Chromosome numbers of phanerogams from Morocco and Algeria

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246 chromosome numbers of 188 flowering plants are reported from collections made in Morocco and Algeria. 79 new counts are reported for some 67 species. The remainder are additional counts of previously counted species. Taxonomic comments are provided for those taxa where new counts have been made.

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This paper is one of a series dealing with taxonomic problems of the Maghreb flora (Humphries 1977, 1978, in prep.) and is confined to reporting chromosome numbers of phanerogams collected mostly in Morocco and a few in Algeria. All of the results reported in Table 1 are counts from new areas. Discussion is confined to new numbers reported for species and infraspecific taxa and problematical groups, but chromosome numbers the same as those in previous publications are listed without comment.

Material and methods

Most of the material used for this study was collected by C. J. Humphries, S. L. Jury, J. M. Mullin and I. B. K. Richardson (HJMR) during a field trip to Morocco in May/June 1974, and by G. Bocquet, R. Borel and A. Reist (BBR) from Morocco in 1971. Other results were obtained from collections made by D. Bramwell, B. G. Murray and I. B. K. Richardson (BMR) from Morocco, 1972, D. A. and S. Sutton (SS) from Algeria, 1976 and C. J. and A. R. Humphries (HH) from Morocco, 1976. Voucher specimens for HJMR, HH and SS collections are deposited in the herbarium of the British Museum (Natural History) (BM), BMR collections at Reading University (RDG) and BBR collections at the Institut für Spezielle Botanik, Zürich (ZT). BBR collections were counted by Vasudevan, the remainder by Humphries and Murray.

Chromosome numbers were obtained either from somatic mitoses of root tips of plants raised from seed or from meioses in buds collected from plants growing in the field. Preparations involved conventional aceto-orcein and aceto-carmine squashes for buds and leucobasic fuchsin squashes in 45% acetic acid and/or aceto-orcein for root tips.

Monocotyledons

Gramineae

Hyparrhenia hirta. Our count of $n=18$ for this wide-ranging subtropical and Mediterranean weed is a new number. Previously reported numbers are $2n=30$, 40, 44, 45, 46, 60 (see Clayton 1969 for review), $2n=30$ being the most common.

Liliaceae

Dipcadi serotinum. Our new count of $2n=32$ is indicative of the cytological complexity of this species. Various other reports have been given, suggesting a polyploid series based on $x=4$, ranging from 2n = 8 (+1–5 B) (Fernandes & Queiros 1971 a, Valdés 1970, Van Loon et al. 1971, Löve & Kjellquist 1973), to 2n = 40 (Sen 1973) and 2n = 64 (Borgen 1974). *D. serotinum* is a widespread and polymorphic species; however, from the evidence available there is little correlation between chromosome number, ecology and morphology.

Fritillaria messanensis. All previous counts for this species give 2n = 24 (La Cour 1951, Gori 1958, Küpfer 1969). Our new count of 2n = 36 suggests that at least two ploidy levels exist within the species. The base number is probably x = 6.

Dicotyledons

Campanulaceae

Campanula filicaulis. Our two counts for this species both give n = 13. The only previously published counts (Quézel 1957) are n = 8 and 24.

Jasione corymbosa. Our count of 2n = 12 is a first report for this species. Many counts have been made in other species of the genus, demonstrating a polyploid series based on x = 6. This North-African-Iberian annual endemic is thus probably a diploid taxon.

Caryophyllaceae

Polycarpon polycarpoides. Our new count of n = 7 suggests that the N African populations are diploids based on x = 7. The single previously published report of 2n = 54 (Kliphuis & Wiefering 1972) is from Europe.

Silene. The counts for *Silene imbricata, S.* aff. *canopica* and *S. setacea* are all new. 2n = 24 is by far the most common number in *Silene*.

Vaccaria pyramidata. 2n = 30 has been reported for all cytologically studied species of *Vaccaria,* with an additional count of 2n = 60 for populations of *V. pyramidata* (Favarger 1946). Our report of 2n = 24 for *V. pyramidata* is in striking contrast.

Compositae-Anthemideae

Chlamydophora pubescens (*Matricaria pubescens* (Desf.) Sch. Bip.). Our count of 2n = 10 differs from the previous report of 2n = 18 (Reese 1957). We believe that Reese's count is erroneous, since the species shows closer affinities to northern hemisphere members of the genus *Cotula,* a polyploid series based on x = 5, than to the *Matricaria/Anthemis* complex, which is based on x = 9.

Chrysanthemum macrocarpum. Fruit and floret morphology shows that this species does not belong to *Chrysanthemum* L. s.str.; it is an annual sister species of the diploid endemic North African perennials of *Leucanthemum* Miller subgen. *Chrysanthemopsis* Maire. This first report of 2n = 18 fits in well with the prevailing diploid number of this tribe.

Leucanthemum. Four out of the species of *Leucanthemum* have not previously been studied cytologically. There are, however, reports of 2n = 18 for *L. catananche* (Dowrick 1952) and for *L. atlanticum* Maire (Quézel 1957). Thus, at least 5 out of the currently accepted 12 species in the monophyletic group, *Leucanthemum* subgen. *Chrysanthemopsis* Maire (Wilcox 1977), are diploids. Together with morphological and distributional data this suggests that the group has evolved allopatrically at the diploid level, a pattern very different from the sympatric polyploid series of the Eurasian species of the genus.

Ormenis scariosa. n = 9 for this species is a new count. It agrees with the common number for diploid species in the *Anthemis* complex.

Compositae-Calenduleae

Calendula. The chromosome numbers of *Calendula* range from 2n = 14 to 2n = 44. Our counts of 2n = 14 for *Calendula algeriensis* confirm the report by Meusel & Ohle (1966), who gave 2n = 14 and 2n = 44 for Mediterranean populations of this species. Chromosome counts of *C. arvensis* are few, previous reports giving 2n = 36 (Negodi 1935, 1937, Janaki Ammal & Sobti 1962), 2n = 42 (Borgen 1974, Löve & Kjellquist 1974) and 2n = 44 (Meusel & Ohle 1966, Fernandes & Queiros 1971 a, b, Borgen 1975, Queiros 1973). The plants studied by us had 2n = 18 and may represent a normal diploid in an x = 9 series. However, a new count of 2n = 14 for *C. arvensis* var. *parviflora* confirms that there is intraspecific aneuploidy in addition to polyploidy.

Compositae-Cardueae

Carduncellus pinnatus. The counts on *Carduncellus* are usually 2n = 24 and 48 (Reese 1957, Roberts 1976). Our new count of 2n = 26 for *C. pinnatus* suggests that two base numbers of x = 12 and 13 occur.

Carthamus fruticosus. This S Moroccan endemic has not been cytologically studied previously. 2n = 24 is not unusual for the genus (Ashri & Knowles 1960, Schank & Knowles 1964).

Centaurea. Of the six chromosome counts given in Table 1, three are new, viz. those of the Iberian-Moroccan endemic, *C. clementei* (2n = 18) and the Maghreb endemics *C.* sp. aff. *nana* (n = 10) and *C. involucrata* (2n = 22). The numbers are all typical for the genus. Our report of n = 9 for *C. sulphurea* differs from previous reports of 2n = 24 (Fernandes Morales 1974, Powell et al. 1974). Neither count is based on N African material. The taxonomy of this variable species is worthy of detailed investigation.

Galactites tomentosa. Our two counts of n = 10 and 2n = 20 differ from reports based on material from the Canaries (Borgen 1974, Larsen 1960, Van Loon 1974) and various other parts of the European Mediterranean (Larsen 1955, Dahlgren et al. 1971, Fernandes & Queiros 1971 b) where the number is 2n = 22.

Jurinea humilis. Our counts of 2n = 24 and 2n = 58 represent radical departures from previous European records of n = 17 (Küpfer 1969) and 2n = 34 (Majovsky et al. 1974) for this species. Numbers for other species in the genus include 2n = 30, 34, 35, 36 (Majovsky et al. 1974, Kuzmanov & Ancev 1973), all of which have been found in *J. mollis* (L.) Reichenb. Probably both polyploidy and aneuploidy have accompanied evolution in the group. The count of 2n = 24 probably represents a tetraploid based on x = 6, which provides some explanation for counts of 30 and 36, and for the hypothesis that counts of 2n = 34 and 88 are aneuploid derivatives of the hexaploid and decaploid conditions.

Xeranthemum inapertum. With this new count of 2n = 30 three out of the six species of *Xeranthemum* L. have been counted. The previous counts are 2n = 12 (*X. annuum* L.) and 2n = 20 (*X. cylindraceum* Sibth. & Dum.).

Compositae-Inuleae

Asteriscus. The counts of n = 7 and 2n = 14 for *A. imbricatus* are new ones and agree with those of various other N African and Macaronesian species such as *A. graveolens* (Forsk.) DC. (Reese 1957, Amin 1972), *A. sericeus* L. fil. (Larsen 1958, 1960, Borgen 1969) and *A. aquaticus* (L.) Less (Borgen 1970). The count of 2n = 10 for *A. pygmaeus* is a new one for the species and differs from a previous count of 2n = 12 (Reese 1957). Other counts of 2n = 16 for *A. sericeus* (Powell et al. 1974) and 2n = 18 for *A. daltonii* (Webb) Walp. (Borgen 1975) suggest that considerable variation occurs in the genus. In fact, these numbers form an aneuploid series of x = 5, 6, 7, 8 and 9. Borgen (1975) suggests that x = 7 is the most common and therefore the ancestral condition in the genus, and that all the other numbers are derived from it. This might indicate common ancestry for the Macaronesian and Atlantic species *A. graveolens, A. sericeus, A. aquaticus* and *A. imbricatus* , but it is in no way suggestive of an ancestral condition for the rest of the genus. Detailed cytotaxonomic investigations are required before the relationships of these species can be resolved.

Bombycilaena discolor (*Micropus bombicinus* Lag.). This annual species, although a common Mediterranean weed, has not been studied cytologically. 2n = 28 is a fairly common number in other species of the subtribe Filaginineae.

Evax pygmaea subsp. *pygmaea*. Our new count of 2n = 18 is at variance with the only previous report for this species (Tongiorgi 1942), 2n = 26 and 3n = 39. These latter numbers have also been reported for the Tyrrhenian endemic *Evax rotundata* Moris (Contandriopoulos 1962).

Leysera leyseroides (*Asteropterus leyseroides* (Desf.) Rothm.). Our first count of 2n = 14 differs from the counts of 2n = 8 for the S African species *Leysera gnaphalodes* (L.) L. (Nordenstam 1967) and *L. tenella* DC. (Bremer 1978). However, in the subtribe Athrixiinae as a whole x = 7 is the most common base number (Pinkava & Keil 1977).

Phagnalon. The new count of 2n = 18 for the Moroccan montane endemic *Phagnalon embergeri* is the same as other members of the genus. However, the new count of 2n = 14 for *P.*

helichrysoides is a radical departure from the previous count of 2n = 18 (Quézel 1957).

Pulicaria. Several chromosome counts have been made in *Pulicaria* which demonstrate an apparent aneuploid series. Hitherto, 2n = 14 has been reported for *P. wightiana* Clarke (Chopde 1965), and 2n = 18 for *P. angustifolia* DC. (Baquar & Abid Askari 1970), *P. dysenterica* (L.) Bernh. (Fernandes & Queiros 1971 b), *P. crispa* Sch. Bip., *P. odora* (L.) Reichenb. (Björkquist et al. 1969, Fernandes & Queiros 1971 b, Queiros 1973), *P. petiolaris* Jaub. & Spach, *P. paludosa* Link (Fernandes & Queiros 1971 b) and *P. uliginosa* Stev. (Kuzmanov & Kozuharov 1970). 2n = 20 has been given for both *P. crispa* (Singh 1951 and *P. dysenterica* (Tischler 1934, Rodolico 1933, Gadella & Kliphuis 1967). In addition, Portuguese plants of *P. odora* have been demonstrated to have between 1 and 6 B chromosomes (Queiros 1973). Our report of 2n = 16 for *P. odora* confirms the presence of intraspecific variation in this species and demonstrates the wider presence of 2n = 16 in the genus. The new count of n = 6 for *P. mauritanica* is the lowest known in the genus. The aneuploid series in the genus thus comprises x = 6, 7, 8 and 9, almost an exact parallel to the situation in the closely related genus *Astericus*.

Compositae-Cichorioideae

Andryala canariensis subsp. *mogadorensis*. Our count of n = 9 for this SW Moroccan endemic is new. This number is typical for the genus.

Picris. Remarkably few counts are available for species in the closely related genera *Leontodon* L., *Picris* L., *Urospermum* Scop. and *Hypochoeris* L. However, on the limited data available, *Picris hispanica* (2n = 20) seems to fit better in *Picris* than in *Leontodon*, since *P. echioides* L. and *P. hieracioides* L. both have 2n = 10. The new count of n = 5 for the Maghreb endemic *Picris cupuligera* confirms the base number and suggests that this is a diploid species. Species of *Leontodon*, by contrast, have base numbers of x = 4, 6 and 7. In a recent review, Sell (1975) finds little justification for separating these genera, so on the basis of chromosome numbers there seems to be a genuine need for a phylogenetic investigation into the relationships of these genera.

Scorzonera pseudopygmaea (*Scorzonera pygmaea* Sibth. & Sm. sensu Maire). Our count of 2n = 12 + 1 B for this species differs from the only previous count of 2n = 14 made by Quézel (1957), but is not unusual for the genus.

Euphorbiaceae

Andrachne aspera. Our new count of 2n = 24 for *A. aspera*, a widespread coastal species of N Africa and the Mediterranean region, is the same as that for the fairly common weed, *A. telephioides* L. (Reese 1957). The only other counts available are those for *A. cordifolia* Merell, which appears to be diploid, with two base numbers: x = 11 and 12 (Gill et al. 1973, Choda & Mehra 1972).

Euphorbia. Our count of 2n = 22 for *E. paralias* bears little apparent relationship to the previous counts of 2n = 16 (Perry 1943, Leveque & Gorenflot 1969, Björkquist et al. 1969, Van Loon 1974). Our count suggests that an aneuploid series exists within the species. Our count of 2n = 20 for *E. exigua* also appears rather surprising at first sight but fits into an extensive aneuploid series when compared to the previous counts of 2n = 16 (Wulff 1939, Bauer 1971), 2n = 24 (Rutland 1941, Bauer 1971, Dahlgren et al. 1971, Nilsson & Lassen 1971) and 2n = 28 (Perry 1943). Our count of 2n = 16 for *E. dracunculoides* confirms previous reports for the species (Malik 1960, Gill et al. 1973), but the new count of n = 20 for Middle Atlas material suggests that aneuploidy occurs in this species. The count of 2n = 14 for the Moroccan endemic *E. megatlantica* is new.

Fumariaceae

Sarcocapnos crassifolia. Our count of n = 12 is a new number for the genus. Previous records for this species as well as for the related *S. enneaphyllus* (L.) DC. are 2n = c. 32 (Ryberg 1960).

Guttiferae

Hypericum australe. This taxon belongs to the group which also contains *H. linarifolium* Vahl and *H. humifusum* L. (Robson 1977). Previous counts on *H. linarifolium* (Robson & Adams

1968, Robson 1956) and *H. humifusum* (Winge 1925, Chattaway 1926, Robson 1956) give 2n = 16, suggesting a base number of x = 8. 2n = 18 for *H. australe* is a more usual number for the genus and either suggests that some degree of aneuploidy can occur within sections or that *H. australe* is a misplaced species.

Labiatae

Mentha gattefossei. The chromosomes of this species are remarkably small, which probably accounts for the variation in previously published counts (2n = ±32, Harley & Brighton 1977, 2n = 40, 48, Makarov & Reznikova 1972). Our count of 2n = 36 has been obtained many times from four separate plants of field origin, which lends further support to the hypothesis that *M. gattefossei* is the sister species of *M. cervina* L., another species with 2n = 36 chromosomes (Makarov & Reznikova 1972, Harley & Brighton 1977). The erection of the monotypic section *Preslia* (Harley & Brighton 1977), on the basis of digitately lobed bracteoles and 4 calyx teeth (instead of the 5 in *M. cervina*) seems rather spurious.

Salvia. Salvia aegyptica is a widespread and rather oligotypic species of the Saharo-Sindian element of the N African flora. Our count of 2n = 42 is the third count for the species. Previous counts are based on Libyan (2n = 38, Bhattacharya et al. 1971) and unlocalised Botanic Garden material (2n = 28, Delestaing 1954). Our new count of n = 7 for *Salvia blancoana* is typical for diploid taxa within the genus. The new counts of 2n = 26 and n = 13 for *S. taraxacifolia* represent the first reliable ones for wild material of this endemic species. The only previously published record (2n = 28, Delestaing 1954) was based on material growing in the Paris Botanic Garden. Its rather isolated position in the genus (Hedge 1975) is reflected in its unusual chromosome number.

Leguminosae

Adenocarpus. The new counts of n = 24 for *A. anagyrifolius* Coss. & Balansa and *A. bacquei* Batt. & Pitard seem to indicate that these species have closer relationships with the E African *A. mannii* Hook fil. complex (see Lems 1958) which has 2n = 48 (Frahm-Leliveld 1969), than with Mediterranean members of the *A. complicatus* J. Gay group.

Genista. A wide range of chromosome counts has been reported for this genus (see Polhill 1976 for review). However, our new count of 2n = 26 for the Moroccan endemic *G. microphylla* (*G. maroccana* Briquet) is a very uncommon number in the genus. The new count of 2n = 72 for *G. vepres* represents a previously unrecorded number for the genus.

Medicago truncatula. Most previous counts for this rather widespread weed give 2n = 16. Our count of 2n = 14 is new for the species, but 2n = 16 and 14 have also been recorded in *M. hispida* Gaertner (Heiser & Whitaker 1948, Heyn 1956), *M. polymorpha* L., *M. rigidula* (L.) All. (Heyn 1963) and *M. tuberculata* Willd. (Mariani 1963).

Onobrychis peduncularis. Our new count of n = 16 would suggest that this W Mediterranean perennial is a tetraploid based on x = 8.

Plantaginaceae

Plantago albicans. Our count of n = 5 is the first report of diploids in this species. Previous reports are 2n = 20 (Chater & Cartier 1976) and 2n = 30 (Runemark 1967).

Rubiaceae

The new counts of n = 22 for *Asperula hirsuta* and n = 11 for *Galium ephedroides* are common tetraploid and diploid numbers for these genera.

Sapotaceae

Argania spinosa. Our count of n = 12 differs from the previous report (2n = 20, Miège 1954). However, the family appears mostly to have n = 12 or 13.

Scrophulariaceae

Acanthorrhinum ramosissimum. Previously only diploids with 2n = 16 chromosomes have been reported (Baur 1932, Reese 1957). One of the populations studied by us is diploid, but we also report the tetraploid number (n = 16) from buds fixed in the field.

Anarrhinum fruticosum. This species has not previously been studied cytologically. However, like all related species within the genus it has 2n = 18.

Linaria. The counts for *L. ventricosa* and *L. tingitana* are new. 2n = 12 is the prevailing number in the genus.

Scrophularia arguta. 2n = 36 at first seems at odds with previous counts (n = ca. 30, Vaarama & Leikas 1970, 2n = 58, Grau 1976). *S. arguta* is similar to *S. peregrina* L. which also has 2n = 36 (Kramer et al. 1972). It is possible that these numbers represent polyploid derivatives based on x = 6: 2n = 36 would be a hexaploid and 2n = 60 and 58 a decaploid and its derivative.

Scrophularia auriculata. n = 29 is a new record for this species, but rather common in the genus. Previously reported numbers for the species include 2n = 78 on Danish and Dutch material (Vaarama & Hiirsalmi 1967, Gadella & Kliphuis 1963), 2n = 80 on British material (Maude 1940), 2n = 84, 86 on French material (Vaarama & Leikas 1970) and 2n = 84 in various European localities (Grau 1976). Vaarama & Hiirsalmi (1967) indicate that most previous counts are based on Atlantic collections.

Veronica sibthorpioides is sometimes placed in *V. hederifolia* which can be divided up into 4 subspecies (Walters 1972). Three of them, subsp. *triloba* (Opiz) Čelak., subsp. *lucorum* Klett & Richter and subsp. *hederifolia* belong to a polyploid series based on x = 9. The N African populations that we have examined all belong to subsp. *sibthorpioides*. A Middle Atlas collection of this subspecies gave n = 15, which confirms previous records of 2n = 30 given by Hofelich (1935), Lehmann & Schmitz-Lohner (1954) and Löve & Kjellquist (1974). On the basis of chromosome number this morphologically distinctive taxon appears not to be a subspecies of the *hederifolia* polyploid complex (see Fischer 1967).

Veronica rosea. Our count of n = 8 is the first report for this species.

Umbelliferae

Daucus. The first count of 2n = 22 on Moroccan material of *Daucus durieua* Lange, although differing from previous counts of 2n = 20 on eastern Mediterranean plants (Queiros 1972), is not unusual for the genus as a whole. There are three common base numbers of x = 9, 10 and 11 in *Daucus* (Bolkhovskikh et al. 1969) but intraspecific aneuploids are rare. n = 11 for *D. setifolius* is a first record; it is the same number as for various other members of the *D. crinitus* group.

Scandix pecten-veneris. Most previous counts (Melderis 1930, Tischler 1934, Delay 1947, Cauwet 1968) based especially on material of European origin, but also those based on specimens from Afghanistan (Podlech & Dieterle 1969) and N America (Heiser & Whitaker 1948) 2n = 16. Our count of n = 13 confirms the previous record of 2n = 26 by Tamamsin (1933; cited from Bolkhovskikh et al. 1969).

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Table 1. Chromosome counts of flowering plants from Morocco and Algeria. – A Algeria, I Iberia, M Morocco, NA N Africa. – BBR Bocquet, Borel & Reist 1971, BMR Bramwell, Murray & Richardson 1971, HH C. J. & A. R. Humphries 1976, HJMR Humphries, Jury, Mullin & Richardson 1974, SS D. & S. Sutton 1976. – AA Anti Atlas, CN Maroc centrale, partie septentrionale, ES Maroc oriental steppique, GA Grand Atlas, H Maroc meridional, MA Moyen Atlas, R Rif, SW secteur Macaronesian marocain, T Tanger, WD Maroc désertique occidental, Z monts des Zaïan. – O1 Oranais, Sahels littoraux, K2 petite Kabylie, K3 Numidie, C1 Tell constantinois, SS2 sous-secteur oriental du Sahara Septentrional, H2 Hauts-plateaux constantinois. – An asterisk indicates new or deviating counts.

