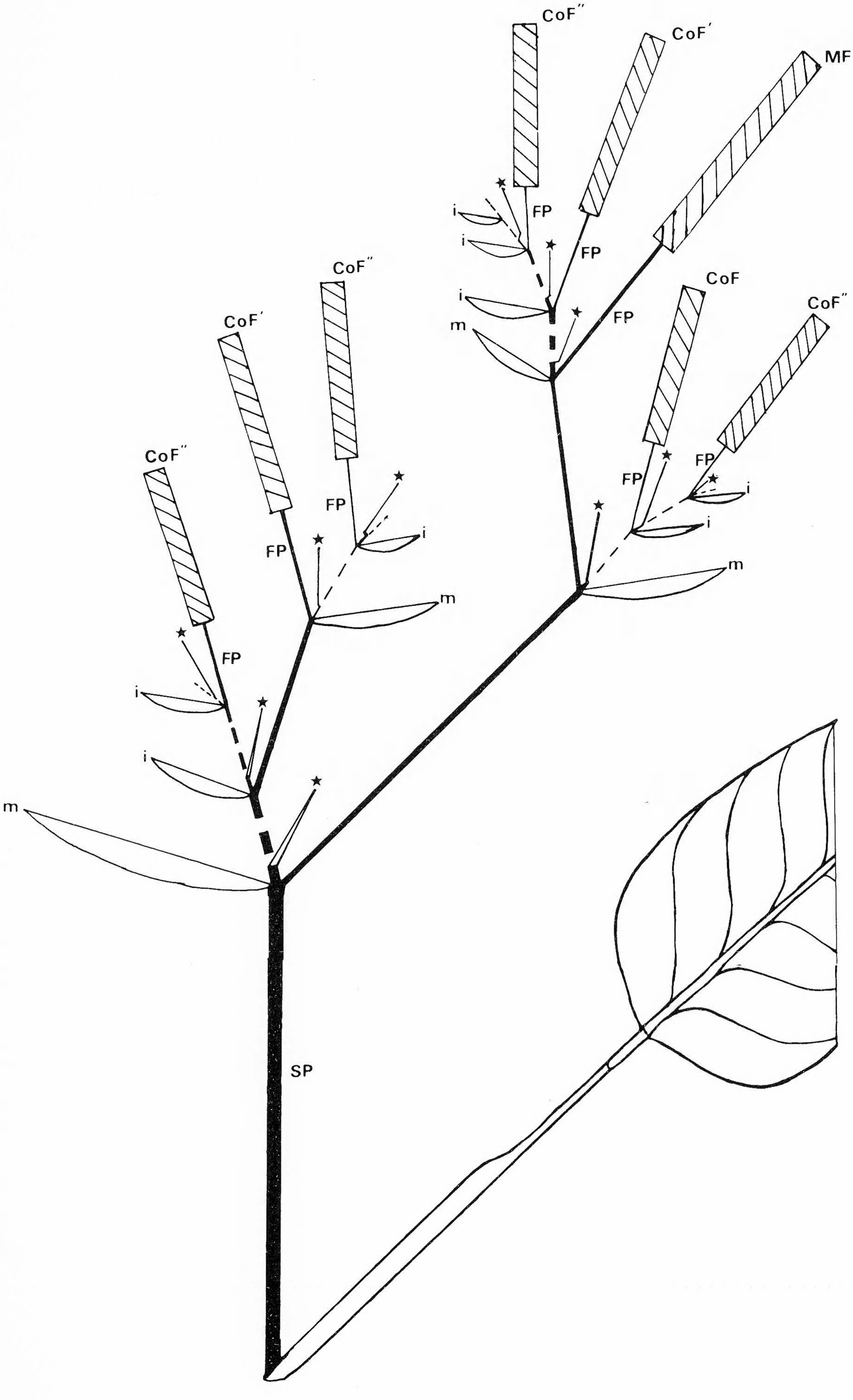
My experience of the Marantaceae lies mainly with the South American genera, in particular *Ischnosiphon* Koern. but also *Calathea* G. F. W. Mey., *Maranta* L., *Monotagma* Schum., *Stromanthe* Sond. and *Thalia* L.

The major branching system has been studied in herbarium specimens and live material dissected in the field. All neotropical species represented in S have been investigated.

Florescence components have been studied under a dissection microscope using softened herbarium material and material collected in the field and preserved in alcohol or Karpeschenko's fluid. I have studied c. 500 florescence components of *Ischnosiphon* and material from one or a few plants of each of the species in other genera included in the investigation, viz. *Calathea* (4 spp.), *Cominsia* Hemsl. (1 sp.), *Ischnosiphon* (c. 20 spp.), *Maranta* (3 spp.), *Monophrynium* Schum. (1 sp.), *Monophyllanthe* Schum. (1 sp.), *Monotagma* (3 spp.), *Myrosma* L. fil. (1 sp.), *Phrynium* Willd. (1 sp.), *Sarcophrynium* Schum. (1 sp.), *Stromanthe* (1 sp.) and *Thalia* (1 sp.).

Serial sections of young florescences of *Ischnosiphon arouma* (Aubl.) Koern. and *Monotagma laxum* (P. & E.) Schum. have been prepared from material collected in the field and fixed in Karpeschenko's fluid.

The vascularization of the florescence component was studied in some plants after treating for 5–30 minutes with hot concentrated lactic acid (Sporne 1948).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MAJOR BRANCHING OF THE INFLORESCENCE

The most suitable species for study of the major branching of the marantaceous inflorescence are some large species of *Calathea* (e.g. *C. insignis* Peters. and *C. casupito* (Jacq.) G. F. W. Mey.), many species of *Ischnosiphon* (e.g. *I. leucophaeus* (R. & P.) Koern., *I. arouma* and *I. obliquus* (Rudge) Koern.) and the small genus *Pleiostachya* Schum. The inflorescences of these species are sufficiently branched to demonstrate the principles but are still lax enough not to obscure them. The description below is based on a specimen of *Ischnosiphon arouma*, the inflorescence of which is analyzed in Fig. 1. Fig. 2 A shows the habit of the inflorescence of the same specimen.

The first inflorescence arising on an aerial shoot of *Ischnosiphon arouma* is terminal which is usual among the Marantaceae, although there are exceptions (e.g. *Ischnosiphon* sect. *Bambusastrum* Schum.). After flowering and fruiting the inflorescence is shed, and a condensed lateral shoot which gives rise to a new generation of leaves in due time terminates in a new inflorescence which is thus lateral to the main shoot. The formation of two generations of inflorescences has been established in *Ischnosiphon arouma* and *I. obliquus*.

For descriptive purposes, at least, it would be convenient to regard the internode elevating the inflorescence above the leaf cluster as the first internode of the inflorescence and to term it *synflorescence peduncle*. (The use of the term synflorescence is explained below.) Depending on the habit of the species it can differ somewhat from the vegetative internodes (e.g. *Ischnosiphon arouma*) or wholly resemble them (e.g. many species of *Maranta*). In *Monotagma*, many species of *Calathea* and other taxa it is the only elongated aerial internode.

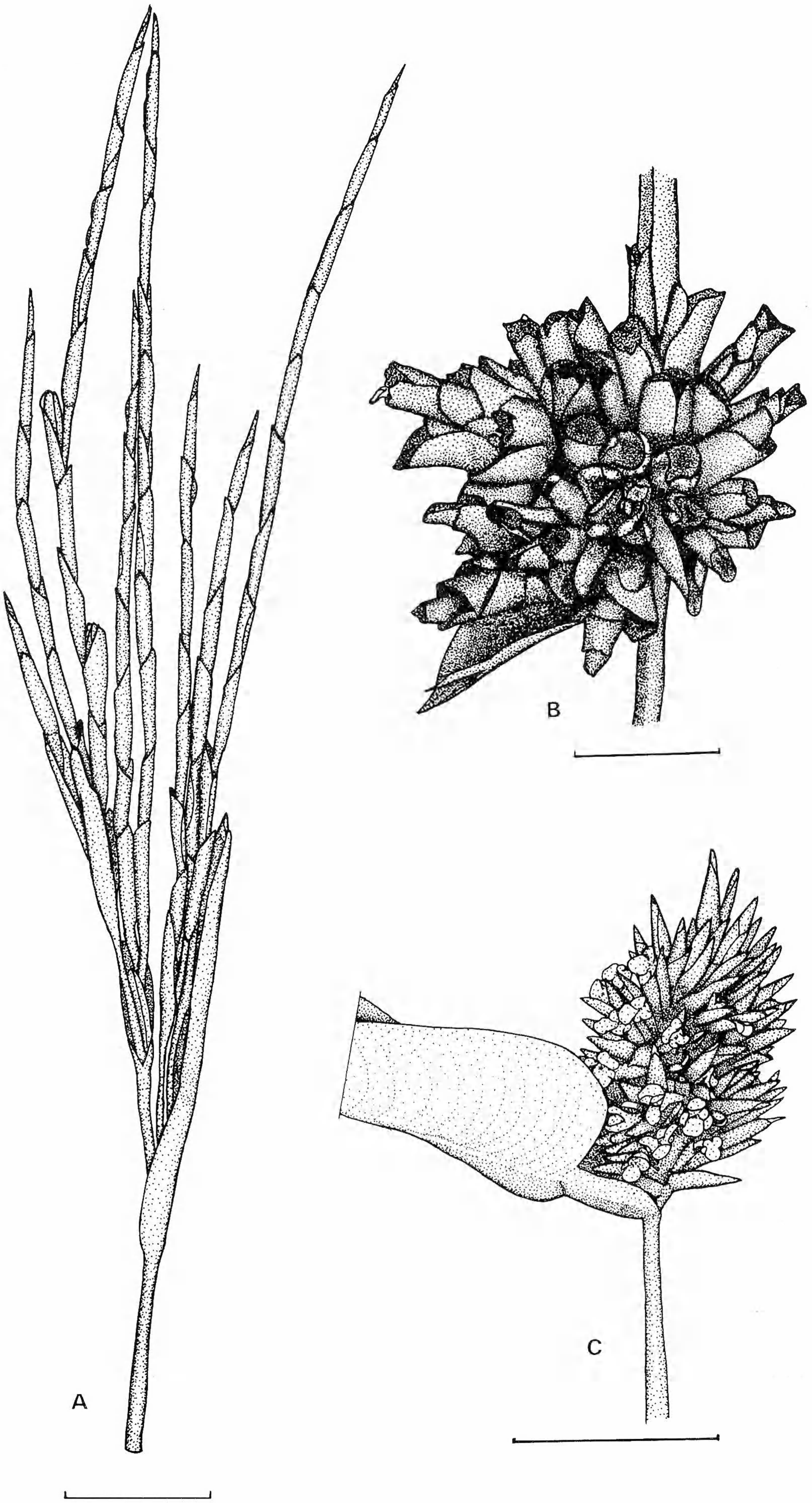
The inflorescence of the Marantaceae is composed of a varying number of mostly quite distinct flowering units, florescences (Troll 1964 pp. 145 et seq.), each shoot of the inflorescence terminating in a florescence. The florescences of *Ischnosiphon* are spiciform with densely imbricated bracts thus forming an easily recognizable structural element (Fig. 2 A). The florescences are discussed in greater detail below.

The main axis of the inflorescence in *Ischnosiphon arouma* generally forms four internodes before a florescence is formed. The proximal one is the synflorescence peduncle and the distal one is the basic internode (Grundinternodium, Troll 1964 p. 148). The basic internode and the internodes proximal to lateral florescences (co-florescences) could for descriptive purposes conveniently be termed *florescence peduncles*. Thus in this case there are three nodes on the main axis below the main florescence, each with a large bract. These bracts, together with the bracts of the first order on the main florescence, have often been called primary bracts. To avoid confusing them with the florescence bracts I suggest the term *main bracts*. This term could also be applied to the bracts on lateral branches occurring between the interphyll and the first florescence bract. (This phyllome was termed "mesophyll" by Schumann (1902), Holttum (1951) and others but the term "interphyll" of Tomlinson (1961) is better. The term mesophyll has already been used in both gross morphology and anatomy to designate other structures.) If a distinction has to be made the epithets primary, secondary, etc. could be used for the main shoot, lateral shoot of first order, etc. In *Ischnosiphon arouma* all main bracts are bracteose. In other species (e.g. *I. obliquus* and species of *Monotagma* the first primary main bract at least may be frondose.

As the number of nodes on the main axis is a taxonomically useful character a term is needed to describe it. I suggest that inflorescences with one, two, three, etc. nodes on the main axis should be termed *uni-, bi-, trinodate,* etc.

Lateral shoots (paracladia of the first order) arise in the axils of the main bracts eventually terminating in a co-florescence. The first two internodes of the paracladia are very short so that the interphylls are hidden within the main bracts of the primary axis. In the axils of the

Fig. 1. Major branching of the synflorescence in *Ischnosiphon arouma*, constructed from Florschütz & Maas 2763. – Symbols: * prophyll, CoF co-florescence, FP florescence peduncle, i interphyll, m main bract, MF main florescence, SP synflorescence peduncle. Broken lines indicate condensed axes.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secondary main bracts and the interphylls of the primary paracladia, paracladia of the second order may arise repeating the pattern of the primary ones. In Figs. 1 and 2 A there are no paracladia of an order higher than the second but these are common in other genera. As the first two internodes of the paracladia are always very short the co-florescences become fasciculately crowded in the axils of the main bracts.

The inflorescence here described conforms very well to the definition of a polytelic synflorescence (Troll 1964 pp. 149 et seq.).

The other scitaminean families have, as far as I know, always a simple or sparsely branched and usually terminal inflorescence. This has probably also been the case in primitive Marantaceae. Among most derived genera of the family, however, there is a strong tendency for an increased number of paracladia to form which, coupled with a shortening of internodes, ultimately results in synflorescences with numerous florescences aggregated into a dense, more or less head-like cluster. Excellent examples are the synflorescences of *Calathea lateralis* (R. & P.) Lindl. (Fig. 2 B) and *Monotagma* aff. *secundum* (Peters.) Schum. (Fig. 2 C). The synflorescence in Fig. 2 B, is shown to be tetranodate and composed of 17 florescences with paracladia of three orders. In these very dense synflorescences the strictly distichous plan of branching is modified in various ways. The phyllotaxy of such synflorescences has been dealt with by Eichler (1884 pp. 29–36).

In some genera (e.g. *Calathea* and *Ischnosiphon* sect. *Bambusastrum*) the opposite trend can be seen, the result being a strongly reduced synflorescence composed of the solitary main florescence often with one or a few empty main bracts on the peduncle.

Excessively branched synflorescences with the internodes not condensed can be studied in some species of *Thalia* (e.g. *T. geniculata* L.), in *Myrosma stromanthoides* Macbr. and some species of *Stromanthe*. They are reminiscent of a grass panicle in habit but nevertheless fundamentally agree with all other marantaceous synflorescences.

THE FLORESCENCE

The main axis, or rachis, of the florescence is always monopodial and carries a number of bracts. In the axils of these bracts more or less complicated flower aggregates, the *florescence components*, are found. The phyllotaxy of the florescence varies considerably (see Eichler 1884 pp. 29–30) but distichous bracts seem to be the primitive state. In *Ischnosiphon arouma* and *Monotagma laxum*, which have spirally arranged bracts in mature florescences, I have observed that the bracts are distichously initiated (Fig. 4 A). The spiral phyllotaxy in these two species is obviously a secondary phenomenon due to the ontogenetic twisting of the rachis.

In taxonomic literature the florescence has been differently described according to the habit, "raceme" and "spike" being the commonest terms used. Since each bract subtends a sympodial florescence component and not a solitary flower (see below) the most appropriate term would appear to be "thyrse", which as far as I know has not previously been applied.

The relative positions and phyllotaxy, the anatomy and thus the texture, and the persistence of the florescence bracts are of great taxonomic importance and better use could probably be made of these characters than hitherto.

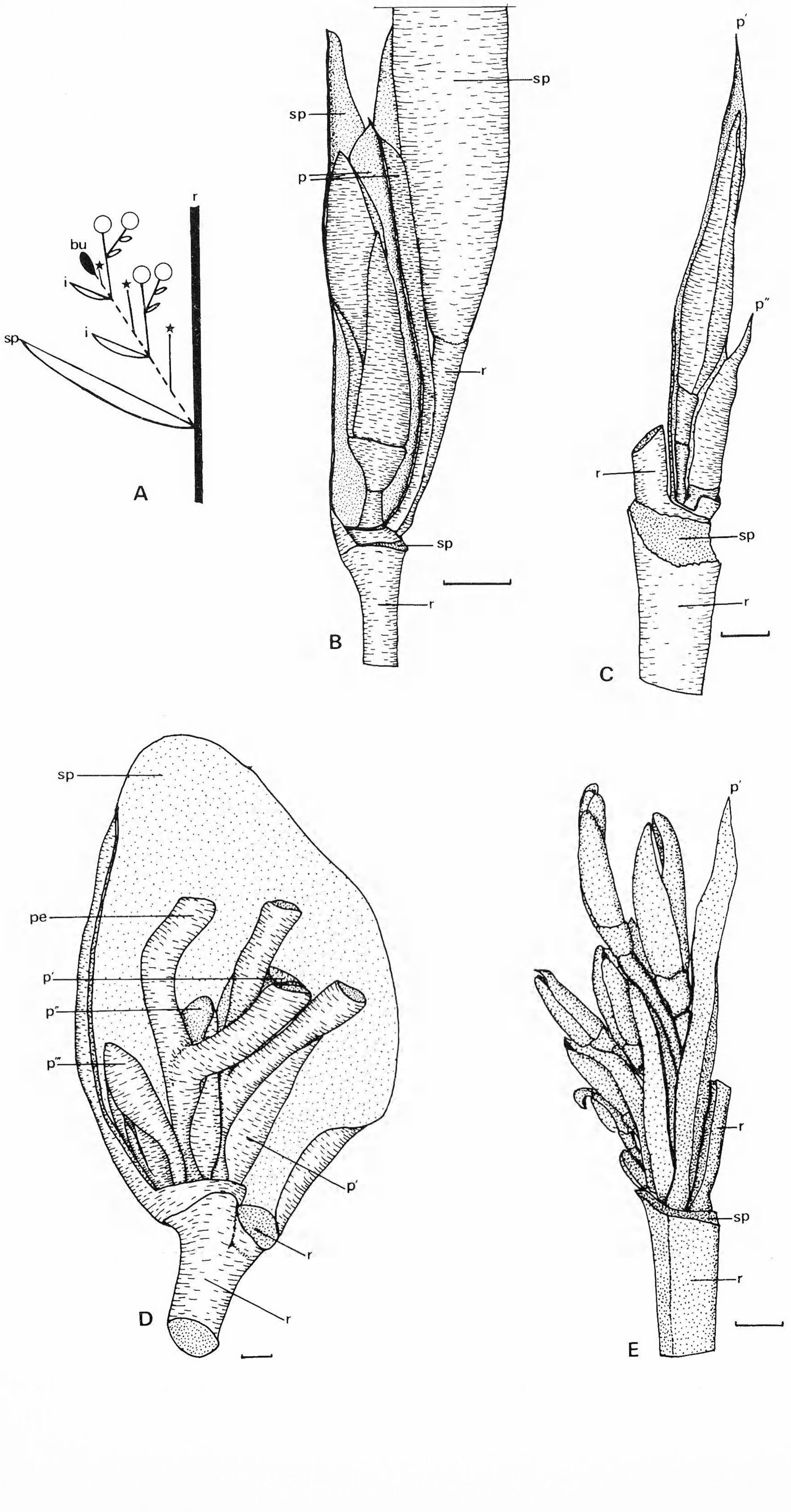
The usual term for the florescence bract is simply "bract", a term that is too vague when applied to complicated synflorescences. The term spathe would be more appropriate.

THE FLORESCENCE COMPONENT

Troll (1964 p. 149) called the more or less complicated components of a florescence "partial florescences" (Partialflorescenzen), a term that is, however, linguistically inconsistent. I prefer the term "*florescence component*" suggested by K. H. Mattisson (pers. comm.).

The florescence component of the Marant-

Fig. 2. Synflorescences. – A: *Ischnosiphon arouma* (Florschütz & Maas 2763). – B: *Calathea lateralis* (Harling & Andersson 11595). – C: *Monotagma* aff. *secundum* (Andersson 12). – Scales 5 cm.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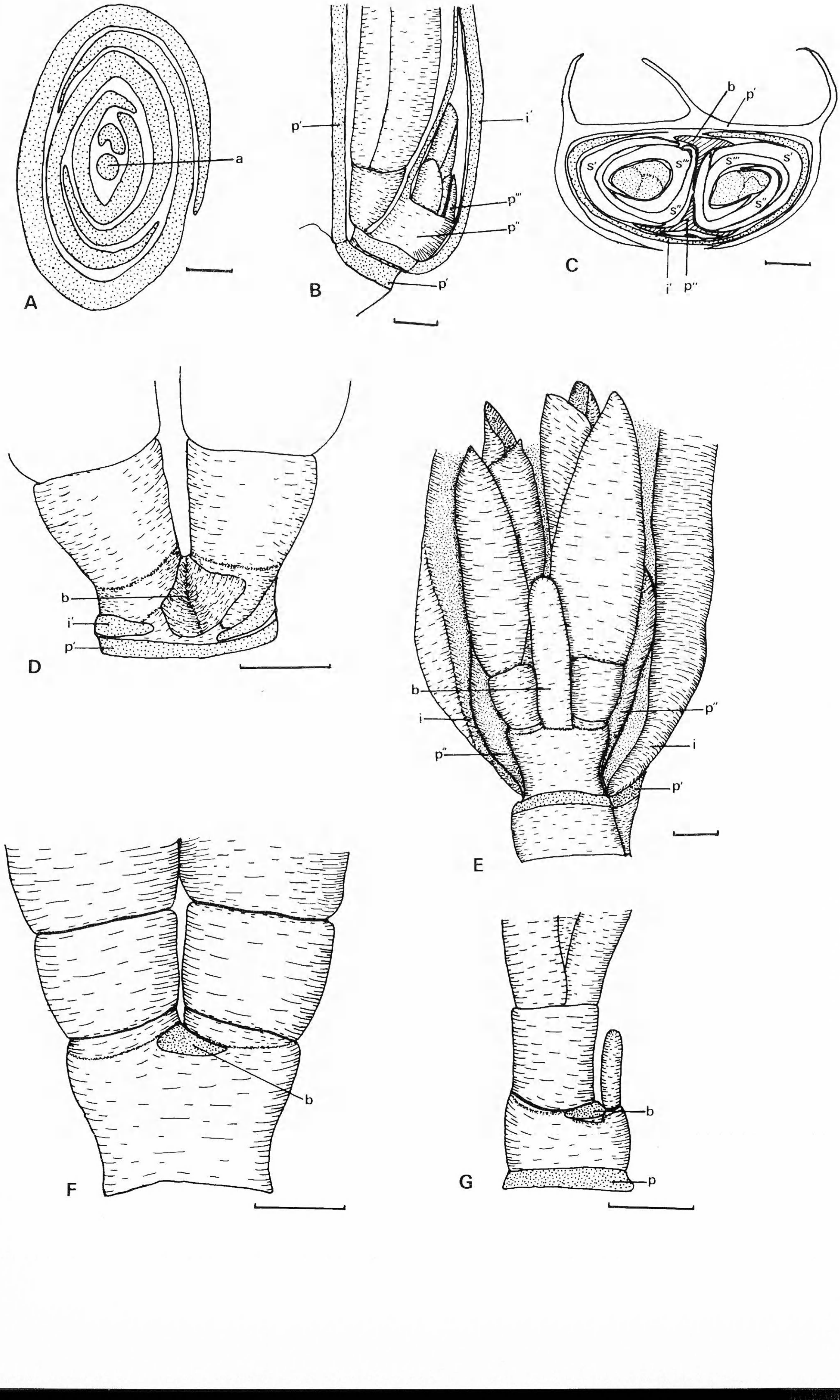
aceae (Figs. 3, 4 B–C) is a shoot system built up of sympodial axes in which the degree of branching varies greatly. The axes are often much condensed. The flowers are usually borne in pairs but the two flowers do not develop quite simultaneously. One flower is always the mirror image of the other. At the base of a flower pair and backing the parent axis, is a prophyll. This first prophyll is always two-keeled. Subsequent prophylls (see below) may be either two-keeled or three-keeled and both types may be present in the same florescence component. Above the prophyll and opposite it is sometimes an interphyll which is characteristic of many species of *Calathea* but also of species belonging to other genera (see Holttum 1951). In some species which normally lack interphylls in the florescence components they may occur sporadically. In *Ischnosiphon arouma* and *I. obliquus* they are present in c. 8% of the c. 400 florescence components examined.

The florescence component is enriched by a prophyllate bud which always arises in the axil of the interphyll where present (Fig. 4 B). It thus can be assumed that prophyllate buds of the second and higher orders are always "axillary" to interphylls, even if the interphyll itself is reduced as is mostly the case. The florescence component may be made up of the products of up to 20 prophyllate buds though usually only five or less.