Taxon	n	2n	Endemic status	Voucher	Origin
MONOCOTYLEDONS					
Gramineae					
Aegilops ovata L.	.	28	.	HJMR 507	M: AA, Igherm, 1300 m, 20 km from Tafraoute
Do.	14	.	.	BBR 10147	M: CN, Beni-Sadden, 600 m, entre Fès et Birtam-Tam
Alopecurus arundinaceus Poiret	14	.	.	BBR 10442	M: MA, Aguelmame de Sidi-Ali, rives du lac, 2100 m
Avena alba Vahl	14	.	.	BBR 10154	M: CN, Beni-Sadden, 600 m, entre Fès et Birtam-Tam
Briza minor L.	.	10	.	HJMR 421	M: AA, N of Tafraoute, Jbel Lekst, 1400 m
Bromus hordeaceus L.	14	.	.	BBR 10651	M: GA, Jbel Ayachi, cirque de Jaffar, 2200 m
B. macrostachys Desf.	.	28	.	BBR 11026b	M: GA, gorges du Moulay Brahim, 42 km de Marrakech 1100 m
B. madritensis L.	14	.	.	BBR 10080	M: T, Tetouan, 12 km au nord de Chechaouen, 320 m
B. rubens L.	14	.	.	BBR 10156	M: CN, Beni-Sadden, 600 m, entre Fès et Birtam-Tam
Do.	.	28 + 4 B	.	BBR 10720	M: ES, entre Mibladen et mines de Tazensout, 1200 m
Do.	14	.	.	BBR 10867	M: GA, jardin du "Cercle" de Msemrir, 1900 m
Do.	14	.	.	BBR 1056	M: MA, plaine entre Itzer et Midelt, 1500 m
B. tectorum L.	7	.	.	BBR 10087	M: T, Tetouan, 5 km au nord de Chechaouen, 340 m
Do.	14	.	.	BBR 10866	M: GA, jardin du "Cercle" de Msemrir, 1900 m
Do.	7	.	.	BBR 10872	M: GA, 2–3 km en amont de Msemrir, 1900 m
Do.	14	.	.	BBR 10839	M: GA, gorge entre les vallées du Todra et du Dadès 2300 m
Dactylis glomerata L.	7 + 2 B	.	.	BBR 11032	M: GA, gorges du Moulay Brahim, 42 km de Marrakech, 1100 m
D. hispanica Roth	14	.	.	BBR 10901	M: GA, Tizi-n-Aguelmous, region d'Agouim, 1700 m
Gaudinia fragilis (L.) P. B.	.	14	.	HJMR 44	M: WN, 8 km S of Arbaoua, 250 m
Haynaldia hordeacea (Coss. & Dur.) Hack.	14	.	NA	BBR 10563	M: MA, plaine entre Itzer et Midelt, 1500 m
Hordeum glaucum Steudel	7	.	.	BBR 10865	M: GA, jardin du "Cercle" de Msemrir, 1900 m
Do.	.	14	.	HJMR 603	M: GA, Tizi-n-Test, 2150 m
Do.	.	14	.	HJMR 112	M: SW, Cap Beddouza, 30 m
Hyparrhenia hirta (L.) Stapf*	18	.	.	BBR 11027	M: GA, gorges du Moulay Brahim, 42 km au sud de Marrakech, 1100 m
Lolium rigidum Gaud.	.	14, 14 + 2 B	.	BMR 453	M: AA, Tafraoute, south-west side of Tizi Mlil
Lophochloa phleoides (Vill.) Reichenb.	14	.	.	BBR 10348	M: CN, Fès, 350 m
Melica ciliata L. var. *nebrodensis* (Parl.) Coss. & Dur.	9	.	.	BBR 10843	M: GA, gorges entre les vallées du Todra et du Dadès, 2300 m
Phalaris paradoxa L.	7	.	.	BBR 10155	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
P. brachystachys Link	6	.	.	BBR 10851	M: WD, avenue de Ouarzazate, 1160 m
P. minor Retz.	14	.	.	BBR 10864	M: GA, jardin du "Cercle" de Msemrir, 1900 m
Do.	14	.	.	BBR 11029	M: GA, gorges du Moulay Brahim, 42 km au sud de Marrakech, 1100 m
Schismus barbatus (L.) Thellung	6	.	.	BBR 10572	M: MA, plaine entre Itzer et Midelt, 1500 m
Taeniatherum caput-medusae (L.) Nevski	7	.	.	BBR 10906	M: GA, route de Telouet
Trachynia distachya Link	.	30	.	HJMR 301	M: AA, above Aït-Baha, 1200 m
Triticum turgidum L.	14	.	.	BBR 11072	M: H, banlieue de Marrakech, 450 m

Taxon	n	2n	Endemic status	Voucher	Origin
Liliaceae					
Asphodelus fistulosus L.	.	28	.	HJMR 144	M: SW, 2 km S of Safi, 20 m
Dipcadi serotinum (L.) Medikus*	.	32	.	SS 79	A: KZ, 30 km E of Skikda
Fritillaria messanensis Rafin.*	.	36	.	BMR 393	M: AA, gorge 20 km E of Tiznit
DICOTYLEDONS					
Asclepiadaceae					
Periploca laevigata Ait.	.	22	.	BBR 11041	M: SW, 20 km au nord d'Agadir
Boraginaceae					
Echium plantagineum L.	8	.	.	BBR 10030	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
Campanulaceae					
Campanula filicaulis Dur.*	13	.	NA	BBR 11052	M: T, col entre le Cap Malabata et Ceuta, 550 m
Do.*	13	.	NA	BBR 10798	M: GA, gorges dans le haut Dadès, 2300 m
Jasione corymbosa Poiret*	.	12	IMA	HJMR 1112	M: T, Tanger, Cap Spartel, 10 m
Caryophyllaceae					
Cerastium arvense L.	18	.	.	BBR 10428	M: MA, Timahdite, province de Meknes, 1850 m
Do.	18	.	.	BBR 10256	M: MA, Jbel Bou Iblane, Taffert, 1780 m
Do.	18	.	.	BBR 10359	M: MA, 5 km d'Ifrane vers Azrou, 1600 m
C. brachypetalum Pers.	46	.	.	BBR 10362	M: MA, 5 km d'Ifrane vers Azrou, 1600 m
Minuartia verna (L.) Hiern	.	26	.	HJMR 822	M: WD, Ouarzazate/Ksar-es-Sour road nr. Skoura
Polycarpon polycarpoides (Biv.) Zodda*	7	.	.	BBR 10744	M: GA, montée au-dessus de la plaine de Midelt, 1750 m
Silene imbricata Desf.*	.	24	NA	HJMR 1110	M: T, Cap Spartel, 10 m
S. sp. aff. *canopica* Boiss.*	.	24	.	HJMR 1081	M: R, Taounate to Ketama
S. setacea Viv.*	.	24	.	HJMR 187	M: SW, 3 km S of Essaouira, 20 m
S. ayachica Humbert	.	24	M	HJMR 969	M: GA, Jbel Ayachi, cirque de Jaffar, 2227 m
Spergularia diandra Heldr. & Sart.	9	.	.	BBR 10306	M: CN, environs de Fès, 350 m
S. rubra Pers.	9	.	.	BBR 10693	M: GA, entre Mibladen et Tazensout, gorge, 1200 m
Stellaria media L.	20	.	.	BBR 10363	M: MA, à 5 km d'Ifrane vers Azrou, 1600 m
Vaccaria pyramidata Medikus*	.	24	.	HJMR 561	M: S, 10 km E of Taroudant, 200 m
Chenopodiaceae					
Beta vulgaris L.	.	18	.	HJMR 143	M: SW, 2 km S of Safi
Cistaceae					
Helianthemum pilosum (L.) Pers.	10	.	.	BBR 10586	M: GA, Jbel Ayachi, cirque de Jaffar, 1700 m
Tuberaria guttata (L.) Fourr.	.	24	.	SS 733	A: K3, 15 km W of El Kala
Cleomaceae					
Cleome arabica L.	.	22	.	HJMR 818	M: WD, Ouarzazate/Ksar-es-Souk road, nr. Skoura, 1350 m
Do.	10	.	.	BBR 10785	M: ED, piste Erfoud/Touroug (sur le tracé de Tinerhir), 850 m
Compositae-Anthemideae					
Achillea odorata L.	9	.	.	BBR 10807	M: GA, Telouet, du Col de Tichka, 1800 m
Anacyclus pyrethrum (L.) Cass. var. *depressus* (Ball) Maire	9	18	IMA	HJMR 867	M: GA, Dadès, gorge between Msemrir and Tamtattouchte
Do.	9	18	IMA	HJMR 757	M: GA, Oukaïmeden, Jbel Angour, 2650 m
Do.	.	18	IMA	HJMR 635	M: GA, 5 km N of Ijoukak, 1159 m
Do.	9	18	IMA	HH 13	M: MA, Mischliffen, 1200 m
Do.	.	18	IMA	HJMR 1035	M: Z, Zaïan, 5 km NE of Mischliffen, 1934 m

Taxon	n	2n	Endemic status	Voucher	Origin
A. pyrethrum var. *pyrethrum*	.	18	MA	HJMR 926	M: GA, cirque de Jaffar, Jbel Ayachi, 2135 m
A. radiatus Lois. var. *radiatus*	.	18	.	HJMR 1064	M: CN, Fès, 16 km from El Hajeb on road to Fès
A. radiatus var. *coronatus* Murb.	9	18	M	HJMR 182	M: SW, 3 km S of Essaouira, 20 m
Do.	9	18	M	HJMR 274	M: AA, ESE of Aït Melloul
Do.	9	18	M	HJMR 562	M: S, Oued Sous, 10 km E of Taroudannt, 200 m
A. valentinus L.	.	18	.	HH 71	M: MA, Tizi-n-Aït-Ouira near El Ksiba
Do.	9	18	.	HJMR 535	M: AA, 6 km from Igherm, 1800 m
Do.	9	18	.	HJMR 674	M: GA, Asni, 7 km from Tahanaoute to Oukaïmeden, 1200 m
Do.	9	18	.	HJMR 624	M: GA, Tizi-n-Test, 1700 m
Do.	9	18	.	HH 77	M: GA, 10 km N of Oukaïmeden, 1600 m
Do.	9	.	.	BBR 11001	M: GA, gorge du Moulay Brahim, près d'Asni, 100 m
A. clavatus (Desf.) Pers.	9	18	.	HJMR 1057	M: Z. Zaïan E of Azrou, 1350 m
Do.	9	18	.	HH 65	M: MA, Ajabo 5 km S of Aïn Leuh
Anthemis arvensis L.	.	18	.	HJMR s.n.	M: MA, Jbel Ayachi, cirque de Jaffar, 22.6.1974
Chamaemelum mixtum (L.) All.	9	.	.	BBR 11056	M: WN, Kenitra
Do.	.	18	.	HJMR s.n.	M: T, Tanger, Cap Spartel, 10 m, 29.6.1974
Chlamydophora pubescens (Desf.) Coss. & Kral.*	.	10	NA	SS 600	A: SS2, 5 km E of Biskra
Chrysanthemum carinatum L.	.	18	M	HJMR 338	M: SW, 40 km S of Agadir, 5 m
C. macrocarpum Coss. & Kral.*	.	18	NA	HJMR 291	M: AA, above Ait Baha, 1200 m
Coleostephus myconis (L.) Reichenb. fil.	.	18	.	SS 736	A: K3, 15 km W of El Kala
Heliocauta atlantica (Litard. & Maire) Humphries	9	18	M	HH 101	M: GA, Refuge Neltner, Jbel Toubkal, 3200 m
Leucanthemum arundanum (Boiss.) Cuatr. var. *mairei* (Humbert) Maire*	.	18	M	HJMR 941	M: GA, Jbel Ayachi, cirque de Jaffar, 20 km, 2135 m
L. catananche (Ball) Maire	.	18	M	HJMR 602	M: GA, Tizi-n-Test, 2150 m
L. gayanum (Coss. & Dur.) Maire* subsp. *gayanum*	.	18	M	HJMR 249	M: SW, Imouzzer-des-Ida-Outanane, 1000 m
L. gayanum subsp. *antiatlanticum* Emb. & Maire*	.	18	M	HJMR 530	M: AA, 4 km from Igherm, 1700 m
Do.*	.	18	M	HJMR 586	M: GA, Tizi-n-Test, 4 km on road to Taroudant, 1900 m
L. redieri Maire* var. *sericeum* (Humbert) Maire	.	18	M	HJMR 965	M: GA, Jbel Ayachi, 20 km from Midelt, 1530 m
Do.*	9	.	M	BBR 10446	M: MA, Aguelmane de Sidi-Ali, 2200 m
Ormenis scariosa (Ball) Litard. & Maire*	9	.	M	BBR 10793	M: Ga, col au dessus de Tamtattouchte, 2300 m
Compositae-Astereae					
Bellis caerulescens (Coss.) Ball	.	18	M	HJMR 611	M: GA, Tizi-n-Test, 1 km N of pass, 2000 m
Compositae-Calenduleae					
Calendula sp. aff. *algeriensis* Boiss. & Reut.	.	14	.	HJMR 1066A	M: CN, Fès, El-Hajeb
C. algeriensis Boiss. & Reut.	7	.	.	BBR 10150	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
Do.	.	14	.	BBR 10319	M: CN, Fès, 350 m
Do.	7	.	.	BBR 10341	M: CN, Fès, 350 m
C. arvensis L.*	.	18	.	HJMR 671	M: GA, Asni, 7 km from Tahanaoute on road to Oukaimeden, 1200 m
C. arvensis var. *parviflora* (Willk.) Batt.*	.	14	.	HJMR 826	M: WD, 41 km from Ouarzazate in Jbel Sarhro
Compositae-Cardueae					
Atractylis cancellata L.	10	.	.	BBR 11020	M: GA, gorge du Moulay Brahim près d'Asni, 1100 m
Carduncellus pinnatus Desf.*	.	26	.	HJMR 500	M: AA, Igherm, 20 km from Tafraoute, 1300 m
Carthamus fruticosus Maire*	.	24	M	HJMR 829	M: WD, 41 km from Ouarzazate in Jbel Sarhro, 1500 m

Taxon	n	2n	Endemic status	Voucher	Origin
Do.*	.	24	M	HJMR 419	M: AA, Jbel Lekst, 1150 m
Centaurea aspera L.	.	44	.	HJMR 366	M: SW, 40 km from Agadir, estuary of Oued Massa, 5 m
C. clementei Boiss.*	.	18	IM	HJMR 1106	M: T, Tetouan-Chechaouèn, Mont Kraa
C. involucrata Desf.*	.	22	NA	HJMR 922	M: GA, Midelt, track to Jbel Ayachi, 2135 m
C. sp. aff. *nana* Desf.*	10	.	NA	BBR 10834	M: GA, gorge entre les vallées du Todra et du Dadès, 2300 m
C. pullata L.	11	.	.	BBR 10314	M: CN, Fès, 350 m
C. sulphurea Willd.*	9	.	IMA	BBR 11007	M: GA, gorge de Moulay Brahim, près de Asni, 1100 m
Galactites tomentosa Moench*	10	20	.	BBR 10311	M: CN, Fès, 350 m
Jurinea humilis (Desf.) DC.*	.	58	.	HJMR 776	M: GA, Oukaïmeden, W cliffs of Col du Tizrag, 2680 m
Do.*	.	24	.	HH 18	M: MA, Mischliffen, 1220 m
Silybum marianum (L.) Gaertner	.	34	.	SS 661	A: H2, 60 km S of Constantine, Ouled Zouai
Xeranthemum inapertum (L.) Miller*	.	28	.	HJMR 947	M: GA, Jbel Ayachi, 20 km from Midelt, 2211 m
Compositae-Inuleae					
Asteriscus imbricatus Cav.*	.	14	M	HJMR 354	M: SW, 40 km S of Agadir, estuary of Oued Massa, 12 m
Do.*	7	.	M	BMR 237	M: SN, Tamri, Cap Ghir
A. pygmaeus Coss. & Kral.*	.	10	.	HJMR 821	M: WD, S of Ouarzazate/Ksar-es-Souk road, Bou Skour 20 km to Skoura
Bombycilaena discolor (Pers.) Laínz*	.	28	.	HJMR 916	M: AA, Tafraoute, 28 km to Igherm, 1500 m
Evax pygmaea (L.) Brot.* subsp. *pygmaea*	.	18	.	BMR 85	M: WN, between Larache and Ksar-el-Kebir
Leysera leyseroides (Desf.) Maire*	.	14	.	HJMR 454	M: AA, 5 km from Tafraoute, 1100 m
Pallenis spinosa (L.) Cass.	5	.	.	BBR 10583	M: GA, Jbel Ayachi, 12 km from Midelt, 1700 m
Do.	5	.	.	BBR 10709	M: ES, gorge de l'Oued Moulouya, 1100 m
Phagnalon embergeri Humbert & Maire*	.	18	M	HJMR 963	M: GA, Jbel Ayachi, N cliffs, 2211 m
P. helichrysoides (Ball) Coss.*	.	14	M	HJMR 765	M: GA, Jbel Angour, 3200 m
P. saxatile (L.) Cass.	.	18	.	HJMR 402	M: AA, W side of Col du Kerdous, 1050 m
Do.	.	18	.	BBR 10748	M: GA, près de Midelt, 1750 m
Pulicaria arabica (L.) Cass.	.	16	.	HJMR 456	M: AA, 5 km from Tafraoute, 1100 m
P. odora Reichenb.*	.	16	.	HJMR 1107	M: T, Tanger, Cap Spartel, 10 m
P. mauritanica Coss.*	6	.	NA	BMR 300	M: AA, Imouzzer valley, Oulria
Compositae-Mutisieae					
Warionia saharae Benth. ex Coss.	17	34	NA	HJMR 278	M: AA, Above Aït-Baha, 1000 m
Compositae-Senecioneae					
Hertia maroccana Maire	10	.	M	BMR 558	M: GA, gorges du Dadès
Compositae-Cichorioideae					
Andryala canariensis Lowe* subsp. *mogadorensis* (Coss. & Ball) Maire	9	.	M	BMR 236	M: SW, Tamri, near Cap Ghir
Catananche caerulea L.	9	.	.	BBR 10689B	M: GA, gorge de l'Oued Moulouya, 1100 m
Crepis vesicaria subsp. *haenseleri* (Boiss. ex DC.) P. D. Sell	.	12	.	SS 225	A: O1, La Macta, between Mostaganem and Oran
Do.	4	.	.	BBR 10312	M: CN, Fès, 350 m
Hedypnois rhagadioloides (L.) F. W. Schmidt	.	10, 10+1 B	.	HJMR 206	M: SW, 5 km above Oulma, 700 m
Hyoseris radiata L.	.	16	.	HJMR 1111	M: T, Tanger, Cap Spartel, 10 m

Taxon	n	2n	Endemic status	Voucher	Origin
Lactuca tenerrima Pourret	.	16	.	HJMR 556	M: AA, 15 km from Igherm towards Taroudannt, 1500 m
Do.	.	16	.	HJMR 575	M: GA, Tizi-n-Test, 1800 m
Do.	.	16	.	HJMR 426	M: AA, Djebel Lekst, 1500 m
Picris cupuligera (Dur.) Walp.*	5	.	NA	BBR 10771	M: GA, à 20 km de Meski en direction de Erfoud, 1000 m
P. hispanica (Willd.) P. D. Sell*	.	20	.	HJMR 934	M: GA, 20 km from Midelt to Ayachi, 2135 m
Reichardia tingitana (L.) Roth	.	16	.	HJMR 355	M: SW, 40 km S of Agadir, Oued Massa, 5 m
Do.	.	16	.	HJMR 633	M: GA, 5 km N of Ijoukak, 1159 m
Scorzonera pseudopygmaea Lipsch.*	.	12 + 1 B	M	HJMR 513	M: AA, 18 km from Igherm on road to Tafraoute, 1800 m
Taraxacum obovatum DC.	16	.	.	BBR 10683	M: MA, rives de l'Aguelmame de Sidi-Ali, 2150 m
Tragopogon crocifolius L.	.	12	.	HJMR s.n.	M: GA, Oukaïmeden, Jbel Angour, 2650 m, 14.6.1974
T. porrifolius L. var. *australis* (Jord.) Batt.	.	12	.	HJMR 1038	M: Z, Zaïan, near Ifrane, 1700 m
Cruciferae					
Aethionema saxatile (L.) R. Br.	16	.	.	BBR 10447	M: MA, rives de l'Aguelmame de Sidi-Ali, 2200 m
Do.	.	48	.	HJMR 2050	M: Z, Zaian, Ras-el-Mar, 1650 m
Biscutella didyma L. subsp. *lyrata* (L.) Murb.	8	.	.	BBR 11013	M: GA, gorge du Moulay Brahim, 1100 m
Crambe hispanica L.	30	.	.	BBR 10692	M: ES, Mibladen, gorge de l'Oued Moulouya, 1200 m
Farsetia aegyptiaca Turra	.	c. 72	.	HJMR 820	M: WD, S of Ouarzazate to Kar-es-Souk road, Bou-Skour 20 km from Skoura, 1350 m
Isatis tinctoria L.	.	28	.	HJMR 574	M: GA, Tizi-n-Test, 1800 m
Lobularia maritima (L.) Desf.	12	.	.	BBR 10702	M: GA, gorge de l'Oued Moulouya, Tazen-Sout, 1100 m
Malcolmia parviflora DC.	.	24	A	SS 105	A: 50 km W of Ténès, Cap Margraoua
Matthiola parviflora (Schousb.) R. Br.	.	8	.	HJMR 324	M: AA, 35 km SW of Aït-Baha, 500 m
Morettia canescens Boiss.	11	.	.	BBR 10767	M: GA, plaine de Rich, 1300 m
Moricandia suffruticosa (Desf.) Cass.	14	.	.	BBR 10691	M: ES, gorge de l'Oued Moulouya, 1200 m
Do.	14+4 B	.	.	BBR 10728	M: GA, gorge & 10 km de Rich, 1400 m
Raffenaldia primuloides Godr.	10	.	M	BMR 604	M: GA, Col du Zad
Dipsacaceae					
Scabiosa sp. aff. *maritima* L.	8	.	.	BBR 10789	M: GA, gorges du Todra, 1700 m
S. stellata L. subsp. *monspeliensis* (Jacq.) Rouy	.	18	.	HJMR 258	M: SW, Imouzzer-des-Ida-Outanane, 1000 m
Euphorbiaceae					
Andrachne aspera Spreng.*	.	24	.	HJMR 213	M: SW, Cap Ghir, 4 m
Euphorbia dracunculoides Lam.	.	16	.	SS 601	A: SS2, 5 km E of Biskra
Do.*	20	.	.	BBR 10579	M: MA, plaine entre Itzer et Midelt, 1500 m
E. exigua L.*	.	20	.	HJMR 218	M: SW, 5 km N of Oulma, 700 m
E. megatlantica Ball*	.	14	M	HJMR 802	M: GA, Tizi-n-Tichka, 1 km N of Igherm-n-Ougdal, 1900 m
E. paralias L.*	.	22	.	HJMR 349	M: SW, 40 km S of Agadir, estuary of Oued Massa, 5 m
E. segetalis L.	8	.	.	BBR 10139	M: GA, ras de la colline de Taounate, 450 m
Fumariaceae					
Sarcocapnos crassifolia (Desf.) DC.*	12	.	IMA	BBR 10448	M: MA, Aguelmame de Sidi-Ali, près de Timahdite, 2200 m

Taxon	n	2n	Endemic status	Voucher	Origin
Geraniaceae					
Erodium glaucophyllum (L.) L'Hérit.	.	20	.	SS 580	A: SS2, 10 km N of Biskra, Col de Sfa
E. malacoides (L.) L'Hérit.	.	20	.	SS 784	A: K2, 30 km E of Skikda, Toret des Senhadja
Do.	10	.	.	BBR 10955	M: GA, Tizi-n-Test, vers Agadir, 2000 m
Guttiferae					
Hypericum australe Ten.*	.	18	.	SS 729	A: K3, 15 km W of El Kala
Labiatae					
Mentha gattefossei Maire*	.	36	M	HH 10	M: MA, 8 km S of Ifrane, Boulimene
Salvia aegyptiaca L.*	.	42	.	BMR 409	M: SW, Tiznit
S. blancoana Webb & Heldr.*	7	.	IMA	BBR 10581	M: GA, Jbel Ayachi, cirque de Jaffar, 1700 m
S. taraxacifolia Coss. ex Hook. fil.*	13	.	M	BBR 11014	M: GA, gorge du Moulay Brahim, 1100 m
Do.*	.	26	M	HJMR 576	M: GA, Tizi-n-Test, 22 km along road from Taroudannt, 1800 m
Stachys ocymastrum (L.) Briq.	9	.	NA	BBR 10338	M: CN, Fès, 350 m
Leguminosae					
Adenocarpus bacquei Batt. & Pitard*	24	.	NA	BBR 10584	M: GA, Jbel Ayachi, 12 km de Midelt, 1700 m
A. anagyrifolius Coss. & Balansa*	24	.	M	BBR 10805	M: GA, Tizi-n-Aguelmous, 2100 m
Biserrula pelecinus L.	8	.	.	BBR 10073	M: T, Tetouan, 5 km au nord de Chechaouen, 340 m
Genista microphylla (Ball) Coss. & Dur.*	.	26	NA	HJMR 323	M: AA, 35 km SW of Aït-Baha, 500 m
G. vepres Pomel	.	72	NA	HJMR 167	M: SW, 12 km along road from Essaouira to Saji, 300 m
Hippocrepis scabra DC.	.	14	.	HJMR 924	M: GA, Jbel Ayachi, 20 km from Midelt, 2135 m
Lotus creticus L.	7	.	.	BBR 10746	M: GA, Midelt, 1750 m
Medicago truncatula Gaertner*	.	14	.	SS 75	A: O2, 5 km E of El Asham
Onobrychis peduncularis (Cav.) DC.*	16	.	.	BBR 10585	M: GA, Jbel Ayachi, cirque de Jaffar, 1700 m
Ononis natrix L. subsp. *natrix*	15	.	.	BBR 10808	M: GA, Telouet
Do.	16	.	.	BBR 10741	M: GA, Jbel Ayachi, cirque de Jaffar, 1750 m
O. natrix subsp. *hispanica* (L. fil.) Coutinho	16	.	.	BBR 10933	M: GA, Tizi-n-Test, 1700 m
Ornithopus compressus L.	.	14	.	SS 807	A: K2, El Halia, 20 km E of Skikda
Scorpiurus muricatus L. subsp. *sulcatus* (L.) Thell.	.	28	.	BBR 11110	M: T, Cap Malabata, 20 m
Do.	.	28	.	BBR 10040	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
Tipuana tipu (Benth.) Kuntze (cultivar)	10	.	.	BBR 11044	M: GA, Marrakech, 450 m
Trifolium campestre Schreber	7	.	.	BBR 10308	M: CN, Fès, 350 m
T. lappaceum L.	8	.	.	BBR 11116	M: T, Cap Malabata, 20 m
T. scabrum L.	5	.	.	BBR 10034	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
T. stellatum L.	7	.	.	BBR 10033	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
T. tomentosum L.	.	16	.	BBR 10320	M: CN, Fès, 350 m
Plantaginaceae					
Plantago afra L.	.	12	.	HJMR 259	M: SW, Imouzzer-des-Ida-Outanane, 1000 m
P. albicans L.*	5	.	.	BBR 10711	M: ES, gorge de l'Oued Moulouya, 1100 m
P. amplexicaulis Cav.	.	10	.	HJMR 197	M: AA, above Aït-Baha, 1200 m
P. arenaria Waldst. & Kit.	6	.	.	BBR 10715	M: ES, gorge de l'Oued Moulouya, 1100 m

Taxon	n	2n	Endemic status	Voucher	Origin
Plumbaginaceae					
Limonium pruinosum (L.) O. Kuntze	.	16	.	SS 604	A: SS2, 5 km E of Biskra
Polygonaceae					
Rumex vesicarius L.	.	18	.	HJMR 302	M: AA, above Aït-Baha, 1200 m
Primulaceae					
Primula vulgaris L.	.	22	.	BBR 10205	M: MA, Jbel Bou Iblane, versant nord, 2180 m
Ranunculaceae					
Ranunculus ophioglossifolius Vill.	.	16	.	SS 762	A: K3, 5 km W of El Kala, Lac Oubeïra
Rosaceae					
Sanguisorba minor (L.) Scop.	.	56	.	HJMR 265	M: SW, Imouzzer-des-Ida-Outanane, 1000 m
Rubiaceae					
Asperula hirsuta Desf.*	22	.	I, NA	BBR 10806	M: GA, Telouet, à partir du col de Tichka, 1800 m
Galium ephedroides Willk.*	11	.	IM	BBR 10745	M: GA, montée au dessus de la plaine de Midelt, 1750 m
Sapotaceae					
Argania spinosa (L.) Maire*	12	.	M	BBR 10960	M: GA, versant sud du Tizi-n-Test entre Tachguelte et Tafinegoult, 1000 m
Scrophulariaceae					
Acanthorrhinum ramosissimum (Coss. & Dur.) Rothm.*	16	.	NA	BBR 10733	M: GA, gorge à 10 km de Rich, 1400 m
Do.*	.	16	NA	HJMR 634	M: GA, 5 km N of Ijoukak, 1159 m
Anarrhinum fruticosum Desf.*	.	18	NA	SS 630	A: CI, 2 km from Kasrou, N of Batna
Do.*	9	.	NA	BBR 10751	M: GA, montée au dessus de la plaine du Midelt, 1750 m
Antirrhinum majus L. subsp. *tortuosum* (Bosc) Rouy	.	16	.	SS 874	A: K2, corniche of Kabylie, 5 km W of Ziama and Mansouria
Linaria reflexa (L.) Desf.	.	12	.	SS 316	A: O1, 5 km N of Bou Ttelis
L. tingitana Boiss. & Reut.*	.	12	NA	SS 173	A: O1, 30 km W of Cap Khamis, E of Sidi Lakhdar
L. ventricosa Coss.*	.	12	M	HJMR 271	M: SW, 5 km E of Tamrhakht, road to Imouzzer
Do.*	6	.	M	BBR 10790	M: GA, gorges du Todra, 1700 m
Scrophularia arguta Ait.*	.	36	.	HJMR 97	M: WS, Cap Beddouza, 30 m
S. auriculata L.*	29	.	.	BBR 11087	M: GA, Tizi-n-Test, 1000 m
Veronica sibthorpioides Debeaux, Degen & Hercvier*	15	.	I, NA	BBR 10459	M: MA, au sud de l'Aguelmame de Sidi-Ali, près de Timahdite, 2200 m
V. rosea Desf.*	8	.	NA	BBR 10582	M: GA, Jbel Ayachi, cirque de Jaffar, 1700 m
Solanaceae					
Datura metel L.	24	.	.	HJMR 373	M: SW, 40 km S of Agadir, Oued Massa
Umbelliferae					
Ammi majus L.	11	.	.	BBR 11058	M: WN, Kenitra
Bupleurum semicompositum L.	.	16	.	HJMR 307	M: AA, 4 km WSW of Aït Baha, 1000 m
Carum atlanticum Litard. & Maire	11	.	M	BBR 10680	M: GA, gorge de l'Oued Moulouya, 1200 m
Daucus carota L. subsp. *hispidus* (Arcangeli) Heywood	.	18	.	HJMR 147	M: SW, 2 km S of Safi, 20 m
D. durieua Lange*	.	22	I, NA	HJMR s.n.	M: GA, 7 km S of Asni, 15.6.1974
D. sahariensis Murb.	.	18	NA	HJMR 883	M: ED, Goulmina, 58 km W of Ksar-es-Souk, 1100 m

Taxon	n	2n	Endemic status	Voucher	Origin
D. setifolius Desf.*	11	.	I, NA	BBR 10305	M: MA, Fès, 350 m
Ferula communis L.	.	22	.	HJMR 337	M: SW, 40 km S of Agadir, estuary of Oued Massa, 5 m
Foeniculum vulgare Miller	11	.	.	BBR 11045	M: H, Marrakech, 450 m
Pseudorlaya pumila (L.) Grande	.	16	.	HJMR 149	M: SW, 5 km S of Safi
Do.	.	16	.	HJMR s.n.	M: T, Cabo Negro near Ceuta, 29.6.1974
Scandix pecten-veneris L.*	13	.	.	BBR 10026	M: CN, Beni-Sadden, entre Fès et Birtam-Tam, 600 m
Zygophyllaceae					
Peganum harmala L.	.	24	.	HJMR 813	M: WD, Jbel Sarhro, 41 km S of Ouarzazate/Ksar-es-Souk road

Achnanthes fogedii, a new subfossil diatom from S Sweden

Hannelore Håkansson

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Achnanthes fogedii sp. nov. is described from a brackish water sediment in the Spjälkö area, S Sweden. Its closest ally seems to be *A. holsatica* Hust.

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Achnanthes fogedii Håkansson, sp. nov.

Valvae ellipticae, 7–9 μm longae, 4.5–5 μm latae. Raphovalvae raphe recta, striae interruptae, 22–25 in 10 μm; striae areovalvae marginales (per microscopium luminarium vix visibiles).

Typus: Spjälkö 2723 1977, Laboratory of Quaternary Biology, Tornavägen 13, Lund.

Valves elliptical, c. 7–9 × 4.5–5 μm, 22–25 striae/10 μm. The striae on the rapheless valve are only on the edge of the valve, and are sometimes hard to recognize in the light microscope. The striae on the raphe valve are interrupted on the valve face. As can be seen in SEM (Fig. 1 E) the two striae "pieces" are connected by a furrow. They follow the bending of the valve. Axial area narrow, expanding slightly in the central area. At the polar ends there are one or more uninterrupted striae. The raphe is straight.

The rapheless valve is easily overlooked in LM, since it sometimes appears as a structureless light-refractive plate, especially when seen from the inside (Fig. 1 A–C). This species will then be mistaken for a small species of *Navicula*.

Achnanthes fogedii most closely resembles *A. holsatica* Hust. (Hustedt 1936 Taf. 407, Fig. 67–72, 1950 S. 344, Taf. 35, Fig. 1–6), but is distinguished from this by the interruption of the striae on the raphe valve and by having the same striae on the raphe valve as on the rapheless valve.

A. fogedii occurs in the sediment of Spjälkö, prov. Blekinge, S Sweden (R. Liljegren unpubl.) together with *Mastogloia smithii* Thw. var. *lacustris* Grun., *M. elliptica* (Ag.) Cl., *M. braunii* Grun., *Cyclotella caspia* Grun., *C. meneghiniana* Kütz., *Achnanthes hauckiana* Grun., *Campylodiscus clypeus* Ehr., *Amphora commutata* Grun., *A. coffeaeformis* Ag. and *Nitzschia scalaris* (Ehr.) W. Smith, which are mostly "Brackwasserformen, häufig in den Küstengebieten" (Hustedt 1930, 1959).

Acknowledgements. I wish to name this species *fogedii* because of my gratitude to Dr Niels Foged, Odense, for all the help he has given me over the years. I want to thank Dr Risto Tynni for advice and critical reading of the manuscript, and Dr Peter Beales for correcting the language.

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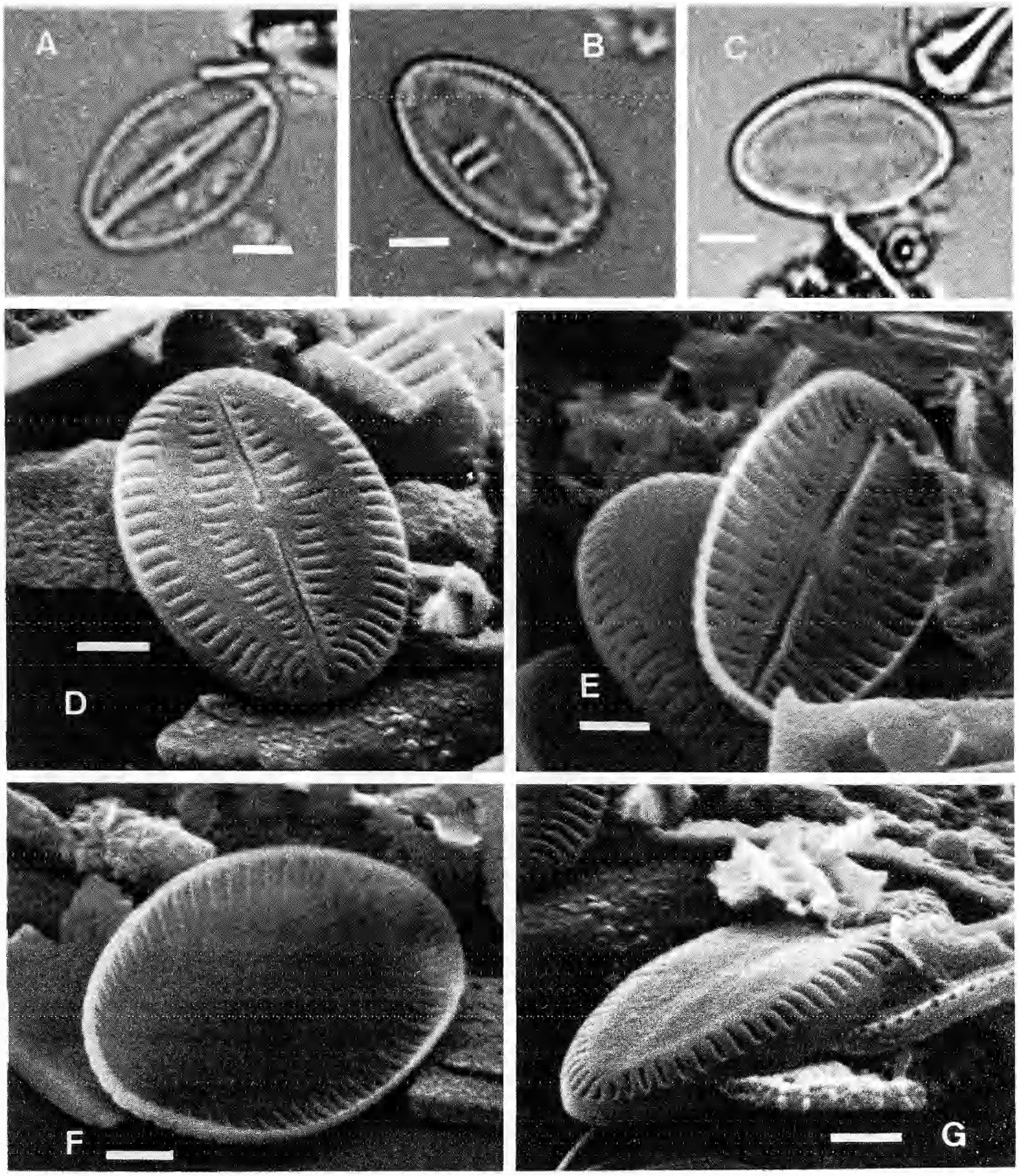

Fig. 1. *Achnanthes fogedii*. – A: Raphe valve. – B–C: Rapheless valve. – D: Exterior view of a raphe valve. – E: Interior view of a raphe valve showing that the "pieces" of the striae are connected by furrows. – F, G: Interior and exterior virews of a rapheless valve. – A–C: LM, scale unit 2 μm, D–G SEM, scale unit 1 μm.

Festuca brevissima Jurtz. in Alaska

Signe Frederiksen

Frederiksen, S. 1978 12 15: Festuca brevissima Jurtz. in Alaska. *Bot. Notiser 131:* 409–410. Stockholm. ISSN 0006-8195.

The diploid taxon *Festuca ovina* L. ssp. *alaskana* Holmen is conspecific with *F. brevissima* Jurtz., which thus occurs on both sides of the Bering Strait.

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Holmen (1964) described *Festuca ovina* L. ssp. *alaskana* from Alaska. It was said to differ from typical *F. ovina,* e.g. in the poorly developed mechanical tissue of the leaf-blade. In the original description the anthers of *F. ovina* ssp. *alaskana* were reported to be 2–3 mm long. Reexamination of the type material as well as other plants from the area clearly show that they have very short anthers (c. 1 mm), however. Moreover, young leaf-sheaths are splitting only halfway or less, while in *F. ovina* they split to the base (cf. Hackel 1882). It therefore appeared unlikely that the Alaskan taxon should be regarded as a subspecies of *F. ovina.*

Löve & Löve (1975) included *F. ovina* ssp. *alaskana* in *F. auriculata* Dobr., a diploid species occurring in the arctic parts of the Soviet Union. Like *F. ovina* it has relatively long anthers (c. 2 mm). In *F. auriculata* the mechanical tissue of the leaf-blade forms three bundles (Cvelev 1976), whereas there are normally seven in *F. ovina* ssp. *alaskana* (Fig. 1). The leaf sections in Holmen (1964) do not seem to illustrate normal conditions in the latter. The differences in anther length and leaf anatomy appear to rule out the possibility that *F. ovina* ssp. *alaskana* should be conspecific with *F. auriculata.*

The short anthers, the poorly developed mechanical tissue of the leaf-blade, and the fact that the leaf-sheaths do not split to the base make it more probable that *F. ovina* ssp. *alaskana* belongs in the *F. brachyphylla* group. This is a polyploid complex consisting of at least one hexaploid (*F. brachyphylla* s. str.), two tetraploids (*F. baffinensis* Polunin and *F. hyperborea* Holmen ex Frederiksen; cf. Frederiksen 1977), and one recently described diploid (*F. brevissima* Jurtzev). The latter has only been reported from the Chukotsk Peninsula in eastern Siberia (Jurtzev & Cvelev 1972, Jurtzev & Žukova 1972). Morphologically it is very similar to *F. brachyphylla* and *F. hyperborea,* but differs in having an open panicle with spreading branches at the time of anthesis. Holmen (1964) made the same observation for *F. ovina* ssp. *alaskana,* and the habitat described by him is also remarkably similar to that reported by Jurtzev & Žukova (1972) for *F. brevissima.*

A closer study of the diagnosis of *F. brevissima* (Jurtzev & Cvelev 1972) as well as an isotype of this taxon showed great similarity with *F. ovina* ssp. *alaskana.* Transverse sections of leaves are practically identical (see Fig. 1 and Jurtzev & Žukova 1972). It seems clear that *F. ovina* ssp. *alaskana* must be included in *F. brevissima.* The only differences appears to be that some specimens from Alaska are more luxuriant, having 2–3 spikelets on the lowermost branches, whereas *F. brevissima* has only one. This certainly falls within a normal range of variation, however. A pale yellowish-green form of *F. ovina* ssp. *alaskana* was reported by Holmen, but

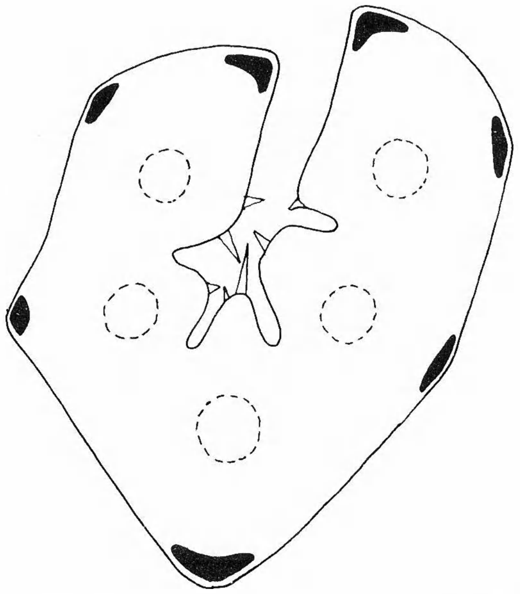

Fig. 1. Transverse section of basal leaf from type specimen of *Festuca ovina* ssp. *alaskana;* mechanical tissue black. – × 100.

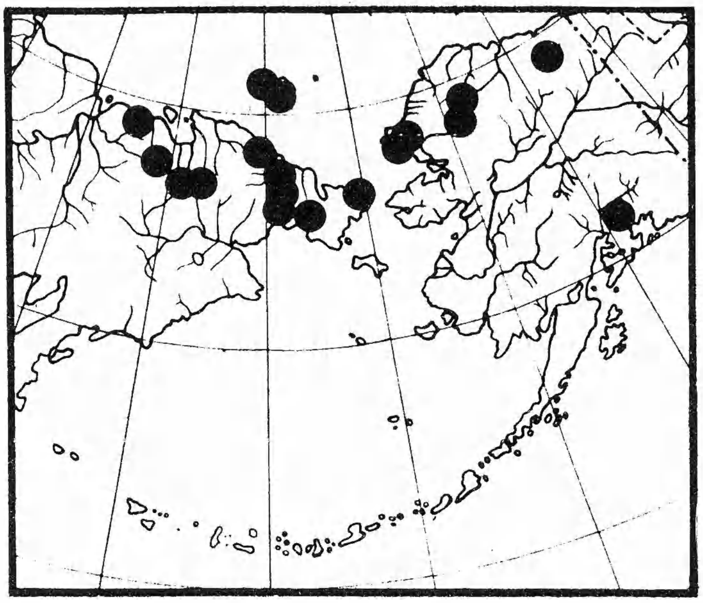

Fig. 2. Distribution of *Festuca brevissima*. The distribution in the Chukotsk Peninsula is based on specimens cited by Jurtzev & Cvelev (1972).

such forms occur also, for instance, in *F. brachyphylla* s.str. (Polunin 1940) and appear to be of no taxonomic significance.

As mentioned, *F. brevissima* can be distinguished from *F. brachyphylla* and *F. hyperborea* on the open panicle with spreading branches at the time of anthesis as well as on the lower chromosome number. It also differs from *F. brachyphylla* in the smaller overall size, short blade of the culm leaves, fewer spikelets, and glaucous colour (fresh green in *F. brachyphylla*). From *F. hyperborea* it differs in the very dense tufts, straight basal leaves, erect culms, somewhat longer anthers and lanceolate lemmas with a terminal erect arista (broader, with a subterminal arista in *F. hyperborea*).

F. brevissima is thus an endemic Beringian species, which has apparently survived the glaciations in this area (Fig. 2). Its distribution matches for instance with that of *Melandrium macrospermum* Porsild (Hultén 1968, Kožančikov & Tolmačev 1971).

Cvelev (1976) suggested that *F. brevissima* should be close to *F. minutiflora* Rydb., another species with very short anthers and poorly developed mechanical tissue. It occurs particularly in the Colorado Rocky Mountains at high altitudes, thus far from the area of *F. brevissima*. I have had the opportunity to study type material of *F. minutiflora,* and this appears quite distinct from *F. brevissima*.

This discussion is based on material from C and L (isotype only).

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Tulostoma niveum sp. nov. (Gasteromycetes), described from Sweden

Lars E. Kers

Kers, L. E. 1978 12 15: Tulostoma niveum sp. nov. (Gasteromycetes), described from Sweden. *Bot. Notiser 131:* 411–417. Stockholm. ISSN 0006-8195.

Tulostoma niveum Kers, sp. nov. is a small, white species confined to central E Sweden. It grows in moss tufts on limestone rocks. A distribution map is presented. The species is considered to come close to *T. moravecii* Pouzar.

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I have been studying the *Tulostoma* flora of C Sweden since 1972. It is not easy to make a taxonomic subdivision of the collected material. This genus is notorious for its troublesome taxonomy. Lloyd called it "the most difficult genus in the puff ball world" (Lloyd 1906 p. 27). In order to reduce the obstacles, I have based my investigation on freshly collected specimens, e.g. fully comparable gastrocarps. As far as possible I have tried to avoid studies of aged "mummies". Quite a large number of herbarium collections are composed of several species or of an otherwise heterogeneous material. Because some species are easily confused, these mixed collections may lead to a misunderstanding of the intra- and interspecific variation. Each of my collections, therefore, consists of gastrocarps which were gathered from one and the same individual swarm of specimens. The principle of the collecting method has been discussed in my paper on *Disciseda* (Kers 1975 p. 407).

Apart from the fairly well known *T. brumale* Pers. and *T. fimbriatum* Fr. there are some specimens in my material which do not represent either these two species or *T. melanocyclum* Bres. They will be studied further. A more distinct entity is described here as a new species: *T. niveum*. The description of its habitat is based on my field studies. The material consists of 88 collections.

Tulostoma niveum Kers, sp. nov.

T. moravecii Pouzar simile, differt statura multo minore, capitulo residuis substrati non contaminato, collo brevissimo a stipite distincte separato, areola circum os non griseo-nigra sed endoperidio plerumque concolorata, ore late conico raro plano ergo in partem superiorem capituli sensim transiente, endoperidio tenuiore, crystallis tetragonis numerosis inter sporas adspersis.

Descr.: Species pusilla tenuisque usque ad 25 mm alta, in Suecia centrali inter muscos in rupibus calcareis siccis crescit. *Capitulum* album, ovatum vel conicum, basi applanatum, in statu humefacto 2–7 mm altum et 3–9.5 mm latum, residuis substrati destitutum, mox collabens. *Os* late conicum, raro planum, a parte superiore capituli haud distincte separatum, album, raro leviter ochraceum, margine orbiculari, sublaevi. *Collum* vero inconspicuum, quam stipite circiter duplo latiore, margine integro. *Fovea capituli* in speciminibus siccis late conica. *Exoperidium* in speciminibus adultis tenuissimum, membranaceum, album, dilabens, substrato non contaminatum. *Endoperidium* subchartaceum, exile, velutinum, ab initio album, mox collabens. *Gleba pulverulenta* e capillitio, sporis et crystallis composita. *Hyphae capillitii* 2–5 μm crassae, hyalinae, incoloratae, parce ramosae, ad septa plerumque non vel unilateraliter incrassatae, laeves. *Sporae* globosae vel subglobosae, (4–)4.5–5(–6) μm diam., minute aculeatae vel per microscopium observatae fere inornatae, sub microscopio dilute lutescentes, pedicello inconspicuo non vel paullo aculeos superante. *Stipes* tenuis, cavus, in statu humefacto 4–21 mm longus et 0.5–2 mm crassus, primo albus demum stramineus vel pallide brunneus, laevis vel striatus, interdum squamulis albis vel stramineis adpressis ornatus vel saepe non ornatus, substrato raro contaminatus.

Typus speciei: Suecia centro-orientalis, Uplandia, pa-

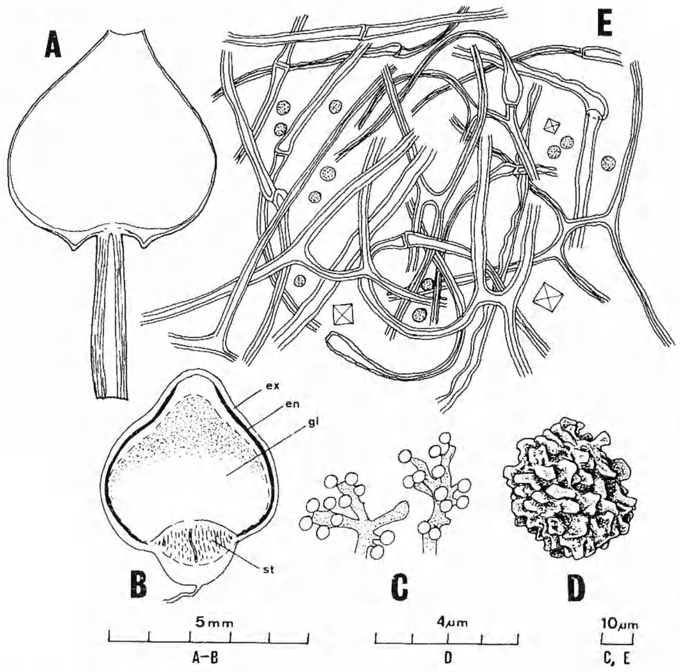

Fig. 1. *Tulostoma niveum*. – A: Capitulum and upper portion of the stipe in vertical, median section. Capillitium and spores not indicated. – B: Young, hypogean gastrocarp in vertical, median section. ex exoperidium, en endoperidium, gl gleba, st stipe primordium. – C: Ends of hyphae with basidia and young basidiospores. Drawn from a gastrocarp younger than in B. – D: Spore, drawn from a SEM photo. – E: Capillitium, spores and crystals. – A Kers 3947, B Kers 3917, C Kers 3931, D, E Kers 4264 (all in S).

rochia Djurö, Insula Munkö, in parte orientali prope mare, 23.9.1973, Kers 4264 (S holotypus, UPS isotypus).

The new species resembles the Czechoslovakian *T. moravecii* Pouzar (Moravec 1953, Pouzar 1958 pp. 596, 814). Both species are white and they have similar stipe surface, capillitium and spores. According to their macroscopic characters they seem to be well distinguished from other European species of *Tulostoma*. I have not found the Swedish material to be identical with any American or Russian species (Wright et al. 1972, Schwartsman & Filimonova 1970, Sossin 1973). The new species has been compared with type material of *T. moravecii* (leg. Z. Moravec, 21.9.1952, PRM).

Tulostoma niveum is smaller than *T. moravecii*. The thin and slender stipe is especially characteristic in contrast to that of *T. moravecii*. The gastrocarps of *T. niveum* collapse comparatively soon in the autumn or winter due to their small size and delicate texture. Accordingly specimens will rarely be found in April–May. It is likely that *T. moravecii*, which has about the same size and texture as *T. brumale*, resists weathering for several months and thereby forms "mummies".

The gastrocarps of *T. niveum* are pure white already when they emerge. Old herbarium specimens tend to discolour and become a pale yellowish shade. The new species is easily distinguished from all other Scandinavian species by its whiteness. When samples of the other species are whitish in colour it is a secondary feature gained by weathering of the originally brownish gastrocarps. *Tulostoma moravecii* is also white from the beginning.

No substrate adheres spontaneously to the peridium of *T. niveum*. Fragments of moss debris can be found on some of my samples but it represents contamination which has stuck to the specimens during the transport. *Tulostoma moravecii* has soil particles firmly stuck to the peridium. It is therefore less obviously white than is *T. niveum*. In *T. moravecii* there also exists a thin earth case at the base of the capitulum.

The lateral outline of the capitulum/mouth is a very distinct feature of *T. niveum*. The mouth is not clearly demarked below since the capitulum is ovate or onion shaped and the mouth is broadly conical (Figs. 1 A, 2). The mouth of *T. moravecii* seems to be more clearly separated from the capitulum proper than in the new species. The outline has been studied on freshly collected and on moistened gastrocarps. In dry material and especially in pressed gastrocarps the typical outline is usually much damaged or distorted. The mouth is opened by abscission of a very minute and almost flat lid. The same opening mechanism is found in *T. brumale*, *T. melanocyclum* and probably in all species which have a tubular or conical mouth.

Numerous tetragonal crystals are mixed with the dry capillitium and spores (Fig. 1 E). Their shape and chemical tests indicate that they are composed of trihydrate of calcium oxalate. They were found to be soluble in saturated Na_2HPO_4 and in 1 M HCl, but insoluble in 25% NH_3 and in concentrated CH_3COOH. I have not found this type of crystals in the dry gleba of *T. moravecii*, nor in my Swedish material of *T. brumale*.