One or two bracteoles are often associated with the flowers. They vary greatly in shape and size from mere rudiments, as in some species of *Stromanthe* (Fig. 5 C) and in *Monophyllanthe oligophylla* Schum. (Fig. 5 A), to large, bract-like structures as in many species of *Calathea*. In *Donax* Lour. (Holttum 1951 Fig. 1 B), *Schumannianthus* Gagnep., *Sarcophrynium* (Fig. 5 B) and others they are small and fleshy and in *Ischnosiphon* and many species of *Calathea* the proximal part is long and ribbon-like, while the distal part (*clavicula*) is hardened, more or less swollen and generally club-shaped. The position of the bracteoles has often become modified during the extensive condensation of the florescence component as in *Calathea* and *Ischnosiphon*. Even in serial sections the bracteoles usually appear to be inserted on different axes, i.e. each one appears to have a pedicel of its own. Such an arrangement would make the branching of the pedicel system difficult to explain since no other phyllomes, from the axils of which the pedicel can branch out, have been encountered. However, in *Stromanthe porteana* A. Gris (Fig. 5 C), *Monophyllanthe oligophylla* (Fig. 5 A), *Sarcophrynium brachystachyum* (Benth.) Schum. (Fig. 5 B), *Donax grandis* (Miq.) Ridl. and probably others one finds an expanded axial system with bracteoles or bracteole rudiments in a presumably primitive position. This lends strong support to an interpretation of the flower pair of the Marantaceae as a monochasial cyme. Each flower pair with its axial system and associated prophyll, interphyll and bracteoles can for brevity of description, be termed a *cymule*.

In *Monotagma* and *Monophrynium* the flowers are unpaired, which is apparently a derived condition. *Monotagma* has a florescence component composed of one-flowered cymules (Fig. 3 C), the number of cymules in a florescence component being three or four. In some species of *Monotagma* there are small bracteoles (Schumann 1902), in others they are absent. *Monophrynium fasciculatum* (Presl) Schum. bears only one flower and the associated prophyll in the axil of each spathe (Fig. 3 B). In *Ischnosiphon arouma* atavistic cymules are sometimes found in which one flower is reduced to a small cylindrical axis (Fig. 4 G). Such forms may be taken as an indication that the single-flowered cymule is a reduced form of the two-flowered one.

Fig. 3. Florescence components. – A: Diagram showing the hypothetical organization of the florescence component of a primitive Marantaceae. Broken line indicates condensed axis. – B: *Monophrynium fasciculatum* (Ramos & Edaño s. num.). – C: *Monotagma laxum* (Harling & Andersson 13994). – D: *Myrosma stromanthoides* (Harling & Andersson 12258). – E: *Maranta bicolor* Ker. Drawn from a live specimen cultivated at the Botanical Gardens of Göteborg. – Symbols: * prophyll, bu bud, i interphyll, p prophyll, pe pedicel, r rachis or rachis scar, sp spathe or spathe scar. – B drawn from softened herbarium material, C and D drawn from fixed material. – Scales 1 mm.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INTERPRETATION OF THE FLORESCENCE COMPONENT

The interpretation of the much-derived marantaceous florescence component has been widely discussed. The commonest interpretation is still that proposed by Eichler (1875, 1884) who interpreted the flower pair as a three-flowered dichasium, in which the primary flower has been lost by reduction. This view was supported by Müller (1885), who found a sterile, minute axis in the florescence component of an un-named species of *Stromanthe*. It was also reported that this axis sometimes produced a third flower. Jonker-Verhoef & Jonker (1957), describing some species of *Calathea*, also refer to these sterile axes. Their interpretation is, however, erroneous, the structure observed by them being an unpaired, subterete bracteole (Fig. 4 E–F). Further support for Eichler's theory was found in the supposed equality ("Gleichwertigkeit") of the two flowers of a pair. He considered that the differences in the degree of development of the two flowers were of no importance, whereas in actual fact the flowers belong to different shoot generations.

A second theory is that put forward by Thompson (1933). On the basis of extensive studies of inflorescence ontogeny and on the assumption (probably false, see Tomlinson 1962 p. 205), that the primitive phyllotaxy of the Scitamineae is spiral, he argued that the florescence component was a much transformed spike with flowers and bracts distributed on a deformed, primitively conical axis, all belonging to the same shoot generation. This theory, which is based almost entirely on ontogeny and the geometrical distribution of the structures and which disregards facts of comparative morphology, has received little support from subsequent research workers and failed to give a sound morphological interpretation.

A third interpretation, that favoured by the present author, regards each flower pair with its

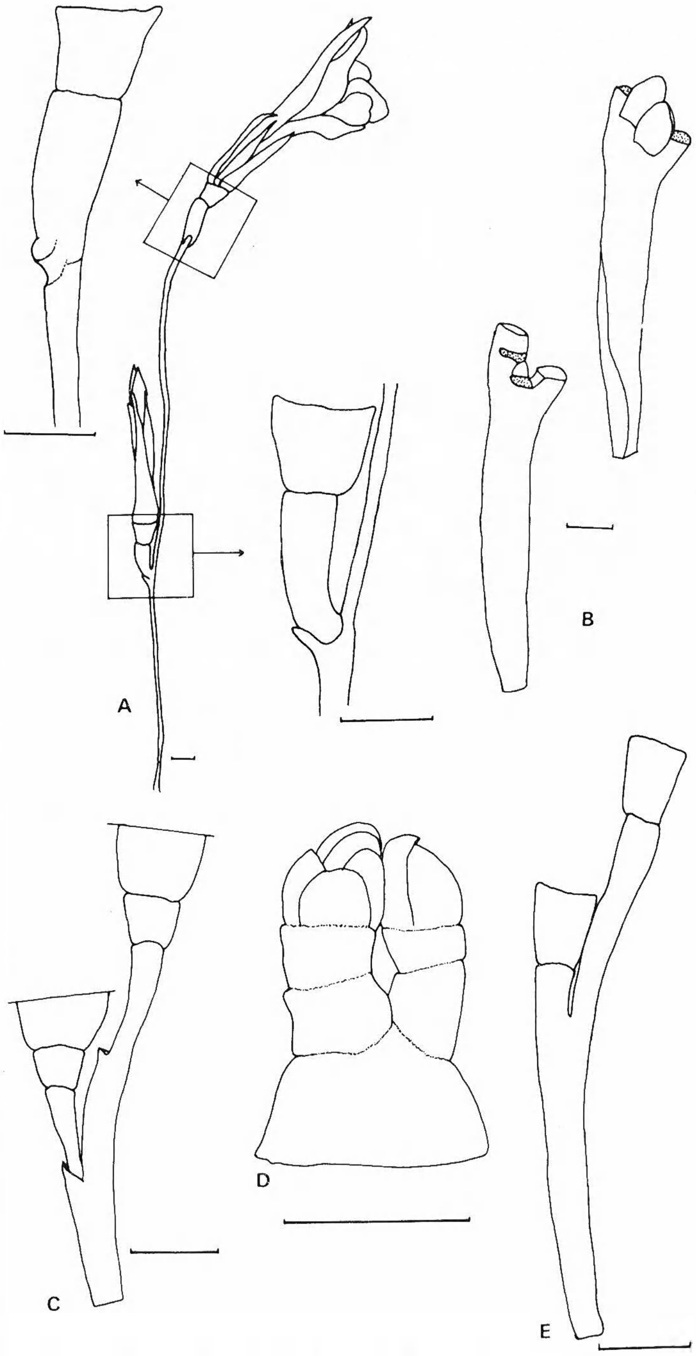

Fig. 5. Cymules (prophylls omitted). – A: *Monophyllanthe oligophylla* (Wessels Boer 1206). – B: *Sarcophrynium brachystachyum* (Arnold 5115). – C: *Stromanthe porteana* (Gardner s. num.) – D: *Myrosma stromanthoides* Macbr. (Harling & Andersson 12258). – E: *Maranta bicolor* Ker. Drawn from live material cultivated at the Botanical Gardens of Göteborg. – A–C illustrate mature structures, D–E are young structures. A–C drawn from softened herbarium material, D drawn from fixed material. – Scales 1 mm.

Fig. 4. A: Cross-section through apical portion of a florescence of *Monotagma laxum* (Andersson 2). – B: Part of florescence component of *Calathea comosa* (L. fil.) Schum., lateral view. Second interphyll omitted (Harling & Andersson 11750). – C: D:o, cross-section of young florescence component. – D: D:o, young cymule. – E: *Calathea* sp., young florescence component, dorsal view (Harling & Andersson 11792). – F: D:o, young cymule. – G: *Ischnosiphon arouma*. Young, atavistic cymule (Andersson 16). – Symbols: a apex, b bracteole or bracteole scar, i interphyll or interphyll scar, p prophyll or prophyll scar, s sepal. – All drawings made from fixed material. – Scales 1 mm.

prophyll, interphyll and bracteoles as a two-flowered monochasium (Fig. 3 A) with the one flower lateral to the other. That, provided the flowers are asymmetric, such arrangements may produce a series of flowers where one flower is the mirror image of the preceding one is exemplified by *Commelina* (see Eichler 1875 p. 145, Fig. 70 B). This interpretation does not disagree with the observations made by Müller (1885), since his illustrations can be interpreted as, and actually give the impression of being, a three-flowered monochasium rather than a dichasium. Furthermore such an arrangement repeats the branching type of the synflorescence and agree with the organization of the inflorescence in other scitaminean families.

The strongest support for this interpretation is, however, the position of the bracteoles on the expanded axes found in *Stromanthe, Monophyllanthe, Sarcophrynium* etc. Further evidence was sought in the vascularization of the florescence components and adjacent parts of the rachis, but the extent of derivation of the vascular structure proved to be so great that it actually provided less information than the superficial structures.

Ontogenetical studies, on a very limited scale, gave little additional information. Ontogenetically the florescence component has also become derived and little information on the primitive state could be obtained from it. The only interesting result obtained from these studies was that the nodes can sometimes be seen on young, though far from primordial, cymules, although the phyllomes are lacking. Such young cymules show the same axial organization as those carrying bracteoles (Fig. 5 D).

ACKNOWLEDGEMENTS

I am much indebted to Professor Gunnar Harling for the opportunity to carry out field studies and for a critical reading of the manuscript. Thanks are also due to Dr. Uno Eliasson and Karl Henning Mattisson for their criticism of the manuscript. Financial support for the field work was received from the University of Göteborg.

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APPENDIX

List of specimens cited

Andersson 2: Peru, Loreto, SW of Iquitos, Puerto Almendra (GB) – Andersson 12: Peru, Loreto, road Iquitos–Quista Cocha, Juanacasa (GB) – Andersson 16: Guyana, Essequibo River, Bartica (GB) – Arnold 5115, Ghana, Daban Ash (K) – Florschütz & Maas 2763, Suriname, between Kabalebo River and West Coppename River (U) – Gardner s. num., Brazil, Minas Geraes (K) – Harling & Andersson 11595, Ecuador, Pichincha, Nanegal (GB) – Harling & Andersson 11750, Ecuador, Napo, Cañon de los Monos, ca 12 km north of Coca (GB) – Harling & Andersson 11792, Ecuador, Napo, Coca (GB) – Harling & Andersson 12258, Ecuador, Carchi, 3–4 km NW of Maldonado (GB) – Harling & Andersson 13994, Ecuador, Zamora-Chinchipe, La Saquea on Río Yacuambi–Yanzatza (GB) – Ramos & Edaño s. num., Phillipines, Luzon, Tayabas, Mt Binuang (K) – Wessels Boer 1206, Suriname, at the confluence of River Paloemen and River Tapanahoni (K).

Euphrasia in Sweden: hybridization, parallelism, and species concept

Thomas Karlsson

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A survey of the Swedish *Euphrasia* taxa is presented. Five groups of taxa are well delimited. *E. salisburgensis, rostkoviana, bottnica, micrantha,* and *stricta* are the most wellknown taxa in these groups. A subdivision of each group into "biological units" is attempted. Some of these are indigenous, others are synanthropic, among these some of the commoner ones. Hybridization is of limited importance in undisturbed habitats, but in man-made habitats the limits between biological units sometimes break down completely.

Number and length of internodes, branching habit, seed size, capsule and leaf form and size are correlated and appear to form adaptive complexes dependent on habitat and climatic factors.

No formal taxonomy is made, but a treatment recognizing five Swedish species only is suggested.

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The genus *Euphrasia* (Scrophulariaceae) shows an extremely intricate variation in NW Europe (Denmark, Finland, Norway, Sweden). Representatives of the genus are fairly common on most kinds of open ground all over the region. They are hemiparasitic annuals. There is a great and seemingly continuous variation in habit, hairiness, leaf and capsule form and size, and flower colour and size. The genus has been subdivided into an increasing number of taxa, some of which are extremely diffusely defined.

In order to elucidate the background for this variation I began in 1970 a study of the genus in southern Sweden. Field studies and cultivation and crossing experiments indicate that there is a quite impressive hereditary adaptation to different environments, and that hybridization with subsequent establishment of hybrid derivatives is common between some taxa.

Field experience from northern Sweden was gained from a trip to the province of Jämtland in 1975.

THE PRIMARY GROUPINGS

Field experience, crossing experiments, herbarium and literature studies have shown that there are some fundamentally distinct units within *Euphrasia*. The Swedish (and NW European) taxa can be grouped into five complexes between which hybrids and other intermediates are rare or non-existent.

(1) The *salisburgensis* complex (*E. lapponica* Th. C. E. Fries, *E. salisburgensis* Funck).

(2) The *rostkoviana* complex (*E. rostkoviana* Hayne subsp. *rostkoviana* and subsp. *montana* (Jordan) Wettstein, *E. fennica* Kihlman).

(3) *E. bottnica* Kihlman.

(4) The *micrantha* complex (*E. micrantha* Reichenbach, *E. scottica* Wettstein).

(5) The *stricta* complex (all other species reported from the region).

The complexes (1), (2) and (3) are well-defined by distinct key characters: the lack of cilia in the capsule apex for the *salisburgensis* complex, the long-stalked glandular hairs for the *rostkoviana* complex, and the extremely small flowers for *E. bottnica*. The *micrantha* complex is morphologically somewhat less clearly distinguished from the *stricta* complex, but seems to be fairly well genetically isolated however, as hybrids are rare. *E. gratiosa* Wiinstedt, believed to be a descendant from *E. micrantha* × *stricta* (Wiinstedt 1946), seems not to be a natural unit. Swedish specimens (in S) designated *E. gratiosa* by Wiinstedt himself are clearly *E. micrantha* and *E. stricta* variants without obvious signs of hybridization.

The above five groups at least, are no doubt specifically distinct from each other. *Euphrasia officinalis* L. is no natural unit at the species level. Hultén (1976 p. 360) goes too far in generalization when he states: "In the Northern Hemisphere the genus *Euphrasia* behaves as a complex species, *E. officinalis* s. lat. ... It consists of a highly variable circumpolar lowland population, and superimposed on this and poorly differentiated from it a group of arctic-montane taxa (*E. frigida – minima, E. salisburgensis – lapponica*)." *Euphrasia salisburgensis* and related species are commonly regarded as a distinct subsection, *Angustifoliae* Wettstein.

Within the complexes mentioned above there are, however, many hybrids and other transitional forms; and widely divergent opinions as to the rank of taxa have been put forward. In our area, this particularly applies to the *stricta* complex. The other complexes have their centres of variation in other regions, so the problems they present here are far less serious.

SUBDIVISION OF THE STRICTA COMPLEX

The following discussion is chiefly concerned with conditions in Sweden, but is probably valid for most of NW Europe. In the westernmost, extremely coastal areas, the variation is however more complicated (cf. Yeo 1971).

The *stricta* complex can be subdivided into six form series. (1) to (4) have small, predominantly white flowers; (5) and (6) have generally large, more or less lilac flowers. In all form series, simple hairs may occur on the leaves, but only in (6) do short-stalked glandular hairs occur.

(1) *Euphrasia frigida* Pugsley, a very variable mountain plant.

(2) *E. frigida* var. *palustris* (Jørgensen) Nordhagen, a well-defined variant in western mountain mires.

(3) The *baltica* type (Nannfeldt in obs.), occurring along the Bothnian Sea and Gulf of Bothnia, there being sympatric with *E. bottnica*.

(4) *E. nemorosa* (Persoon) Wallroth, a very variable lowland plant. This taxon has been known as *E. curta* (Fries) Wettstein, or *E. glabrescens* (Wettstein) Wiinstedt if subglabrous. It was included in *E. nemorosa* by Yeo (1971).

(5) *E. hyperborea* Jørgensen, a mountain plant from western N Sweden, with a wider distribution in N Norway.

(6) The *Euphrasia stricta* group. All that has been included under the names *E. brevipila* Burnat & Gremli, *E. tenuis* (Brenner) Wettstein 1896, *E. stricta* Wolff ex Lehmann (including var. *gotlandica* Ahlfvengren), *E. suecica* Murbeck & Wettstein, and part of what has been called *E. reuteri* Wettstein, forms one single unit with a seemingly continuous variation in many characters. There are, however, geographical and ecological trends in the variation and further research may make a subdivision possible. The oldest name within the group is *Euphrasia stricta* (Yeo 1971).

Yeo (1971, 1972) made *E. tenuis* (including *E. suecica*) a subspecies under *E. arctica* Lange; further subspecies of *E. arctica* are what have been known as *E. borealis* (Townsend) Wettstein from the W coasts of Denmark and Norway. According to Yeo the difference between *E. arctica* and *E. stricta* lies in the more rounded leaves of the former. Indeed, *E. borealis* collections look extremely different from the more eastern *E. stricta*, among other things in leaf form. Nevertheless, if the NW European material is subdivided on leaf form, we get a subdivision that is as unnatural as that previously made on the presence or absence of glandular hairs (Wettstein 1896). To me it seems that the Scandinavian material makes it impossible to retain *E. arctica* sensu Yeo as a species distinct from *E. stricta*.

What is here termed the *Euphrasia stricta* group is thus roughly equivalent to *E. brevipila* sensu Hylander (1945), but includes also part of what he referred to *E. brevipila*×*curta*. It is roughly comparable to the sum of Yeo's (1972) *E. stricta* and *E. arctica*, and is thus not at all the same as his *E. stricta* group.

In this paper the epithets *brevipila, tenuis, stricta, suecica,* and *gotlandica* will be used for more or less distinct units within the *E. stricta* group. The epithets *suecica* and *tenuis* will be used according to Wettstein's (1896) definition, i.e. for eglandular and glandular aestival variants, respectively.

A BASIC PRINCIPLE

Thus it is possible to subdivide *Euphrasia* in Sweden into a limited number of biological units. The local populations of each such biological unit are linked in space and time by habitat preferences, modes of dispersal and pollination biology, and a supposed common origin which is also expressed as an overall morphological similarity. However, there may be greater or lesser variation between the local populations of every biological unit. With a particular character, one biological unit may have a range that covers the gap between two other biological units. This implies that classification on "sub-complex level" in difficult genera like *Euphrasia* should not be made without sufficient field studies in the area concerned. If the classification is made on the basis of herbarium material only, one is likely to produce erroneous subdivisions, as nothing indicates where the boundaries between the natural entities go.

An example: The common form series of the *E. stricta* group (known as *E. brevipila*) and *E. nemorosa* may well be distinguished on a population basis by flower size in southern Sweden. However, another, geographically

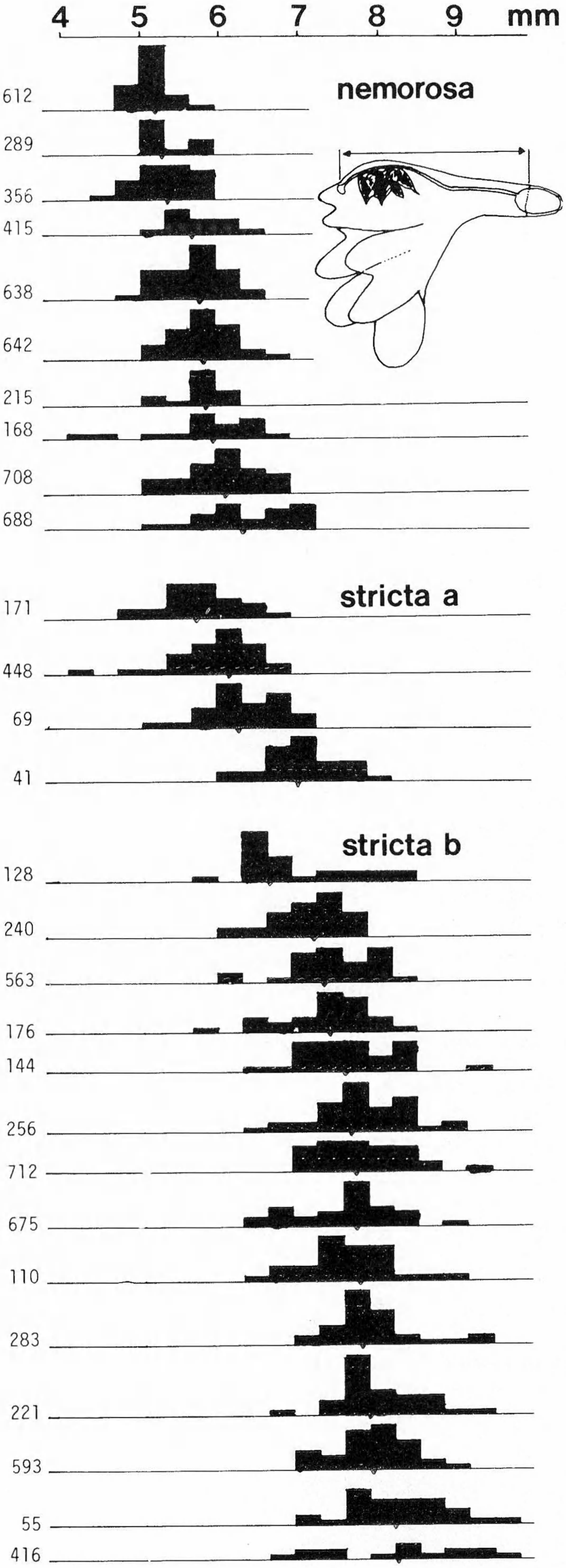

Fig. 1. Corolla length of three *Euphrasia* taxa. Cultivated material from 28 randomly selected populations from Skåne, southern Sweden.

limited race of the *E. stricta* group has a flower size that covers the gap between, and overlaps with, both of them (Fig. 1). Wiinstedt, who apparently had not seen this race in the field, determined some sheets to *E. stricta*, others to *E. gratiosa*, and still others to *E. glabrescens*.

Three factors seem to have been of particular importance in building up the present variation in *Euphrasia* in Sweden. The first one is vegetation history: there are indigenous *Euphrasia* taxa as well as taxa that have been introduced, or at least have distributions which have grown much larger owing to the activities of man (synanthropous taxa). The second factor is hybridization. The third is the presence of parallel, ecologically conditioned variation.

INDIGENOUS EUPHRASIA TAXA

I consider the following *Euphrasia* taxa to be definitely indigenous in Sweden, that is they have reached their localities, or by far the greater part of them, before man had any heavy influence on the environment.

E. lapponica – dry, wind-swept calcareous heath in the mountains (Nordhagen 1952).

E. salisburgensis – *Schoenus ferrugineus* fens on Gotland. The Swedish material represents a distinct variant (Pettersson 1958 p. 111, 1965).

E. bottnica – land upheaval zone of the Gulf of Bothnia (Julin 1965).

A glabrous, polymorphic race of the *E. stricta* group on limestone pavement of Öland and Gotland and some further small areas (Sterner 1938 p. 150).

E. stricta var. *gotlandica* – a poorly understood variant in calcareous, wet habitats on Gotland (*E. gotlandica* (Ahlfvengren) Hylander 1955, not validly published).

E. hyperborea – subalpine and low alpine fens and *Betula* groves (Lange 1938 p. 139).

E. frigida – a widespread and polymorphic northern and alpine species, also scattered along the big rivers (Wistrand & Lundqvist 1964).

E. frigida var. *palustris* – a distinct variant in *Trichophorum caespitosum* fens in the mountains (Smith 1920 p. 221, Sernander 1941 p. 101).

The *baltica* type – land upheaval zone along the Bothnian Sea and Gulf of Bothnia (Julin 1965, Ericson 1973 pp. 39, 55).

Some of these distinctly native taxa show a tendency to invade man-made habitats. This is true for e.g. *E. frigida*, which occurs on roadsides far down in the woodlands and also in mown meadows in or near the mountains (information on herbarium labels; Arwidsson 1930).

Some of the native taxa, on the other hand, appear to be extremely specialized, e.g. *E. frigida* var. *palustris*, *E. lapponica*, and *E. salisburgensis*. They show little or no tendency to occupy new habitats, and therefore they may be threatened by environmental changes.

SYNANTHROPOUS EUPHRASIA TAXA

I consider the following *Euphrasia* taxa to be more or less completely synanthropous in Sweden, that is, they have reached their present, often very wide distributions by way of colonizing man-made habitats. I have never seen, nor have I any knowledge of occurrences of the taxa listed, which could with confidence be regarded as indigenous. This leaves the possibility that such localities exist, especially perhaps in areas with broken topography. Even if so, these areas are vanishingly small in relation to the present areas inhabited.