The density of the spore ornamentation varies in the new species, also within a single gastrocarp. The SEM-photos show the verrucae to be distant in some spores whereas they are more

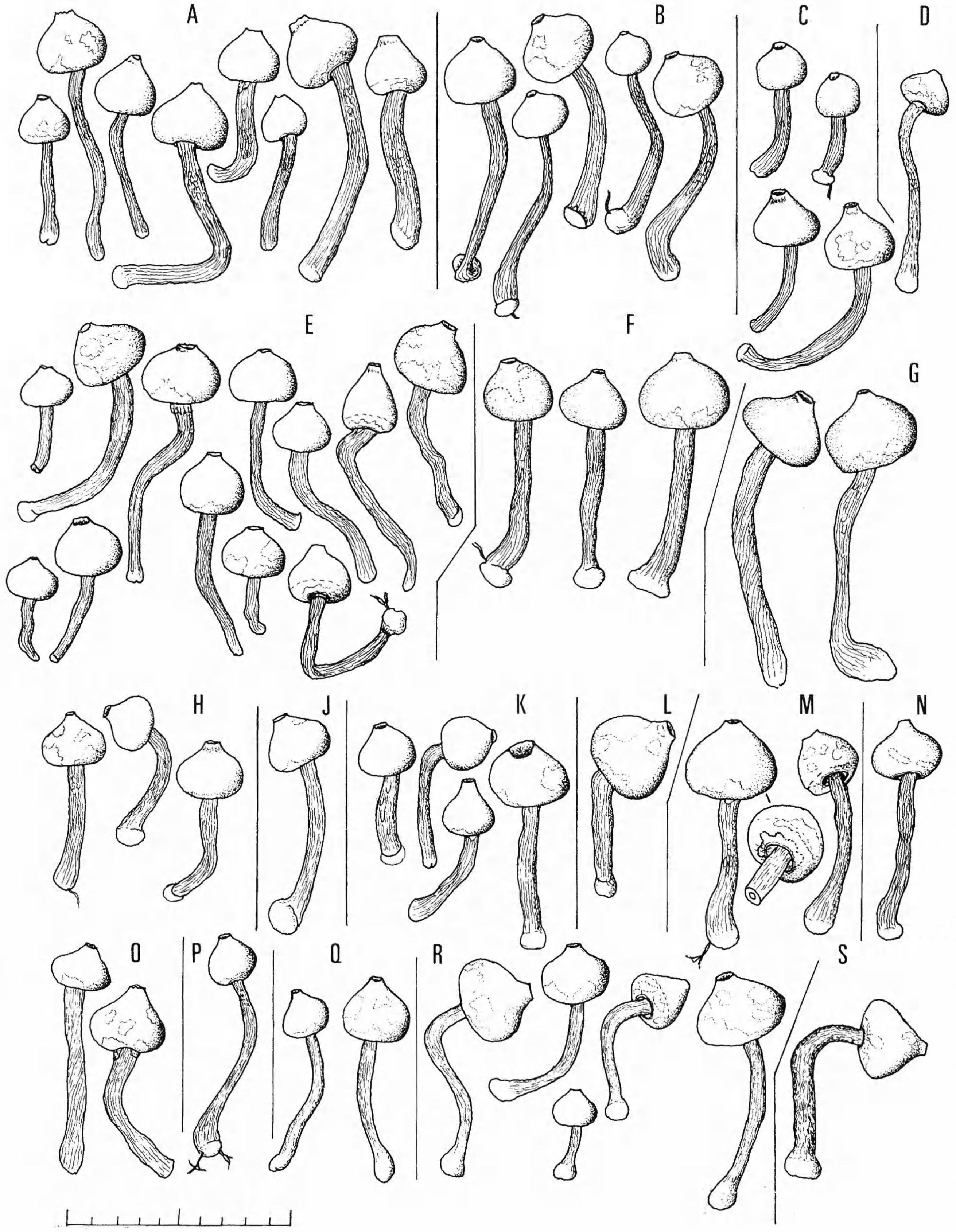

Fig. 2. *Tulostoma niveum*. Variation in the general habit of the gastrocarps. The specimens drawn from moistened gastrocarps belonging to 18 collections (A–S).

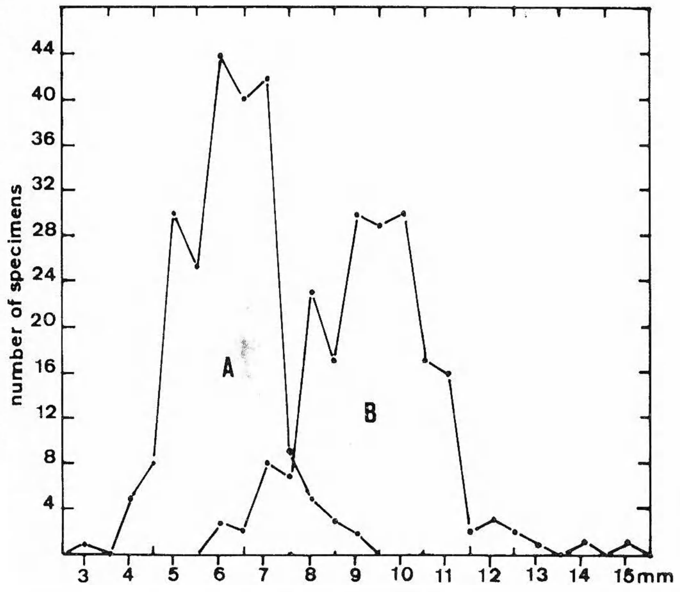

Fig. 3. Diagram showing the difference in capitulum size of *Tulostoma niveum* (A) and *T. brumale* (B). Diameter of capitulum measured from moistened specimens. Material from central E Sweden (all in S).

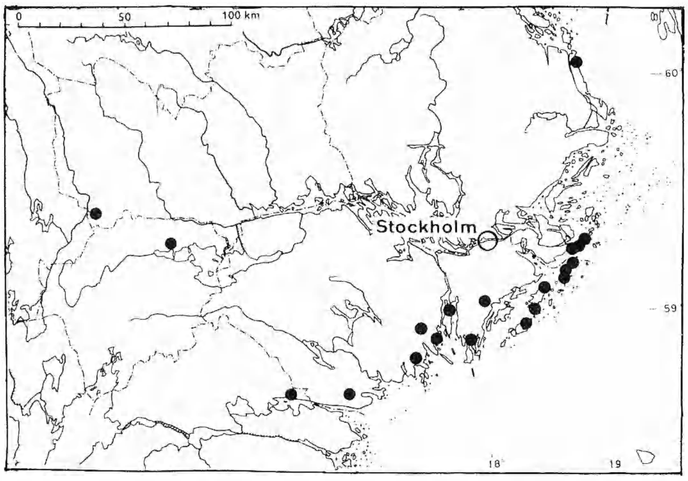

Fig. 4. Distribution of *Tulostoma niveum*. The species is confined to archaean limestone rocks in central E Sweden.

numerous and densely clustered in other spores. The usual, "clustered" type is illustrated in Fig. 1 D. It is composed of unevenly thickened verrucae which tend to form anastomoses and short ridges. *T. moravecii* has, according to SEM photos added to the type material, a similar ornamentation. It may be common in the genus; *T. xerophilum* Long shows the same type (Eckblad 1971 Fig. 16).

The dry spore mass of *T. niveum* has the same ochraceous colour as in *T. moravecii* and *T. brumale*.

Tulostoma niveum and *T. moravecii* may also differ in their habitat preferences. In its only known locality *Tulostoma moravecii* grows in soil (calcareous) where it is found associated with *Festuca valesiaca, Stipa capillata* and *Erysimum crepidifolium* (Pouzar 1958 p. 597). The Swedish species grows in *Tortello-Sedetum* communities on limestone rocks, where it is strictly confined to moss tufts in particular situations.

It is sometimes difficult to separate *T. niveum* from small, much bleached "mummies" of *T. brumale*. These specimens of *T. brumale* can be distinguished by their tubular mouth and by their capillitium threads which are generally much swollen at the septa. The difference between *T. niveum* and *T. brumale,* exemplified by a quantitative character, viz. the size of the capitulum, is shown in Fig. 3. *Tulostoma niveum* is not a habitat modification of *T. brumale*. Both species grow close to each other in a number of localities but the species always behave as distinct. Although there exists a large number of intermediate micro habitats in these localities, no intermediate specimens have been found. It should have been very remarkable, of course, if a species of *Tulostoma* would modify in the very important specific character found in its capillitium, viz. swollen contra not swollen septa!

Mr R. Rydberg was the first to collect this species from the Stockholm archipelago. During the last few years his material has been available for studies (in S). He applied several names to the material, e.g. *T. albicans* White, *T. bresadolae* Petri, as well as some manuscript names. None of these names were mentioned in his article on the Swedish Gasteromycete flora in which he expressed the opinion to have found seven species new to Sweden (Rydberg 1949).

The American *T. albicans* White has been suggested to be identical with *T. jourdani* Pat. (Long 1947 p. 121). It differs from *T. niveum* in its large and globose capitulum, the tubular mouth, the sand coated peridium, the yellowish ("buff") coloured endoperidium, the prominent collar and the thicker stipe ("3–5 mm") (White 1901 Plate 31, Figs. 4, 5, Long 1946). The American *T. mcalpinianum* Lloyd and *T. pygmaeum* Lloyd, which are compared with *T. albicans* by Lloyd, also clearly differ from *T. niveum* (Lloyd 1906 pp. 15, 16, Stevenson & Cash 1936 p. 195). *Tulostoma bresadolae,* described from Italy, dif-

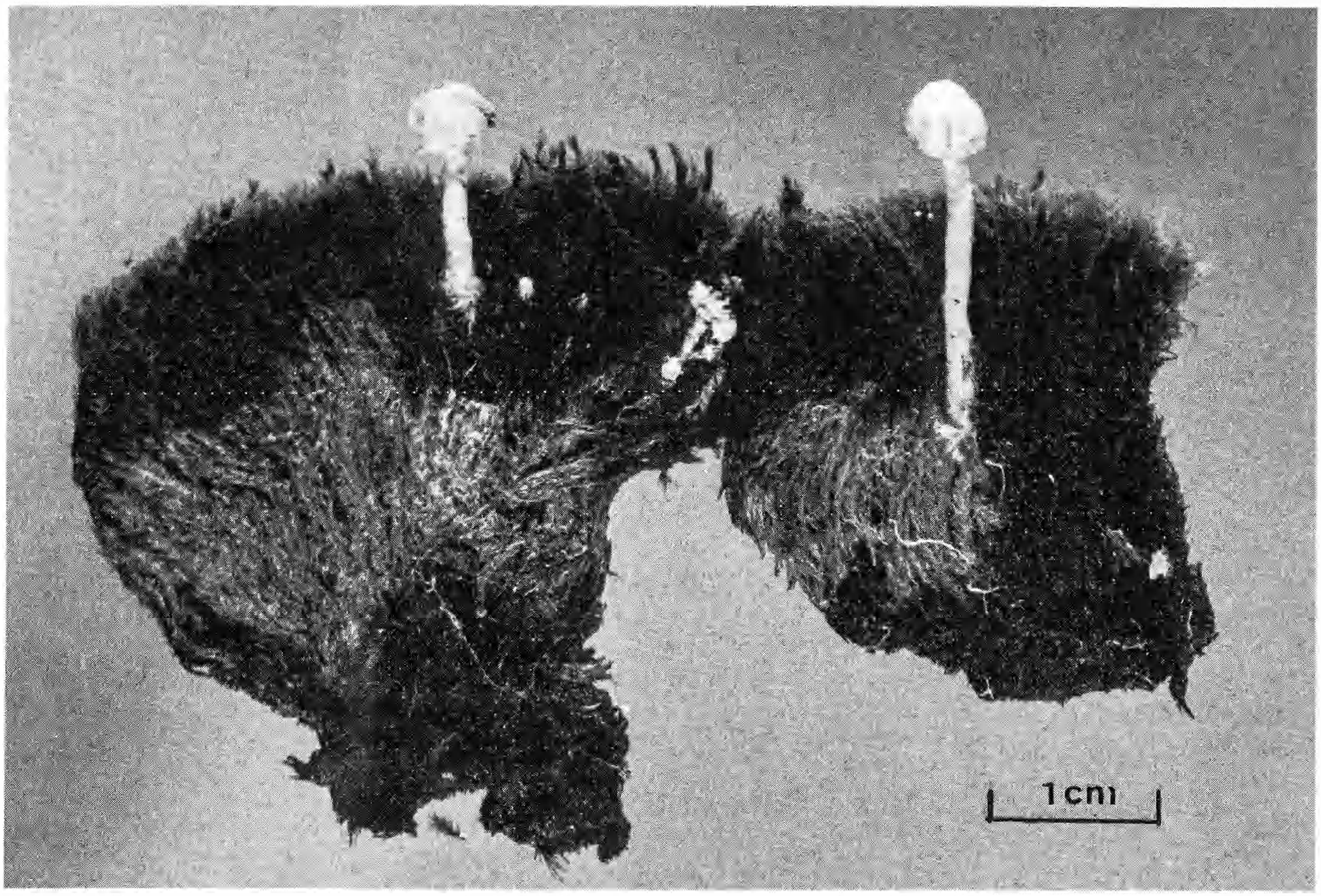

Fig. 5. *Tulostoma niveum*. Two gastrocarps growing in a tuft of *Ditrichum flexicaule*. Note the pale, mycelium infected portion of the moss substrate. – Kers 4264 (S). Photo B. Ekberg, SVA, Stockholm.

fers from *T. niveum* in its globose capitulum, tubular mouth, coloured capillitium, larger spores ("5–8 μm"), thicker endoperidium and scaly stipe (Petri 1904, 1909 p. 121).

Habitat, field notes

Tulostoma niveum is quite frequent in open situations on archaean limestone rocks in central E Sweden (Fig. 4). It is more common than *T. brumale* there. Most finds have been made in the Stockholm archipelago. Vast areas of treeless, unexploited limestone rocks with a broken topography are particularly common there.

One reason why the species has escaped attention for so long is the comparatively short duration of its gastrocarps. Samples of *Tulostoma* have generally been collected during the spring or early summer and then in the form of "mummies". During that part of the year the gastrocarps of *T. niveum* are regularly much disintegrated and collapsed and therefore hardly detectable. Few botanists have visited the localities when the fresh gastrocarps emerge, viz. in late autumn and early winter.

In a number of localities it is possible to find *T. brumale* and *T. niveum* occurring within the same rocky area. The two species then occupy different micro habitats. Although they may grow close to each other, I have never found them mingled or associated. Descriptions of their habitats are given below.

Tulostoma brumale usually grows in deep deposits of fine sand. However in rocky habitats in central E Sweden this species occurs in a moss/lichen community situated on more or less sloping rocks which are covered with a thin layer of sandy soil. The water which drains from the higher parts of the rock surface regularly passes the sandy pockets or depressions in which this species is growing. The soil substrate dries up easily and is never seriously water-soaked. There is no fundamental difference between this kind of "rocky" habitat and the more usual ones for this species. In both cases the mycelium of *T. brumale* develops in the humus-rich, sandy soil which is present just beneath a layer of a scanty vegetation.

Tulostoma niveum is restricted to moss tufts which grow directly on the bare rocks. The basalmost portion of these tufts is more or less decomposed to form a thin layer of organic soil. There is no mineral soil beneath these tufts, although particles of sand or fine sand are regularly found scattered within the tufts (Fig. 5).

The moss tufts occupy topographically characteristic positions. They are situated on the tops of ridges, on small crests, on knobs etc. Consequently, a much broken topography offers a greater number of suitable habitats than does a plane rocky area. Due to their position, the tufts are above the level of the drainage, which neatly follows the inclination and surface structures of the rock. Sometimes the species occurs on precipices where water does not filter regularly. I have also found *T. niveum* on the steep sides of large boulders. The mycelium of *T. niveum* develops in the inner portion of the tufts where it grows in a moss substrate free from mineral soil.

The detailed situation of the tufts means that they are moistened directly by the rain, melting snow and fog. The water has not previously passed over the rock surface and it has not therefore been enriched with humus, mineral salts etc. A second characteristic of these tufts is that they are never water-soaked. They always hold a large proportion of air, but only a small amount of water. Consequently the moss substrate remains unfrozen for a long time during the cold season, or else becomes just slightly frozen during the nights. Because of the small water content, the substrate also thaws easily, even in the weak winter sun. If quite close to the sea shore, the species may grow in north-facing or in other shady situations. When observed in these unexpected situations the moss tufts were unfrozen owing to the mild air temperature prevailing near the sea.

The characteristics of the micro habitats of *T. niveum* can be summarized as follows. The species is confined to those moss tufts which are very little affected by drainage water, which are never watersoaked, and which, therefore, do not easily become permanently frozen in late autumn and winter. It is doubtful whether the water chemistry is of real importance for *T. niveum*. On the other hand, the physical peculiarities of the moss tufts must be of great importance for a successful colonization.

The tufts are generally composed of pure stands of *Tortella tortuosa* (Hedw.) Limpr. or *Ditrichum flexicaule* (Schleich.) Hampe. Some other moss species may be present, but then in small quantities, e.g. *Abietinella abietina* (Hedw.) Fleisch., *Bryum capillare* Hedw., *Homalothecium sericeum* (Hedw.) Br. Eur., *Hypnum cupressiforme* Hedw. and *Schistidium apocarpum* (Hedw.) Br. Eur.

The saprophytic mycelium grows densely interwoven with the moss substrate in which it forms a sharply delimited stratum (Fig. 5). The infected portion of the moss tuft differs from the surrounding parts in its pale colour and soft texture. Developing gastrocarps can easily be found in the late autumn when moss tufts, gathered from suitable micro habitats, are split up. The intense transformation of the moss substrate clearly indicates where the young gastrocarps are to be sought.

The mycelium is certainly perennial. Gastrocarps have been observed developing in one and the same moss tuft over several years.

Material studied

The information in this list has been abbreviated for a few localities in which a great number of samples have been gathered. Full citations will be found in a list which has been deposited in the library, Swedish Museum of Natural History (S).

Östergötland. Krokek parish, Marmorbruket, c. 300 m E of Fagervik, On boulder, 18.11.1972, Kers 3941 (S).

Närke. Glanshammar parish, 450 m NNE of Glanshammar church, 11.11.1973, Kers 4280 (S); 650 m E of Glanshammar church, 11.11.1973, Kers 4273 (S); 1 km E of Glanshammar church, 11.11.1973, Kers 4774 (S).

Västmanland. Viker parish, W of lake Älvlången, 11.7.1965, N. Hakelier (UPS).

Södermanland. Bälinge parish, 750 m SSW of Nynäs manor house, 25.2.1973, Kers 3944 (S). – Dalarö parish, Utö island, 350 m E of Kroka, 5.11.1972, Kers 3917 (S), Utö island, in the NW, 5.11.1972, Kers 3919, 3924, 3943 (S); Utö island, in the NE, 15.6.1952, R. Rydberg (S) – Mörkö parish, Egelsvik, 5.5.1973, L. Thorán (S) – Nämdö parish, Mörtö island, 12.11.1972, 12.8.1973, 25.5.1973, Kers 3914, 3920, 3922, 3925–3928, 3935–3937 (S); Uvö island, in the S, 17.12.1972, Kers 3916, 3930, 3933 (S) – Trosa-Vagnhärad parish, Jättarsberget, N of Anderviken, on the precipice, 8.8.1972, Kers 3918 (S); Skorvan island, 19.9.1975, M. Ryberg (S) – Tunaberg parish, 1 km NNE of Tunaberg church and 300 m NW of Fingerkulla, 22.10.1973, Kers 4267, 4268, 4276 (S) – Vårdinge parish, E of lake Sillen, 1.7 km S of Vårdinge church, 9.11.1975, Kers 4231 (S) – Ösmo parish, 500 m NW of Jursta and 200 m N of Drakboda, 1.5.1973, Kers 3923 (S); Malhuvud island, in the SW, 25.11.1972, Kers 3945, 3947, 4773 (S) – Österhaninge parish, Ornö island, 300 m ENE of Näset, 27.1.1974, Kers 4278 (S); Ornö island, in the N, 30.5.1948, R. Rydberg (S).

Uppland. Djurö parish, Runmarö island, 33 collections made between 1945 and 1975 by E. Haglund & R. Rydberg, R. Rydberg, P.-E. Holmberg and Kers (S); Munkö island, 12 collections made between 1948 and 1973 by R. Rydberg and by Kers (S, Kers 4264 also in UPS); Skarp-Runmarö island, 28.10.1972, Kers 3942 (S); Risselö island, 11.11.1972, Kers 4275 (S) – Väddö parish, Nothamn, just S of the old quarry and the harbour, 23.11.1972, Kers 3932 (S).

Acknowledgements. I am indebted to the Curators of PRM, S and UPS for placing material at my disposal. I also thank the following persons in Stockholm: Dr Siwert Nilsson for preparing SEM-photos, Dr Ulf Hallmén for help with identification of the crystals found in the gleba, Mr Thor-Björn Engelmark for determinating the moss species, Professor Tycho Norlindh for correcting my Latin text, and Miss Sally Brown for revising the English manuscript. Last but not least I wish to express my gratitude to my friends in Stockholm who made it possible to visit some of the localities by providing transport facilities, viz. Lars-Åke Ericsson, Per-Erik Holmberg, Lars Thorán and Hans Rydberg.

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Elaphomyces maculatus found in Sweden

Lars E. Kers

Kers, L. E. 1978 12 15: Elaphomyces maculatus found in Sweden. *Bot. Notiser 131:* 419–422. Stockholm. ISSN 0006-8195.

The first Scandinavian find of *Elaphomyces maculatus* Vitt. is reported from central E Sweden (Ascomycetes, Plectascales). The fungus was found in a dense stand of *Corylus* and *Quercus*.

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Specimens of *Elaphomyces* with a brown, verrucate cortex are frequent in Sweden. They form ectomycorrhiza with our common forest trees. Previous finds of *Elaphomyces* in Scandinavia were summed up by T. M. Fries (1909). No black species were known from Sweden at that time, although Fries listed some old records. However, these were doubtful since no material had been kept, viz. *E. persoonii* Vitt. and *E. anthracinus* Vitt. vel affine (Fries 1909). The present find of *Elaphomyces maculatus* Vitt. is the first verified Swedish record of a black-coloured *Elaphomyces*. The discovery of this rare fungus is a result of a methodical search for Fungi hypogaei carried out during the autumn of 1977 by Mr Evert Plahn, Stockholm.

Description of the Swedish material

Ascocarps (0.6–)1–2.5(–3.5) cm in diam., spherical to oblong or irregularly rounded, when large often with deep depressions, rarely with single, round, elevated areas; wall hard, black, not easily breaking; fruit-bodies light, hollow, surrounded by a densely adherent crust composed of the roots of vascular plants, soil particles and a dark brown mycelium which may be grey or green in places. *Cortex* 300–400 μm thick, black, very hard, cracking in dried specimens, surface appearing smooth to the naked eye, indistinctly and very minutely verrucose under the microscope in places, tips of the verrucae usually covered by a thin, loose layer of dark brown mycelium, cortex glossy black in section, homogeneous to the naked eye, exterior half composed of densely packed rods which are intimately connected by plates of tangentially arranged dark brown hyphae. *Peridium* (1.5–)2.5–3 mm thick when fresh, pure white at first, irregularly pale grey when dry, firm in mature specimens, almost cartilaginous in fully mature ascocarps, formed of densely interwoven hyphae; hyphae 2.5–3 μm thick and partially sclerenchymatic near the cortex, 6–10 μm thick near the gleba; peridium clearly distinguished from the cortex by its texture and colour. *Gleba* cottony white at first, discoloured brownish black by the maturing spores, multiseptate to leave a small amount of capillitium, gleba not extending to the centre of the ascocarps. *Asci* spherical, 75–80 μm in diameter, 8-spored, stalk gently curved and 15–20 μm long. *Ascospores* spherical, 29–35(–43) μm in diam., exospore 5–8 μm thick, composed of radially arranged elements, young spores hyaline to pale brown and smooth, mature spores dark brown to almost black, with a dense ornamentation of 1–1.5 μm high verrucae in small, angular groups thereby giving the spore surface an indistinct, reticulate pattern.

Swedish material. Uppland, Litslena parish, 2.8 km E of Grillby and 450 m S of Prästtorp. Deciduous woodland with *Corylus* and *Quercus,* Plahn 9.VIII.1977 (S); Kers & Plahn 30.VIII.1977 (S, UPS).

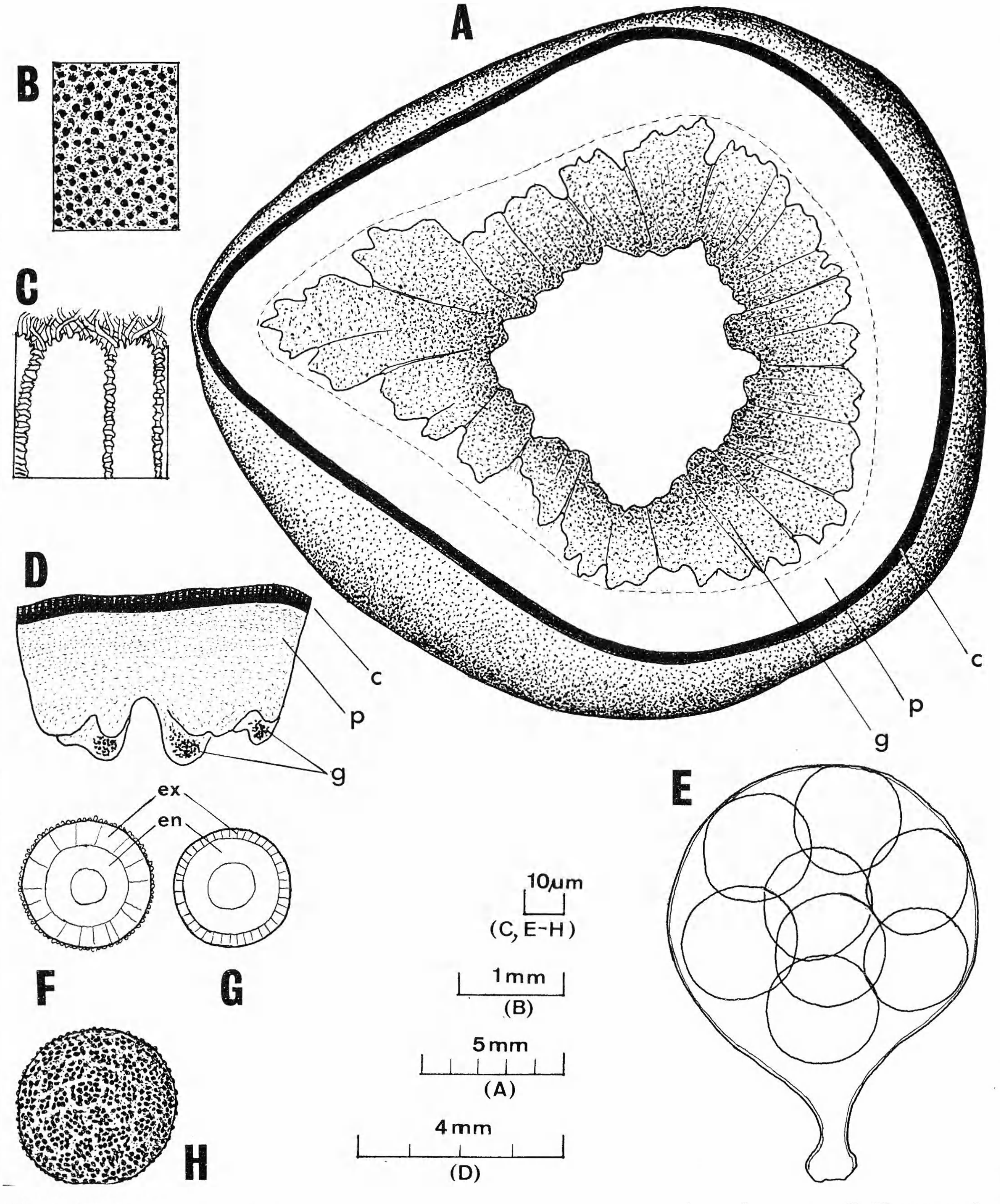

Fig. 1. *Elaphomyces maculatus*. – A: Ascocarp, median section. – B: Surface of cortex. – C: Upper portion of cortex in vertical section. – D: Portion of young ascocarp with initial stage of gleba formation. – E: Young ascus with ascospores. – F–G: Young ascospores in optical section. – H: Nearly mature ascospore showing ornamentation. – c cortex, en endospore, ex exospore, g gleba, p peridium. – Kers & Plahn 30.VIII.1977 (S).

Discussion

Among those *Elaphomyces* species which have a black-coloured, smooth to almost smooth cortex, *E. maculatus* Vitt. and *E. septatus* Vitt. are easily distinguished by their large-sized spores (32–43 μm in diameter). Both species are rare and little known. Hollós (1911) considered that *E. septatus* represented an immature form of *E. maculatus*, an opinion supported by Szemere (1965). Other authors, e.g. Dodge (1929), Lange (1956) and Ceruti (1960) have considered them as being distinct species.

I have identified the Swedish material as being *E. maculatus*, and not *E. septatus*, because of the following observations and arguments. The peridium is white throughout and it is quite distinct from the cortex in both colour and texture. The peridial tissue of the mature ascocarp is not "pseudoparenchymatous" (Dodge 1929), "soft-fibrillose" (Lange 1956), or "molliusculum" (Ceruti 1960), but is rather tough and composed of mainly tangentially-arranged, densely-interwoven, hyphae (cf. Ceruti 1960 Plate 8, fig. 2). The ornamentation of the young, translucent spores does not agree with that illustrated for *E. septatus* (Fontana 1908, Lange 1956, Ceruti 1960), but instead corresponds rather well with that shown for *E. maculatus* (Vittadini 1831 Plate 4, fig. 5, Tulasne & Tulasne 1841 Plate 1, fig. 1, Knapp 1952 Plate 6, fig. 7, and Ceruti 1960 Plate 8, fig. 2). In the Swedish material the spores are up to 43 μm in diameter, whereas the maximum size of those of *E. septatus* is stated to be 38 μm.

If *E. septatus* were merely an immature stage of *E. maculatus*, then the young spores of both should be identical. No spores similar to those illustrated for *E. septatus* have been found in the Swedish material. Transparent spores from small, immature ascocarps, as well as spores from large, mature ones, have been studied.

Corda's illustrations of *Ceratogaster maculatus* (Vitt.) Corda (=*E. maculatus* Vitt.) resemble material of *E. septatus*, due to the pseudoparenchymatic peridium and the sparsely-verrucated spores (Corda 1842 Plate C1, figs. 7–10).

Szemere (1965 Plate 2, fig. d) synonymized the two species and his illustrations of *E. maculatus* may include elements of both. The description and illustrations of *E. maculatus* given by Richon & Roze (1888 pp. 248, 249, Plate LXXI, figs. 22–28) are not especially instructive, since no details of spore ornamentation are shown. Furthermore, the asci are stated to be 6-spored and oblong, which is not characteristic for *E. maculatus*. In his figure of *E. septatus*, Hollós (1911 Plate 2, figs 35, 36) shows no spore details either, so that it too may represent *E. maculatus* instead. Because the spores have been drawn differently by different authors, it is likely that two taxa are concerned. I consider it unlikely that the two species are conspecific, as has been suggested by some authors.

The green maculae on the cortex (hence "maculatus") are due to firmly adherent, green mycelium. They are absent from many ascocarps. Similar green maculae are also occasionally present in *E. anthracinus* Vitt. and *E. leveillei* Tul. A patchy greenish colouration of the mycelium which forms the crust was observed when the present material was collected. This colour, however, later disappeared and certainly does not form a reliable character. The spore ornamentation at first consists of isolated, very low verrucae in small, angular groups of 5–15 together, which give the exospore wall a cracked appearance. In almost mature, but still transparent, spores, the verrucae in each individual group coalesce basally. The very narrow sinuses which separate these groups give the spore surface a reticulate pattern, although this is obscure and scarcely visible in fully mature, opaque spores. This surface patterning has not previously been noted for *E. maculatus*.

Distribution

Elaphomyces maculatus was not previously known from Scandinavia. Other black-coloured species had been reported, viz. *E. aculeatus* Vitt., *E. septatus* Vitt., *E. anthracinus* Vitt., *E. uliginosus* Hesse and *E. leveillei* Tul. (Fries 1909, Lange 1956, Eckblad 1961, 1971). The Danish record of *E. septatus* was mentioned as somewhat doubtful by Ceruti (Ceruti 1960 p. 8). Very likely all these black-coloured *Elaphomyces* species have a southern distribution in Scandinavia.

Literature records of *Elaphomyces maculatus* are not always reliable, due to possible confusion with *E. septatus*. Reliable records, however, at least exist from N Italy, Hungary, France and Germany.

The Swedish occurrence is remarkable from a phytogeographical point of view. It is worthwhile noting, however, that this species was found only 1.4 km from a locality for *Elasmomyces krjukowensis* (Buch.) Sacc. & Sacc., another mainly C. European, hypogeous fungus (Kers 1978).

Habitat, field notes

The locality is situated about 50 km NW of Stockholm, at an altitude of 6 m above sea-level and just N of the lake Mälaren. The finds were made on a short, south-facing slope at the foot of a high precipice. The slope was covered by a very dense thicket of *Corylus avellana,* with isolated, large *Quercus robur* and a few *Ulmus glabra.* Due to the deep shade in summer, herbs were almost absent, except for some stands of *Dryopteris filix-mas.* Rhizomes and bulbs of some spring-flowering plants were found, e.g. *Anemone nemorosa, Corydalis fabacea,* and *Gagea lutea.* Other fungi observed here were: *Tuber rufum* Pico ex Fr., *Hymenogaster* cfr. *griseus* Vitt., *Melanogaster ambiguus* (Vitt.) Tul. (=*M. macrosporus* Vel.) (all hypogeous), *Helvella crispa* Scop. ex Fr. and *H. lacunosa* Afz. ex Fr. The slope was grazed by cattle, though less intensely within the wooded area in question.

The very weathered, slaty rock at the foot of the precipice was apparently quite base-rich, since in damp habitats, seepage water, produced from small fissures, had a calciphilous flora, e.g. *Linum catharticum* and a number of mosses: *Amblyodon dealbatus, Barbula recurvirostris, Bryum intermedium, Distichium inclinatum, Ditrichum flexicaule, Encalypta vulgaris, Homalothecium sericeum, H. lutescens, Myurella julacea, Tortella tortuosa, T. fragilis, Riccia glauca* and *Pellia endiviifolia* (leg. & det. E. Plahn. Nomenclature: Arnell 1956, Nyholm 1954–1969).

Elaphomyces was found on a deposit of fine sand, which was rich in humus and covered by a layer of decomposed leaf litter. Specimens were found at 2–5 cm depth at several points along a strech of about 50 m. They grew in association with the fine roots of trees and shrubs, viz. *Corylus* and/or *Quercus.* The central hollow of some of the ascocarps was filled with water, a peculiarity also seen in other species. The fruit-bodies were light in weight, compared with those of *E. granulatus* and *E. muricatus.* Only the largest specimens had a mature gleba. When just opened, the specimens gave off a distinct odour resembling that of ether. The material consists of 34 ascocarps in various stages of development.

The habitat, the vegetation and the flora in this locality appear to be quite "natural". There were no obvious indications that the fungus could have been introduced into this area with imported, deciduous trees.

Acknowledgement. Many thanks are due to Mr Evert Plahn, Stockholm, who discovered this rare fungus and under whose guidance I visited the locality.

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Epidermal leaf structures in species of Strobilantheae and Petalidieae (Acanthaceae)

Per-Olof Karlström

Karlström, P.-O. 1978 12 15: Epidermal leaf structures in species of Strobilantheae and Petalidieae (Acanthaceae). *Bot. Notiser 131:* 423–433. Stockholm. ISSN 0006-8195.

Epidermal leaf structures on the upper and lower epidermis (cell structure, stomata, non-glandular and glandular hairs, cystoliths) of fifteen species of Strobilantheae Lindau (*Dyschoriste* Nees, *Hemigraphis* Nees, *Mimulopsis* Schweinf., *Goldfussia* Nees, *Perilepta* Bremek., *Pseudaechmanthera* Bremek.) and of seven species of Petalidieae Lindau (*Blechum* P. Br., *Phaulopsis* Willd. emend. Spreng., *Petalidium* Nees) were studied. Most of the material originated from plants cultivated in greenhouses. Additional observations have been made on herbarium specimens. *Petalidium* differs from the other genera in the occurrence of special types of glandular hairs and of thick-walled, branched, non-glandular hairs. The cystoliths in *Petalidium* are also larger and partly of another type and stomata are more numerous on the upper epidermis than in the other genera. These differences support the placement of *Petalidium* in a separate subtribe, Petalidiinae. The proposed transfer of *Dyschoriste* to the Petalidiinae is unsupported. The genera *Dyschoriste, Hemigraphis, Goldfussia, Perilepta, Pseudaechmanthera* and *Mimulopsis* should be included in a single subtribe, Strobilanthidinae. The proposed transfer of *Blechum* to a separate subtribe, Blechinae, is not justified on the basis of the epidermal structures of the leaves.

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Among other genera Lindau (1895) included *Dyschoriste* Nees, *Hemigraphis* Nees, *Strobilanthes* Bl. (including *Goldfussia* Nees) and *Mimulopsis* Schweinf. in the Strobilantheae Lindau. The genera *Blechum* P. Br., *Phaulopsis* Willd. emend. Spreng. (=*Micranthus* Wendl.) and *Petalidium* Nees were placed in the Petalidieae Lindau. Bremekamp (1944, 1965) transferred *Dyschoriste* and *Mimulopsis* to the subtribe Petalidiinae and *Blechum* to the subtribe Blechinae of the Ruellieae, while placing *Hemigraphis* and *Strobilanthes,* together with *Goldfussia* and two of his new genera *Perilepta* Bremek. and *Pseudaechmanthera* Bremek., in the subtribe Strobilanthidinae of the Ruellieae.

The present studies were made in order to find out whether or not epidermal characters might be helpful in the delimitation of the Strobilantheae and the Petalidieae.

Material and methods

Most of the material studied was taken from plants cultivated for several years in the greenhouses of the Department of Systematic Botany, University of Göteborg. The plants were grown under closely similar conditions (temperature, illumination, relative humidity). The central areas of mature and healthy leaves, from approximately the same positions on all plants, were examined.

The cuticles were peeled or scraped off with a razor blade, placed in water on slides, and studied under the microscope. When herbarium specimens were studied, the leaves were warmed in an aqueous solution of saponine before the cuticles were peeled off. To find out whether or not this treatment had any effect on the epidermal structures, fresh leaves were treated in the same way. I did not find any signs that the saponine treatment could have any effect on the results obtained.

All quantitative measurements are the mean values of 100 readings.

The following species have been examined: *Dyschoriste fischeri* Lindau (3 plants), *D. perrottetii* (Nees) O. Kuntze (6 pl.), *D. thunbergiflora* (S. Moore) Lindau (4

Table 1. Cell structure and size and stomatal characters in plants growing under greenhouse conditions. – L lower epidermis. U upper epidermis. – sin sinuouswalls, sl sin slightly sinuous walls, str straight walls. – * stomata rare, only occurring in close vicinity of veins.

Species	Cell structure in intervenous areas		Cell size, midrib		Stomatal frequency per mm^2		Stomatal size (μm)		Stomatal index	
	L	U	L	U	L	U	L	U	L	U
Dyschoriste fischeri	sin	sin	73 × 19	71 × 19	162	*	21 × 13	20 × 12	15.2	–
D. perrottetii	sin	sl sin	47 × 14	43 × 19	175	25	20 × 13	22 × 12	12.6	–
D. thunbergiflora	sin	sin	62 × 15	58 × 17	219	*	19 × 12	20 × 12	16.2	–
Hemigraphis alternata	sl sin	sin	28 × 19	35 × 22	167	*	23 × 13	19 × 12	15.6	–
H. repanda	str or sl sin	sl sin	26 × 20	35 × 27	141	*	24 × 14	26 × 14	13.8	–
Goldfussia glomerata	sin	sin	55 × 14	68 × 17	225	0	23 × 14	–	12.9	0
G. isophylla	sl sin	sl sin	43 × 22	41 × 24	169	0	25 × 15	–	18.4	0
G. penstemonoides	sin	sin	30 × 15	49 × 16	269	0	22 × 14	–	17.8	0
Perilepta dyeriana	sin	sin	38 × 21	48 × 24	225	0	20 × 13	–	14.8	0
Pseudaechmanthera glutinosa	sin or sl sin	sin	28 × 14	41 × 14	225	*	21 × 13	21 × 11	13.9	–
Phaulopsis dorsiflora	sin	sin	64 × 14	42 × 17	188	0	20 × 12	–	15.0	0
Blechum pyramidatum	sin or sl sin	sl sin	52 × 21	42 × 19	155	19	21 × 14	23 × 13	16.7	–
Petalidium crispum	sin or sl sin	sin or sl sin	66 × 25	85 × 24	119	94	22 × 14	26 × 15	13.9	12.6

pl.), *Hemigraphis alternata* (Burm. f.) T. And. (4 pl.), *H. repanda* (L.) Hall. f. (3 pl.), *Goldfussia glomerata* Nees (=*Strobilanthes glomerata* (Nees) T. And.; 3 pl.), *G. isophylla* Nees (=*S. isophylla* (Nees) T. And.; 6 pl.), *G. penstemonoides* Nees (=*S. penstemonoides* (Nees) T. And.; 4 pl.), *Perilepta dyeriana* (Mast.) Bremek. (=*S. dyeriana* Mast.; 4 pl.), *Pseudaechmanthera glutinosa* (Nees) Bremek. (=*S. glutinosa* Nees; 3 pl.), *Blechum pyramidatum* (Lam.) Urb. (=*B. brownei* Juss.; 5 pl.), *Phaulopsis dorsiflora* (Retz.) Santapau (=*P. parviflora* Willd.; 4 pl.), and *Petalidium crispum* A. Meeuse ex P. G. Meyer (5 pl.).

Additional observations were made on herbarium material of the following species: *Dyschoriste angusta* Small. (1 specimen), *D. linearis* Gray (1 sp.), *D. oblongifolia* (Michaux) O. Kuntze (1 sp.), *D. perrottetii* (4 sp.), *D. radicans* Nees (2 sp.), *D. thunbergiflora* (2 sp.), *Petalidium aromaticum* Oberm. (1 sp.), *P. englerianum* C. B. Cl. (1 sp.), *P. oblongifolium* C. B. Cl. (1 sp.), *P. setosum* C. B. Cl. (1 sp.), and *Mimulopsis elliotii* C. B. Cl. (1 sp.).

Voucher specimens are deposited at GB.

Observations

The following is a summary of the observations made. The detailed descriptions with drawings of the upper and lower epidermis of leaves of each genus are held at the Department of Systematic Botany, University of Göteborg and copies can be obtained from the author.

Cell structure

Intervenous areas. The epidermal cells are irregular with sinuous or slightly sinuous walls (Fig. 1 A–D, Table 1). The degree of undulation is normally more pronounced on the lower than on the upper epidermis. *Hemigraphis repanda* differs in having cells on the lower epidermis with straight, or only slightly sinuous, walls (Fig. 1 E).

No important size differences between intervenous epidermal cells from the upper and lower epidermis were found. The cells of the upper epidermis, however, are somewhat larger than those of the lower in *Dyschoriste perrottetii, Petalidium crispum* and *Goldfussia isophylla.* This size difference is even more pronounced in *Hemigraphis repanda.*

Fig. 1. Cells from intervenous areas and costal cells. – A, C: Cells with sinuous walls (A int, le; C int, ue). – B, D: Cells with slightly sinuous walls (B int, le; D int, ue). – E: Cells with straight or slightly sinuous walls (int, le). – F, G: Costal cells (le). – A: *Perilepta dyeriana.* – B: *Goldfussia isophylla.* – C: *G. glomerata.* – D: *Dyschoriste perrottetii.* – E, G: *Hemigraphis repanda.* – F: *Phaulopsis dorsiflora.* – int intervenous area, le lower epidermis, ue upper epidermis.

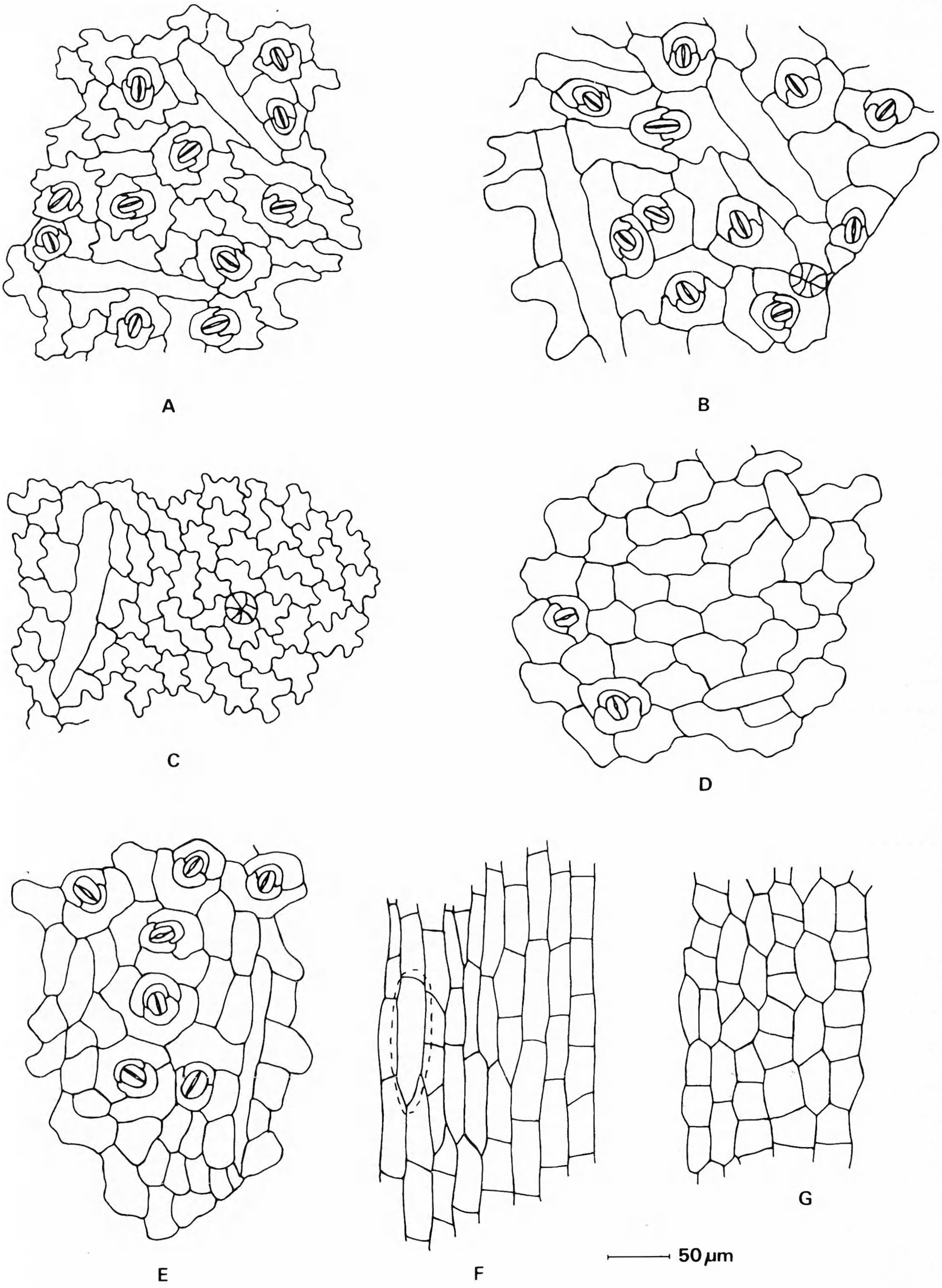

A
B
C
D
E
F
G
50 µm

Table 2. Measurements of stomatal size (μm) and stomatal frequency per mm^2 of herbarium specimens. The values for stomatal frequency are only approximate, due to the insufficiency of the material – L lower epidermis, U upper epidermis.

Species	size		frequency	
	L	U	L	U
Dyschoriste perr. 1971	19 × 12	19 × 12	260	130
D. perrottetii 1973	18 × 11	16 × 9	190	60
D. thunbergiflora	20 × 12	–	280	0
D. angusta	22 × 13	22 × 13	280	90
D. linearis	20 × 11	21 × 12	230	110
D. oblongifolia	19 × 12	20 × 13	300	160
D. radicans	21 × 14	21 × 15	320	170
Petalidium aromaticum	22 × 16	22 × 17	230	210
P. oblongifolium	19 × 14	20 × 14	220	200
Mimulopsis elliotii	20 × 11	–	170	0

On veins. The costal cells were straight-walled, more or less elongated, and arranged in rows, in all the species studied (Fig. 1 F). In *Dyschoriste* and *Goldfussia isophylla* those on the upper and lower epidermis are equal in size (Table 1). In *Hemigraphis* the costal cells of the upper epidermis are somewhat larger than those of the lower one. The costal cells of the upper are longer than those of the lower epidermis in *Goldfussia glomerata, G. penstemonoides, Perilepta dyeriana, Petalidium crispum,* and *Pseudaechmanthera glutinosa,* while the opposite holds true for *Phaulopsis dorsiflora* and *Blechum pyramidatum* (Table 1). The costal cells of *Hemigraphis* leaves were shorter than those of the other genera (Fig. 1 G).

Stomata

The ontogenesis of the stomata of all the species which I was able to study belong to the diallelocytic type, as defined by Payne (1970). The stomatic guard cells always had contact with two subsidiary cells (Fig. 1).

Among the species grown under greenhouse conditions no stomata were present on the upper epidermis of the following species: *Goldfussia isophylla, G. glomerata, G. penstemonoides, Perilepta dyeriana,* and *Phaulopsis dorsiflora.* Stomata were sparse in the upper epidermis and occurred only in the immediate vicinity of veins in *Dyschoriste fischeri, D. thunbergiflora, Hemigraphis alternata, H. repanda,* and *Pseudaechmanthera glutinosa.* In *Dyschoriste perrottetii, Blechum pyramidatum* and *Petalidium crispum* the stomata were scattered in the intervenous areas on the upper epidermis. In *Petalidium crispum* they were more numerous than in the other two genera (Table 1).