E. rostkoviana – the majority, if not all the present-day occurrences are dependent on human activity. This applies to both subsp. *rostkoviana* and subsp. *montana*.

E. stricta group – except for races specified as indigenous. All the glandular races (known as *E. brevipila* subsp. *brevipila* and subsp. *tenuis* (Brenner) Wettstein) thus seem to be synanthropous.

E. micrantha.

E. nemorosa.

Some of these distinctly synanthropous taxa show a tendency to invade natural vegetation. Thus the *E. stricta* type known as *E. brevipila* subsp. *tenuis* invades banks of water courses in parts of N Sweden (Wistrand 1962 p. 137).

For *E. nemorosa* and the *E. stricta* group the majority of occurrences seem to be along roadsides or in similar places. However, at least in parts of their areas, all taxa listed occur as normal constituents of semi-natural grasslands that have been grazed or mown for hundreds of years. They are as a rule locally extremely good phytosociological indicators, i.e. appear as extremely specialized. However, all taxa except *E. micrantha*, which is associated with *Calluna* on poor soils over its entire Swedish area, show a remarkable lack of consistency in sociological behaviour from area to area. A morphologically fairly homogeneous taxon known as *E. brevipila* subsp. *tenuis* thus occurs on roadsides in N Sweden, in one extremely well-defined type of mown meadow on Gotland, in quite another type of mown meadow on the W coast, and in still another in the inland. The reason for this curious phenomenon is not quite clear.

Several *Euphrasia* taxa of semi-natural grasslands have become rare today as old agricultural practices are given up; some of them are on the verge of extinction and will only survive in reserves. This fact is strong evidence for their synanthropous character.

Euphrasia scottica is not classified above. I have not been able to find it again at its single known locality in Sweden, Marstrand (Hylander 1945 p. 288).

An original area of synanthropous taxa

The *Euphrasia* taxa classified as synanthropous in Sweden may have had their areas of origin in several different regions. For two reasons, however, I would suggest that heathland and other coastal habitats in W Europe have been of particular importance.

(1) The genus is distinctly more polymorphic in westernmost Europe. Several more form series are met with in addition to most of those previously discussed. On the W coast of Norway *E. scottica* becomes commoner, and one polymorphic taxon, *E. arctica* subsp. *borealis* (Townsend) Yeo is added. In westernmost Denmark, *E. arctica* subsp. *minor* Yeo (*E. borealis* auct. dan.) and *E. dunensis* Wiinstedt are added. Further to the south-west, and on the North Sea islands there are still other taxa. The possibility of subdividing the *stricta* complex into one small-flowered, (1)–(4), and one large-flowered, (5)–(6), group, as suggested above (p. 00) seems to be excluded in these areas. Even the difference between the *stricta* complex and the *micrantha* complex seems to become quite subtle towards the west.

Furthermore there is indication that *E. micrantha*, whose present wide European distribution is in all likelihood dependent on man, is more variable towards the west. The occurrence of purple-flowered variants (var. *primaria* (Fries) Hylander) in the western part of its Swedish area (Hylander 1945 p. 286) is well known.

(2) Most authors dealing with heath communities are in agreement that heath vegetation has for long been characteristic of certain coastal locations (Gimingham 1972 p. 17), but that its spread over large parts of W Europe is associated with man. In our time there is a strongly maritime belt with poor or no forest growth along great parts of the Scandinavian west coast. The poor forest growth seems to be climatically conditioned (Sjörs 1967 p. 111).

It may well appear that those *Euphrasia* taxa which have a vast synanthropic distribution today have originated by selection from such areas of biotypes well suited for colonization of habitats opened up by man.

My knowledge of extreme western *Euphrasiae* and vegetation is very limited. The above reasoning is thus simply a hypothesis, which can only be tested through field studies by botanists acquainted with local vegetation and its history in the areas concerned.

HYBRIDIZATION

The indigenous and synanthropic taxa listed above are the main building blocks in the complex variation of Swedish *Euphrasia*. The pattern has been much obscured by hybridization.

Hybridization under undisturbed conditions seems to be of limited importance. *Euphrasia stricta* var. *gotlandica* and *E. salisburgensis* occur side by side in Gotlandian spring mires, but hybrids are found as single plants only. The same relation seems to be present between *E. frigida* and *E. lapponica*, and between the *baltica* type and *E. bottnica*. Some transitional forms are admittedly present between *E. hyperborea*, *frigida* and *frigida* var. *palustris*.

Man's re-structuring of the environment made, however, many *Euphrasia* taxa spread over new ground. During this spread they came in contact with each other in new constellations. If there are sufficient internal or external barriers to gene exchange between taxa, they coexist without losing their identity. In some places in Sweden, *E. rostkoviana* comes in close contact with a race of the *E. stricta* group. In a Skåne locality (Högestads mosse) I have searched in vain for hybrids in mixed colonies of these two taxa; Albertson (1942) did the same in Västergötland (Skogastorpskärret).

However, if the original material was not sufficiently differentiated to make hybridization rare or impossible, and if the habitats colonized were sufficiently close to one another, the limits between the biological units broke down locally or over large areas. This is what has happened between races of the *E. stricta* group and *E. nemorosa* in Skåne, on the W coast, and in E Central Sweden, to cite just those regions from which the phenomenon is best documented by herbarium material. (In the last-mentioned area things seem to be still more complicated by the presence of a hairy *E. stricta* race impossible to distinguish from recent hybrids.) Hybrid swarms between *E. frigida* and a *stricta* race (*E. brevipila* subsp. *tenuis*) are very prominent in the mountains (Smith 1920 pp. 220, 222).

Thus has Nature in an enormous experiment tested the taxonomic status of the biological units, more rigorously than we can ever hope to do in our experimental gardens. The test has shown that *E. stricta, nemorosa* and *frigida,* in the combinations just discussed, are not valid species, assuming that valid species are expected to show at least some degree of reproductive isolation. We can with some justice regard them as ecotypes in the Clausen sense of the word (cf. the well-known example of *Potentilla glandulosa,* Clausen 1951). Yeo (1966 p. 243) reached the same conclusion.

In the cases of *E. rostkoviana* versus *stricta, stricta* versus *salisburgensis, frigida* versus *lapponica,* and *bottnica* versus *baltica,* the test of natural coexistence has, on the other hand, shown that the entities are reproductively isolated and thus we can confidently regard them as specifically distinct.

PARALLELISM

In *Euphrasia,* as in some other European genera of annual hemiparasites, different species often appear in quite similar variants in similar or identical habitats. This is mainly the result of parallel selection of well-adapted biotypes, although phenotypic modification also plays a part. The phenomenon has been put in relation to hemiparasitism in an earlier paper (Karlsson 1974) and was illustrated with *Euphrasia* material from southern Sweden. Let us now examine the parallelism in greater detail on a slightly different array of taxa.

Length and number of internodes

Length of internodes. The length of internodes in the middle part of the stem is obviously correlated with the height of the surrounding vegetation, other external factors being the same. Long internodes are found, for example, in plants from fen and meadow habitats, where the vegetation is tall (10–30 cm) but moderately dense; and roadsides, when there is a verge of tall grasses and herbs. The selective force may well be competition for light.

Short internodes are found chiefly in plants from extremely wind-swept areas, like coastal and alpine habitats, and from heavily grazed areas. The selective forces may well be water stress (water loss being minimized in small compact plants) and grazing (tall plants being bitten off and thus prevented from setting seed).

Number of internodes. The number of internodes to the lowest flower is strongly correlated with the length of the vegetation period. This is conceivable as the lower the node of flowering is, the earlier the flowering starts, and the earlier are mature seeds produced. A rather high number of internodes is found in southern plants in general. A low number of internodes is found in northern and alpine plants in particular; but southern plants from meadows where the vegetation period is artificially shortened by mowing in the middle of July also exhibit this characteristic. This relation between latitude and habit is immediately seen when any northern *Euphrasia* is compared with its counterpart from southern Sweden, but it is best demonstrated in the *E. stricta* group which occurs all over the country (Fig. 2).

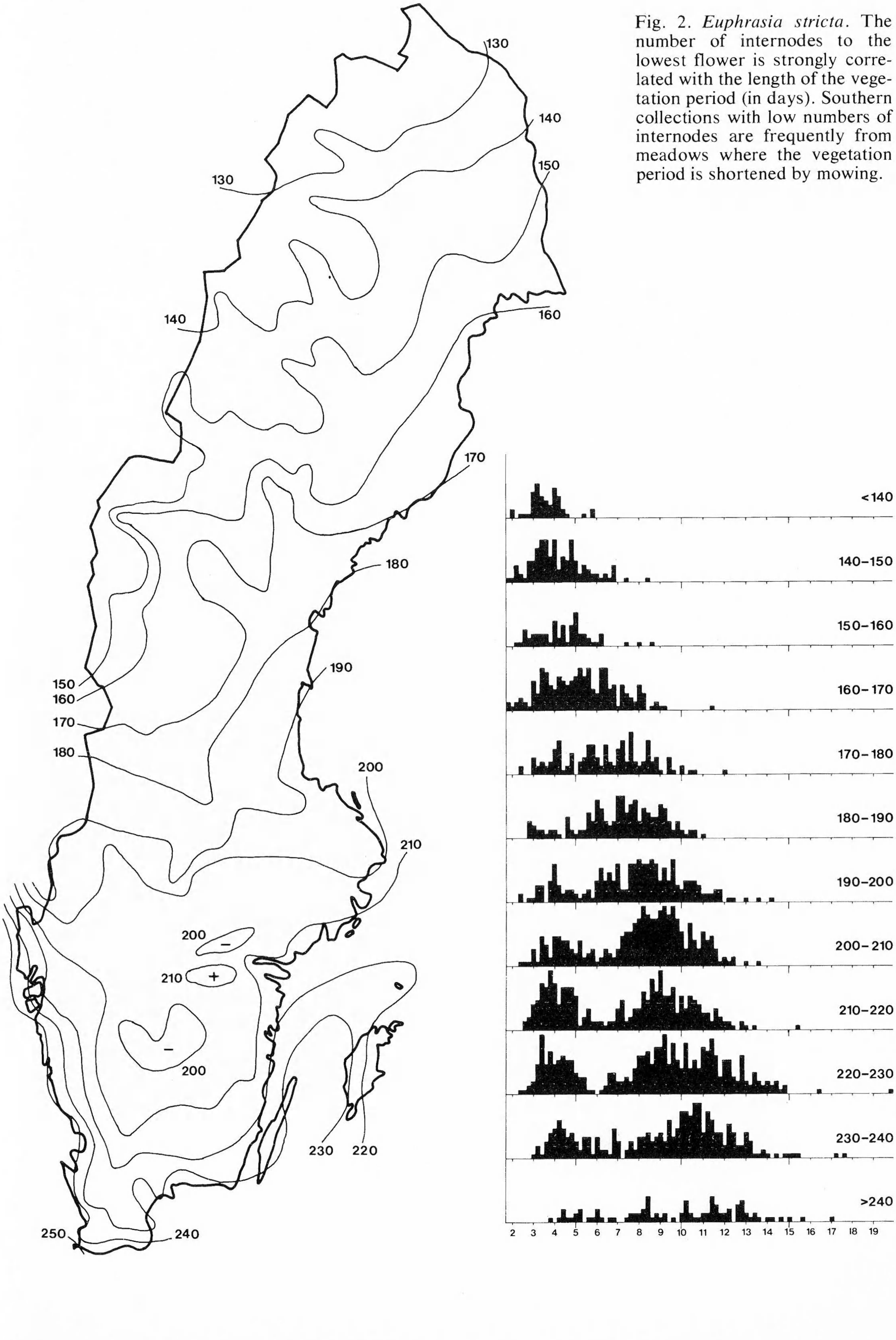

Fig. 2. *Euphrasia stricta*. The number of internodes to the lowest flower is strongly correlated with the length of the vegetation period (in days). Southern collections with low numbers of internodes are frequently from meadows where the vegetation period is shortened by mowing.

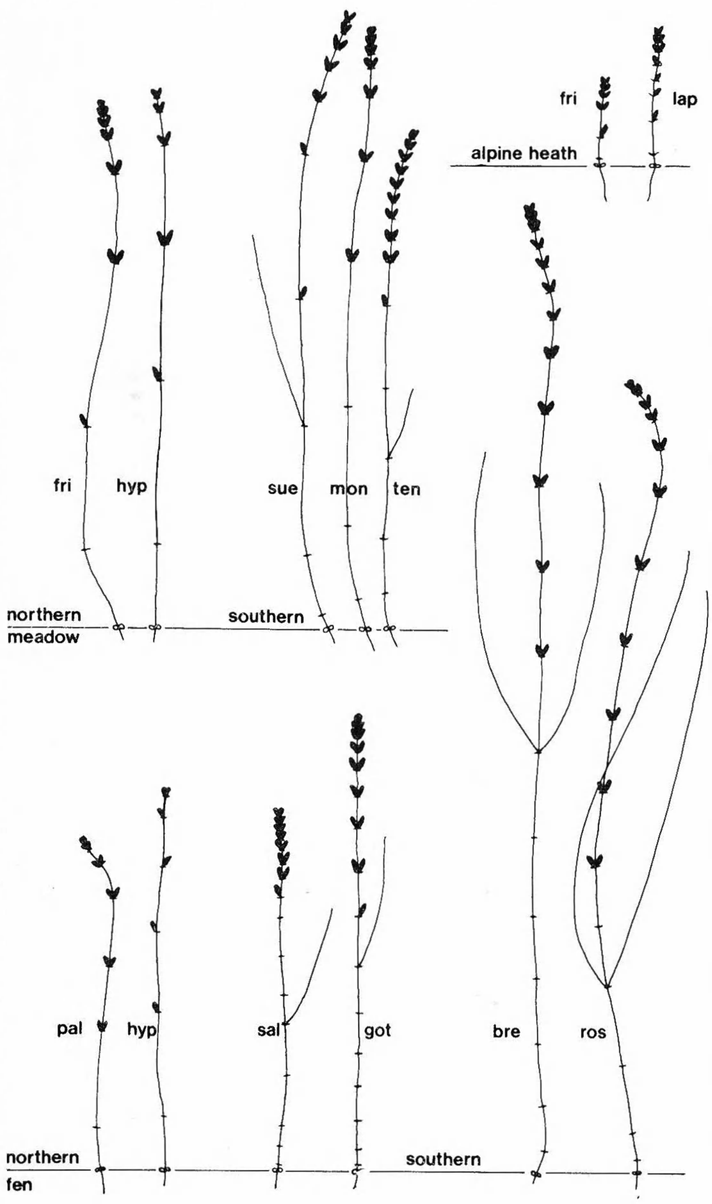

Fig. 3. Parallel, habitat-correlated variation in *Euphrasia*. The specimens illustrated were randomly selected from collections which were in turn randomly selected from those with a sufficient habitat description. Spontaneous material. All 1/4 natural size.

Given the average ecological conditions for any Swedish *Euphrasia* type, it is in fact possible to predict its average habit in terms of length and number of internodes. Thus the northern *Trichophorum caespitosum* fen plants *E. frigida* var. *palustris* and *E. hyperborea* are expected to be mutually similar, but to have fewer and (by way of compensation) longer internodes than *E. stricta* var. *gotlandica* and the Gotland population of *E. salisburgensis*. These last two taxa grow in *Schoenus ferrugineus* fens where the tussocks are of about the same height as in the *caespitosum* fens. Variants of *E. stricta* and *E. rostkoviana* from southern fens with a taller vegetation of *Carex* species and herbs are expected to have about the same number of internodes as the Gotlandian fen taxa, only longer. All of these predictions have been quite strikingly verified (Fig. 3, bottom row).

Euphrasiae from subalpine *Betula* groves with a fairly tall field layer are expected to have as long and few internodes as plants from southern mown meadows exhibit. In fact they have still fewer internodes, which suggests that the vegetation period in the subalpine meadow is in reality shorter than the effective vegetation period in the southern mown meadows (Fig. 3, middle row).

E. frigida from wind-swept alpine heath has a habit that is strikingly different from that of the same species in subalpine meadow; but it is closely paralleled by *E. lapponica* which grows in exactly comparable sites (Fig. 3, top row).

Branching. The mode of branching is partly determined by the number of nodes available for

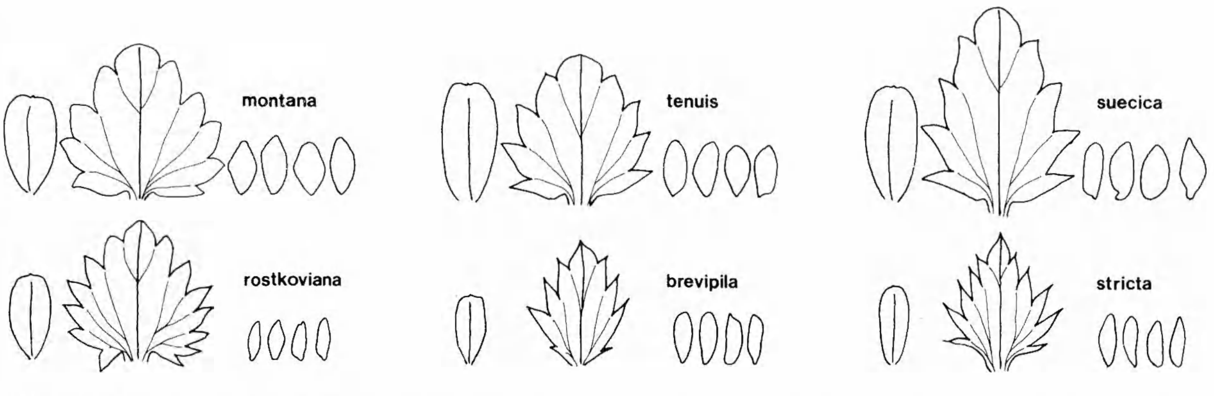

Fig. 4. Capsules, lower bracts, and seeds from *Euphrasia*. Upper row: taxa with few internodes; lower row: related taxa with many internodes (*E. hyperborea* has no obvious counterpart). The illustrated populations and specimens were randomly selected. Spontaneous material.

branching. Thus the northern plants in general are very sparsely branched. The average number of seeds necessary for survival in different habitats is another factor of obvious importance. The greater the number of branches, the greater will be the number of capsules and seeds. In the alpine environment with a wet spring and a short summer, the mortality is obviously much lower than in e.g. a dry sandy field in the south; there is no need for a great excess of seeds and the low degree of branching is thus no serious disadvantage for the population. A similar explanation may be hypothesized for the low number of branches in southern fen *Euphrasiae* in relation to plants from drier habitats (Karlsson 1974 Fig. 1). In addition, seed size may have a compensatory effect (cf. below).

Seeds, capsules, leaves

Large seeds, large emarginate capsules, and leaves with few obtuse teeth are found in all Swedish few-internoded *Euphrasiae*. This is still more striking when comparison with their closest relatives with many internodes is made (Fig. 4). It is extremely improbable that this association of four attributes over six pairs of taxa should be due to chance. The explanation for the association may be (1) that the characters have been selected for as forming a working unit, (2) that they are due to pleiotropic effects of a limited number of genes, or (3) that they are logically correlated. The first and third alternatives can easily be applied.

If the conclusion is accepted that a low number of internodes is an adaptation to a short vegetation period, the large seeds rich in stored nutrients may be seen as another adaptation. The seedlings from large seeds are themselves large (checked in cultivation), a great percentage of them will be established and rapid establishment will result in the flowering and fruiting stages being reached more rapidly. Under such circumstances the inherent disadvantage in producing few seeds, which is common to all the few-internoded taxa, may well be compensated for. Salisbury (1942 pp. 4–36) showed that seed size was related to habitat conditions, and concluded that large seeds are advantageous when rapid growth in the seedling stage is needed for survival.

Capsule size and form may be partially dependent on the number and size of seeds.

The fact that a low number of internodes is associated with few obtuse leaf teeth seems to be a case of logical correlation of characters. In few-internoded as well as many-internoded taxa there is a gradual transition along the shoot from leaves with few obtuse teeth nearest to the cotyledons, via leaves with many acute or acuminate teeth in the middle of the shoot, to leaves with few aristate teeth in the very top of the plant (Fig. 5). In the few-internoded plants the first flower is situated rather low down on this "scale" of leaf forms. When leaf form in *Euphrasia* is discussed the lower bracts are generally considered. Then the few-internoded taxa will of necessity be classified as having leaves with few obtuse teeth, the number of internodes and the leaf dentation being nothing but two directly related scales for describing flower position.

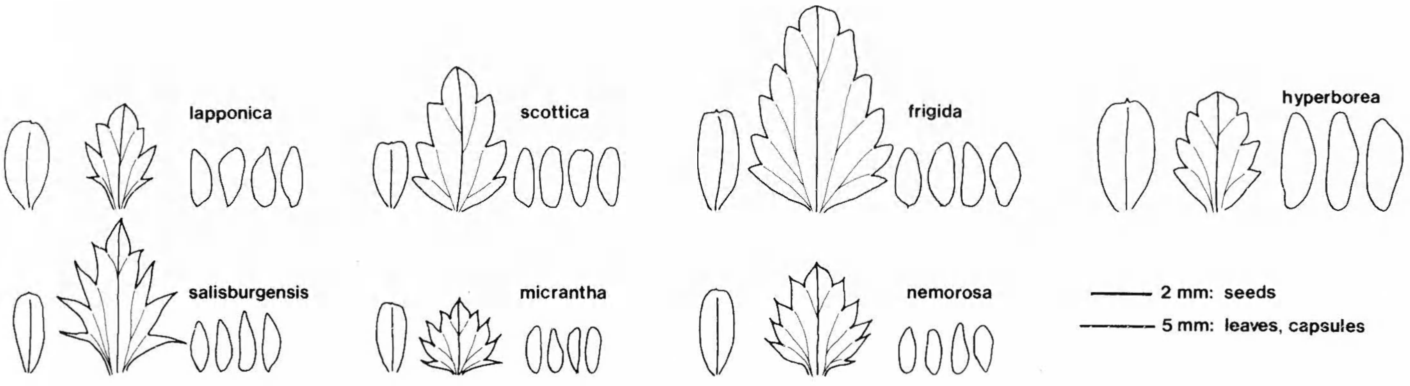

Fig. 4 (continued).

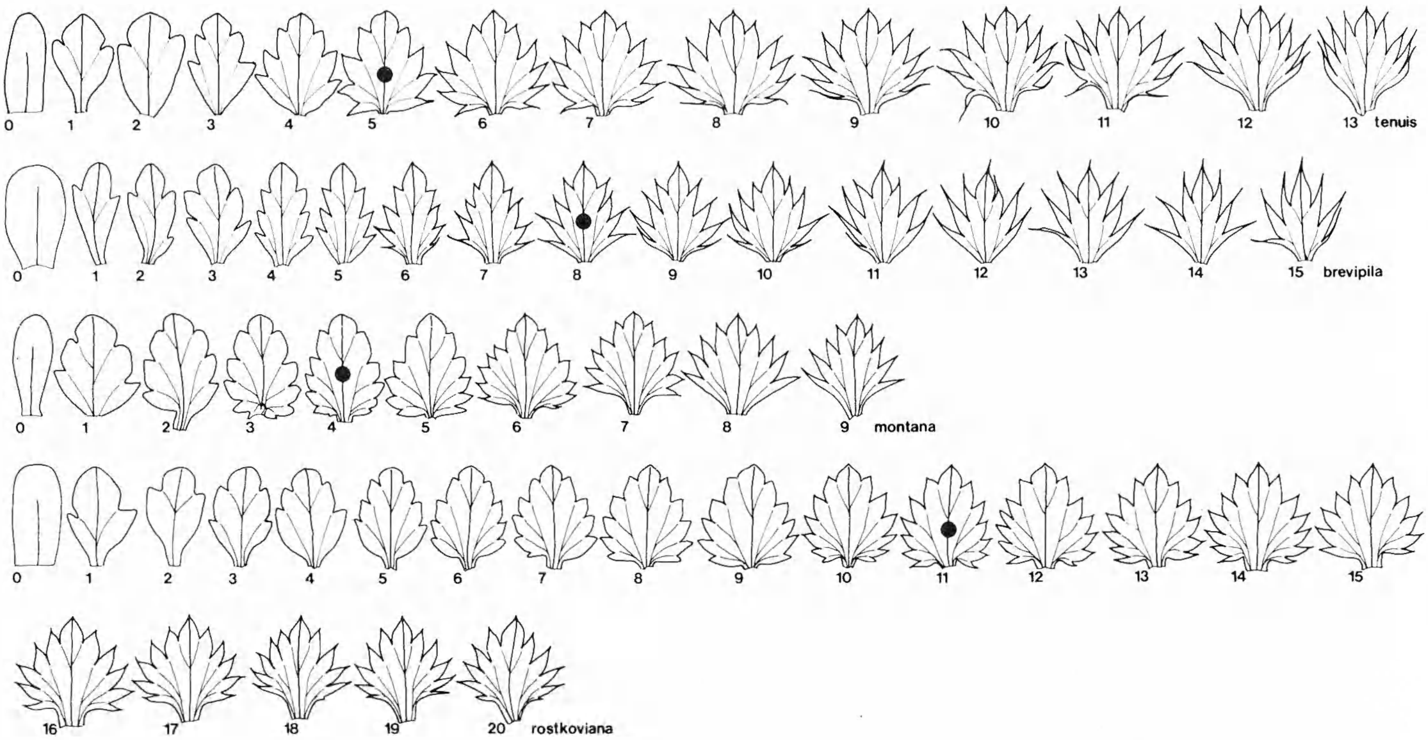

Fig. 5. Leaf series from four *Euphrasia* specimens selected at random; *tenuis* and *montana* are few-internoded, *brevipila* and *rostkoviana* corresponding many-internoded taxa. Numbers refer to nodes; the lowest leaf subtending a flower is marked. Magnification variable, leaf length being kept constant in all drawings.