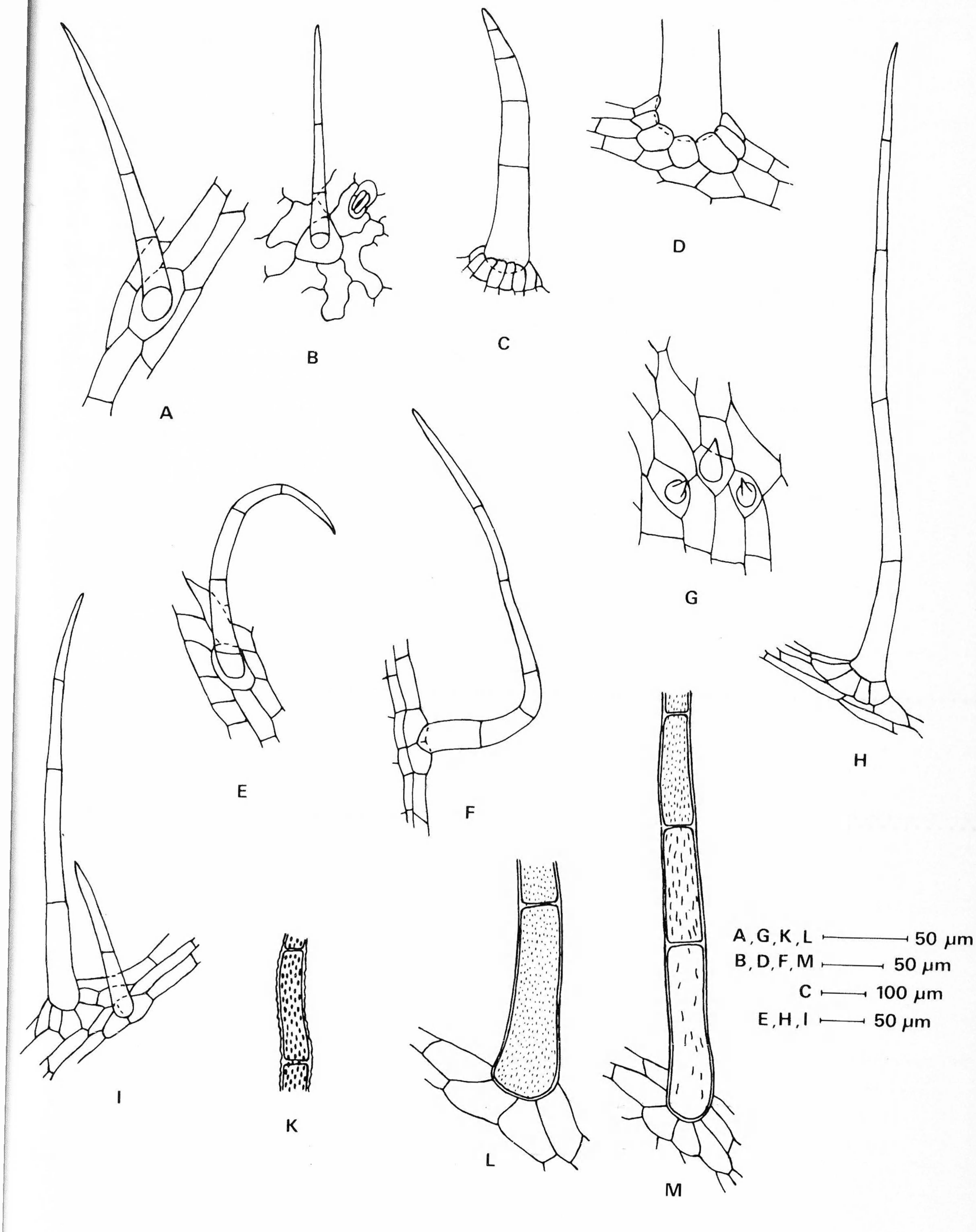
Among the species of which herbarium material was studied *Dyschoriste thunbergiflora* and *Mimulopsis elliotii* were the only ones which lacked stomata on the upper epidermis. In the other species, i.e. *Dyschoriste* spp. and *Petalidium* spp., stomata occurred in the intervenous areas. The stomatal frequencies, however, were much lower on the upper than on the lower epidermis in *Dyschoriste,* while in *Petalidium* similar frequencies were recorded from both leaf surfaces (Table 2).

In species which have stomata on both leaf surfaces there was no difference in stomatal size (i.e. the size of guard cells) between the upper and the lower epidermis. *Petalidium crispum,* however, differs in having somewhat more elongate stomata on the upper epidermis. The other species of *Petalidium* examined did not show this difference in stomatal size.

Non-glandular hairs

Uniseriate, multicellular hairs, with thin, ornamented walls, occur in most of the species studied. They normally arise from a single epidermal cell (Fig. 2 A, B). In *Goldfussia, Perilepta, Pseudaechmanthera,* and *Phaulopsis* the epidermal cells which surround the basal part of a hair differ from the other epidermal cells both in size and in the pattern in which they are arranged. The basal cell of the hair is more or less embedded in the surrounding epidermal cells.

Fig. 2. Non-glandular hairs. – A, B: Uniseriate hairs arising from a single epidermal cell (A midrib, le; B int, le). – C, D, H: Uniseriate hairs with the basal part, together with the surrounding epidermal cells somewhat lifted above the general plane of the epidermis (C int, ue; D midrib, ue; H midrib, le). – E, F: Curved hairs (midrib, ue). – G: Short, 1-celled hairs (midrib, le). – I: Different types of hairs occurring together (midrib, le). – K–M: Hairs showing cell wall ornamentation (midrib, le). – A, B: *Goldfussia glomerata.* – C, G: *Perilepta dyeriana.* – D, F, M: *Phaulopsis dorsiflora.* – E: *Blechum pyramidatum.* – H, I, L: *Pseudaechmanthera glutinosa.* – K: *Hemigraphis repanda.* – int intervenous area, le lower epidermis, ue upper epidermis.


A
B
C
D
E
F
G
H
I
K
L
M
A, G, K, L 50 μm
B, D, F, M 50 μm
C 100 μm
E, H, I 50 μm

The basal part of the hair, together with the surrounding cells, is raised somewhat above the general level of the epidermis (Fig. 2 C, D, H). These hairs are long and multicellular. Often the non-glandular hairs are straight (Fig. 2 H, I), but in *Phaulopsis* and *Blechum* markedly curved hairs occur (Fig. 2 E, F). The type of ornamentation of the cell walls is much the same in all species (Fig. 2 L), with the exception of *Hemigraphis* (Fig. 2 K), the cell walls of which are provided with short tubercles. The wall of the basal cell is often less ornamented than those of the other cells (Fig. 2 M). Sometimes the basal cell is entirely unornamented. In *Pseudaechmanthera, Blechum* and *Petalidium* the cell walls are slightly ornamented. In *Goldfussia glomerata* 2–4-celled hairs without ornamentation occur in intervenous areas on the lower epidermis.

Very short, 1-celled hairs occur in *Perilepta dyeriana* (Fig. 2G). I did not find this type in any of the other species studied.

Yet another type of non-glandular hair occurs in *Petalidium aromaticum* and *P. oblongifolium*. These hairs are multicellular and branched, with more than one lateral branch (Fig. 3 A, B). Their walls are thicker than those of the other genera. This type of hair was not found in any of the other species I studied. In *Hemigraphis alternata* I observed branched hairs on two occasions. In both cases the hairs had only one lateral branch (Fig. 3 C). I do not think that *Hemigraphis* is normally characterized by branched hairs, since they were so rare in *H. alternata* and were not found at all in *H. repanda*. Ahmad (1974 c) did not report branched hairs in *Hemigraphis*. Ahmad (1974 c) also reported that non-glandular hairs were absent from the upper epidermis of *H. alternata*. However, I found that non-glandular hairs were present on the upper epidermis of *H. alternata*. In the intervenous areas they were rare, on the veins they were more numerous.

In *Petalidium englerianum* stellate, non-glandular hairs are very common on both leaf surfaces (Fig. 3 D, K).

The number of cells of the non-glandular hairs and the length of the hairs are presented in Table 3. Due to an insufficiency of material, I was unable to measure the length of the non-glandular hairs of those species for which only herbarium material was available.

Glandular hairs

Subsessile glandular hairs have been reported for many members of the Acanthaceae. In most cases these hairs consist of a globular head, composed of 2–8 cells, and a single-celled stalk.

In the species presently studied the heads normally consist of 4 or 8 cells (Fig. 3 E, F). The heads are globular and their cell walls are thin. *Petalidium* differs in having hairs with a somewhat rectangular head with thicker walls (Fig. 3 G).

In *Petalidium aromaticum* stalked glandular hairs, with 2- or 4-celled heads, occur together with subsessile glandular hairs with 8-celled heads, both on the veins and in the intervenous areas. Their stalks consist of 1–3 short cells (Fig. 3 H, I).

Larger, stalked, glandular hairs occur in all the *Petalidium* species studied. Their stalks are 2–3-celled and their heads multicellular (Fig. 3 L, M). Similar stalked glandular hairs have been found in *Dyschoriste thunbergiflora*. However, their frequency is much higher in *Petalidium*.

Another type of stalked glandular hair occurs in *Goldfussia glomerata* and *Phaulopsis dorsiflora*. The heads of these hairs are more or less globular and up to 8-celled (Fig. 3 N–P).

None of the stalked glandular hairs studied had ornamented stalk cells.

Cystoliths

Cystoliths occur subepidermally, or epidermally, both on the veins and in the intervenous

Fig. 3. Non-glandular hairs, glandular hairs and cystoliths. – A–C: Branched hairs (A, C midrib, ue; B int, le). – D, K: Stellate hairs (midrib, ue). – E–G: Subsessile glandular hairs (E midrib, ue; F int, le; G int, ue). – H, I: Short, stalked glandular hairs (int, le; I seen from above). – L–P: Stalked glandular hairs (L, M midrib, ue; N int, le; O, P midrib, le; M, P seen from above). – R, S: Cystoliths (R midrib, ue; S midrib, le). – A, H, I: *Petalidium aromaticum*. – B: *P. oblongifolium*. – C: *Hemigraphis alternata*. – D, K: *Petalidium englerianum*. – E: *Pseudaechmanthera glutinosa*. – F: *Blechum pyramidatum*. – G, L, M, R: *Petalidium crispum*. – N: *Goldfussia glomerata*. – O, P: *Phaulopsis dorsiflora*. – S: *Dyschoriste fischeri*. – int intervenous area, le lower epidermis, ue upper epidermis.

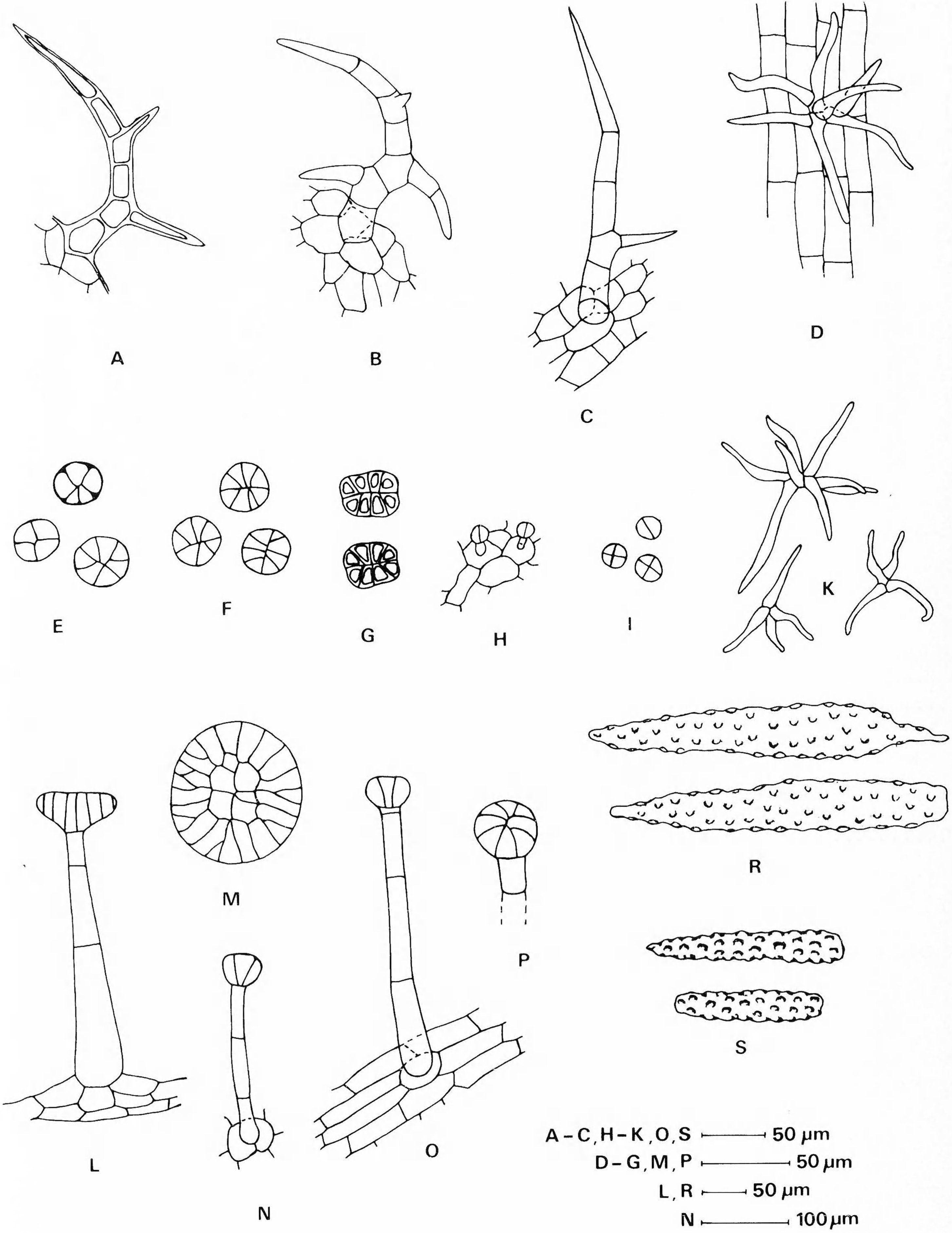

A
B
C
D
E
F
G
H
I
K
L
M
N
O
P
R
S
A-C, H-K, O, S 50 µm
D-G, M, P 50 µm
L, R 50 µm
N 100 µm

Table 3. Length (in μm) and number of cells of non-glandular hairs at midrib and from intervenous areas (int a). Plants growing under greenhouse conditions. – L lower epidermis, U upper epidermis. – [1] sparsely occurring, [2] rare, [3] uppermost 4 cells red-coloured, [4] all or 2–3 apical cells red-coloured, [5] all cells red-coloured, [6] cells lack ornamentation, [7] 2–4 apical cells red-coloured, [8] 2–3 apical cells red-coloured, [9] cells slightly ornamented, [10] curved hairs, [11] straight hairs.

Species	Hair length				Number of cells			
	Midrib		int a		Midrib		int a	
	L	U	L	U	L	U	L	U
Dyschoriste fischeri	327	259	0	42	3–6	3–6	0	2–3[1]
D. perrottetii	104	117	0	0	3–4	3–4	0	0
D. thunbergiflora	314	279	215	69	4–6	4–6	4–6	2–3[1]
Hemigraphis alternata	177	136	49	342	3–5[4]	3–4	2–3[1]	2[2]
H. repanda	279 911	0	0	0	4[5] 6–7[5]	0	0	0
Goldfussia glomerata	2950 204	4227 213	162	1233	11–14[3] 3–5	8–17[7] 3–5	11–14[3] 2–4[6]	–10[8]
G. isophylla	0	0	0	0	0	0	0	0
G. penstemonoides	358	368	0	185	5–7	5–6	0	4[2]
Perilepta dyeriana	20	0	0	696	1[6]	0	0	4–6
Pseudaechmanthera glutinosa	655 147	932 168	249	251	4–7 2–3	5–10 3	3–4[9]	3–4[9]
Phaulopsis dorsiflora	506	339 769	271	424	5–6[3]	5–6[10] 5–6[11]	4	3–4
Blechum pyramidatum	364	848 358	0	675	4–6[9]	5–6[9] 4–6[9]	0	3–5[9]
Petalidium crispum	176	190	0	0	2–5[1]	2–5[1]	0	0

areas. They are simple, elongate, more or less narrow, mostly tapering at one end and blunt at the other (Fig. 3 S, upper one). In *Dyschoriste* they are sometimes blunt at both ends (Fig. 3 S, lower one). Cystoliths are sparsely present in *Hemigraphis,* especially on the veins. In *Pseudaechmanthera glutinosa* cystoliths are absent from the intervenous areas of the upper epidermis, in *Petalidium crispum* they are absent from the intervenous areas of the lower epidermis. In *Petalidium* the cystoliths are markedly broader and longer than those of the other genera (Fig. 3 R).

Another type of cystolith than that described above also occur in *Petalidium*. These cystoliths taper gradually towards one end and are shortly pointed at the other (Fig. 3 R, upper one).

In *Mimulopsis elliotii* I did not observe cystoliths on either side of the leaves.

Discussion

According to Stace (1965) the variation in cuticular characters is due to three major causes: the degree of maturity of the leaf; the environment in which the plant is situated; and the position of the leaf on the plant. The epidermal cell characters generally affected by these three factors are those of size, frequency and degree, rather than the actual anatomy or organisation of a particular epidermal structure.

Epidermal cells. According to Stace (1965) few characters of the epidermis show as much variation as does the degree of cell wall undulation. Therefore its use as a taxonomic character calls for the utmost caution. When the epidermal cell walls are undulate, the degree of undulation is generally more pronounced on the lower than on the upper epidermis (Stace 1965). This condition is also true for acanthaceous genera (Ahmad 1974 a, b). The results of my own studies fully agree with this statement. The only exception is *Mimulopsis elliotii,* where the degree of undulation is more pronounced on the upper than on the lower epidermis.

Generally speaking, the epidermal cells of the upper leaf epidermis are larger than those of the lower (Napp-Zinn 1974). This agrees with my own findings as regards *Dyschoriste perrottetii,* *Petalidium crispum, Goldfussia isophylla,* and *Hemigraphis repanda.*

The dissimilarity in size of the costal cells of the upper and lower epidermis is probably of little value taxonomically, since differences were found between the species in one and the same genus.

Stomatal frequency has commonly been used as a taxonomic aid. However, stomatal frequency often varies on different parts of a single leaf, and on different leaves of one plant. In mature leaves I found no great dissimilarity in the stomatal frequencies of different parts of the same leaf, but the frequencies of young and matured leaves differed. Therefore, as mentioned above, I only studied mature leaves. Furthermore, stomatal frequencies were measured only in the leaf centre. If stomatal frequency is recorded in terms of the proportion of stomata to epidermal cells, i.e. using the stomatal index (Salisbury 1927), then these variations in stomatal frequency can be almost cancelled. As shown in Table 1, I measured the stomatal frequency, as well as the stomatal index for all the species grown under greenhouse conditions. Due to the insufficiency of the material I was unable to measure the stomatal index of leaves of the species for which herbarium specimens were studied. As shown in Tables 1 and 2, there are generic differences in both stomatal frequency and stomatal index, as also between the species in one and the same genus. Stomatal frequency and stomatal index are therefore useless as a taxonomic aid in the species examined. An even more important fact is that in some species no stomata at all were present on the upper epidermis.

Modification of stomatal frequency. Leaves from herbarium specimens of *Dyschoriste perrottetii* collected in Kenya in 1971 were studied to provide comparison with those of the cultivated material (cuttings taken from the same stand). On the herbarium specimens stomata occur on both the upper and the lower epidermis (Table 1, 2). There were approximately 260 stomata per mm^2 on the lower epidermis and 130 on the upper. Leaves from a herbarium specimen, collected in 1973, of a plant grown in the greenhouse were also studied. The respective stomatal frequencies for this specimen were found to be approximately 190 and 60. For the greenhouse (fresh) material from 1977 the corresponding values were 175 and 25. It seems clear that the stomatal frequencies have diminished during the period of cultivation. On the leaves of the cultivated material of *D. fischeri* and *D. thunbergiflora* no stomata were present in intervenous areas of the upper epidermis, although occurring very sparsely in the vicinity of the larger veins. However, since *D. perrottetii* leaves still had some stomata present in the intervenous areas, i.e. not only in the close vicinity of veins, I think that the difference is genetic and not simply environmental.

Trichomes. The variation in the trichome frequencies of different parts of a single leaf is a well-known taxonomic character. However, Stace (1965) stated that the use of trichome frequency as a taxonomic character must be preceded by a series of observations on a wide range of material, in order to discover the cuticular changes which accompany growth and senescence, as well as the degree of phenotypic variation. I have not yet been able to make such a series of observations.

The length of the non-glandular hairs is probably of less value taxonomically. The size variation within a species may be considerable as reported by Ahmad (1978). The occurrence of different types of trichomes and differences in the ornamentation of the cell walls are more important as taxonomic aids.

The occurrence of different types of glandular hairs is however a character of taxonomic value. In the species examined five types could be recognized: subsessile hairs with globular heads; subsessile hairs with rectangular heads; stalked hairs with 2–4-celled heads; stalked hairs with 8-celled heads; and stalked hairs with multicellular heads. In *Strobilanthes heyneanus* Nees long-stalked glandular hairs, with 3–4-celled stalks and 2–several-celled globular or hemispherical heads, occur rarely on the veins (Ahmad 1974 c).These hairs seem to be of the same type as those which occur in *Goldfussia glomerata* and *Phaulopsis dorsiflora.* Long-stalked glandular hairs occur densely in *Dyschoriste vagans* O. Kuntze but sparsely in *D. erecta* O. Kuntze (Ahmad 1978).

Cystoliths. The nature and distribution of cystoliths are valuable generic characters in the Acanthaceae. Many authors have described the structure of cystoliths and sometimes used them

Table 4. The number of generic differences in taxonomically valuable characters of the leaf epidermal structures of all the species studied.

Genus	*Pet*	*Dys*	*Hem*	*Gol*	*Per*	*Pse*	*Pha*	*Ble*	*Mim*
Petalidium	–	5	7	9	9	7	10	7	7
Dyschoriste	5	–	2	4	4	2	5	2	2
Hemigraphis	7	2	–	4	4	2	5	2	2
Goldfussia	9	4	4	–	2	2	1	4	2
Perilepta	9	4	4	2	–	2	3	4	2
Pseudaechm.	7	2	2	2	2	–	3	2	2
Phaulopsis	10	5	5	1	3	3	–	3	3
Blechum	7	2	2	4	4	2	3	–	2
Mimulopsis	7	2	2	2	2	2	3	2	–

as a taxonomic aid (Hobein 1884, De 1967, Ahmad 1974 a, 1975). Hobein (1884) noted that elongate cystoliths, always pointed at one end, occur e.g. in *Dyschoriste, Phaulopsis* and *Blechum* and some other genera. This agrees with my own findings. The same type of cystolith occurs in all the genera *Goldfussia, Perilepta, Pseudaechmanthera,* and *Hemigraphis,* but is only partly true for *Petalidium,* in which genus, as described above, I found another type of cystolith, as well. The only species in which I did not find cystoliths was *Mimulopsis elliotii.*

Taxonomic conclusions

Those differences in leaf epidermis characters found between the genera examined and which, in my opinion, are taxonomically valuable are presented in Table 4, i.e. the absence of stomata from the upper epidermis, the occurrence of different types of non-glandular and glandular hairs, the ornamentation of the cell walls of non-glandular hairs, and the occurrence of different types of cystoliths. From this table it is clear that *Petalidium* differs in many respects from all the other genera studied and supports the placement of *Petalidium* in a separate subtribe, the Petalidiinae as defined by Bremekamp.

The transfer of *Dyschoriste* to the Petalidiinae is unsupported by my results. The genera *Dyschoriste, Hemigraphis, Goldfussia, Perilepta, Pseudaechmanthera,* and *Mimulopsis* should to be included in a single subtribe, the Strobilanthidinae.

The transfer of *Blechum* to a separate subtribe, the Blechinae (Bremekamp 1965), receives no support from the nature of the epidermal structures of its leaves, which have more in common with those of the genera which it is suggested should be placed in the subtribe Strobilanthidinae, than with *Petalidium.* However, I think that further studies (embryological, cytological, anatomical) ought to be made, in order to find out which subtribe *Blechum* should be placed in. This also applies to *Phaulopsis.* Since there are several differences in the leaf epidermal characters of this genus and *Petalidium,* there is no good reason for placing it in the Petalidiinae. On the other hand there are also differences between *Phaulopsis* and the genera which it is suggested should be placed in the subtribe Strobilanthidinae, especially with *Dyschoriste* and *Hemigraphis.* In my opinion, therefore, leaf epidermis structures are useless for elucidating the best taxonomical position for *Phaulopsis.*

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Tremella juniperina, a fungicolous jelly fungus

Anna-Elise Torkelsen

Torkelsen, A.-E. 1978 12 15: Tremella juniperina, a fungicolous jelly fungus. *Bot. Notiser 131:* 435–438. Stockholm. ISSN 0006-8195.

A thorough description of *Tremella juniperina* Karst. is given, the species is lectotypified and its distribution in Fennoscandia is mapped. The species is new to Norway and Sweden; it was previously known only from the original material from Finland. It is not identical with *Exidia grilletii* (Boud.) Neuh. *T. juniperina* is constantly associated with, and probably grows saprophytically on, ascocarps of *Colpoma juniperi* (Karst.) Dennis.

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In the years 1861–70 the Finnish mycologist P. A. Karsten issued *Fungi Fenniae exsiccati,* consisting of ten instalments, altogether 1000 numbers. Number 812 in this exsiccate, issued in 1869, is *Tremella juniperina* Karst., which he described as follows: "Erumpens, subrotunda, vulgo plicato-undulata, livido-pallida. Sporae sphaeroideae. Mustiala, på En, d. 8. Apr. 1869". Twenty years later (Karsten 1889 p. 452) he transferred the species to *Exidia* as *E. juniperina*. A description of *E. juniperina* is given in Swedish; translated into English it runs: "Basidia globose, 10–12 μm in diameter. Branches of *Juniper,* here and there in Tammela". It is possible that Karsten had seen some globose formations in the microscope both times, but without being able to decide if they were spores or basidia. The measurements given show that his last interpretation is correct.

Karsten's reasons for transferring the species to *Exidia* are not clear. The two genera *Tremella* and *Exidia* are similar in many respects. *Tremella* has globose–subglobose basidia and spores, while *Exidia* has subglobose to obpyriform basidia and allantoid spores. The spore form is the best character by which the genera can be distinguished.

Tremella juniperina was not mentioned again in mycological literature, until Donk (1966) wrote his *Check list*. Donk, however, merely included the species under names omitted from the check list proper, and he suspected that it was identical with *Exidia grilletii* (Boud.) Neuh.

A more thorough description of *T. juniperina* is given below, based on the lectotype, the isolectotypes and herb. P. A. Karsten no. 1538, 39 (H), and in part also on fresh material collected by myself.

Tremella juniperina Karst. – Fig. 1, 2

Karsten, Fung. Fenn. exs. 812 (1869; with description) (H lectotype, selected here; K, UPS isolectotypes) – *Exidia juniperina* (Karst.) Karsten 1889 p. 452.

Fructifications gelatinous, 1–2(–3) mm in diameter, at first like small pustules, becoming turbinate and somewhat wrinkled, smooth or faintly pruinose under a lens, hyaline, sometimes with a yellow tint when moist, drying horny, pale yellow and hardly visible. Hyphae 2.0–2.5 μm broad with clamp connections. Hymenium amphigenous; basidia globose, 9.6–12.0 μm in diameter, with four sterigmata of variable length. Spores globose to subglobose, 4.2–5.6(–6.0) μm in diameter, germinating by repetition.

Growing on ascocarps of *Colpoma juniperi* (Karst.) Dennis on twigs of *Juniperus communis* still attached to the shrub.

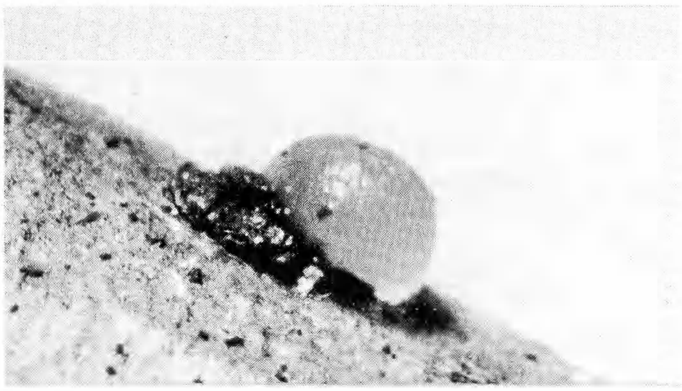

Fig. 1. *Tremella juniperina* (Torkelsen 1022/77, O). Fresh fruit body growing on old ascocarp of *Colpoma juniperi* (seen as a black spot) on branch of *Juniperus communis*. ×10.

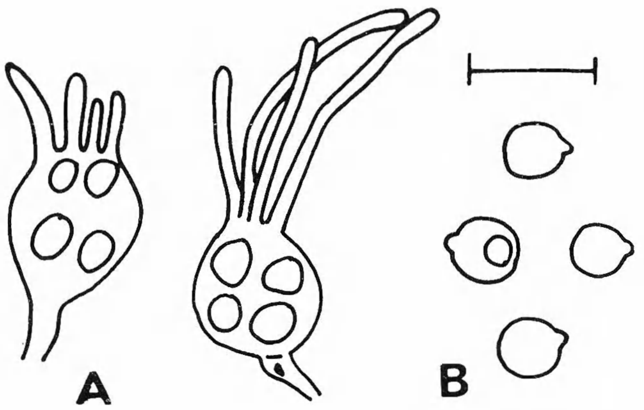

Fig. 2. *Tremella juniperina* (K. Holm 392 f, UPS). – A: Basidia. – B: Spores. – Scale 10 μm.

Substrate

In all specimens seen, including the lectotype, the fruit bodies of *Tremella juniperina* are associated with old ascocarps of *Colpoma juniperi* (Karst.) Dennis (syn. *Clithris juniperi* (Karst.) Rehm), sometimes even growing on them. Asci, ascospores and the characteristic paraphyses can no longer be seen, but fresh, young ascocarps occur on the same twigs, clearly indicating the identity of the species. Thus the substrate for *T. juniperina* should be given as *Colpoma juniperi*. Apparently, Karsten was not aware of the relationship between the two fungi as he did not mention the ascomycete in his diagnosis. The ascomycete was well known to him, issued in Fung. Fenn. exs. as no. 399, *Coccomyces juniperi* Karst.

Up to now 34 gatherings of *Colpoma juniperi* have been made in Norway, and *Tremella juniperina* has been found on 18 of them. This implies that the two species are not always associated, and that *C. juniperi* is more common than *T. juniperina*.

I assume that *Tremella juniperina* is dependent of *Colpoma juniperi*, and it seems to be a hypersaprophyte rather than a parasite. A study of the life cycle of living specimens would be desirable. The fungicolous way of life is not uncommon in the genus *Tremella*. It has been found in *T. encephala, T. globospora, T. indecorata, T. mycophaga, T. obscura, T. polyporina, T. simplex* and *T. versicolor* (Torkelsen 1968, Pilát 1957, Reid 1970). It is often difficult to decide if these fungi are parasites or saprophytes. Bandoni (1961), however, demonstrated experimentally that *T. encephala* grows parasitically upon *Stereum sanguinolentum*. As far as I know, no other cultural experiments on these fungi have been performed.

Distribution

In 1975 K. Holm sent me for identification some twigs of *Juniperus communis* containing gelatinous fungi; among others I could identify *Tremella juniperina*. These specimens were from various parts of Fennoscandia. I have since collected *T. juniperina* several times in different parts of Norway. Specimens from C, H, K, O, TRH, S and UPS have also been studied.

T. juniperina is now known from the following provinces in Fennoscandia. *Norway:* Akershus, Hedmark, Telemark, Aust-Agder, Vest-Agder, Hordaland, Nord-Trøndelag, Nordland. *Sweden:* Dalarna, Hälsingland, Härjedalen, Jämtland, Lappland (Lycksele lappmark), Uppland, Västmanland. *Finland:* Kuusamo, Regio aboensis, Satakunta, Tavastia australis. *USSR:* (formerly Finland): Karelia. *T. juniperina* is so far unknown in Denmark. The distribution is mapped in Fig. 3.

Since *T. juniperina* is always found in connection with *Colpoma juniperi* its distribution is limited by the distribution of the host. According to Holm & Holm (1977), *C. juniperi* has a northern–alpine distribution, being known from Sweden, Norway, Finland, Iceland, Greenland, Switzerland, Austria, Czechoslovakia, Italy and N.Y., USA.

I have also examined ten specimens of *C. juniperi* from C Europe (collections made in the Alps and the Carpathians) in search for *T. juni-*

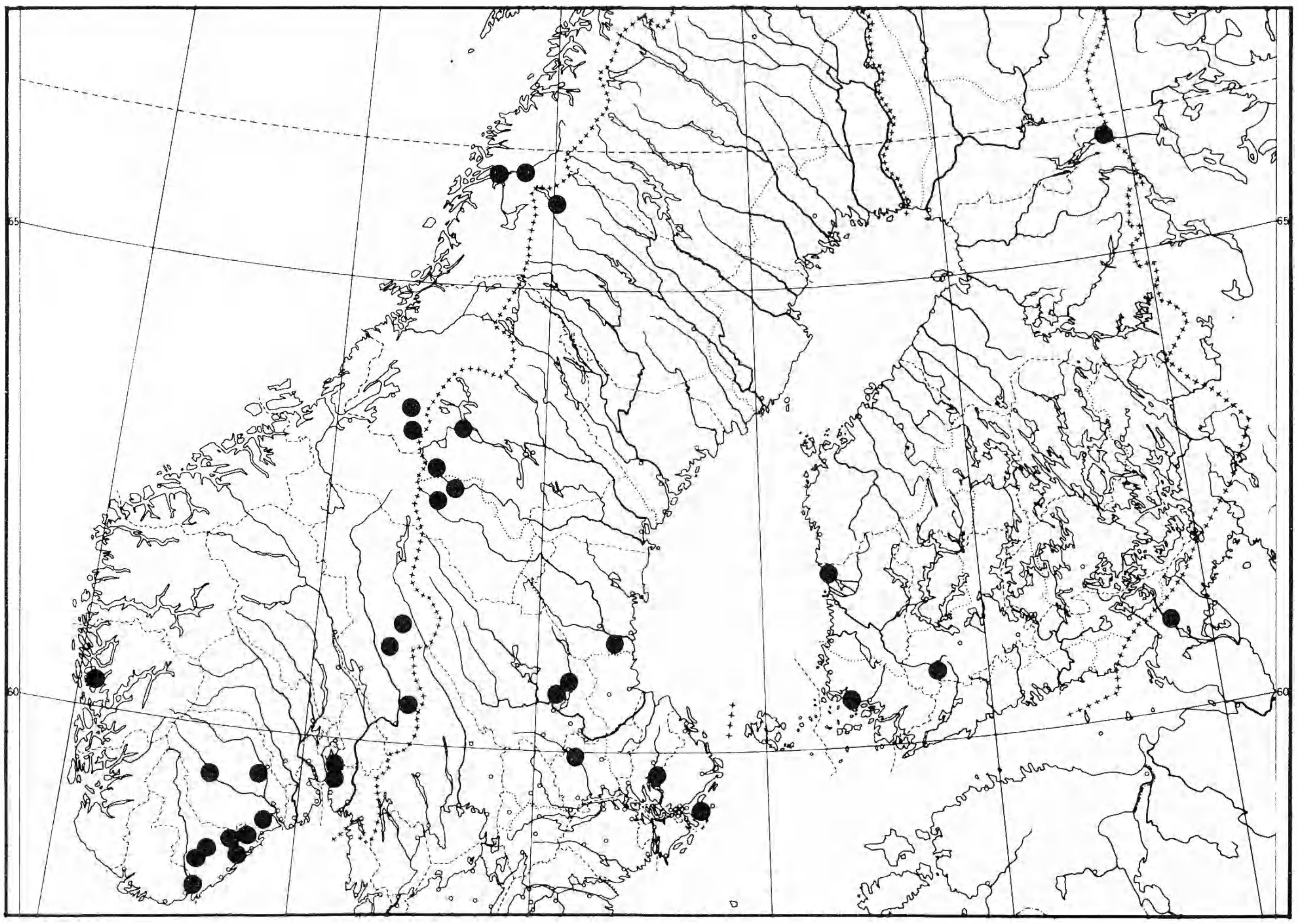

Fig. 3. *Tremella juniperina*. Known distribution in Fennoscandia.

perina, but it was not found. A specimen of *C. juniperi* from Greenland contained no *Tremella*. It seems that *Tremella juniperina* has a more restricted distribution than its host, which grows farther to the south as well as farther to the north. The southernmost locality of *T. juniperina* is in Norway, Jeppestøl, near Kristiansand (58°18′N), the northernmost one is in Finland, Oulanka National Park, N of Biological Station, S slope of hill Ampumavaara (66°22′30 ″N).

Tremella juniperina and Exidia grilletii

As already mentioned Donk (1966) suspected that *Tremella juniperina* was identical with *Exidia grilletii* (Boud.) Neuh. Evidently, Donk did not study *T. juniperina* himself, but relied on observations made by Dennis (in litt.). Dennis based his opinion on the Kew collection of Karsten's exsiccate. This material, according to Dennis, contained small carpophores, which become hyaline when soaked up, with abundant basidia and no spores. Dennis concluded that *T. juniperina* was identical with *E. grilletii,* because of the small basidia, the colour of the carpophores, and the substrate. As *E. grilleti* is known to grow on deciduous wood only, while *T. juniperina* was recorded from *Juniperus,* Dennis noted: ''The host is odd if so, but Karsten's hosts were often wrong''.

I have examined the Kew specimen of Karsten's *T. juniperina,* and it is the same species as the lectotype in H and isolectotype in UPS. Without doubt it is a *Tremella* species. The material is in good condition and contains basidia, some old and empty, and some young, cruciately septate, 7.5–11.3 μm in diameter. The spores, apparently overlooked by Dennis, are few and relatively small, about 5.0 μm in diameter. I have examined the substrate of the exsiccate specimen microscopically and identified it as *Juniperus communis*.

The characters just mentioned show that *Exidia grilletii* and *Tremella juniperina* are two quite different species.

According to Reid (1973) the correct name of *Exidia grilleti* is *Myxarium grilletii* (Boud.) Reid. He had noticed that the obpyriform basidia of the species in question were of the myxarioid type, characteristic of *Myxarium, Protodontia, Stypella* and other genera of Tremellaceae.

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The genus Zygophyllum in Egypt

M. Nabil El Hadidi

El Hadidi, M. N. 1978 12 15: The genus Zygophyllum in Egypt. [The family Zygophyllaceae in Egypt II.] *Bot. Notiser 131:* 439–443. Stockholm. ISSN 0006-8195.

This account is the second and last part of a revision of Zygophyllaceae s. str. in Egypt. It provides additional information on *Zygophyllum* to that given in Täckholm's *Students' flora of Egypt ed. 2* (1974). *Zygophyllum* L. in Egypt includes 10 species. *Z. aegyptium* A. Hosny and *Z. migahidii* Hadidi are new to Egypt. The latter is represented by var. *isthmia* A. Hosny, var. nov., from the Isthmic Desert. *Z. geslinii* Coss. does not occur in Egypt. The name *Z. berenicence* is validated.

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El Hadidi (1972) gave an account of *Fagonia* L. and *Seetzenia* R. Br. in relation to the treatment of Zygophyllaceae in Täckholm's *Students' flora of Egypt, ed. 2* (1974), to give additional information which is essential for any future detailed revision of these genera.

Two other accounts were planned to cover the treatment of the other 4 genera of Zygophyllaceae s.l. in Egypt, viz. *Zygophyllum* L., *Peganum* L., *Tetradiclis* Stev. ex Bieb. and *Tribulus* L. During the last few years, however, it has become obvious that Zygophyllaceae s. str. is rather distinct from Tribulaceae (*Tribulus*) and Peganaceae (*Peganum, Tetradiclis*); see further El Hadidi (1977 a).

Zygophyllaceae s. str. includes Old World genera with opposite, stipulate, usually compound leaves; the fruit is a capsule and the seeds have an endosperm (El Hadidi 1975). It includes 3 genera in Egypt, *Fagonia* L., *Seetzenia* R. Br. and *Zygophyllum* L. This account gives additional information on *Zygophyllum* as a basis for a more detailed study (Hosny 1978).

El Hadidi (1974) reported 9 species of *Zygophyllum* in Egypt. These belong to 4 sections of the 2 subgenera proposed by van Huyssteen (1937). According to Hosny (1977) species of the sections *Bipartia* van Huysst. and *Mediterranea* Engler are apparently polymorphic and can easily be confused. Among the most confused groups is the *Z. album* complex, which includes several taxa with grey pubescent, glandular leaves. El Hadidi (1974) considered that this complex comprises 3 species: *Z. album, Z. propinquum* and *Z. geslinii* Coss. Hosny (1978) showed that the latter species does not occur in Egypt and that *Z. album* comprises 2 varieties. Furthermore, she added *Z. aegyptium* and *Z. migahidii* var. *isthmia* which is described here. Accordingly, *Zygophyllum* is represented in Egypt by 10 species, which can be distinguished from one another according to the key below.

Key to the species of Zygophyllum in Egypt

1. Annual herb; leaves simple, terete .... 3. *Z. simplex*
– Perennial shrubs or shrublets; leaves 2-foliolate 2
2. Leaflets flat 3
– Leaflets terete 4
3. Capsule pear-shaped, up to 10 mm long .... 2. *Z. decumbens*

– Capsule pod-like, 20–30 mm long .... 1. *Z. fabago*
4. Leaflets greyish, glandular, peduncle shorter than flower and capsule 5
– Leaflets green, glabrous, peduncle at least as long as flower and capsule 8
5. Capsule pear-shaped, 5-lobed 6
– Capsule obconical, angular 7
6. Capsules solitary at each node, up to 5 mm broad .... 4. *Z. album*
– Capsules in clusters at each node, 5–8 mm broad .... 8. *Z. aegyptium*
7. Capsules solitary at each node, 5–7 mm long .... 9. *Z. migahidii*
– Capsules in clusters at each node, 8–10 mm long .... 7. *Z. propinquum*
8. Capsule wingless 9
– Capsule with 5 broad wings .... 10. *Z. dumosum*
9. Capsule 5 mm long and broad .... 6. *Z. berenicense*
– Capsule 10 mm long, 5 mm broad .... 5. *Z. coccineum*

1. **Z. fabago** L.

Linnaeus 1753 p. 385 – Orig. coll.: Savage catalogue 544/1 (LINN).

Perennial, green, glabrous shrublet with 2-foliolate leaves; leaflets broadly ovate, flat. Flowers 20 mm in diam.; petals white; filaments pink. Capsule 20–30 mm long, 5 mm broad, pod-like, 5-angled.

Distribution. In Egypt confined to the Isthmic Desert and Sinai; Palestine, Jordan, Syria, Iraq and Iran.

Collections. Egypt: Desert à loin du Caire, 27.1.1831 (FI) – Desert between Cairo and Suez, in wet salty places, 1867, Figari (FI) – Mountainous deserts, salt springs along Suez, eastwards in El Arish and Gaza, 1876, Figari (FI, Webb 29669).

2 a. **Z. decumbens** Del. var. **decumbens**

Delile 1813 p. 221, tab. 27, fig. 3 – Orig. coll.: Valleé dans l'Egaroment, Delile (MPT, FI).

Glabrous, green or yellowish-green shrublet with prostrate branches and 2-foliolate leaves; leaflets broadly obovate, flat. Cymes 4 times branched; flowers 8 mm in diam. Fruit turbinate, 3 × 2 mm; pedicel 3 mm.

Distribution. In Egypt confined to the Arabian Desert along the Red Sea; Sudan (coast) and Somalia (Gulf of Aden).

Collections. Egypt: Djebel Attagah, 2.1877, Letourneux 37 (G, K) – Kosseir–Ras Banas, 3.1864, Schweinfurth 2237 (G) – Wadi Uraq, 3.1877, Schweinfurth 26 (LD) – Wadi Hamata, im nördlichen Theile der oest. Wüste von Ägypten, 13.4.1880, Schweinfurth (C).

2 b. **Z. decumbens** var. **megacarpum** A. Hosny

Hosny 1977 p. 467 – Orig. coll.: Egypt, Eastern Desert (Da. Sept.), Cairo–Suez road, 115 km from Cairo, 4.1976, N. El Hadidi and A. Hosny (CAI holotype).

More robust than the type variety, with decumbent branches; up to 35 cm high. Cymes 2–3 times branched; flowers 12 mm in diam. Fruit 5 × 4 mm; pedicel 6.5 mm.

Distribution. Arabian Desert, and along the Red Sea coast in Egypt, Sudan and Saudi Arabia; also along the coasts of the Gulf of Aden (Yemen and Somalia).

Collections. Egypt: Im nördlichen Theile der östlichen Wüste 1886, Schweinfurth (BM) – Wadi Warag, Da. Sept., 7.8.1925, Simpson 3498, 3499 (K) – Gebel Attaga near Aboud's factory, 6.1955, Botany Dept. excursion (CAI) – Wadi el-Rokham (Suez), 6.1964, Osborn (BM) – Cairo–Suez road, 3.1974, Nabil El Hadidi (CAI) – *Sudan:* Cap Elei–Cap Elba, 12.1864, Schweinfurth 2238 (K) – Wadi Shináab, 4.1933, Jackson 2773 (K) – *Somalia:* Sugavo, 1.1945, Glover & Gilliland 786 (K) – *Arabia:* Jidda, 9.1878, Barton (K) – Wadi Khawat, SW of Rub el-Khali, 1.1960, Thesiger (BM) – Aden, Wadi Duan, 1936, Maxwell-Darling 187 (K) – 40 miles N of Mukella, 5.1955, Heming 520 (BM, K).

3. **Z. simpex** L.

Linnaeus 1767 p. 68 – Orig. coll.: Plant grown in Uppsala Botanic Gardens from seeds collected in Arabia by Forsskål in 1762.

Zygophyllum portulacoides Forsskål 1775 p. 88 – Orig. coll.: Arabia Felix, Môr 1762, Forsskål (C, LD-Retz).

Glabrous, mat-forming herb. Leaves 9–10 mm, simple, cylindrical. Flowers yellow, minute. Capsule pear-shaped, 2 mm in diam., deeply 5-partite.

Distribution. The most widespread species of the genus, known from N Africa, southern Africa, the Cape, the Canary Is. and the Cape Verde Is., in the east through tropical Arabia to Iraq, Iran, Pakistan and India.

4 a. **Zygophyllum album** L. fil. var. **album**

Linnaeus 1762 p. 551 – Orig. coll.: Savage catalogue 544 (LINN).

Zygophyllum proliferum Forsskål 1775 p. 87 – Orig. coll.: Alexandria ad salinas, 4.1762, Forsskål (C).

Blue-green, mealy-pubescent shrub. Leaves 2-foliolate; leaflets ovoid, c. 7 mm. Flowering branches with one flower at each node. Flowers less than 9 mm in diam., almost sessile. Capsule glandular, obconical, 5×5 mm, 5-lobed; lobes obtuse, slightly keeled.

Distribution. Widely distributed throughout the deserts and salt marshes of N Africa. Along the Red Sea coast in Egypt, Sudan, Ethiopia; Gulf of Aden (Somalia). Also known from Palestine, Syria, Cyprus, Arabia and Spain (one locality).

Collections. Egypt: En Aegypto, Forsskål (BM, C) – Egypto, Delile (FI, Webb 29641) – Inter Kahiram et Suez, 3.1846, Boissier (G, K) – Alexandria, Viviani (FI, K, M) – Farafra Oasis, 1873, Ascherson 600 (G) – *Libya:* Tripoli 1773, Rothman (S) – *Sudan:* Suakin near sea, 3.1855, Johnston 15 (K) – *Ethiopia:* Eritrea, Assab, 1.1962, Mooney 8951 (K) – *Somalia:* 3 miles E of Erigavo, 9.1938, McKinnon S/101 (K) – *Arabia:* 3.1846, Boissier (G) – Jidda, 5.1951, Trott 1660 (K) – *Cyprus:* Regio Cyperus, 1880, Sintenis 415 (G) – *Spain:* Catalunia austro-occid., in arenosis salsis ad ostiam ibiri, I. Punta de la Banya, 1.6.1934, Font Quer 52 (S).

4 b. Z. **album** var. **amblyocarpum** (Baker fil. ex Oliver) Hadidi

El Hadidi 1978 – *Z. amblyocarpum* Baker fil. ex Oliver 1895 plate 2358 – Orig. coll.: Hadramaut, Mokalla, Shary Burrock Valley, 21.12.1893, Lunt 51 (K, BM).

Differs from the type variety in being more glandular, whitish and robust (frequently reaching over 1 m in height), and in having a slightly larger capsule with acute, distinctly keeled lobes.

Distribution. In Egypt confined to the salt marshes along the Mediterranean and Red Sea; coastal regions of Sudan, Ethiopia, Somalia and southern Arabia.

Collections. Egypt: Mariut, Burg El Arab, 2.4.1971, Ibrahim & Mahdi (CAI, S) – Wadi Gerawi near Helwan 1896, Schweinfurth (G).

5. **Z. coccineum** L.

Linnaeus 1753 p. 386 – Orig. coll.: Egypt, Memphis, Shaw (BM).

Zygophylum desertorum Forsskål 1775 p. 87 – Orig. coll.: Inter Kahiram et Suez, 8.1762, Forsskål (C, BM, LD).

Glabrous, bright green shrub up to 75 cm. Leaves 2-foliolate; leaflets cylindrical, c. 10 mm. Flowers more than 10 mm in diam., pedicel 3–4 mm. Capsule ± cylindrical, wingless, c. 10×4 mm; apex obtuse.

Distribution. In Egypt from the Libyan and Arabian Deserts and the wadis along the Red Sea, also in coastal Sudan and Ethiopia, and the Dahlak Archipelago. Rare in Sinai and the geomorphological extension, the Naqab Desert.

Collections. Egypt: On Sharagi land, Ain Shindi, Siwa Oases, 27.3.1927, Simpson 4557 (K) – Shallow sandy wady, Batn El Hashish between Dakhla and Kharga, 15.4.1928, Simpson 6097 (K) – Inter Kahiram et Suez, 8.1762, Forsskål (C, BM, LD) – In deserti propi Memphiden, 1819, Sieber (BM) – Circa Citadellam Cahirae, 15.1.1838, Wiest (G, K, S) – Cairo, 1846, Boissier (G, K) – Caire, 18.3.1847, Kralik (G, S) – Inter Abbasia et Montem nigrum, 4.5.1861, Samaritani (S) – Helwan, Seitentahl des Wadi Hof, 2.2.1855, Volkens (C) – Cairo, 30.3.1880, Covetten Gelfes Expd. (UPS) – Chardaga, 5.7.1936, Th. Mortensen (C) – *Sudan:* Nubische Küste 22°N bei Mirsa Gubeta, 3.1864, Schweinfurth 2240 (K) – About 21° sea coast, 1896, Bent (K) – Sea beach at Port Sudan, 11.1929, Burtt Davy 2806 (K) – Near Khor Ashout, Red Sea coast, 70 miles from Port Sudan, 1935, Maxwell-Darling 136 (K) – Port Sudan, 4.1967, Sahmi & Kami 716 (K) – Suakin, 4.1949, Bally 7103 (K) – Aqiq, 1953, Jackson 2788 (K) – Aqiq, 4.1959, Jackson 3931 (K) – *Sinai:* Dans le endroits humides et sales, environs de Tor 1832, Bové 173 (FI) – Wadi El Tayiba, 2.5.1939, Drar 127 (S) – *Palestine:* Wadi Arava near Eilat, 28.6.1966, Wängsjö 1630 (LD).

6. **Z. berenicense** (Muschler) Hadidi, comb. et stat. nov.

Basionym: *Zygophyllum coccineum* L. var. *berenicense* Muschler 1912 p. 578 – *Z. berenicense* Schweinf. in Ascherson & Schweinfurth 1887 p. 56, nom. nud. – Orig. coll.: Egypt, Trummer von Berenice, 7.1864, Schweinfurth 2248 (BM).