Discussion

Valid species are expected to differ in several independent characters. Those just discussed cannot be regarded as such a set of characters, however. They are more correctly looked upon as parts of well-integrated adaptational complexes. Species in *Euphrasia* differing chiefly in habit and habitat-correlated characters should at once be suspected as being misclassified ecotypes in the Turesson sense (e.g. the example with *Hieracium umbellatum*, Turesson 1922). This has far-reaching consequences as length of internodes, node at which the lowest flower is situated, number of branches, shape of leaves, and size and shape of capsule are by tradition regarded as being among the most important taxonomic characters in European *Euphrasia* (Yeo 1972 p. 257).

TAXONOMIC IMPLICATIONS

Serious doubt about the prevailing species concept in *Euphrasia* has been arrived at via two independent ways of reasoning.

Some of the most often used taxonomic characters have been shown to be mutually associated and dependent on habitat. I consider that a number of the 46 *Euphrasia* species today recognized in Europe (Yeo 1972) would, on close examination turn out to be ecotypes in the Turesson sense, more properly recognized at an infraspecific level if at all (cf. the treatment of *Melampyrum* and *Rhinanthus* in Flora Europaea, Soó & Webb 1972).

A more satisfactory basis for the delimitation of taxa at the rank of species seems to be available when at least some of the following, fairly independent characters, coincide and differ between related taxa: flower size and colour, indumentum of leaves, general leaf form, habitat relationships, geographical distribution, and chromosome number. There are, however, quite a number of taxa that show good differentiation in this respect, but still do not stand the test of natural coexistence (p. 54). The extensive breakdown of differences by hybridization makes the species rank inappropriate even in these cases.

In my opinion the only taxonomic treatment that faithfully expresses the facts reviewed above is one which allows five species in Sweden, viz. *E. salisburgensis* (with two subspecies), *E. rostkoviana* (with three subspecies), *E. bottnica*, *E. micrantha* (with two subspecies), and *E. stricta* (with preliminarily six subspecies).

This taxonomy is an obvious break with tradition in the genus. However, although it is generally considered that the criteria on what constitutes a valid species may vary a little from group to group, the present species concept in *Euphrasia* may well be said to be erroneous. It leads to the recognition of at least six endemic species in NW Europe, a glaciated area with a very young flora. No mechanism like alloploidy, apomixis, or pronounced genetic drift, which may lead to rapid speciation, is known within the genus.

The aim of this paper is to give some fresh material to the old debate on the species concept in *Euphrasia*. The principles outlined here will be applied in a series of papers dealing with separate groups of Swedish *Euphrasia* in greater detail.

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APPENDIX

Data on the figures

Fig. 1. Full data on the populations, specified here by the author's collection numbers, will be given in a future publication.

Fig. 2. Means of five counts per locality; all material of the *E. stricta* group in GB, LD, S and UPS was utilized. The locality means were plotted on a map, from which the histograms here presented were constructed. For zone 200–210, only 60% of the material measured was used for the histogram. The data on length of vegetation period is taken from Lundqvist (1953).

Fig. 3. Author's collections (three exceptions). Province, parish, locality, and author's collection number given. Alpine heath: *frigida*, Jämtland Frostviken Mesklumpen (802); *lapponica*, Torne lappmark Pesisvare 17.8 1916 Samuelsson (BG). – Meadow: *frigida*, Jämtland Åre Saxvallsklumpen (780); *hyperborea*, Jämtland Åre Rundhögen (756); *suecica*, Got-

land Vallstena Alvne (735); *montana*, Västergötland Brunn Kälkared 6. 1939 Westfeldt (UPS); *tenuis*, Gotland Öja Lasses (737). – Fen: *frigida* var. *palustris*, Jämtland Åre Täljstensberget (773); *hyperborea*, Jämtland Frostviken Storlidfjället (809); *salisburgensis*, Gotland Hangvar Kvie (748); *stricta* var. *gotlandica*, Gotland Bäl 10.8 1938 E. Th. Fries (S); *brevipila*, Skåne Ramsåsa Ramsingegårdarna (105); *rostkoviana*, Skåne Träne Körning (21).

Fig. 4. Author's collections (five exceptions). Province, parish, locality, and author's collection number given; *montana*, Västergötland Brunn Kälkared 6. 1939 Westfeldt (UPS); *rostkoviana*, Skåne Dagstorp Dagstorps mosse (113); *tenuis*, Gotland Öja Lasses (737); *brevipila*, Skåne V Vram Ringleholm (36); *suecica*, Gotland Vallstena Alvne (735); *stricta*, Gotland Rute Fardume 28.8 1932 E. Th. Fries (S); *lapponica*, Torne lappmark Pesisvare 17.8 1916 Samuelsson (BG); *salisburgensis*, Switzerland Tessin 16.8 1967 Greuter & Hainard (OULU); *scottica*, Norway Hardanger Odda 30.7 1912 Selland (LD); *micrantha*, Skåne N Mellby Sandåkra (557); *frigida*, Jämtland Åre Handöl (772); *nemorosa*, Skåne Långaröd Sjököp (642); *hyperborea*, Jämtland Frostviken Storlidfjället (809).

Fig. 5. Author's collections (one exception). Province, parish, locality, and author's collection number given; *tenuis*, Gotland Öja Lasses (737); *brevipila*, Skåne V Vram Ringleholm (36); *montana*, Skåne S Sandby Kungsmarken 30.6 1897 Simmons (LD); *rostkoviana*, Skåne Dagstorp Dagstorps mosse (113).

Studies in African Cyperaceae XIV

The genus Hellmuthia Steud.

Richard Wheeler Haines and Kåre Arnstein Lye

Haines, R. W. & Lye, K. A. 1976 05 06: Studies in African Cyperaceae XIV. The genus Hellmuthia Steud. *Bot. Notiser 129*: 61–67. Stockholm. ISSN 0006-8195.

The morphology of *Hellmuthia (Scirpus) membranacea* is described and illustrated. This species has spikelets resembling the flowers of Scirpeae, but set between a pair of transversely arranged scales which are ciliate on the margins and strongly ciliate on the keels. It does not belong to Scirpeae, and should be included in Mapanieae. The genus *Hellmuthia* Steud. is reestablished and the new combination *H. membranacea* (Thunb.) R. Haines & K. Lye is coined.

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Scirpus membranaceus Thunb. (Fig. 1) is a striking South African coastal species described and figured by Clarke in the "Flora Capensis" (1901–2) and his "Illustrations of Cyperaceae" (1909) and again by Schönland (1922). It differs from other *Scirpus* species in its large heavy "spikelets", rounded woody fruits and peculiar "perianth", but has always been considered a true member of the Scirpeae. Nees (1835) transferred *Scirpus membranaceus* to *Isolepis,* Kunth (1837) transferred it to *Ficinia,* while Steudel (1855) classified it in a new genus *Hellmuthia* as *H. restioides* Steud.

The species has held a special position in the "synanthial theory" of Mattfeldt (1938) and his followers. Holttum (1948) and Schultze-Motel (1959), using Clarke's work as their source, believed it to indicate the way in which a mapanioid type of synanthium had become transformed into a single flower of scirpoid type. Bentham & Hooker (1883) suggested that *S. membranaceus* connected the two genera *Scirpus* and *Hypolytrum.* Haines (1966), again from Clarke's drawings, suggested that it should perhaps, be transferred from Scirpeae to Mapanieae. Clearly a new examination and assessment of this plant is required and a recent collection, Lye 6660, has provided several new details of its structure.

MORPHOLOGY AND ANATOMY

Scirpus membranaceus Thunb. is a robust tussocky perennial sedge with short woody rhizomes and grey strongly hairy roots. Culms 30–80 cm long and 1.0–2.5 mm thick, terete, glabrous; the central part of the culm consists of brown pith (aerenchyma) which is surrounded by 25–35 (in our material) vascular bundles; between the vascular bundles and the epidermis there is an area of thick-walled sclerenchyma which alternates with chlorenchyma (Fig. 2 A, B). Leaves up to 30 cm long, but usually much shorter, 1–3 mm wide, reniform to lunate (in section) with scabrid margins; the throat and lateral parts of the leaf-sheath membranous, light grey with reddish-brown dots, in older culms breaking up into a filigree pattern; the basal sheaths brown, shorter and thicker, almost scale-like. The leaf is dorsiventral with a single row of vascular bundles arranged in a crescentiform arc (Fig. 2 C, D). The adaxial epidermis-cells are larger than the abaxial. The scleren-


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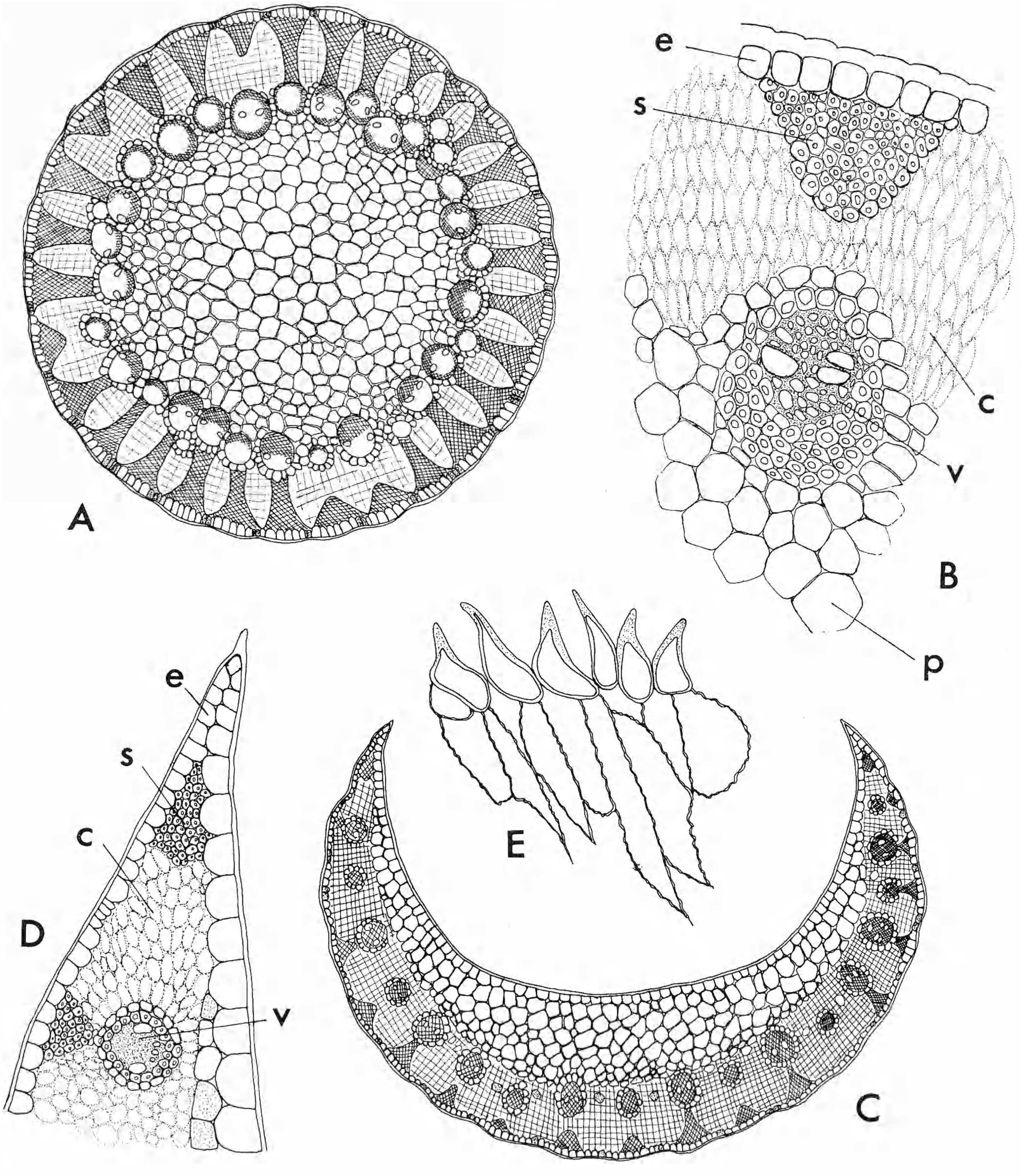

Fig. 2. *Hellmuthia membranacea*. – A: Section of culm, ×30. – B: Section through part of culm showing epidermis (e), sclerenchyma (s), chlorenchyma (c), parenchyma (p) and young vascular bundle (v), ×110. – C: Section of leaf, ×30. – D: Section through leaf-edge showing epidermis (e), sclerenchyma (s), chlorenchyma (c) and young vascular bundle (v), × 110. – E: Edge of cone bract from inflorescence showing minutely dentate margin. – All from Lye 6660. Drawn by Gerd Mari Lye.

Fig. 1. *Hellmuthia membranacea*. – A: Habit. – B, C: Inflorescence. – D: Base of shoot. – E: Innovation. – F: Cone of spikelets with basal prophyll (p). – G: Plan of spikelet and subtending cone bract (b). – H: Cone bract. – I: Spikelet. – J: Keeled scales of spikelet. – K: Base of spikelet. – L: Keeled scale. – M: Stamen. – N: Achene with filaments (f). – Drawn from Lye 6660.

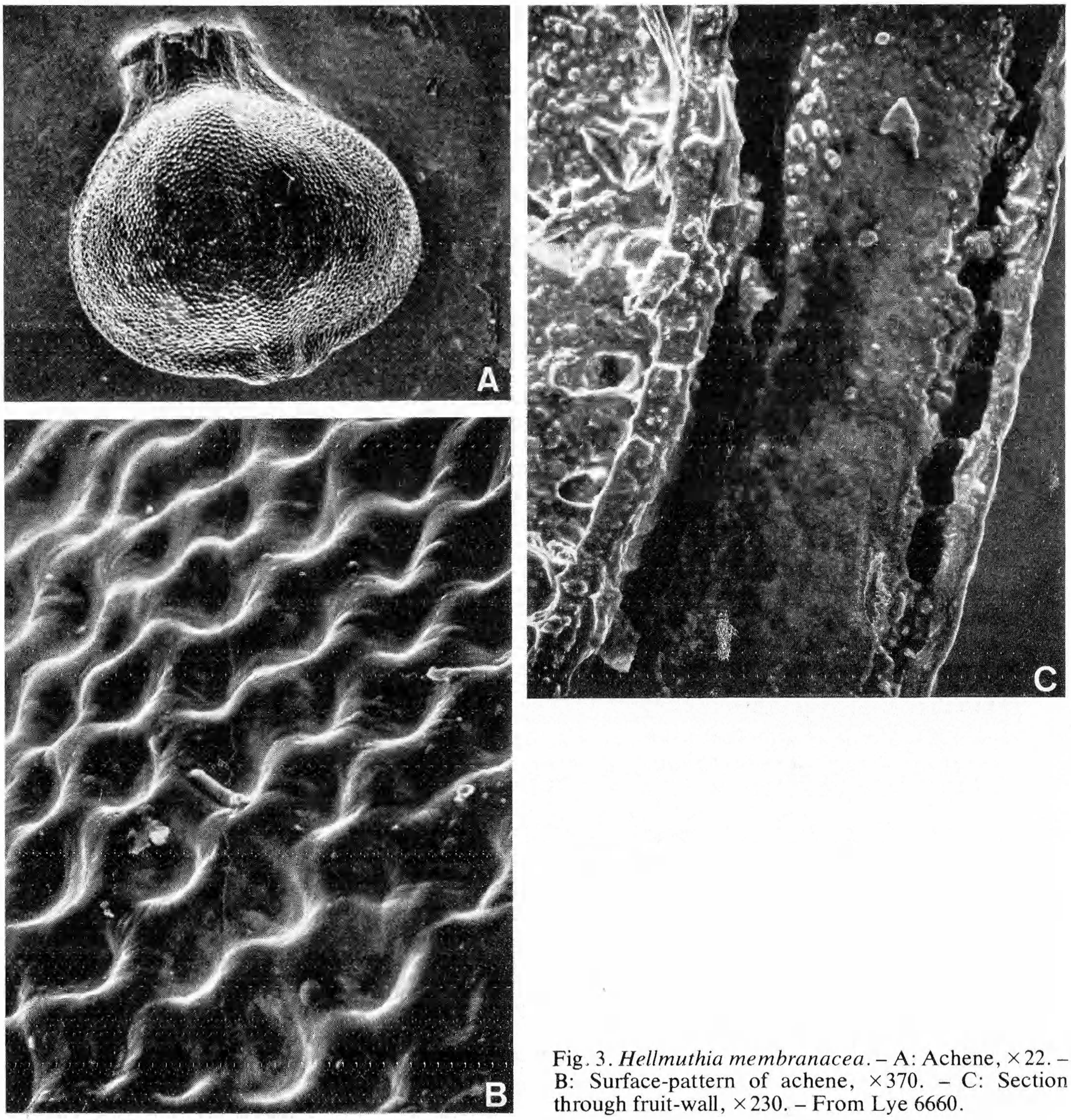

Fig. 3. *Hellmuthia membranacea*. – A: Achene, ×22. – B: Surface-pattern of achene, ×370. – C: Section through fruit-wall, ×230. – From Lye 6660.

chyma consists of small thick-walled cells which surround the vascular bundles or are situated below the abaxial epidermis opposite the vascular bundles.

Inflorescence a solitary cone or more commonly a condensed head of 2–10 sessile cones. Main inflorescence-bracts leafy with membranous base, usually 3 per inflorescence, more rarely 2–5, usually longer than the inflorescence; additional bracts are entirely membranous or with a green midrib. Cones 10–30 mm long and 6–10 mm wide, ovoid, obtuse; each cone has a wide, transversely wrinkled prophyll at its base and numerous closely imbricate scales spiralled round the cone axis. Scales 7–9 mm long and 4–5 mm wide, broadly ovoid with minutely dentate (Fig. 2 E) and torn margin, concave, membranous, light rusty-brown with dark reddish-brown dots, near the apex stiffer and darker. Each scale, even the lowest, subtends a single

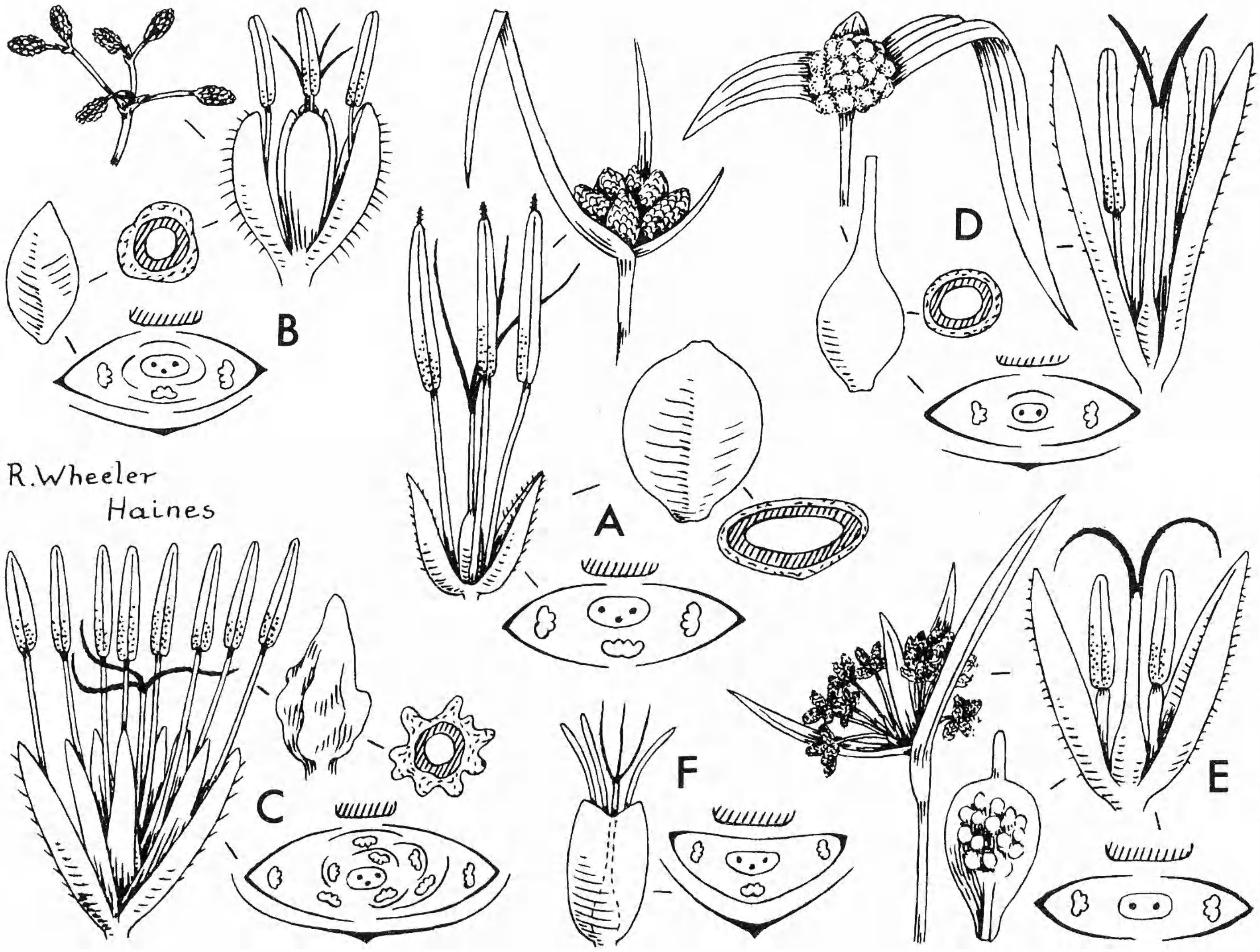

Fig. 4. *Hellmuthia* compared with other Mapanieae. – A: *Hellmuthia*; inflorescence, spikelet, plan, achene and section of achene. – B, C: *Thoracostachyum bancana* Kunz and *Scirpodendron costatum* Kunz (from Clarke 1909). – D, E: *Mapania rhynchocarpa* G. Lourougnon & J. Raynal and *Hypolytrum secans* (K. Schum.) J. Raynal (from Raynal 1968 a, b). – F: *Principia grandis* Uitt. (from Uitten 1935).

bisexual "flower" with 3 stamens and a sharply trigonous ovary with a 3-fid style. But whereas the upper "flowers" of the cone are naked the lower 4–6 have a membranous "perianth" at the base. Anthers 2.5–4.0 mm long and 0.3–0.5 mm wide, yellow, linear, ending in a triangular reddish-brown ciliate apex; filaments 7–9 mm long and 0.4–0.5 mm wide, pale, much flattened. Style 6–7 mm long, reddish-brown with style-branches 4–5 mm long.

Achene 2.2–2.6 mm long and 2.0–2.2 mm wide, dark greyish-black, almost circular in outline, but with a cuneate base; it is much flattened with hardly any trace of the original trigonous state of the ovary (Fig. 3 A). Its surface is marked by hollows and undulating ridges (Fig. 3 B). It falls with the stout filaments of the 3 stamens attached to its narrowed base. The achene wall has a 1-layered exocarp with a thick cuticula, a thick almost woody mesocarp and a thin endocarp (Fig. 3 C). In our material fruits were ripened only by the upper "flowers" without "perianths", those with "perianths" having failed to develop. Clarke's drawing, however, shows a ripening ovary in a "flower" provided with scales, so there is little doubt that all the "flowers" are potentially fertile.

Clarke (1909) figured "flowers" both with and without the "perianth", showing it as a pair of somewhat irregular folded keeled scales with toothed margins placed transversely. Schönland (1922) noted that "structures which most botanists would consider as prophylls were also occasionally found", but did not figure them. We have found the scales joined adaxially below, ciliate, not toothed, at the margins and strongly ciliate on the keels. They bear no resemblance to the true perianth members found in other species of *Scirpus* s. lat. They can, however, be matched precisely, particularly as regards the ciliation of the keels, in the inflorescences of Mapanieae (Fig. 4). *Principia* appears to be the only genus of Mapanieae in which the keels are not ciliate and *Chrysithrix* the only genus without keeled scales, though in *Scirpodendron* they are lacking in the upper "flowers" as in *Scirpus membranaceus* (Kern 1962). Otherwise the keeled scales are uniform throughout the tribe.

The *Cyperus* type embryo is figured by van der Veken (1965) who classifies our plant in *Scirpus* sect. *Holoschoenus* (Link) Koch, but mentions the possibility of its being a *Ficinia,* as suggested by its narrow fruit base and geographical distribution. In *Mapania* and *Hypolytrum,* the only genera of Mapanieae in which the embryo is known, it is extremely immature, resembling that of a *Juncus* (Juguet 1970). But Didrichsen (1897) found such an embryo in *Cladium,* whereas most Rhynchosporeae have advanced embryos (Verbelen 1970). Possibly immature embryos are associated with slow germination.

TAXONOMIC POSITION

The tribe Mapanieae or Hypolytreae, as it is sometimes called, is separated from Scirpeae because of its two outer hypogynous scales, transverse, folded and sharply keeled, ciliate or spinulose on the keel, free or sometimes connate on the adaxial side.

Mapanieae with relatively simple spikelets were placed together as Mapaniinae by Pfeiffer (1925). *Thoracostachyum* and most species of *Hypolytrum* have panicled inflorescences (Fig. 4). *Mapania* and a few species of *Hypolytrum* have condensed heads (Nelmes 1955, Raynal 1968 b). All have the paired, ciliate–keeled basal scales, each subtending a solitary stamen, but in some species the scales are joined (Koyama 1959, 1961, Kern 1962). In *Hypolytrum* these are usually the only scales and stamens in the spikelet, but there may be a third unkeeled abaxial scale subtending a third stamen. In *Mapania* and *Thoracostachyum* there are, besides the 2 or 3 scales subtending stamens, 2 or 3 additional empty scales above. All the scales and stamens are crowded on a very short rachilla ending in a naked ovary and 2- or 3-fid style. In all genera the fruit is a woody-walled rounded nut. We suggest that *Scirpus membranaceus* should be placed in Mapaniinae because of its keeled and ciliate hypogynous scales and thick-walled achene and the genus *Hellmuthia* Steud. be reestablished for this species. It differs in its habitat from most members of the group which grow along the poorly lit margins and on the floors of damp forests, especially along streams, and are slow-growing broad-leaved plants (Raynal 1968 a), but it resembles certain South American species of *Hypolytrum* (Koyama 1967, 1970).

NEW COMBINATION

Hellmuthia membranacea (Thunb.) R. Haines & K. Lye, comb. nov. Basionym: *Scirpus membranaceus* Thunb. in Prodr. Plant. Capensium p. 17 (1794). Syn. *Hellmuthia restioides* Steud. in Syn. Pl. Glum. 2, p. 90 (1855); *Isolepis membranacea* Nees in Linnaea 9, p. 291 (1835) and *Ficinia membranacea* Kunth in Enum. 2, p. 252 (1837).

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A nomenclatural note

Aponogeton afroviolaceus K. Lye, nom. nov.

Basionym: *A. violaceus* K. Lye in Norw. Journ. Bot. 18, p. 187 (1971) and Bull. Jard. Bot. Nat. Belg. 43, p. 205 (van Bruggen 1973), non *A. violaceus* Lagerh. in Svensk Bot. Tidskr. 14, p. 168 (1920).

I would like to thank Dr T. Yamashita of Tokyo who has found Lagerheim's description of *A. violaceus* hidden away in an embryological paper by Afzelius. The name *A. violaceus* Lagerh. has been overlooked by the compilers of Index Kewensis, by myself (Lye 1971) and by the world monographer of *Aponogeton* Dr van Bruggen (1968, 1973).

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On pollen of Campanulaceae

III. A numerical taxonomic investigation

Anita Dunbar and Hans-Georg Wallentinus

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A numerical method has been applied to the study of the pollen grains of 38 species of Campanulaceae chosen as being representative of the different morphological types of the family. The recorded factors are weighted as to presumed taxonomic value and the percentual similarity is calculated. The result is presented as a dendrogram. Species of Goodeniaceae and Sphenocleaceae have been included for comparison. The method used demonstrates the compound pattern consisting of more than one type of fine structure of the sexine. Palynological evidence suggests a new circumscription of the subfamily Cyphioideae.

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Hans-Georg Wallentinus, Royal Institute of Technology, Department of Land Improvement and Drainage, S-100 44 Stockholm 70, Sweden.

A numerical method has been used to study the pollen grains of 38 species of Campanulaceae and a few species of Goodeniaceae and Sphenocleaceae. The investigation is based upon information gained in Dunbar (1975 a, b). Since then further species of the genera *Githopsis, Adenophora, Nemacladus, Isotoma* and *Lobelia* have been examined using scanning and transmission electron microscopy. In general the pollen grains of *Githopsis, Nemacladus* and *Isotoma* show a close relationship to those investigated in Dunbar (1975 a, b) while in *Adenophora* some difference is evident. The *Lobelia* species show similarity either to the reticulate-striate pattern of *Lobelia dortmanna* or to the strictly striate type of sexine of *Lobelia zeylanica*.

In Dunbar (1975 a, b) 80 species of Campanulaceae were investigated while in the present paper only one of two or more similar species of a genus is represented. Most authors divide the family into three subfamilies: Campanuloideae, Cyphioideae and Lobelioideae. This subdivision will be used in the present paper.

METHOD

This investigation is to be regarded as a test of the suitability of using pollen grain characters in numerical taxonomy. Since characters of the surface ultrastructure only are included, the number of characters is limited. The characters of the pollen grains are given a numerical value, viz. 1, 3, or 6 (Table 1) according to their presumed taxonomic value. This series was employed since the computer program applied was originally designed for use in plant sociology where these values were used. The aperture condition is considered to be the most important together with the presence or absence of spinules and verrucae.

The taxa (operational taxonomic units, OTUs, of this investigation) are compared as to weighted percentual similarity according to formula (1), where P is the per cent of similarity.

$$P = 100\,(1 - \frac{\Sigma\Delta t}{\Sigma t_i + \Sigma t_j}) \qquad (1)$$

t is the numerical value of each factor (Table 1) and $\Sigma\Delta t$ is the difference in t between two compared OTUs. i and j are the two OTUs compared. Σt is the sum of the numerical values of the t's for each OTU. These values are given in Table 1.

Some examples of the way P is calculated will be given here. *Campanula rapunculoides* and *C. uniflora* have P=90%, $\Sigma\Delta t$ is 2 (1+1, with the differences in factors 11 and 12), the sum of the t's is 20 (10+10).

Table 1. The numerical values of characters used. Taxon numbers refer to Fig. 1.

Factor	Taxon number	3–4 porate	6 porate	12 porate	3 colporate	5–6 colporate	3 colpate	6–10 colpate	spinules	verrucae	absence of spinules/verrucae	ridges	ridges, top end bent upwards	fingerlike structures	protrusions	reticulate, low relief	reticulate, high relief	irregular ridges, atypical	perforated tectum	pits	granulate	striate	number of factors	Σt
Factor number		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
Campanulaceae																								
Campanula rapunculoides	1	6	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
C. uniflora	2	6	.	.	.	.	.	.	3	.	.	.	1	.	.	.	.	.	.	.	.	.	3	10
C. alliarifolia	3	6	.	.	.	.	.	.	3	.	.	1	.	.	1	.	.	.	.	.	.	.	4	11
C. carpatica	4	6	.	.	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	.	3	10
C. speciosa	5	6	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	3	10
C. trachelium f. *alba*	6	6	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	.	3	10
C. americana	7	.	.	6	.	.	.	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	3	10
Asyneuma canescens	8	6	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
Phyteuma scheuchzerii	9	6	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
Symphyandra armena	10	6	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
S. hofmannii	11	6	.	.	.	.	.	.	3	.	.	1	.	.	1	.	.	.	.	.	.	.	4	11
Edraianthus serpyllifolia	12	6	.	.	.	.	.	.	3	.	.	1	.	.	1	.	.	.	.	.	.	.	4	11
Wahlenbergia denticulata	13	6	.	.	.	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
W. krebsii	14	6	.	.	.	.	.	.	3	.	.	1	.	.	.	1	.	.	.	.	.	.	4	11
W. undulata	15	6	.	.	.	.	.	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	3	10
Adenophora sp.	16	6	.	.	.	.	.	.	3	.	.	1	.	.	1	.	.	.	.	.	.	.	4	11
Jasione montana	17	6	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	3	10
Roella sp.	18	6	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	3	10
Githopsis specularioides	19	.	6	.	.	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	3	10
Prismatocarpus pedunculatus	20	6	.	.	.	.	.	.	3	1	.	.	.	.	1	.	.	.	.	.	.	.	4	11
Platycodon grandiflorum	21	.	.	.	.	6	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
Campanumoea lancifolia	22	.	.	.	6	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	3	10
C. maximowiczii	23	.	.	.	.	6	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	.	3	10
Canarina eminii	24	.	.	.	6	.	.	.	3	1	.	.	.	.	1	.	.	.	.	.	.	.	4	11
C. abyssinica	25	.	.	.	6	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	3	8
Ostrovskia magnifica	26	.	.	.	.	.	.	6	.	1	.	.	.	.	1	.	.	.	.	.	.	.	3	8
Cyananthus sp.	27	.	.	.	.	.	.	6	.	1	.	.	.	.	.	.	.	.	1	.	.	.	3	8
Codonopsis sp.	28	.	.	.	.	.	.	6	3	1	.	.	.	.	.	1	.	.	.	.	.	.	4	11
Cyphia sp.	29	.	.	.	6	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	1	.	3	13
Parishella californica	30	.	.	.	.	.	.	6	3	.	.	.	.	.	.	.	.	.	.	1	.	.	3	10
Nemacladus rubescens	31	.	.	.	6	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	3	10
Cyphocarpus sp.	32	.	.	.	6	.	.	.	.	.	6	.	.	.	1	.	1	.	.	.	.	.	4	14
Laurentia petraea	33	.	.	.	.	.	6	.	.	.	6	.	.	.	1	.	1	.	.	.	.	.	4	14
L. carnosula	34	.	.	.	6	.	.	.	.	.	6	.	.	.	1	.	.	.	.	.	.	1	4	14
Lobelia dortmanna	35	.	.	.	.	.	6	.	.	.	6	.	.	.	.	.	1	.	.	.	.	1	4	14
L. zeylanica	36	.	.	.	.	.	6	.	.	.	6	.	.	.	.	.	.	.	.	.	.	1	3	13
Isotoma anemonifolius	37	.	.	.	6	.	.	.	.	.	6	.	.	.	1	.	1	.	.	.	.	.	4	14
Downingia elegans	38	.	.	.	6	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	1	3	13
Goodeniaceae																								
Scaevola sp.	39	.	.	.	6	.	.	.	3	.	.	.	.	.	.	.	.	.	1	.	.	.	3	10
Sphenocleaceae																								
Sphenoclea zeylanica	40	.	.	.	6	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	1	.	3	13
Frequency		18	1	1	11	2	3	4	28	6	9	12	1	1	15	6	4	2	2	2	2	4	21	63

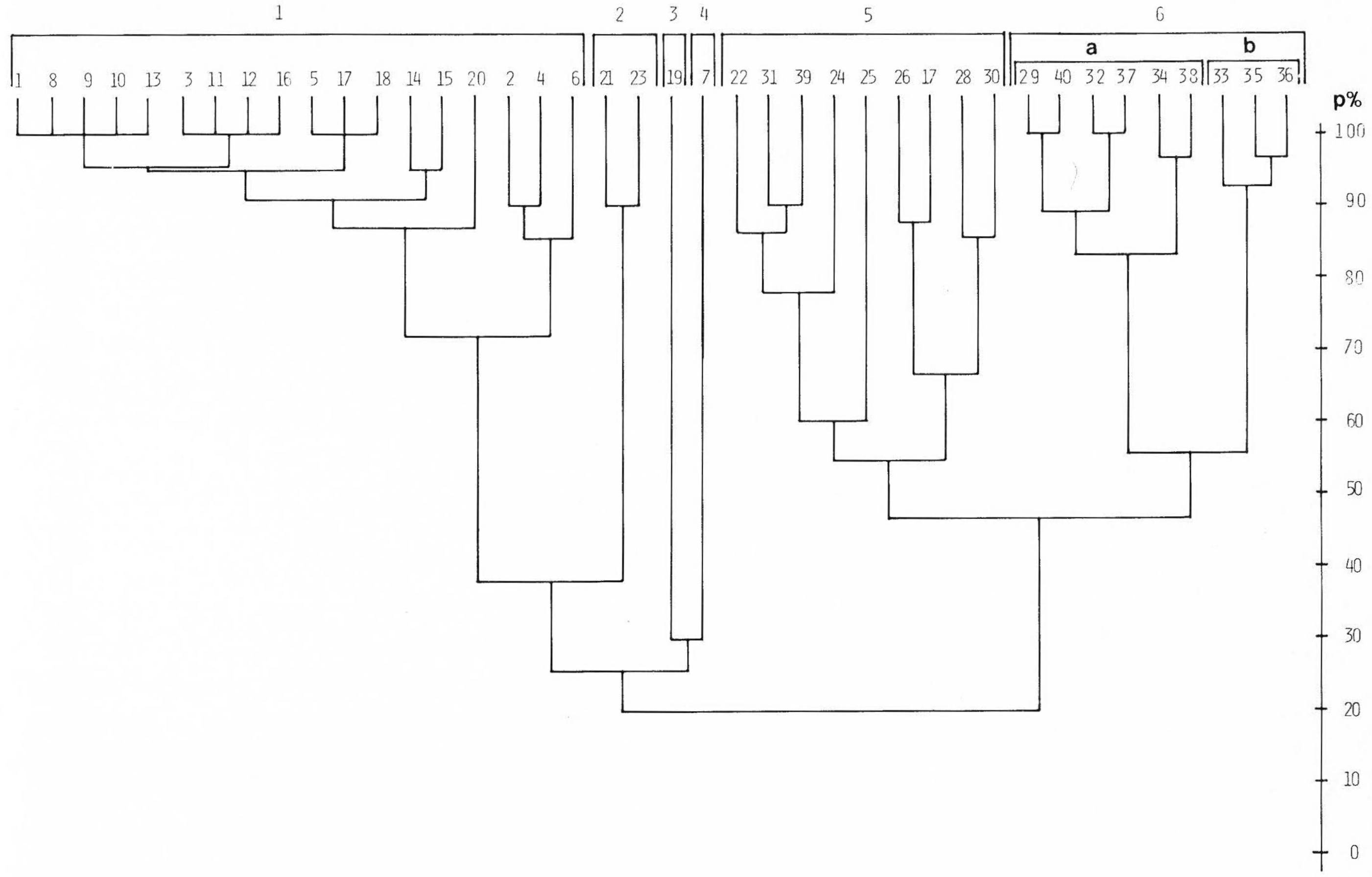

Fig. 1. Dendrogram of representatives of Campanulaceae, Goodeniaceae and Sphenocleaceae, based on pollen grain characters.

90% could be directly calculated from formula (1). *Platycodon grandiflorum* and *Campanumoea lancifolia* differ in aperture condition and $\Sigma\Delta t$ will thus be as high as 12 (6+6 for factors 5 and 4 resp.), sum of the t's is 20 (10+10) and the similarity is 40%. *Sphenoclea zeylanica* and *Parishella californica* has $P=0$ since $\Sigma\Delta t$ is 23 (6+6+3+6+1+1) and the sum of the t's is also 23.

All taxa are compared in this way. The two most similar OTUs are then connected in a diagram (Fig. 1) at the level indicated by P. In the first step several taxa are found to be identical as to the factors measured. An example of this is *Asyneuma canescens*, *Phyteuma scheuchzerii*, and *Symphyandra armena*. These species are connected at $P=100\%$. In the next step the two combined OTUs are treated as a new OTU containing *all* the characters from the two "parents". For example, the combination *Campanula rapunculoides* and *C. alliarifolia* has $P=95\%$. The new OTU will contain the same factors as *C. alliarifolia*. If, on the other hand, *C. rapunculoides* and *C. uniflora* had been combined ($P=90\%$) the new OTU would have added one factor and the sum of t would have increased from 10 to 11.

After this primary combination, the new OTU is considered together with all the other OTUs and again the most similar OTUs are combined and connected as in Fig. 1. The procedure is continued until only one OTU remains, comprising all taxa and all factors.

RESULTS AND DISCUSSION

At the 50% level the dendrogram could be divided into six groups (Fig. 1). Groups 1–4 enclose genera and species of Campanuloideae, group 5 of Campanuloideae and Cyphioideae while group 6 consists of species and genera belonging to Cyphioideae and Lobelioideae. Group 1 encloses all the 3–4-porate pollen grains, while 6- and 12-porate pollen grains belong to groups 3 and 4 respectively. The 5–6-colporate pollen grains of the family belong to group 2, and due apparently to similarities in characters which have been given lower value they are connected to the 3–4-porate group at the 37% level. However the 6- and 12-porate grains only show a 30% similarity to the 3–4-porate group. Group 5 encloses 6–9-colpate and 3-colporate pollen grains with spinules/verrucae. Group 6 consists of 3-colpate–colporate pollen grains lacking spinules/verrucae.

The method demonstrates the compound pattern consisting of two types of fine structure in the sexine (Dunbar 1975 a, b) in the species 3–16. They are distinctly recognized from the clusters of the species 1–13 with one component of the compound pattern and also from the clusters of the species 5–18 containing the other component of the compound pattern (Fig. 1).

As regards the suggested line of evolution of the fine structure from ridges to finger-like elements (see Dunbar 1975 b p. 118, Fig. 9) the presumedly more advanced patterns in species 2 and 4 together with the atypical pattern in species 6 show a similarity of 72% to the rest of the species in group 1.

A similarity of only 20% connects the porate pollen grains with the colpate–colporate grains (except group 2). The 3–9-colpate and 3-colporate pollen grains are divided into two groups with a similarity of 47%. In group 5 rather different characters of lower values are represented, no species being joined at the 100% level (Fig. 1). Group 6, on the other hand, shows a slightly higher degree of similarity with two subgroups, (a) and (b); the species of subgroup (a), 29–38, characterized by 3-colporate apertures, the species of subgroup (b), 33–36, by 3-colpate apertures.

The suggestion in Dunbar (1975 b) that Cyphioideae provides a link between the two other subfamilies in Campanulaceae, Campanuloideae and Lobelioideae is supported by the results in the present investigation. On the other hand, with regard to homogeneity the delimitation of Cyphioideae is, from a palynological point of view, open to discussion. The species 30 and 31, *Nemacladus rubescens* and *Parishella californica*, are similar to some genera of Campanuloideae rather than to the genus *Cyphia*. With regard to pollen morphology they could be removed from Cyphioideae to Campanuloideae, while 32 *Cyphocarpus* (Cyphioideae), strongly resembling for example *Isotoma anemonifolius* (Lobelioideae), could be placed in the subfamily Lobelioideae.

The families Goodeniaceae and Sphenocleaceae are closely connected to Campanulaceae. This may be due to the fact that only surface ultra structural characters and no characters revealed by TEM (transmission electron microscopy) are included in this investigation. Further TEM investigations may give evidence of a less close similarity between the three families.

As different factors have been given different numerical values the factors with higher values will often be determining in separating the groups. But within the groups factors with low values and intermediates between such factors will be determining.

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Meiosis in Greek Brassica of the oleracea group

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Meiosis has been studied in *Brassica cretica* Lam. ssp. *cretica* and ssp. *nivea* (Boiss. & Spr.) Onno. Plants grown from spontaneous seed and experimental hybrids were investigated. Almost all had 2n=18. Only 6 out of over 1,000 F_1 and F_2 hybrids showed deviating chromosome number in root-tip mitosis. At M I quadrivalents were observed in several cases, other types of disturbances being rare. At A I, cells with bridges and/or laggards were observed. The interpretation of these disturbances is discussed. In the material as a whole no significant correlation between meiotic disturbances and pollen stainability was found. The presumed nature of the breeding barriers is discussed.

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Investigations on meiotic behaviour in cultivated varieties of *Brassica oleracea* L. as well as in spontaneous material have been carried out by Catcheside (1937), Wills (1966), Mizushima (1968, 1969), Zdráhalová (1969), Curran (1970), Sampson (1970), and others. This investigation forms part of a more comprehensive study that aims at elucidating the biological and phytogeographical relationships between Mediterranean taxa of the *Brassica oleracea* group.

The aim of this particular investigation was to elucidate: (1) to what extent meiotic irregularities occur in natural populations of *B. cretica* Lam.; (2) the effects of these irregularities on male fertility; and (3) meiotic behaviour in F_1 offspring representing crosses within and between taxa. Other indications of hybrid vigour and fertility were also observed: seed germination, vegetative development, pollen stainability and seed setting.

THE BRASSICA CRETICA COMPLEX

The material treated belongs to sect. *Brassica* in a limited sense, i.e. the 18-chromosome group of species closely related to *Brassica oleracea* L. The *B. cretica* complex occurs in Greece in the Ionian Islands, Peloponnisos, Attica, Crete, the Aegean islands and peninsulas northwards to Athos, and in the southwestern coastal parts of Turkey. The complex as a whole is recognized by the shrubby habit and glabrous, stiff, fleshy leaves without pointed lobes. The populations inhabit cliffs or small rocky islands and are generally small, i.e. less than 1,000 individuals, some even consisting of less than 50 individuals.

The variation within the *B. cretica* complex is of two types: regional variation between forms from parts of Crete and Peloponnisos and those from the rest of the area, and considerable local variation between single populations or groups of populations. Local variation is especially pronounced between isolates in the Kikladhes. The variation is so irregular, however, that we cannot accept taxonomic rank for any of the S Aegean forms despite the decidedly deviating appearance of some of them. Some of these forms have been referred to as *B. aegaea* Heldr. & Hal. A detailed report on the variation pattern and a formal taxonomic treatment will be published separately. We accept the following two subspecies:

B. cretica Lam. ssp. **cretica**

Leaves ± short-stalked, either lobed basally or simple, decurrent on the petiole, usually semi-amplexicaul. Flowers yellow or rarely cream-coloured. Ornamentation of seeds varied but with the meshes never as distinct as in ssp. *nivea*.

Greece: Ionian Islands, coastal localities of Peloponnisos and Crete, the Aegean area. Turkey: The SW parts.

B. cretica Lam. ssp. **nivea** (Boiss. & Spr.) Onno

Leaves ± long-stalked, if lobed only on the long-stalked lamina, sometimes decurrent on the petiole, usually not semi-amplexicaul. Flowers white, small. Seed with a distinct large-meshed reticulum.

Greece: Parts of Peloponnisos, mountain and gorges of W Crete.

Intermediates between the subspecies occur on the NW coast of Crete and in some localities in the S part of Peloponnisos. There are several such populations with the same combination of *cretica*-like lobed leaves, *nivea*-type seed pattern and small, cream-coloured flowers.

MATERIAL AND METHODS

Our experiments include 1 population of the above-mentioned intermediates, 4 populations of ssp. *nivea* and 19 populations of ssp. *cretica*. The material originates from different parts of the area of distribution with several different types of the Kikladhes isolates represented. Some of the populations chosen are situated close together and are morphologically similar (Fig. 1). Seed was collected in the field and sown in the greenhouses at the Department of Plant Taxonomy, Lund, Sweden.

Meiotic preparations were made according to the usual acetic-orcein method. Unfixed buds were used. The coverslips were removed with Arcton 12 (Swedish ICI, Örebro, Sweden). Meiotic investigations were made on PMCs only.

Mitotic preparations were made from root tips fixed in the Navashin-Karpechenko fixative. The root tips were sectioned and stained in crystal violet. In some cases root tips were fixed in Carnoy, stained in Feulgen and squashed.

Male fertility was estimated by calculating the percentage of stainable pollen after staining in cotton blue. Several independent calculations were made on each individual, each calculation being based on 500 pollen grains. The maximum value of these calculations was used.

For the crossings, 2–5 flowers were emasculated on each plant, isolated in a pergamine bag and left for about one week before pollination. After pollination the flowers were again isolated and left in the bag until the seeds were harvested.

Each individual was given a number composed of a population number or F_1 family number, followed by an individual number. The code to the numbers is given in Appendices 1 and 2.

RESULTS

The somatic chromosome number 2n=18 was found in all plants originating from spontaneous seed. In 6 out of over 1,000 F_1 and F_2 plants representing interpopulational crosses of ssp. *cretica* and of ssp. *nivea* deviating chromosome numbers were found, viz. 2n=17, 27 and 36. Endopolyploidy and aneusomaty were often observed, but not sufficiently investigated to allow an estimation of definite frequencies to be made. The mitotic chromosomes of the diploid complement are fairly similar, being metacentric to submetacentric and about 4μ long. The chromosome set includes one pair of satellited chromosomes.

Since our main aim was to check the chromosome numbers we nearly always used the quick and reliable method of sectioning root tips. The preparations obtained by this method are usually not suitable for the analysis of chromosome morphology and we have consequently very limited information on it.

Meiosis

Plants grown from spontaneous seed

Twenty plants of ssp. *cretica* and 3 of ssp. *nivea* were investigated. An average of 68 cells/individual were analysed at M I, 149/individual at A I and 35/individual at M II.

At diplotene–diakinesis associations of two bivalents were frequently found. In some cells two such "quadrivalents" were observed. At

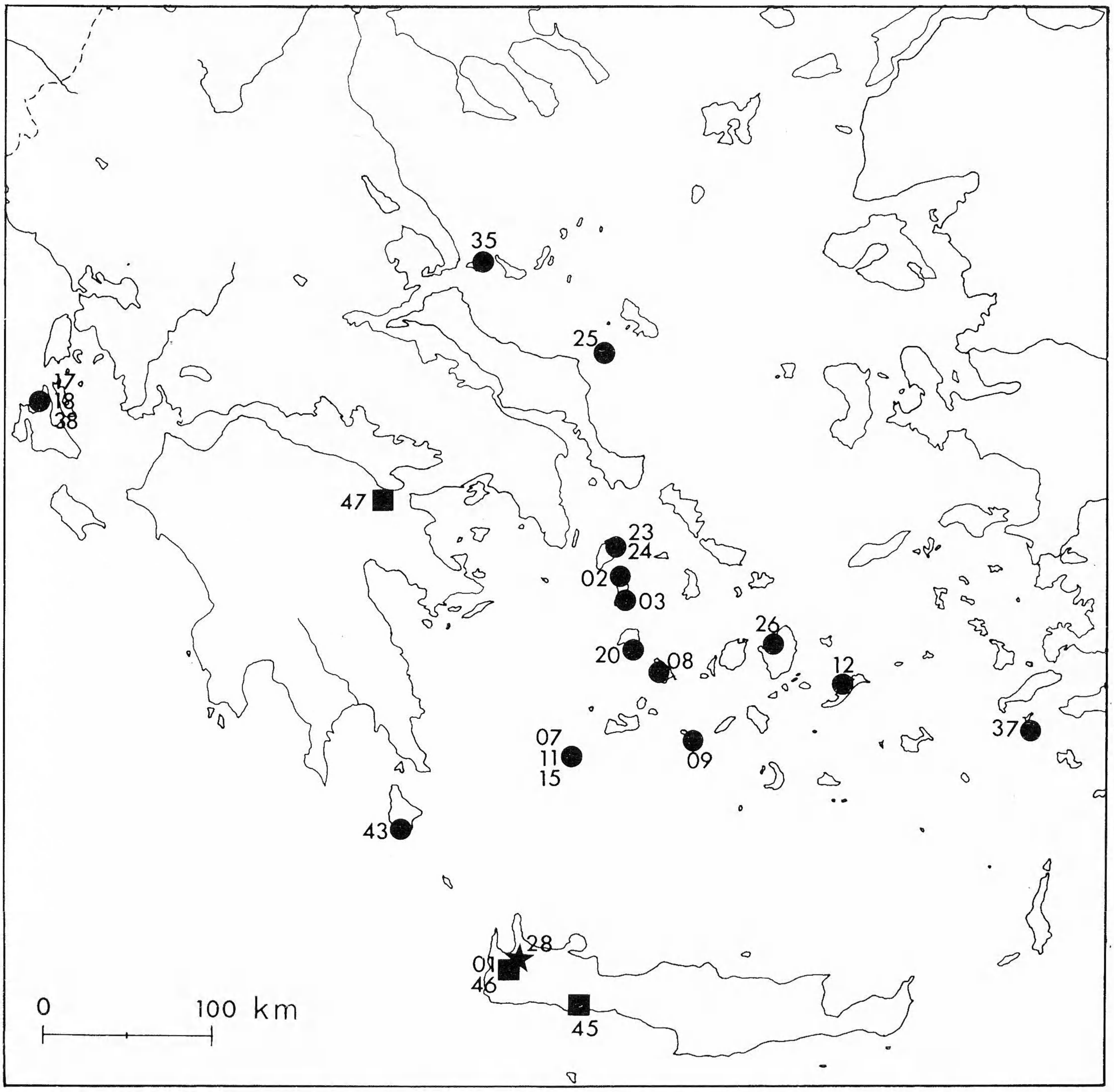

Fig. 1. Collection sites for the populations investigated. Dots indicate populations of *B. cretica* ssp. *cretica*, squares populations of *B. cretica* ssp. *nivea*, and the star an intermediate population. Exact localities are given in the Appendix.

M I, one quadrivalent was found in the cells of 10 out of a total of 23 individuals investigated. In no instance were two quadrivalents observed. The frequency of cells with one quadrivalent varied between plants from 1% to 39%. Cells with two univalents were seldom observed, viz. only 1–4% in 6 individuals.

At A I the most frequent disturbance was the formation of bridges usually without visible fragments. Bridges were observed in 16 out of 23 individuals, in two of these at high frequencies, viz. 18% and 6% respectively. In addition lagging chromosomes and bridges with fragments were observed at A I. No significant correlation exists between disturbances at M I and A I (r=0.20).

M II was investigated only to check on the amount of non-disjunction at A I and in 4 plants only was non-disjunction observed.

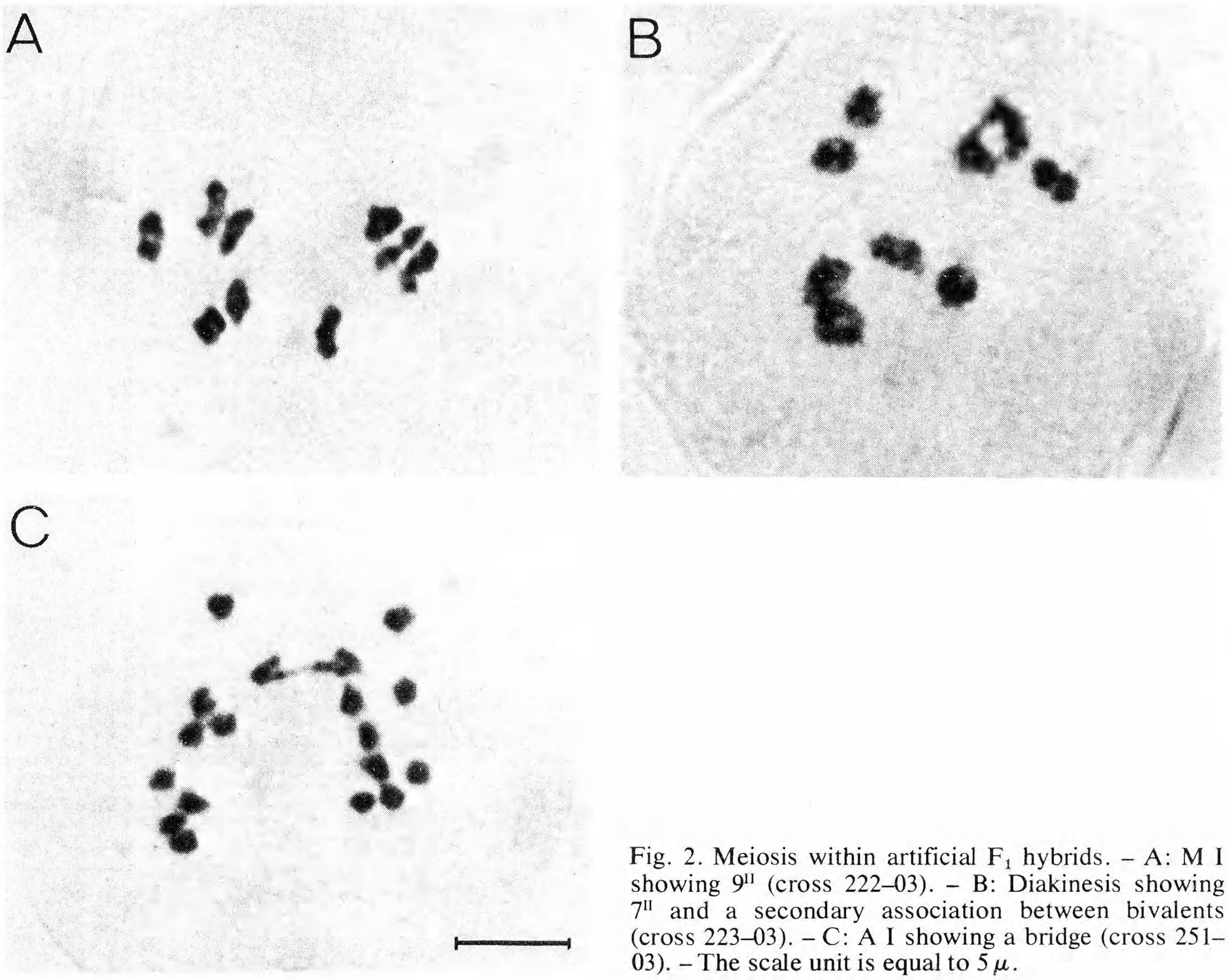

Fig. 2. Meiosis within artificial F_1 hybrids. – A: M I showing 9^{II} (cross 222–03). – B: Diakinesis showing 7^{II} and a secondary association between bivalents (cross 223–03). – C: A I showing a bridge (cross 251–03). – The scale unit is equal to 5 μ.

F_1 hybrids

A total of 64 plants was investigated. The number of cells per plant examined at each stage was roughly as for the wild material. Meiotic behaviour seems to be similar in all F_1 hybrids whether they are crosses within or between taxa. In the following report all F_1 hybrids have been lumped together.

The most conspicuous feature of the M I stage was the frequent occurrence of one quadrivalent. In the earlier stages, viz. diplotene–diakinesis, there were considerably more cells with one quadrivalent than at M I. Obviously many apparent quadrivalents are in fact secondary associations without chiasma formation. These secondary associations break up into bivalents during late diakinesis–M I. In a few cases two quadrivalents/cell were observed in the premetaphase stages but never at M I. In a total of 35 out of 54 individuals cells with one quadrivalent were observed. The frequency of such cells/individual varied from 1% to 23%. In 28 individuals cells with $8^{II}+2^{I}$ were observed. The highest frequency of cells with univalents within an individual was 8%. Other types of M I disturbances were very rare.

At A I the most frequent type of disturbance was the formation of chromatin bridges (Fig. 2C), usually not associated with fragments. In 41 of 54 F_1 plants investigated some cells with bridges were found, the frequency of such cells varying from 0.5% to 10%. Few cells with bridges and fragments were noted, the maximum frequency being 2% found in 10 plants. One (seldom more) laggard per cell occurred in cells from 23 plants but the maximum was only 2%.

There was no significant correlation between

Table 1. A survey of meiosis in plants of natural origin as well as in various F_1 hybrids. PS indicates pollen stainability (%), n the number of cells analysed, BF bridge with visible fragment, B bridge without visible fragment and OI other irregularities.

Code	PS	MI					AI							MII			
		9^{II}	$1^{IV}+7^{II}$	$8^{II}+2^{I}$	OI	n	Laggard		Bridge		OI	Normal	n	9+9	10+8	11+7	n
							1	2	BF	B							
WILD MATERIAL																	
B. cretica ssp. **cretica**																	
02–01	87	18	.	.	.	18	.	.	.	2	.	17	19	2	.	.	2
02–07	95	.	.	.	.	.	.	.	.	.	.	13	13	108	1	.	109
03–01	97	141	.	2	3	146	2	1	1	5	.	185	194	23	1	.	24
07–03	99	110	.	1	.	111	.	.	.	1	.	151	152	.	.	.	.
09–01	99	7	.	.	.	7	2	.	.	1	.	161	164	.	.	.	.
11–02	99	109	4	.	.	113	.	.	.	.	.	.	.	.	.	.	.
12–02	99	22	.	.	.	22	5	.	1	3	.	370	379	16	.	.	16
12–03	95	50	32	.	.	82	4	.	.	2	.	70	76	45	1	.	46
15–01	99	21	.	.	.	21	.	.	.	1	.	112	113	100	.	.	100
15–06	99	177	.	.	.	177	3	.	.	1	.	179	183	47	.	.	47
17–03	97	104	12	5	.	121	7	.	3	27	1	395	433	27	.	.	27
17–04	97	6	.	.	.	6	.	.	.	.	.	53	53	.	.	.	.
18–02	97	.	.	.	.	.	1	.	.	2	.	110	113	12	.	.	12
20–08	99	79	.	3	.	82	.	.	.	2	.	61	63	77	.	.	77
28–03	99	68	1	.	.	69	1	.	.	.	.	94	95	.	.	.	.
28–04	99	79	.	2	.	81	2	.	2	6	.	156	166	45	1	.	46
35–05	97	96	3	1	.	100	1	.	.	.	.	81	82	11	.	.	11
37–03	95	95	29	.	.	124	5	.	.	1	.	91	97	22	.	.	22
38–05	99	127	4	.	.	131	1	.	.	46	.	200	247	35	.	.	35
43–02	99	46	3	.	.	49	.	.	.	9	.	219	228	16	.	.	16
B. cretica ssp. **nivea**																	
01–04	99	21	6	.	.	27	.	.	.	.	.	.	.	.	.	.	.
01–05	99	31	8	.	.	39	.	.	.	.	.	31	31	3	.	.	3
45–08	97	6	.	.	.	6	.	.	.	2	.	216	218	6	.	.	6
F_1 HYBRIDS																	
B. cretica ssp. **cretica** × ssp. **cretica**																	
206–04	99	116	35	.	.	151	2	.	.	.	.	512	514	8	.	.	8
206–07	89	.	.	.	.	.	.	.	.	5	.	84	89	23	.	.	23
206–16	99	32	1	.	.	33	.	.	.	2	.	174	176	.	.	.	.
214–10	93	230	22	.	.	252	.	.	.	1	1	192	194	.	.	.	.
214–11	93	87	.	.	.	87	6	.	.	5	.	470	481	5	.	.	5
215–02	97	53	5	.	.	58	1	.	.	1	.	42	44	4	.	.	4
215–04	67	114	18	.	.	132	3	.	.	2	.	281	286	16	.	.	16
215–05	55	88	27	1	.	116	.	.	.	.	.	.	.	.	.	.	.
215–10	45	73	12	2	.	87	2	.	.	2	.	365	369	69	3	.	72
216–06	53	.	.	.	.	.	3	1	.	.	.	438	442	8	.	.	8
216–12	73	138	.	3	.	141	.	.	.	.	.	250	250	9	.	.	9
218–03	83	147	.	1	.	148	2	.	1	3	.	167	173	3	.	.	3
218–04	79	.	.	.	.	.	3	.	.	21	.	344	368	.	.	.	.
221–06	99	129	6	1	.	136	.	.	.	.	.	150	150	.	.	.	.
222–02	31	.	.	.	.	.	.	.	.	.	.	194	194	54	.	.	54
222–03	21	124	37	1	1	163	.	.	.	2	1	68	71	4	.	.	4
222–04	13	174	32	2	.	208	.	.	.	.	.	.	.	.	.	.	.

Table 1 (continued).

Code	PS	MI					AI							MII			
		9^{II}	$1^{IV}+7^{II}$	$8^{II}+2^{I}$	OI	n	Laggard		Bridge		OI	Normal	n	9+9	10+8	11+7	n
							1	2	BF	B							
222–07	27	27	.	.	.	27	.	.	.	2	.	181	183	26	.	.	26
229–04	91	40	2	.	.	42	.	.	.	.	.	162	162	39	.	.	39
230–04	87	9	.	.	.	9	.	.	.	3	.	35	38	8	.	.	8
230–07	59	.	.	.	.	.	.	.	.	.	.	54	54	12	.	.	12
231–10	97	46	.	.	.	46	.	.	.	.	.	.	.	.	.	.	.
232–09	99	17	.	1	.	18	.	.	.	1	.	149	150	101	.	.	101
232–10	77	123	1	2	.	126	.	.	.	.	.	.	.	.	.	.	.
238–01	63	97	13	.	1	111	.	.	.	.	.	.	.	.	.	.	.
241–03	75	97	3	1	2	103	.	.	.	1	.	87	88	8	.	.	8
242–08	77	43	.	.	.	43	2	.	.	1	.	153	156	.	.	.	.
244–01	81	140	1	.	.	141	.	.	.	2	.	258	260	7	.	1	8
244–10	93	91	3	1	.	95	.	.	.	1	.	13	14	.	.	.	.
244–12	81	101	4	.	.	105	1	.	.	1	.	97	99	.	.	.	.
244–13	89	30	6	.	.	36	2	.	.	3	.	199	204	70	.	.	70
248–04	85	119	.	4	1	124	.	.	.	.	.	.	.	.	.	.	.
248–09	77	162	2	14	.	178	1	.	.	2	.	137	140	16	1	.	17
249–03	89	126	11	.	.	137	1	.	.	2	.	63	66	10	.	.	10
251–03	83	59	.	6	1	66	3	.	.	16	.	154	173	.	.	.	.
251–05	93	89	.	2	.	91	1	.	.	1	.	37	39	.	.	.	.
252–03	71	.	.	.	.	.	3	.	.	1	.	240	244	7	.	.	7
253–01	71	9	.	.	.	9	3	.	1	7	.	263	274	23	.	.	23
253–10	43	.	.	.	.	.	3	.	.	2	.	272	277	41	.	.	41
255–09	83	13	.	.	.	13	1	.	1	9	.	357	368	31	.	.	31
255–11	73	39	5	1	1	46	.	.	.	.	.	.	.	.	.	.	.
257–25	99	27	2	.	.	29	.	.	1	3	.	114	118	.	.	.	.
258–01	91	123	.	2	.	125	.	.	.	.	.	14	14	24	1	.	25
258–13	93	44	.	3	.	47	.	.	.	.	.	36	36	82	1	.	83
263–03	91	.	.	.	.	.	.	.	1	.	.	123	124	21	.	.	21
266–10	73	111	.	7	2	120	.	.	.	.	.	212	212	.	.	.	.
277–08	83	21	.	.	.	21	1	.	1	.	.	49	51	.	.	.	.
277–09	71	.	.	.	.	.	.	.	.	1	.	79	80	40	1	.	41
280–08	97	13	.	.	.	13	2	.	.	17	.	158	177	34	.	.	34
281–07	95	20	2	1	.	23	.	.	.	.	.	.	.	.	.	.	.
281–12	75	98	8	1	.	107	1	.	.	8	.	182	191	5	.	.	5
B. cretica ssp. **nivea** × ssp. **nivea**																	
207–03	99	49	8	4	10	71	3	.	.	25	.	480	508	.	.	.	.
207–09	99	134	5	3	1	143	1	.	.	9	1	312	323	22	.	.	22
B. cretica ssp. **cretica** × ssp. **nivea**																	
201–05	89	60	6	.	.	66	1	.	2	3	.	332	338	56	.	.	56
203–01	81	173	50	.	1	224	5	.	1	19	2	386	413	4	.	.	4
209–03	75	17	4	.	.	21	1	.	.	1	.	77	79	.	.	.	.
209–05	87	86	.	1	.	87	8	.	1	24	.	407	440	.	.	.	.
245–12	95	6	1	1	.	8	.	.	.	3	.	242	245	24	.	.	24
245–14	91	70	1	2	.	73	.	.	.	.	.	.	.	.	.	.	.
246–03	99	167	45	5	5	222	1	1	1	.	.	231	234	14	.	2	16
246–08	75	.	.	.	.	.	1	.	.	3	.	130	134	106	.	.	106
246–10	85	89	6	.	.	95	.	.	.	.	.	.	.	.	.	.	.
246–15	85	98	2	3	1	104	.	.	.	3	2	112	117	.	.	.	.
260–01	93	20	3	.	.	23	.	.	.	2	.	31	33	7	.	.	7

Table 2. Number of chiasmata/cell in different individuals representing wild material as well as F_1 hybrids. Pollen stainability (PS) given.

Code	PS	Numbers of chiasmata per cell											Mean
		10	11	12	13	14	15	16	17	18	19	20	
Wild material													
03–01	97	.	1	1	2	13	13	15	2	1	.	.	15.0
11–02	99	.	.	.	.	3	4	3	3	.	.	.	15.5
12–03	95	.	.	1	1	4	2	2	1	.	.	.	14.5
15–06	99	.	.	1	2	5	6	.	.	.	.	.	14.1
F_1 hybrids													
203–01	81	.	.	.	2	8	2	.	3	1	.	.	14.8
207–09	99	.	.	.	.	1	4	1	2	2	.	.	15.0
215–05	55	.	1	2	12	12	9	7	8	.	.	.	14.5
221–06	99	.	.	1	4	7	2	4	.	.	.	.	14.2
231–10	97	.	.	.	.	.	3	7	1	.	1	1	16.4
232–10	77	.	.	.	4	3	8	5	4	1	.	.	15.2
241–03	75	1	4	7	2	6	3	1	.	.	.	.	12.9
241–05	99	.	1	.	.	2	2	3	5	1	.	.	15.7
245–14	91	.	.	.	2	.	3	4	1	1	.	.	15.5
246–03	99	1	1	3	3	3	2	.	.	.	.	.	12.9
246–10	85	.	.	1	5	4	5	4	3	.	.	.	14.7
246–15	85	.	.	.	1	1	5	2	1	.	.	.	15.2
248–09	77	.	.	1	7	7	7	11	2	.	.	.	14.7
249–03	89	.	.	.	.	2	4	4	6	.	.	.	15.9
251–05	93	1	1	3	1	2	2	2	1	.	.	.	13.6
255–11	73	.	.	2	4	5	1	1	1	.	.	.	13.9
258–13	93	.	.	.	2	5	5	.	.	.	.	.	14.3

Analysis of variance for number of chiasmata/cell in different plants.

Source of variation	df	SS	MS	F
Between plants	20	269.8592	13.4929	5.3876***
Within plants	382	956.6866	2.5044	
Total	402	1226.5459		

disturbances at M I and A I (r = −0.099). In 5 of the 38 plants investigated non-disjunction was found in cells at M II. The percentage of individuals displaying regular meiosis appears to be somewhat higher in the material grown from spontaneous seed than in the F_1 hybrids. At A I and M II no difference has been observed between the groups of plants (Table 1).

Chiasma formation

In 21 plants (4 from spontaneous seed and 17 F_1 hybrids) chiasma formation and the frequency of chiasma formation were observed in 10 or more cells from each plant. Only very rarely were interstitial chiasmata observed at diplotene. At diakinesis and M I all chiasmata were terminal, indicating a terminal localization in most cases and complete terminalization in the remaining cases.

When counting the number of chiasmata per cell difficulties sometimes arose in interpreting some bivalents. Since the chromosomes are comparatively small it was difficult to distinguish between ring and rod bivalents when the bivalents were unfavourably oriented. The number of chiasmata per cell (Table 2) should therefore be interpreted with caution. The

Table 3. Frequency (%) of quadrivalents in various F_1 hybrids with a pollen stainability (PS) over 90%, between 90 and 70%, and under 70% respectively. n indicates the number of F_1 hybrids investigated.

PS	% quadrivalents									n
	0		10		20		30		40	
>90		29		2		5		1		37
90–70		18		3		1		.		22
<70		1		4		2		.		7

Table 4. Differences in percentage of meiotic disturbances at MI and AI in F_1 hybrids from repeated crosses of the same populations. The pollen stainability (PS) is given.

Cross no.	Population nos.	PS	MI	AI
B. cretica ssp. **cretica** × ssp. **nivea**				
201–05	28×01	89	9	2
203–01	01×28	81	23	7
B. cretica ssp. **cretica** × ssp. **cretica**				
242–08	28×03	77	0	2
248–04	28×03	85	4	.
248–09		77	9	2
214–10	37×28	93	9	1
214–11		93	0	2
215–02	37×28	97	9	5
215–04		67	14	2
215–05		55	24	.
215–10		45	16	1
281–07	37×28	95	13	.
281–12		75	9	5

number of chiasmata per cell usually varied greatly between cells of a single plant. In one of the parent plants between 11 and 18 chiasmata per cell were observed. No pronounced difference in chiasma frequency between parent plants and F_1 plants was observed. Differences between single plants exist, however (F=5.39***). In two F_1 hybrids a difference in the number of chiasmata per cell was noted between cells with one quadrivalent and those where only bivalents were observed. In the former there appear to be on the average up to 0.5 chiasmata more per cell.

Table 5. Percentage meiotic disturbances in F_1 hybrids obtained through crosses within and between phytogeographical regions. The entire F_1 material is pooled without keeping the different hybrids separate. Regions: 1 Crete, Kithira. 2 Kephallinia. 3 Kikladhes. 4 Nisiros. 5 Northern Sporades.

Regions	MI															AI						
	0		5		10		15		20		25		30		35	0		5		10		15
Within regions																						
1×1		.		1		.		.		.		.		1			1		1		.	
2×2		.		.		.		.		.		.		.			.		.		1	
3×3		2		3		.		.		.		.		.			3		1		.	
5×5		.		.		.		.		.		.		.			1		.		.	
Between regions																						
1×2		.		.		1		.		.		.		.			3		.		.	
1×3		7		1		1		.		.		.		.			8		1		1	
1×4		1		5		1		1		2		.		.			8		1		.	
1×5		1		.		.		1		1		.		.			4		1		.	
2×3		.		.		.		.		.		.		.			2		.		.	
2×4		1		.		.		.		.		.		.			2		.		.	
2×5		.		.		.		.		.		.		.			2		.		.	
3×4		.		1		.		.		.		.		.			1		.		.	
3×5		.		.		.		.		1		.		.			3		1		.	

Pollen stainability

The percentage of stainable pollen was high in the plants grown from spontaneous seed in which meiosis was investigated. In all plants except one stainability was more than 90%, in most cases more than 95%. In the F_1 hybrids, however, pollen stainability varied considerably within as well as between the different F_1 families, from 10% to 100%. There proved to be only a weak correlation between pollen stainability and degree of meiotic disturbances for a given individual. In the parent material the percentage of disturbances at M I was not significantly correlated with pollen stainability (r=−0.14) nor was there any significant correlation between pollen stainability and disturbances at A I (r=0.35). In the total F_1 material the trend was similar. Pollen stainability was not significantly correlated either with the degree of disturbance at M I (r=−0.26), the A I disturbances (r=0.14) or chiasma frequency (r=0.17). However, if the few hybrids with pollen stainability below 70% are considered separately (Table 3), they prove to have a considerably higher frequency of individuals with many quadrivalents. This indicates that in addition to the general occurrence of quadrivalents based on homoeology there are also quadrivalents due to other causes in the hybrids with the most reduced fertility. This would indicate that differences caused by translocations are involved in establishing strong genetic barriers between populations. On the other hand, there is no such strong reduction of interfertility and raised frequency of quadrivalents in the crosses between the subspecies.

The F_1 hybrids, though representing different types of crosses, showed no marked differences in the distribution of meiotic irregularities, the crosses within taxa displaying a distribution of meiotic disturbances similar to that in crosses between taxa. When the same populations were crossed repeatedly using different individuals, the resulting F_1 hybrids usually displayed fairly similar meiotic behaviour though apparent differences were at times observed (Table 4).

The Aegean area has been divided into phytogeographical regions (Rechinger 1943, Greuter 1971), but the meiotic behaviour of the F_1 hybrids obtained from crosses both within and between these regions was about the same (Table 5).

DISCUSSION

The most conspicuous type of disturbance at M I found in this investigation was the formation of quadrivalents, a phenomenon that has been elucidated by Haga (1938), Sikka (1940), Wills (1966), Chiang & Grant (1975) and others. Some authors have pointed out the frequent secondary pairing that occurs at premetaphase to metaphase stages in many plants of *B. oleracea*, e.g. Catcheside (1934, 1937), Haga (1938).

The question arises as to whether secondary pairing and quadrivalent formation are two phases of the same phenomenon. Catcheside (1937) concludes that *B. oleracea* is a secondary polyploid with a basic chromosome number of six, three of the basic chromosomes being present in duplicate the remainder being single. The haploid set would be AA BB CC DEF. The same conclusion was reached by Haga (1938), while Sikka (1940) regarded the basic chromosome number as five. In actual fact the genomes of the genus *Brassica* with the present chromosome numbers 2n=16, 18 and 20 are now presumed to have evolved from a basic chromosome number of six (see Prakash 1973).

From prometaphase to metaphase Catcheside (1937) found a varying degree of secondary associations but no multivalents or univalents. Haga (1938) found multivalent associations as well as secondary associations. Röbbelen (1960) reported finding secondary pairing between bivalents in only c. 13% of the PMCs he investigated. Wills (1966), on the other hand, reported that in his material it was hardly possible to find any PMCs where there were no bivalents associated at diakinesis. In addition to a pronounced frequency of secondary associations he also reported high frequencies of true multivalents, primarily quadrivalents. Wills (1966) concludes that the quadrivalents are the result of secondary associations that have been able to form chiasmata. He noticed that in cells with quadrivalents chiasma frequency was somewhat higher than in other cells. Furthermore he stated that synapsis in *B. oleracea* can be under genetic control. Thompson (1956) showed that in the meiosis of a few haploid *B. oleracea* two bivalents were found in 4 cells of the 54 investigated. In 12 cells one bivalent was observed. It is thus reasonable to consider that at least four of the chromosomes are homoeologous and subsequently that both secondary associations and quadrivalent formations at diploid level arise from the same cause.

In this investigation our results in the main support the views of Wills (1966). It is, however, somewhat puzzling that quadrivalents were found at such high frequencies, whereas there was an almost entire absence of trivalents accompanied by univalents. In the material investigated by Wills (1966) trivalents also seem to be comparatively rare. If chiasma frequency is directly responsible for the number of multivalents formed, the chance of trivalent associations being formed should be higher compared with quadrivalents. In our material we have found no clear evidence that the cells with quadrivalents also displayed higher chiasma frequency although there was a trend in that direction. The fact that pollen stainability in any given plant, either from spontaneous seed or an F_1 hybrid, was not significantly correlated with the number of disturbances at M I or A I supports the theory that the multivalents are usually not the result of translocations except in F_1 hybrids with low fertility. Provided that disjunctional segregation exists, as was usually the case, quadrivalents involving homologous or homoeologous chromosomes need not necessarily bring about an increase in pollen abortion. It is not possible to state to what extent chromosomes involved in a particular quadrivalent are homologous. Curran (1970) obtained 13 seedlings from a desynaptic plant of *B. oleracea* eleven of which were hyperdiploids and two diploids. He suggested that the genes for viability are distributed throughout the diploid complement since no hypodiploids were found, which implies that it is not probable that any four chromosomes in the complement are homologous but rather, to some extent at least, homoeologous. Since the chiasmata are almost exclusively terminal the homologous parts of the chromosomes involved in quadrivalent formation should be the terminal parts.

The disturbances at A I were in most cases bridges without fragments. Although there was no correlation between disturbances at M I and A I it is to be suspected that bridges without fragments generally reflected separation difficulties in quadrivalents (cf. Wills 1966). Another explanation is of course inversion heterozygosity. Since the chiasmata are more or less terminal the crossing-over within an inversion loop would give rise to a very small acentric fragment that could easily escape notice. However, crossing-over within inversion loops would almost certainly result in decreased male fertility. This was not the case in our material. We could not find any correlation between disturbances at A I and the percentage of stainable pollen in the material as a whole. In some cases where the bridges were associated with an acentric fragment a paracentric inversion could be suspected of being the cause. Laggards could perhaps also be explained as resulting from quadrivalent separation difficulties as the frequency of univalents at M I was not high enough to provide the only reason for the high frequency of laggards at A I.

In much of the plant material from Greece, chiefly in that from the Aegean area, the effective isolation of populations has generated considerable morphological diversification, e.g. in *Erysimum* (Snogerup 1967 a, b), *Nigella* (Strid 1970), *Malcolmia* (Stork 1972), *Leopoldia* (Bentzer 1973), *Allium* (Bothmer 1974). In some instances this morphological diversification has been accompanied by breeding barriers between populations. It has not been conclusively shown in any of these genera to what extent the breeding barriers have arisen from chromosomal differentiation. They may also be merely due to differences in genes or gene combinations. In *B. cretica* the trend of morphological differentiation between populations resembles the general trend in other material from the area. It also seems quite clear that there are breeding barriers between certain populations or, more correctly, between certain plants of certain populations. In the *B. cretica* ssp. *cretica* and ssp. *nivea* material from spontaneous seed pollen stainability was generally high although meiotic disturbances were present. In the F_1 material pollen stainability was on the average considerably reduced. This indicates that in the total F_1 material meiotic disturbances are largely due to secondary pairing and multivalent formation, while decreased male fertility is caused by differences in the genic or micro-structural composition of the genomes. The frequency of reduced interfertility seems to be as great within the two subspecies as between them.

Secondary pairing between homoeologous bivalents indicates that the chromosomal architecture of the general *Brassica* genome is very conservative.

CONCLUSIONS

(1) Meiotic disturbances can often be traced back to secondary pairing or to its consequences.

(2) The degree of meiotic disturbance was similar in the parent material and in F_1 hybrids obtained through crosses within and between subspecies as well as between plants from the same or different geographic regions.

(3) In the material as a whole there is no general correlation between degree of meiotic disturbance and pollen stainability.

(4) The breeding barriers between populations are probably chiefly caused by genic or microstructural differences rather than by major chromosomal differences. Only in some cases of

much reduced fertility in hybrids between isolated populations do translocations seem to be involved.

(5) The breeding barriers, expressed in terms of reduced pollen stainability, were often pronounced in interpopulational crosses. The variation between repeated crosses as well as between full sibs may at times be considerable.

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APPENDIX 1

Code to populations grown in cultivation. All the populations have 2n= 18, and originate from Greece.

Population	Origin
B. cretica ssp. **cretica**	
02	Kithnos, Yavalido Bay, maritime cliffs, 1968, R & E
03	Kithnos, W of Stenon Kanalas, maritime cliffs, 1968, R & E
07	Milos, Ananes, the NW-islet, 1967, R & Be
08	Sifnos, S of Kamares, maritime cliffs, 1967, R & Be
09	Folegandros, 2 km W of Pelagia, maritime cliffs, 1967, R & Be
11	Milos, Ananes, the S-islet, 1967, R & Be
12	Amorgos, Nikouria, maritime cliffs, 1967, R & Be
15	Milos, Ananes, the S-islet, 1967, R & Be
17	Kephallinia, the peninsula outside Assos, maritime cliffs, 1966, Sn
18	Kephallinia, 1 km S of Assos, maritime cliffs, 1966 Sn
20	Serifos, the islet Mikronisi, 1967, R & Be
23	Kea, 0.5 km SSW of Kastriani, maritime cliffs, 1968, Sn & B
24	Kea, 0.5 km N of Kastriani, maritime cliffs, 1968, Sn & B
25	Euboea, the islet Scopulus Prasouda, Phitos
26	Naxos, 5 km E of the town Naxos, 1964, R
35	Skiathos, 4 km N of the town, maritime cliffs, 1966, Phitos
37	Nisiros, Mandrakion, maritime cliffs, 1971, Phitos
38	Kephallinia, Assos, maritime cliffs, 1971, Phitos
43	Kithira, 1973, B

Population	Origin
B. cretica ssp. **nivea**	
01	Kriti, 2 km S of Topolia, gorge, 1967, Sn
45	Kriti, 15 km W Chora Sphakia, Agia Rumeli, maritime cliffs, 1973, G
46	Kriti, 1 km S of Topolia, 1973, G
47	Peloponnisos, Akrokorinth, cliffs exposed towards N, 1973, G
Intermediate population	
28	Kriti, Nomos Chanion, 9 km ESE Kastello, the gorge SE of Rocca, 1964, Sn

APPENDIX 2

Code to the F_1 hybrids meiotically investigated. All the hybrids have the chromosome number 2n=18 except the following: F_1 hybrids: 231–21 (2n=36), 242–01 (2n=27), 262–18 (2n=27), 262–03 (2n=27), 265–03 (2n=27); F_2 hybrid: 242-02-08 (2n=17).

Cross number	Parent populations	Cross number	Parent populations
Within **B. cretica** ssp. **cretica**			
206	02×35	244	28×23
214	37×28	248	28×03
215	37×28	249	23×26
216	38×37	251	28×11
218	28×26	252	35×25
221	02×07	253	38×35
222	28×35	255	35×03
229	28×07	257	38×15
230	28×17	258	02×15
231	11×07	263	02×18
232	02×11	266	37×09
238	38×28	277	18×28
241	02×09	280	18×38
242	28×03	281	37×28
Within **B. cretica** ssp. **nivea**			
207	01×01		
B. cretica ssp. **cretica**× ssp. **nivea**			
201	28×01	245	01×11
203	01×28	246	01×37
209	35×01	260	38×01

A cytotaxonomic reconnaissance of tropical African Anthoxanthum L. (Gramineae)

Inga Hedberg

Hedberg, I. 1976 05 06: A cytotaxonomic reconnaissance of tropical African Anthoxanthum L. (Gramineae). *Bot. Notiser 129*: 85–90. Stockholm. ISSN 0006-8195.

East African *Anthoxanthum nivale* K. Schum. comprises two cytotypes with partially separated geographical and altitudinal distributions, a tetraploid with 2n=20 and a dodecaploid with 2n=60. As the morphological variation is largely overlapping the cytotypes cannot be separated taxonomically. The Ethiopian material, one sample of which had the chromosome number 2n=20, deviates sufficiently from *A. nivale* to be described as a new species, *A. aethiopicum* I. Hedb.

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Of the genus *Anthoxanthum* L. a single species, *A. nivale* K. Schum., is generally recognized in tropical Africa. The close affinity between this species and the European *A. odoratum* L. had been observed by Engler (1904), who pointed out that although very different from *A. odoratum* "*A. nivale* is more related to this species than to any other". The differences between the species are mainly quantitative: thus *A. nivale* has considerably higher culms, broader leaves and larger panicles. Spikelet characters seem, however, to be of little diagnostic value.

In his revision of the Afroalpine flora O. Hedberg (1957) reported two chromosome numbers within *Anthoxanthum nivale,* viz. the tetraploid number (2n=20) in one sample from Mt Muhavura, and the dodecaploid number (2n=60) in one sample from Aberdare and two from Mt Kenya. The limited material then available did not allow taxonomic conclusions to be drawn but a significant difference in pollen size was observed between the tetraploid and the dodecaploid (O. Hedberg 1952). In the present investigation morphological features have been studied in relation to chromosome number using more extensive material.

MATERIAL AND METHODS

During a recent field trip material was collected from four of the high mountains in East Africa, viz. Mt Elgon, Aberdare, Mt Kenya and Mt Meru. In order to secure as much cytological material as possible fixations were made in the field and living plants and seeds were sent to the Botanic Garden at Uppsala University. Though a fair proportion of the plants survived none flowered in cultivation which also applies to the plants raised from seed. Hence a morphological investigation of all plants from which fixations were made was not possible.

Chromosome counts were made from root-tip sections and squashes (I. Hedberg 1967, 1970). The chromosome number has been counted in 22 field collections, 19 of which are of more or less recent date (Table 1). Furthermore the chromosome number was established for 83 plants from 8 seed collections (Table 2).

Earlier collections for which the chromosome number was known have been included in the present investigation as well as some additional herbarium material including specimens from Ethiopia.

Spikelet length was measured with a binocular lens to the nearest 0.1 mm. The values in Fig. 3 represent averages of 5 measurements. Pollen size was measured in lacto-phenol preparations under an ordinary microscope. The values in Figs. 3 and 4 represent means of 25 measurements each. Voucher specimens are deposited at UPS.

Table 1. List of material investigated.
Where not otherwise stated the numbers refer to collections made by I. and/or O. Hedberg.

Locality	Altitude	Voucher	2n
Ethiopia			
Galama Mts	3700 m	4239	20
Bale Mts	2500 m	S. Gilbert 64	–
	3050 m	S. Gilbert 51	–
Uganda			
Ruwenzori	3450 m	351	–
Mt Muhavura	3400 m	2183	20
Mt Elgon	3550 m	S. Bie 66289	20
Kenya			
Mt Elgon	3050 m	5075	20
	3050 m	5076A	20
	3050 m	5076 B	20
	3200 m	4460	20
Aberdare	3150 m	5068	20
	3300 m	5023	20
	3300 m	5057	20
	3500 m	5055A	60
	3500 m	5056	60
	3900 m	1537	60
Mt Kenya	3000 m	4877	60
	3600 m	Coe & Kirika 254	–
	3800 m	5060	60
	3850 m	4312	60
	3900 m	4414	60
	4000 m	4805	–
	4150 m	1779	60
	4200 m	5016	60
	4350 m	1723	60
Tanzania			
Kilimanjaro	3500 m	4372	60
	3800 m	S. Bie 8	–
	3800 m	S. Bie 31	60
	3850 m	S. Bie 123	–
	4400 m	1200	–
Mt Meru	3300 m	2304	–
	3550 m	4754	–

Table 2. Chromosome numbers in plants grown from seed collections.
N number of plants examined.

Locality	Altitude	2n	N
Mt Elgon	3050 m	20	12
Aberdare	3250 m	20	7
Mt Kenya	3000 m	60	11
	3650 m	60	22
	3800–4000 m	60	9
	4000 m	60	6
	4200 m	60	7
Mt Meru	3550 m	60	9

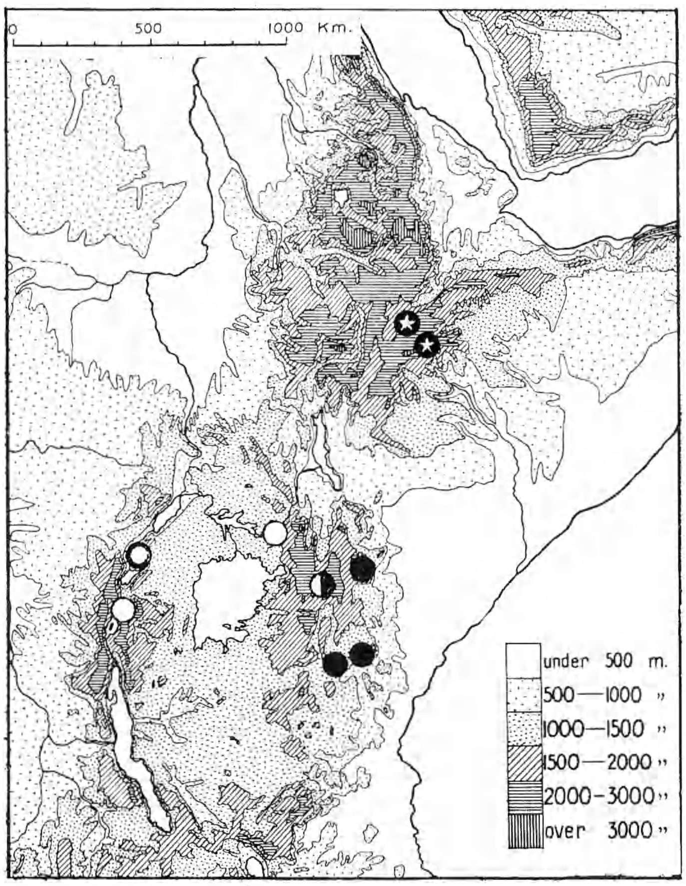

Fig. 1. Origin of *Anthoxanthum* samples investigated. Unfilled circles: tetraploids. Filled circles: dodecaploids. Half-filled circle: tetraploids and dodecaploids on the same mountain. Double ring: sample with unknown chromosome number. A dot with a star: *A. aethiopicum*.

CHROMOSOME NUMBERS

Two chromosome numbers were found, viz. 2n=20 (4x) and 2n=60 (12x). Tetraploids were found on the Galama Mts (Ethiopia), Mt Muhavura and Mt Elgon, dodecaploids on Mt Kenya, Mt Meru (from seed collections only) and Kilimanjaro and both cytotypes on Aberdare (Fig. 1). The material is not extensive enough to allow safe conclusions to be drawn on the geographical distribution of the cytotypes but indicates that tetraploids probably do not occur on Mt Kenya. Where both cytotypes occur on the same mountain the cytotype with a high chromosome number seems to grow at higher altitudes (Fig. 2), which is the opposite of what is found in European *A. odoratum* (I. Hedberg 1969).

No fragments such as those reported by O. Hedberg (1952) in the tetraploid were observed and his report is probably based on misinterpretation. Since some chromosomes have secondary constrictions which do not stain in crystal violet their satellites can easily be mistaken for fragments (I. Hedberg 1970). This may also explain the irregularities mentioned by O. Hedberg (1952) in one of his dodecaploids.

MORPHOLOGY

East African material

The material seems fairly uniform and agrees well with the description given by Clayton

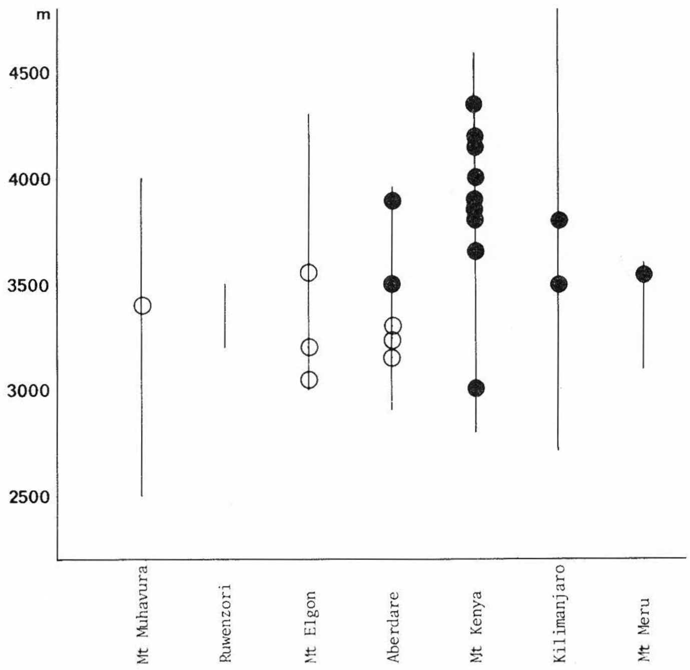

Fig. 2. Altitudinal distribution of *Anthoxanthum nivale* in East Africa. ○ tetraploids, ● dodecaploids.

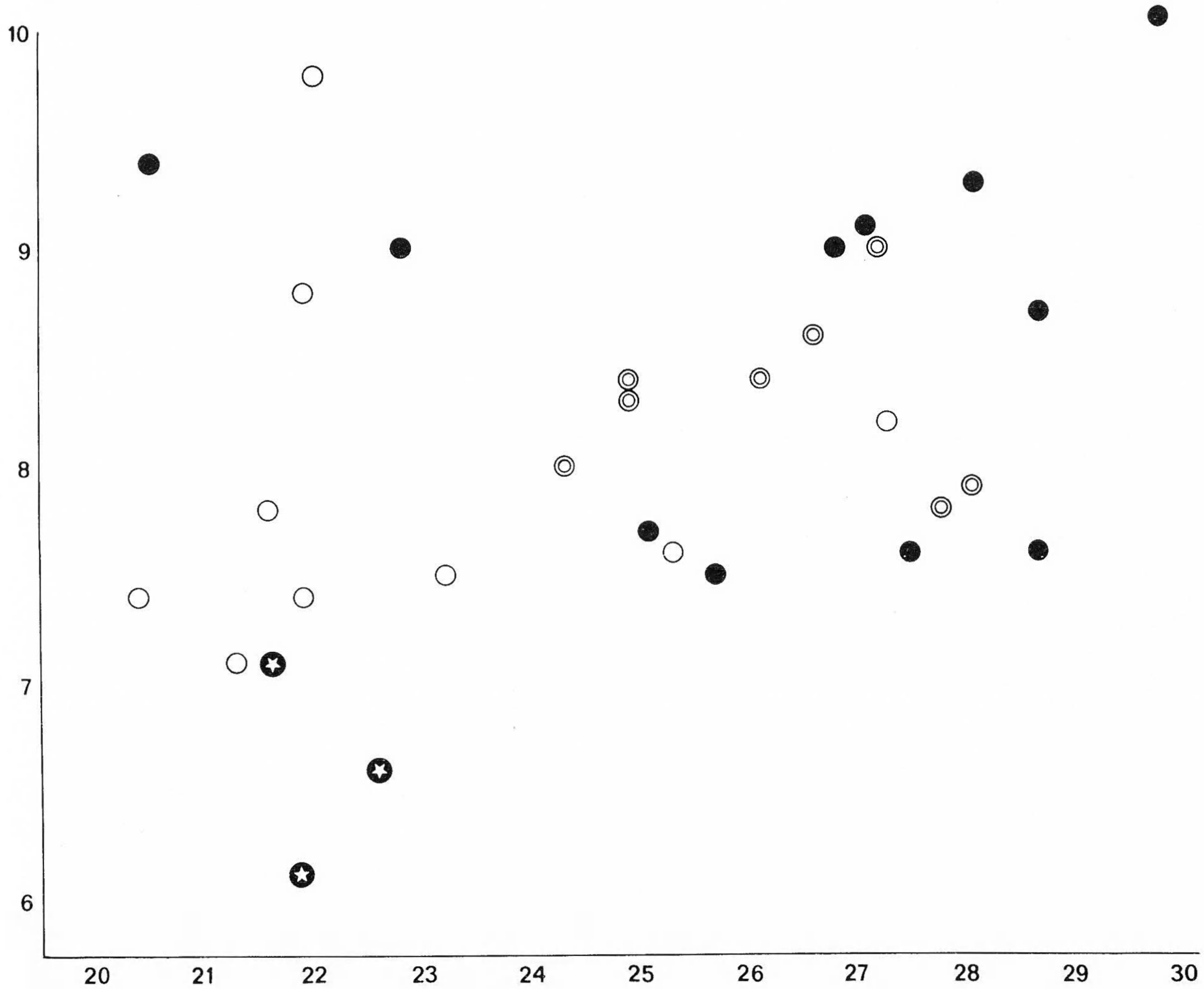

Fig. 3. Correlated variation in pollen size (horizontal axis) and spikelet length (vertical axis) in African *Anthoxanthum*. – Pollen size is given in scale divisions (each equalling 1.7 μ), spikelet length in mm. For explanation of symbols, see Fig. 1.

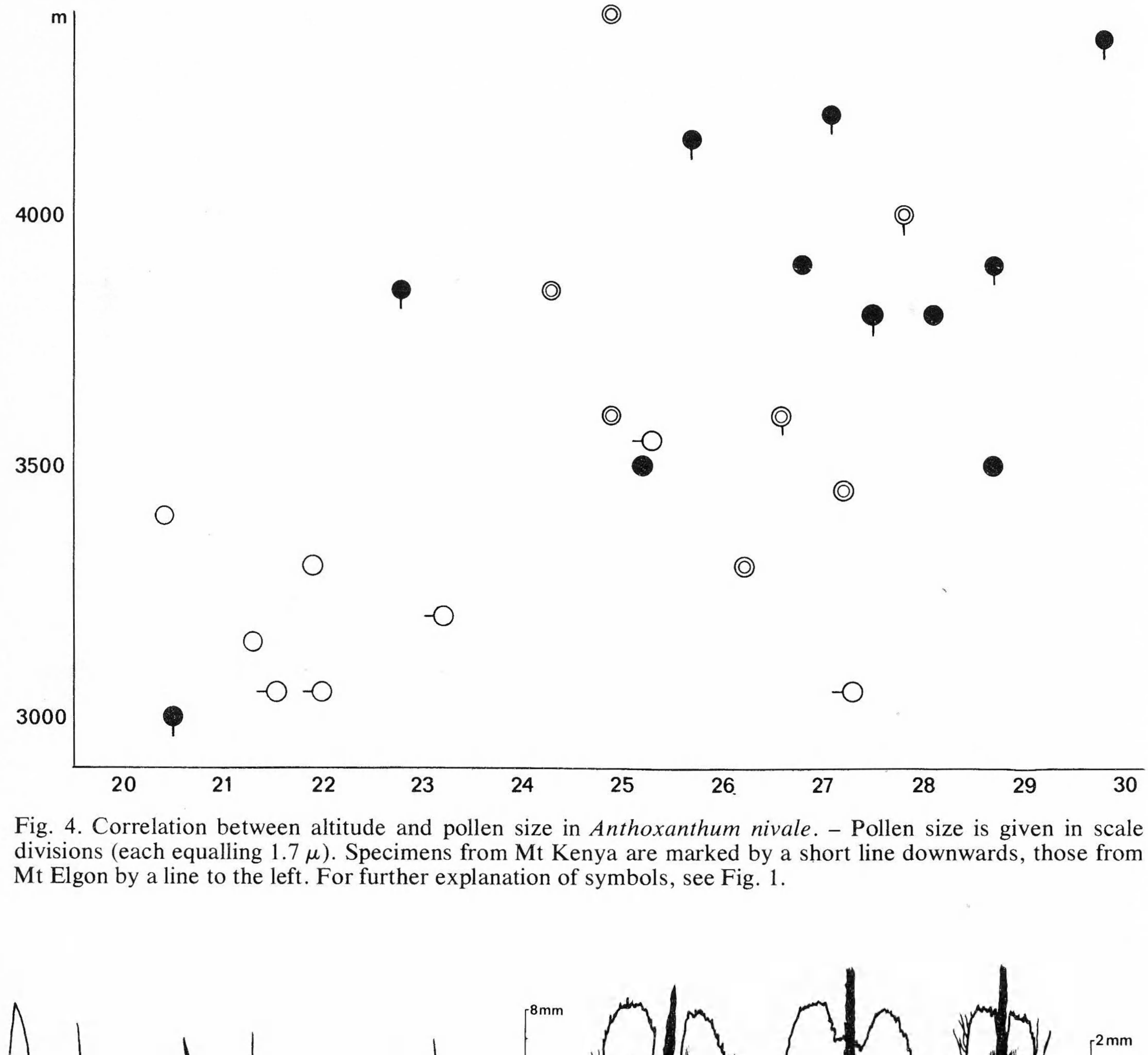

Fig. 4. Correlation between altitude and pollen size in *Anthoxanthum nivale*. – Pollen size is given in scale divisions (each equalling 1.7 μ). Specimens from Mt Kenya are marked by a short line downwards, those from Mt Elgon by a line to the left. For further explanation of symbols, see Fig. 1.

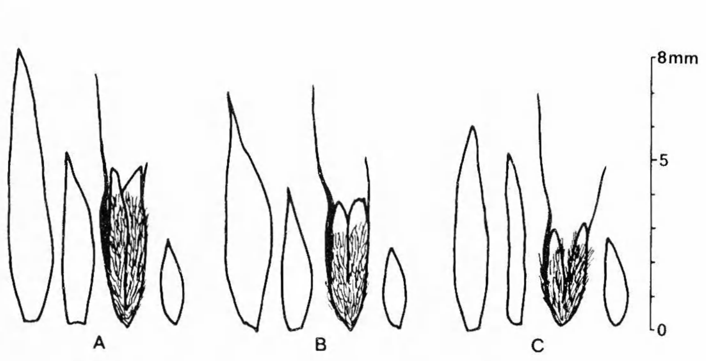

Fig. 5. Glumes, sterile lemmas and fertile lemma in African *Anthoxanthum*. – A: *A. nivale*, Hedberg 4414 (2n=60). – B: *A. nivale*, Hedberg 4460 (2n=20). – C: *A. aethiopicum*, Hedberg 4239 (2n=20).

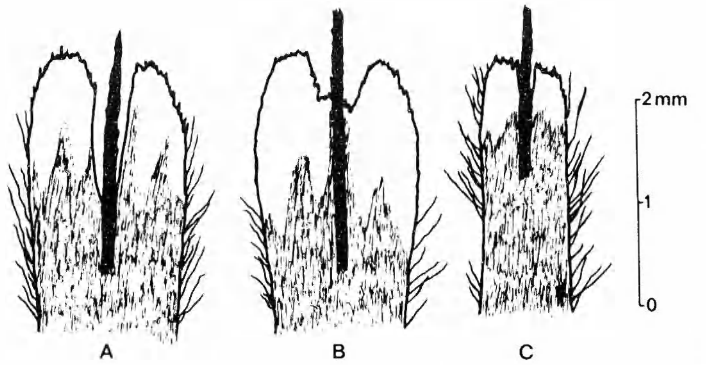

Fig. 6. Upper parts of sterile lemmas in African *Anthoxanthum*. – A: *A. nivale*, Hedberg 4414 (2n=60). – B: *A. nivale*, Hedberg 4460 (2n=20). – C: *A. aethiopicum*, Hedberg 4239 (2n=20).

(1970), although there is a certain variation in habit between the different mountain populations. The (tetraploid) Elgon plants tend to be slenderer with narrower panicles, but since the tetraploids from Aberdare are quite robust the habit does not seem to reflect the chromosome number to any great extent. One of the dodecaploids from a low altitude on Mt Kenya is of the same slender type as the Elgon tetraploids suggesting that this variation may be largely due

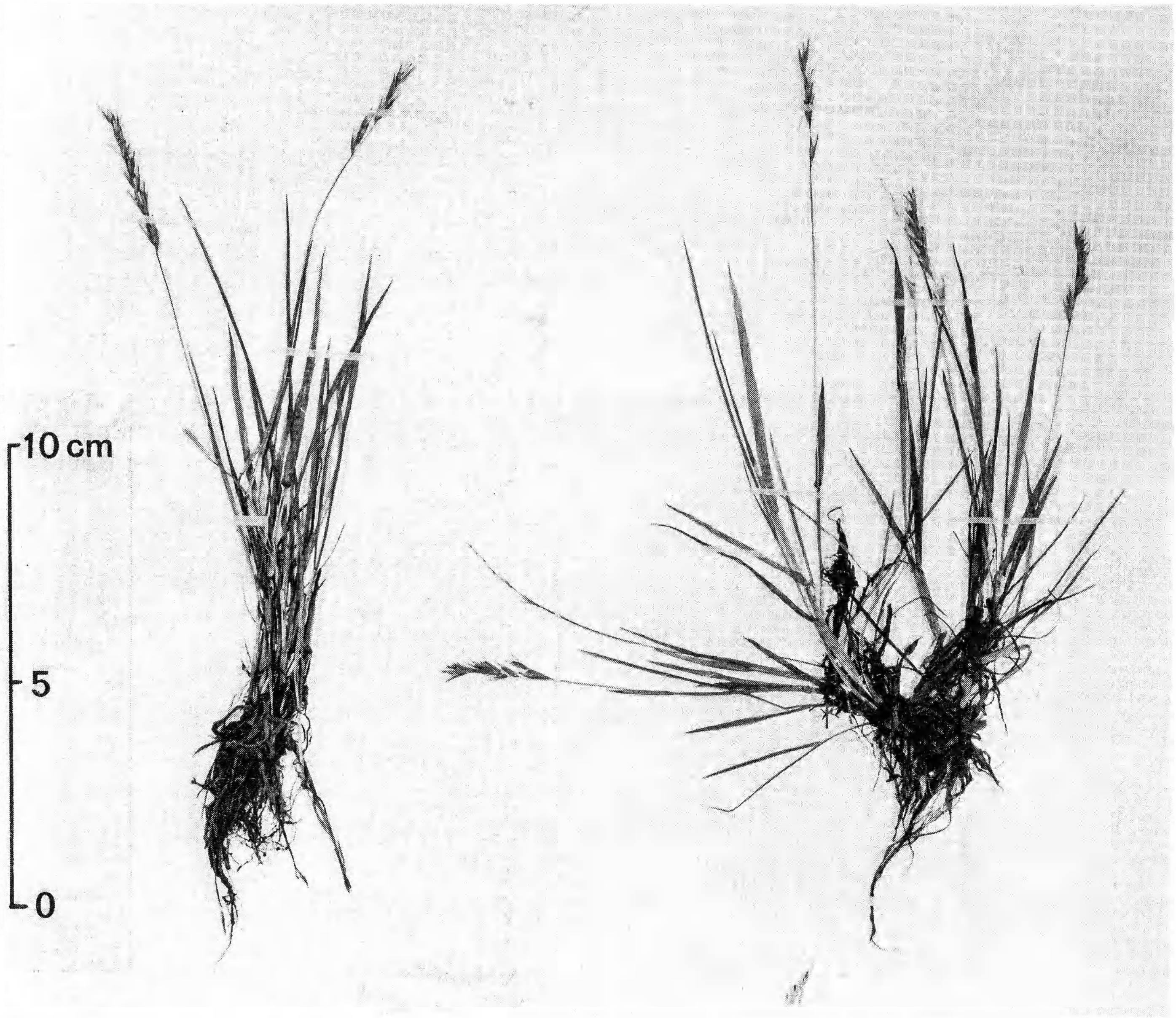

Fig. 7. Part of type collection of *Anthoxanthum aethiopicum* I. Hedb. (Ethiopia, Galama Mts, O. Hedberg 4239, UPS).

to environmental factors. This would also explain the robust appearance of the tetraploids from Aberdare which were growing in an exposed situation on open moorland. The conspicuous difference between individuals from high and low altitudes was pointed out already by Engler (1904).

There is a fairly strong correlation between spikelet length and pollen size (Fig. 3), but whereas there is considerable overlapping in spikelet length there is a strong tendency for the pollen grains of dodecaploids to be larger than in tetraploids. It is, however, difficult to tell whether the difference in pollen size is due to the difference in chromosome number or to the fact that the dodecaploids occur at higher altitudes, since both within the material as a whole and within individual mountain populations pollen size increases with increasing altitude (Fig. 4).

Ethiopian material

The three collections from Ethiopia deviate in general appearance from the East African material in their gracile form and slender panicles (Fig. 7). In these features they more closely resemble European *Anthoxanthum odoratum* (cf. also O. Hedberg 1971). Their glumes are equal or subequal, the sterile lemmas are linear with truncate tips and only about half as long as the glumes and the fertile lemma is the same length as the sterile lemmas (Fig. 5, 6). In the East African material, on the contrary, the lower glume is considerably shorter than the upper, the sterile lemmas are the same length as the lower glume, slightly broader and obtusely bilobed in their upper part and the fertile lemma is only half as long as the sterile lemmas. The only Ethiopian individual from which cytological material was available proved to be tetraploid.

In spite of the limited material available the differences accounted for here justify describing the Ethiopian material as a separate species.

Anthoxanthum aethiopicum I. Hedb., sp. nov.

Quoad habitum ad *A. odoratum* L. accedit sed ab illo et *A. nivali* K. Schum. differt essentialiter glumis subaequalibus, lemmatibus sterilibus quam glumis multo brevioribus, linearibus, apice truncatis, lemma fertilis lemmatibus sterilibus vix brevior.

Orig. coll.: Ethiopia, Arussi Prov., Chillalo Awraja, Galama Mts (c. 30 km ESE of Asella), near the E slope of Boraluco, along a stream, 3700 m. 10.IX 1967, O. Hedberg 4239 (UPS holotypus).

Tufted perennial grass with culms up to 15(–50) cm high, erect (or straggling), leaves up to 3(–6) mm broad, inflorescence slender, spike-like (to open). Spikelets 6(–7.5) mm long, lanceolate, with equal or subequal glumes. Sterile lemmas half as long as the glumes, linear, with truncate tips. Fertile lemma about the same length as the sterile lemmas.

ACKNOWLEDGEMENTS

The collecting trip during which most of my material was assembled was supported by a grant from the Wallenberg Foundation through the Rector Magnificus of Uppsala University. The laboratory work was supported by grants 065–062 and 065–066 from the Swedish Natural Science Research Council. For valuable assistance in various respects I am much indebted to Mrs B. Eklund and to my husband, Professor O. Hedberg.

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Botanical literature

Mollenhauer, D. (ed.) 1975: *Erstes Internationales Desmidiaceensymposium,* Bieber (Spessart), September 1971. Verhandlungen. 316 pp., 46 pl., 39 fig. Beihefte zur Nova Hedwigia 42. J. Cramer, Lehre. Price DM 200.–.

During the past decades huge international congresses have lost much of their importance. Their role has to a great extent been assumed by symposia. These work-shops afford a more inspiring and fruitful opportunity for presentation and discussion of research problems and results. Among the numerous symposia there are of course, phycological ones. The first ones in the field of marine phycology were soon followed by symposia on blue-green algae and on diatoms. The youngest member in the family of phycological symposia has been that arranged for the people working on and with desmids. This symposium was arranged in September 1971 by Dr Dieter Mollenhauer in Bieber (Spessart). He has done good work in making available the results of that symposium which have now been published by J. Cramer. Thus Cramer has taken care of the proceedings from the symposia on diatoms as well as that on desmids. Dr Mollenhauer has not only prepared the proceedings, he has also written a splendid introduction which emphasizes many points of interest. He has furthermore contributed with a comprehensive paper on morphology and phylogenetic relations amongst desmids.

The majority of the papers cover cytology, morphology, and reproduction. However, there are some taxonomical contributions. Dr Andersen has a short note on some problems in the nomenclature of desmids, and on the later starting point rule. The discussion about the advantages and disadvantages of the later starting point which was initiated by the proposal of Nordstedt (1906) is surprisingly long-lived. In the case of *Euastrum binale* it has already been stated by Nordstedt (1906) that Ralfs ought to be quoted as the author, because Turpin's *Heterocarpella binalis* is quite indeterminable. A very good reason indeed. Incidentally, the genus *Cosmarium* was not described by Corda in 1834, only a few species; the generic diagnosis was published first in 1839. *Spirotaenia* was only mentioned by Brébisson in 1844, the description followed first in 1849, one year after the description had appeared in Ralfs (1848).

The following contribution by Dr Bicudo considers the typification of *Arthrodesmus*. It is a problem of which Teiling also was well aware when he published his monograph of *Staurodesmus*. We have very good hopes that Dr Bicudo will consistently follow up the matter with an analysis and rearrangement of all the taxa involved. It should be mentioned that Förster (1972) has suggested that the few taxa of *Arthrodesmus* which were not included in *Staurodesmus* should be included in *Xanthidium,* viz. those with four or more spines per semicell. Thus following Ralfs (1848) who did so with *Arthrodesmus octocornis* Ehrenb. However, one cannot deny that *Arthrodesmus octocornis* Ehrenb. ex Arch. also has strong affinities to *Staurodesmus,* e.g. to *S. extensus* (Borge) Teiling. In Lake Rudsjön near Gävle (Sweden) a rich population of both above mentioned taxa occurs as well as numerous Janus-plants, one semicell with two, the other one with four spines. There are even semicells which have two on one side and only one spine on the other side.

In her paper Dr Mix considers the taxonomic importance of the features characterizing the cell wall of the Conjugatae, and her proposal for modified classification of Conjugatae (Mix 1972).

The contribution of Dr Ružička dealing with some common problems which are applicable not only to desmids but also to many other algae is well worth reading. These matters have been pointed out many times before, but it is abundantly clear that they need reiteration. Therefore, let us emphasize once more the most important of them, viz. that the descriptions, discussions, and records should be accompanied by figures. The figure is of fundamental importance for all work on microscopical algae. Ružička also discusses the use of algal cultures for the study of variation-range of algal taxa, and the consequences of such investigations for taxonomy. I am not very optimistic about this trend of thought. In some cases of course, one can expect some useful information, especially when the cultures are used for the study of interspecific hybridity in order to adopt the sexual criterion in delimiting species, as has been done by Ling and Tyler (1974).

Another way of delimiting desmid taxa has been exemplified in this volume by Dr Kasprik. He has studied the chromosome numbers in *Micrasterias*. The counts range from 25 to 230. The results are not very encouraging, and seem, for the present to be of little use for the taxonomy.

In these days when ecology is the "talk of the town" one is surprised that the proceedings contain only one ecological paper, viz. that by Dr Tassigny. He gives an account of his studies on the desmid flora and vegetation in a number of small oligo- and mesotrophic waters in the vicinity of Paris. Stress has been laid on the relations between the flora and environment.

I have mentioned a few of the papers gathered in this volume. There are many more all of which have some bearing on desmids, and throw a great deal of light on the subject.

Kuno Thomasson

Heslop-Harrison, J. (ed.) 1971: *Pollen: development and physiology.* 338 pp. Butterworth & Co. Ltd., London. Price £ 7.–.

This attractively printed volume is derived largely from papers presented at Symposia and Conferences held at Washington State University, Pullman, U.S.A. and the International Botanical Congress, Seattle, Washington, U.S.A.

In view of the breadth of the subject matter of the included articles, it is helpful for the reader that the Editor, Dr J. Heslop-Harrison, has subdivided the book into the following five Sections: "Nucleus and Cytoplasm in Microsporogenesis", "Pollen Development and the Pollen Grain Wall", "Pollen and Pollen Tube Metabolism", "Pistil-Pollen Interactions", and "Incompatibility".

Each section is documented by at least one fairly substantial Review paper together with Abstracts varying in length from one to several pages. Some 43 persons are involved in the authorship of the 36 contributions.

Since some time has elapsed since this publication first appeared it is of interest to note that several of the included contributions have been widely cited as, e.g., in a recently published review (cf. *Botanical Review* 4: 233–314, 1975). In addition, many of the book's papers relate significantly to continuing researches conducted by several of the participants, among whom are: U. C. Banerjee, E. S. Barghoorn, M. D. Davies, D. B. Dickinson, J. Heslop-Harrison, R. B. Knox, C. Labarca, J. P. Mascarenhas, D. Southworth, and R. G. Stanley (cf. M. Van Campo and C. Millerand, *Pollen et Spores,* Paris, Supplement, Oct. 1975).

The volume includes a brief Foreword composed by the late Professor G. Erdtman in which the reader is reminded, via a quotation from Linnaeus, that "Nature is greatest in its very smallest details"!

A. Orville Dahl

Böcher, T. W. 1975: *Det grønne Grønland.* 256 pp. Rhodos, Copenhagen. ISBN 87 7496 4526, 87 7496 4542 or 87 7496 4569. Price DKr 228.– (clothbound).

Det grønne Grønland (The Green Greenland) is a monumental treatise in Danish on Greenlandic botany. The exploration of the flora and vegetation types from the eighteenth century to our day is outlined in the first part of the book, followed by chapters on environmental factors and on adaptation to arctic and subarctic conditions. Phytogeographical patterns and problems of interpretation are dealt with as well as the phytosociological subdivision of the island. The concluding chapters survey propagation and dispersal, variation and the speciation of Greenlandic plants. The flora is interesting and relatively rich and the vegetation surprisingly luxuriant if one has not been previously aware of the actual extent of ice-free land surrounding the huge glaciated island.

This is obviously a labour of love and Tyge Böcher has produced a personal and charming volume on the island where he has done so much botanical research. The text is abundantly illustrated with attractive photographs, many in colour, taken by Jens Böcher. An international edition would be a great acquisition, making the work accessible to non-Scandinavian readers.

Gunnar Weimarck

O'Connor, M. & Woodford, F. P. 1975: *Writing scientific papers in English. An ELSE-Ciba Foundation guide for authors*. Associated Scientific Publishers. viii + 108 pp. ISBN Excerpta Medica 90 219 4035 3; ISBN American Elsevier 0444-15165-6. Price Dfl 21.00.

For the majority of us scientific authorship presents numerous problems. The output of scientific information has attained gigantic proportions making the need for concentration more imperative than ever, both from the point of view of the reader and with a thought to the increased costs of production.

"Writing Scientific Papers in English" somewhat resembles the CBE Style Manual but concentrates more on European publishing practices and is less comprehensive. We are guided step by step in the planning, preparation and writing of a paper, and are shown how to revise the first draft both structurally and stylistically, and how then to refine the second draft, for instance, rewrite the abstract, check against Instructions to Authors, etc. There is a chapter on how to type the paper, advice on how to correspond with the editor and a section on correcting the proofs. In some short appendices recommended steps in writing a paper, abbreviations of different kinds and expressions to avoid are presented. The advice given in the body of the text goes into considerable detail, and to my mind it is sound and realistic. The book is easy to read and is written with a great deal of humour. I must admit that I found myself wishing at times that I had read the book much earlier.

The cover design is made up of the title of the book surrounded by two concentric rings, the one composed of the names of languages or language groups, the other of the names of different disciplines. The pattern is symbolic of the fact that the book is the core of a system of guidelines to be published shortly as small booklets to be stored in pockets inside the front and back covers. (At the time of going to press the Scandinavian booklet is the only one that has so far appeared). This genial idea will undoubtedly prove a great asset as the difficulties facing an author will vary with linguistic background and discipline. The separate booklets can also be revised oftener than the core volume. The publishers will not be the same as for the book. Information can be obtained from the Secretary of ELSE (European Association of Editors of Biological Journals), address: Dr J. R. Metcalfe, Commonwealth Agricultural Bureaux, Farnham House, Farnham Royal, Slough, Bucks SL 23BN, UK.

From the point of view of the editing I wish to comment on one or two points concerning the layout of the book. Figs. 6 and 8 demonstrate a recommended form of presentation of illustrations – why then has optimal use not been made of the page? As regards the headings the mixture of symmetrical and asymmetrical typography seems to me to be less fortunate.

The book should be acquired and studied in detail by all scientists writing in English. Inexperienced writers will find it a substantial help, and the more experienced will undoubtedly derive much stimulus as regards improving their papers. Editors of journals will be able to refer authors to the recommendations found in the book before submitting manuscripts for publication to the benefit of scientific writing all round.

Gunnar Weimarck

Opera Botanica

Vol. 1. N. Hylander, I. Jørstad and J. A. Nannfeldt: Enumeratio Uredinearum Scandinavicarum. 1953. 102 pp. – H. Horn af Rantzien: Middle Triassic Charophyta of South Sweden. 1954. 83 pp. – H. Hjelmqvist: Die älteste Geschichte der Kulturpflanzen in Schweden. 1955. 186 pp. – Price SKr 30 (15).

Vol. 2. H. Runemark: Studies in Rhizocarpon. I. Taxonomy of the yellow species in Europe. 1956. 152 pp. – H. Runemark: Studies in Rhizocarpon. II. Distribution and ecology of the yellow species in Europe. 1956. 150 pp. – G. Knaben: On the evolution of the radicatum-group of the Scapiflora Papavers as studied in 70 and 56 chromosome species. A. Cytotaxonomical aspects. 1959. 76 pp. – Price SKr 30 (15).

Vol. 3. A. Gustavsson: Studies on Nordic Peronosporas. I. Taxonomic revision. 1959. 271 pp. – A. Gustavsson: Studies on Nordic Peronosporas. II. General account. 1959. 61 pp. – G. Knaben: On the evolution of the radicatum-group of the Scapiflora Papavers as studied in 70 and 56 chromosome species. B. Experimental studies. 1959. 96 pp. – Price SKr 30 (15).

Vol. 4. R. Dahlgren: Revision of the genus Aspalathus. I. The species with flat leaflets. 1960. 393 pp. – Price SKr 30 (15).

Vol. 5. Á. Löve and D. Löve: Chromosome numbers of Central and Northwest European plant species. 1961. 581 pp. – Price SKr 40 (20), bound SKr 48 (28).

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