Similar in habit to *Z. coccineum,* but smaller, with decumbent branches and smaller leaves; leaflets up to 6 mm. Capsule club-shaped, 5×5 mm.

Distribution. Along the Red Sea in Egypt, Sudan and Saudi Arabia.

Collections. Egypt: Wadi Hassani at the mouth in deep

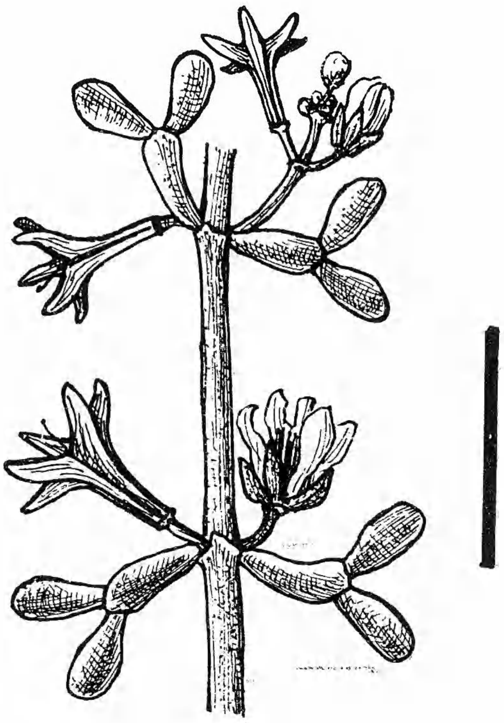

Fig. 1. *Zygophyllum migahidii* var. *isthmia*. Scale 1 cm.

sand, 25.4.1924, Simpson 2798 (K) – Bir Gendeli amongst rocks near the Madfun, 23.8.1927, Simpson 2947 (K) – *Sudan:* Port Sudan, 18.1.1955, Drummond & Hemsley 1002 (K) – *Arabia:* Ad littoris maris prope Geddam, 2.1837, Fischer 95 (K, M) – Ad littore maris prope Djedam, 10.1.1836, Schimper 877 (G, M) – Djedda, 1838, Botta (G) – Shores of Red Sea near Jedda, 12.1950–5.1951, Trott 1659 (K).

7. **Z. propinquum** Decaisne

Decaisne 1835 p. 283 – Orig. coll.: Egypt, terrains humides et saumâtres des environs de Tôr, 6.1832, Bové 171 (P, CAI, G, K).

Glandular, pubescent shrub. Leaves 2-foliolate; leaflets greyish-white, cylindrical, more than 10 mm. Flowering branches with several flowers at each node. Flowers over 10 mm in diam., pedicel 2–4 mm. Capsule obconical, 5-angular, 10–15 × 3–6 mm, apex obtuse; pedicel 4–6 mm.

Distribution. In Egypt confined to Sinai; Iraq, Iran, Afghanistan and Pakistan.

Collections. *Iraq:* Karbella, Musseijib, 3.10.1947, Gillett 9968 (K) – 3 km NW of Alm Sukhair, 11.11.1956, Rawi & Joseph 16259 (K) – *Iran:* Lar, inter Genu et Sarzeh, 250 m, Rechinger 3404 (W) – *Pakistan:* Bela, 12 km W Bela, Rechinger 27587 (W).

8. **Z. aegyptium** A. Hosny

Hosny 1977 p. 467 – Orig. coll.: Egypt, Mediterranean region, Ras El Bar near Damietta, 7.1976, A. El Gazzar (CAI holotype).

Green, glabrous shrub up to 60 cm. Leaves bifoliolate; leaflets unequal, obovate to oblanceolate. Flowering branches with 2–3 flowers at each node. Flowers more than 10 mm in diam., pedicel 2 mm. Capsule glabrous or slightly hairy, obconical, 5-lobed, 5–9 × 5–8 mm, apex retuse, pedicel up to 3.5 mm.

Simpson recognized the distinct characters of this taxon; he named his specimen (Simpson 1890, K) *Z. album* but wrote: ''A very distinct form growing with the type; branches sub-erect but quite flat''.

Distribution: Mediterranean region of Egypt and Tunis; common on Cyprus.

Collections (in addition to those given in Hosny 1978). *Egypt:* In regione Alexandria, Mex, 20.7.1868, Schweinfurth 66 (S) – Basse-Egypte, Ramulé, 3.1877, Letourneux (C) – Salt marsh Sidi Shata near Damietta, 2.5.1922, Simpson 1220 (K) – Sandy ground, El Ibrahimya, Alexandria, 15.3.1923, Simpson 1890 (K) – Ramleh, prope Alexandrie, 5.6.1933, Wall (S) – Sinai-Halbinsel, Sanddünen-vegetation hinter der Mangrove, 29.3.1976, Breckle 3869 (K). – *Cyprus:* Am Salzsee bei Larnaka, 16.7.1880, Sintenis 514 (LD) – Larnaca, 7.4.1912, Haradjian 39 (S) – Distr. Larnaca in salinis, 25.6.1939, Lindberg (S) – Distr. Limasol, 3.7.1939, Lindberg (LD) – Larvacavikeus, shore 3 km NE of Larnaca, 1.7.1971, Julin (S) – Famagusta, 6.4.1974, Wängsjö 5004 (LD) – *Tunis:* Gabes, c. 3 km SE of Telboulbon, 13.4.1963, Wängsjö (LD).

9. **Z. migahidii** Hadidi var. **isthmia** A. Hosny, var. nov. – Fig. 1

Habitu varietati typicae similis, sed floribus et fructibus minoribus. Sepala 3.5 × 2.5 mm; petala 5 × 2 mm, apice dentata. Stamina 10, filamenta 2.5–3 mm longa. Ovarium 5-angulare, pubescens; stylus et stigma simplex, in toto 1.75 mm longum. Capsula 5-lobata, obconica, 5–7 mm longa, in parte apicali 5 mm, in parte basali 1.5 mm diametro. Pedicellus 3 mm longus.

Holotypus: Egypt, Isthmic Desert (Di), E of Qantara (32°20′E, 30°51′N), 3.1974, Adel El Gazzar (CAI).

Similar in habit to the type variety (El Hadidi 1977 b p. 328). Flowers and fruits smaller. Sepals 3.5 × 2.5 mm; petals 5 × 2 mm, apex dentate. Stamens 10, filaments 2.5–3 mm. Ovary 5-angled, hairy; style and stigma simple, together 1.75 mm long. Capsule 5-lobed, obconical, 5–7 mm long, 5 mm in diam. near apex, 1.5 m below. Pedicel 3 mm.

Distribution: Endemic to the Isthmic Desert, only known from the type locality.

10. **Z. dumosum** Boiss.

Boissier 1849 p. 125 – Orig. coll.: Palestine: In aridissimis deserti Arabiae inter Nuckl et Gaza (G).

Woody shrub up to 1 m. Leaves 2-foliolate; leaflets cylindrical, fleshy, mealy pubescent, c. 10 mm. Flowers up to 15 mm in diam., pedicel 3–6 mm. Capsule 5-partite, each part strongly compressed with broadly winged margin.

Distribution: In Egypt confined to the Isthmic Desert and Sinai; Palestine, Jordan.

Collections. Egypt: Sinai, Wadi Feiran 1831, Aucher 793 (FI, G) – Sinai mountain region, 1867, Figari (FI) – Sinai, Wadi Sheikh, 11.1883, Hart (K) – Two days S of Gaza in Tih desert, 3.1882, Post (K) – Sinai, Wadi Tache, 11.5.1891, Cramer (G) – N Sinai, Wadi Heridin S of El Arish, 4.4.1939, Drar (CAI, S) – Isthmic desert, Darb El Hagg at Sudur el Heitam, 10.5.1939, Drar 677 (CAIM, S) – *Palestine:* Desertum prope Neckl, 3.1846, Boissier (G) – Arava valley, envir. of Eilat, 10.1.1957, Safriel 665 (LD) – Versus St. Saba, 1855, Kotschy 559 (G) – Inter St. Saba et Jericho, 1881, Letourneux (K) – Jericho, 1886, Post (BM, K) – Jericho, 1897, Bornmüller 286 (K) – St. George Convent, 4.1911, Dinsmore 6430 (K) – Jerusalem, Wadi El Kelt, 25.3.1912, Meyers & Dinsmore B2430 (LD) – Jordan valley near Jericho, 15.3.1921, Linder (UPS) – Inter Khan Hatrur et Jericho in semideserto lapidoso, 27.4.1932, Samuelsson 629 (LD, S) – Desertum Judaicum, inter Jerusalem et Jericho, Wadi Kelt, 26.3.1933, Samuelsson 2495 (LD, S) – Wadi Kelt, 24.3.1934, Alonzo 100 (S) – Wadi Kelt, 6.1941, Davis 3677 (K) – Maris Mortui, prope mare in collibus, 14.1.1908, Dinsmore 4430 (LD) – Maris Mortui australis, N of Ghor-us–Safiyal, 28.4.1939, Dinsmore 14430 (S) – *Jordan:* Zerka, 4.1945, Davis 9407 (K) – Dead Sea among the ruins, 4.1965, Townsend 65/7 (K).

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Vivi Täckholm biological symposium

Synopses of lectures prepared for a symposium held in Lund, Sweden, in August 1978

On the genus Launaea Cass.

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The genus *Launaea* Cass., family Compositae, tribe Cichorieae, subtribe Crepidinae comprises about 80 species and 12 subgenera. The genus includes herbaceous annuals and perennials and spiny shrubs. The range of distribution is temperate, subtropical and tropical, mainly occurring in C to SW Asia and Africa. There is one species in Western Australia, six in S Europe and a few in the West Indies, C America and Chile. All species have involucral scales with scarious margins and beakless heteromorphic achenes (one type of achene is short-beaked in subg. *Brachyramphus*). The involucral bracts and the achenes are of diagnostic value. The caudex is provided with a rosette of leaves which often differ in shape from the cauline leaves. In some species the rosette is not produced until after anthesis. The heads are usually cylindrical, some almost globose or oblong. The corolla is usually yellow but violet and pink species are also known. The chromosome numbers are x = 7, 8, 9 and 16.

A preliminary assessment of the effect of protection on the vegetation of Mediterranean desert ecosystems

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The western Mediterranean desert of Egypt has a long history of intensive land use which, coupled with austerity of environment and uncertainty of rainfall, has resulted in an advanced stage of desertification. The ecosystems have been shifted beyond their zones of equilibrium and are producing at a lower rate than their normal potential. Practices should be adopted that will allow vegetation to recuperate in order to sustain maximum productivity. These should incorporate possibilities for deferred or rotational grazing and for the establishment of reserves for monitoring the changes in the vegetation and other ecosystem components that would occur if they were completely or partially protected against man-made perturbations.

The present study includes a preliminary evaluation of the effect of fencing on the composition of the vegetation and the biomass and phenology of species in two ecosystems (coastal dunes and non-saline depressions) within the framework of the "Samdene" project sponsored by the University of Alexandria for "Systems Analysis of Mediterranean Desert Ecosystems of Northern Egypt" and supported by the U. S. Environmental Protection Agency and the Ford Foundation.

After three years of protection there was an overall increase of about 38% in the density of species and almost no change in the total cover of vegetation on the coastal dunes. On the other hand, the overall increase in density and cover of species was remarkable in the non-saline depressions (more than 200% for density and 114% for cover). The general pattern of vegetation distribution, however, remained almost the same. The change in biomass varied from species to species and from season to season for a given species. Some species attained a significantly higher biomass than species outside the exclosure, others significantly lower. But because of the marked increase in the density of most species there was an overall increase in biomass of about 870 kg/ha (29%) in the non-saline depressions and 100 kg/ha (2%) on the coastal dunes during spring. The difference in the phenological behaviour of species inside and outside the exclosure was more pronounced in the non-saline depressions than on the coastal dunes. The most obvious difference was that most species exhibited an additional peak of phenological activity (leafing out and flowering) inside the exclosure during late spring and early summer (May–July) at a time when activity was on the decline outside the exclosure. Therefore, it can be concluded that protection for three years has resulted in a general improvement in the primary production and phenological behaviour of species, especially in the non-saline depressions which are more readily accessible to heavy grazing than the coastal dunes.

Some species exhibited a negative response to protection. These may have been palatable species that suffered when deprived of light nibbling and removal of standing dead shoots, a practice which usually promotes vigour and growth, or they may have been unpalatable or of low palatability and were now in direct competition with the protected palatable species. Partial protection and controlled grazing might therefore be more profitable than complete protection. However, it may not be feasible to draw definite conclusions from short-term exclosure experiments such as this, since the effects of the inconsistency of rainfall and the degree of degradation of the ecosystem may exceed the effect of protection during the short period of a few years.

Plant life in Nubia

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Egyptian Nubia comprises the Nubian Desert and the delimiting part of the Nile valley which after the construction of the Aswan High Dam in 1965 was replaced by the reservoir lake (Lake Nasser). The Nubian Desert is the southern province of the Libyan Desert and differs essentially from the northern province (the Libyan Plateau) as regards the underlying rock which here is Nubian sandstone.

The formation of the Nubian Nile began during the Miocene period and during the Pliocene it received its water from the rain which fell in the Arabian Desert. Most of the prominent features of the Nile valley developed during the Pleistocene. Three phases can be distinguished: the Protonile, Prenile and Neonile. The sequence of events during the Neonile phase (30,000 years) are sufficiently well known from archeological evidence and studies of the Nile valley sediments. Periods of high rainfall with savanna vegetation in the Nubian Desert and the apparent elevation of the water level in the Nile alternated with dry periods when the water level was lowered and desert conditions prevailed. The present dry conditions in Nubia seem to have been established during the Old Kingdom (c. 4000 B. C.).

Floristic studies in Egyptian Nubia are in progress in three areas:

(1) Studies of the remains of the original Nile-Nubian plant cover on a group of islands near Aswan

The plant communities show the characteristic features of a type of woodland not known elsewhere in Egypt. "Duns" Island, now a nature reserve, has three vegetation types: Xeromesophytic forest dominated by *Acacia* spp., xerohalophytic shrubs dominated by *Tamarix* spp. and the hydromesophytic meadows including a swamp community dominated by *Cynodon-Panicum–Cyperus*. Among the associated species are new records for the Egyptian flora or new species which have still to be described.

(2) Studies along the shores of Lake Nasser

Plants that succeeded in establishment after the construction of the Aswan High Dam are characteristic of the shores of a lake rather than of the banks of a river. Communities dominated by *Phragmites australis, Tamarix amplexicaulis* or *Salsola baryosma* inhabit the shores of the lake in the two areas of study: Daboud and Abu Simbel. The Daboud area (25 km S of Aswan) includes rich natural vegetation and is uninhabited. The Abu Simbel region (350 km S of Aswan) is the site of the only human settlement on Lake Nasser. About 35 weeds have been recorded from gardens, lawns and experimental fields in this area. In all 55 species have succeeded in becoming established, which constitutes 25% of the species known from Nubia before the inundation of the Nile valley in 1965. *Acacia* seedlings succeeded in establishing and started their vegetative growth within a period of 3 to 4 years.

(3) The Nubian Desert

Floristically, the Nubian Desert is the best-known area in Egypt. The vegetation is sparse and is confined to places where underground water is available for plant growth in particular around the wells and small oases. Palm groves, tamarisks and salt marshes are the prominent types of vegetation. Outstanding are the *Acacia* islets which are related to prehistoric archeological sites. Each islet consists of a single gigantic tree of *Acacia ehrenbergiana* with the vegetative branches resting on top of a sand dune and covering an area of 30 to 50 m in diameter. Radio carbon dating of some of the younger branches points to an age of 350 to 700 years. These remarkable acacias must belong to the period when the water supply enabled the growth of such trees. Artifacts and other remains of ancient human settlement are commonly met with around these islets.

With regard to the memorial forest to be donated by Sweden in memory of the late Vivi Täckholm the following points should be taken into consideration: The forest should consist of indigenous trees growing in their natural habitat, which was what Vivi Täckholm wished. The Nile Nubian region would be a convenient site especially when Lake Nasser has been finally settled. It has been decided to re-settle the region, and the cultivation of trees that belong to the woodland type known earlier in Nubia can help in restoring the original plant cover of Egyptian Nubia. Vivi Täckholm herself lived in the Nile Nubian region for two seasons before its inundation to make a documentary study of the natural flora of the area. She hoped that a nature reserve would be established after the completion of the High Dam. She was also interested in the pre-history of the region.

A comparative study of the effect of fluometuron on the root meristems of wheat and broad beans

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Fluometuron, the common name for N-(3-trifluoromethyl phenyl)N$^-$, N$^-$-dimethyl urea, has been widely used as a selective urea herbicide. Its effects on mitotic and aberration rates were determined and compared in the root meristems of wheat (*Triticum vulgare* L.) and broad bean (*Vicia faba* L.). Wheat grains and roots of bean seedlings were soaked in different concentrations (M, M/10, M/100 and M/1000) of the herbicide and distilled water for different lengths of time. The rate of germination and of seedling growth of treated wheat grains was markedly decreased by increasing the dose (concentration × time). Complete mitotic inhibition accompanied by faint Feulgen staining were observed after treatment with M and M/10 concentrations for 24 hours and 48 hours' recovery. However, the rate of germination was 61% with M/10 for 24 h indicating that this dose had a delayed lethal effect. The mild dose (M/1000 for 2 h) induced a significant increase in the rate of mitotic index (MI) compared with the controls in wheat and bean root meristems. This stimulation of division (short mitotic cycle) was lost when either the time of treatment or the recovery period was prolonged. The increase in the rate of MI due to this treatment was significantly greater in wheat than in bean root meristems. This can perhaps be attributed to the effect of the intact molecule of the compound (resembling a hormonal effect), while the delayed effect (loss of stimulation) was probably due to the action of the degraded products of the herbicide which in wheat were found to be the mono- and dimethylated products rather than the analine products.

Fluometuron induced higher rates of aberration in bean meristems than in wheat root meristems. The rate increased with increase in dose and was inversely proportional to rate of MI. An exception to this trend was found in wheat treated with M/10 for 24 h. The apparent decrease in aberration rate with this treatment could be attributed to the uncalculated heterochromatinization (faint Feulgen staining) which was general. The major types of aberration in both wheat and beans were chromosome stickiness, which ranged from moderately sticky chromosomes to clumpy figures, and heterochromatinization on part of a chromosome, a whole chromosome or even a whole chromosome complement. This indicated that chromosome stickiness and heterochromatinization may be induced by the same mechanism or two closely related mechanisms. Other aberrations such as micronuclei, changes in ploidy and fragments were rare.

The ratio nucleus/nucleolus volumes in late interphase cells decreased more in beans (3.2 control, 1.9 treated seedlings) than in wheat (4.6 control, 3.4 treated grains). The slight difference exhibited in wheat was due to an increase in nucleolar volume (0.5×10^{-6} mm^3 control, 0.9×10^{-6} mm^3 treated), probably as a result of an increase in RNA synthesis. In beans, on the other hand, the difference was due to a decided decrease in nuclear volume (1.8×10^{-6} mm^3 treated, 2.5×10^{-6} control), as a consequence of interference of DNA, nuclear proteins or RNA synthesis.

A preliminary experiment was carried out using bean seedlings to detect a repair mechanism by applying a mixture of nucleotide monophosphate (A, T and G each 400 ppm) after treatment with M and M/10 of the herbicide for 4 h. However, a synergistic effect was obtained, and the rates of aberrations reached 100% accompanied by a decrease in the MI. The nucleotide mixture alone induced 44% aberrations.

Demethylation of fluometuron was found to be the primary detoxification mechanism in resistant crops. Accordingly the induction of chromosomal stickiness and heterochromatinization in both wheat and beans could be due to the difference in the relative amounts of an enzyme system capable of demethylating the herbicide. The greater increase in nucleolar volume in wheat compared with that in beans may indicate an increase in mRNA responsible for the formation of these enzymes. However, the degradation products may form conjugates with cell metabolites which in their turn could be responsible for the induction of aberrations. But since fluorine compounds have been proved to induce stickiness and high rates of aberrations, it may be suggested that the $-CF_3$ side chain has a role in the induction of these aberrations.

Studies on the effect of the protection of vegetation on the soil mesofauna in a Mediterranean desert in Egypt. Preliminary results of studies on population density

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An area in the Omayed Desert 10 km south of the Mediterranean coast and 85 km west of Alexandria was fenced off and protected from grazing for 3 years from 1974 to 1977. In half of this area (10.2 ha) 66% of the grazing pressure prevalent in the area was allowed; and two other areas were fenced in and 66% and 33% of the prevalent grazing pressure was allowed. The soil mesofauna (those which do not pass through a 1 mm-mesh sieve) were sampled from under five species of shrubs in each of these 4 treatments in addition to the free-grazing (100%) area (a total of 294 samples) outside. Preliminary results of the population density of the soil mesofauna per area and per soil volume indicate that the highest means are obtained in the treatments with 3-year protection + 66% grazing pressure and with no previous protection + 33% grazing pressure. The highest population densities occur in summer. It is postulated that the sheep and goats (consumers) have a beneficial effect on soil mesofauna by converting plant biomass into animal necromass (urine) and converted plant necromass (dung) which is more readily usable and assimilable than litter. This beneficial effect outweighs the harmful effect of trampling at intermediate grazing pressures. Populations of the soil mesofauna are in the process of adjusting to changes in plant cover and producer–consumer relationships within the exclosures.

The mitotic apparatus of Haemanthus katherinae in the scanning electron microscope

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The endosperm cells of certain monocotyledonous plants, in particular *Haemanthus katherinae,* have been a suitable subject for studying the organization and function of the mitotic apparatus (MA). Information on giant mitotic configurations and mitosis in these cells comes from light microscopy using phase contrast, Nomarski differential contrast, light polarization and fluorescence. At ultrastructural level sectioned material has been studied in transmission and high voltage electron microscopes, and chromosomes but not the spindle were observed in the scanning electron microscope (SEM).

In the present investigation, the intact MA of *H. katherinae* was analysable in the SEM. The chromatic part, i. e. the chromosomes, and the achromatic part, the spindle, could be clearly distinguished. At metaphase the spindle appeared as a network of fibres and fibre bundles that extended in the direction of the spindle axis. Spindle fibres and fibre arrays were often intermingled with each other and sometimes showed an intimate parallel arrangement. Usually they were either convergent, i. e. fusing or associating with other fibres thus giving rise to a thicker bundle, or divergent in a fan-like formation. Significantly more spindle fibre material was observed at the equatorial plate region than at the polar regions. Frequently the spindle fibres showed ridged or globular surface features. At the kinetochore regions large bundles of kinetochore fibres as well as continuous fibres were seen. The chromosomes appeared to be covered with spindle proteins. Chromatic supercoils were sometimes clearly distinguishable.

The present findings may have some bearing on the hypotheses proposed for chromosome movements based on assembly–disassembly, sliding or zipping of microtubules. They also showed that the MA is preserved intact with least loss of matter.

Plant life in the maritime sand dunes along the Mediterranean in Egypt. The ecology of Ononis vaginalis Vahl

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The genus *Ononis* is circum-Mediterranean. It is represented in Egypt by eight species. The range of distribution of *Ononis vaginalis* Vahl extends along the Mediterranean from Tunisia to Syria with extensions in the Saharo-Arabian region. In Egypt the species is confined to the calcareous maritime sand dunes along the Mediterranean coast.

The distributional pattern of plant species on the maritime dunes from the seashore to the crest of the dune is controlled mainly by the degree of exposure to sea-spray and to the rate of sand accretion.

Ononis vaginalis is a pioneer on the slowly accreting sand in areas protected from sea-spray. It can be considered as the pre-climax stage of maritime sand dune psammosere, the climax being a scrubland represented by *Lygos raetum* Heywood, *Lycium europaeum* L. and *Thymelaea hirsuta* (L.) Endl.

Being a perennial the species shows clear seasonality of growth: an active growth period and a dormant one. Regeneration is either from perennating buds or from seeds. Perennating buds are borne above the sand surface (Chamaeophytes), but due to shallow sand accumulation lower buds become covered with sand (Hemicryptophytes). The dormant buds give new sprouts in October. The new branches bear flowers in January. Peak of flowering is reached in March. Fruit setting starts in March and ends in June. Seed shedding starts in April and ends in July.

Two populations of *Ononis vaginalis* can be distinguished on flower and fruit characters: one with a deep yellow standard with clear purple stripes and with longer pods; the other population with a light yellow standard with faint purple stripes and with shorter pods. Intermediate forms exist.

Average seed weight is 0.5 mg. The seeds have tuberculate seed coats and are of three different colours: yellowish-brown, very pale brown and olive-grey. Seeds are naturally set to depths varying from 0.5 to 5 cm. Seedling emergence is controlled by the onset of and amount of rainfall. Successful emergence took place after twelve days from the onset of 9.3 mm of rain in late November 1976, while 4.3 mm of rain in late November 1975 failed to effect emergence. Germination of seeds kept in the laboratory does not exceed 2%, but in the field it varies from 50 to 100%. It should be noted that the early phase of plumule emergence is critical. It is mainly due to elongation of the cells in the embryo axis (hypocotyl).

The moisture content of the 12-day-old seedlings is seven times the dry weight. Seedling growth was monitored weekly during the rainy season 1976–1977. Root nodules appeared a week after emergence. At the end of 13 weeks seedling biomass averaged 161 mg dry weight.

The species is palatable to grazing animals. Flowers and developing seeds provide food for a number of the insect fauna. Ants collect shed seeds from the soil surface.

Oreoleysera and Antithrixia, new and old South African genera of the Compositae

Kåre Bremer

Bremer, K. 1978 12 15: Oreoleysera and Antithrixia, new and old South African genera of the Compositae. *Bot. Notiser 131:* 449–453. Stockholm. ISSN 0006-8195.

Oreoleysera Bremer, a new monotypic genus, is described. It is based on *Leysera montana* Bolus and the new combination *Oreoleysera montana* (Bolus) Bremer is made. *Antithrixia* DC. with the only species *A. flavicoma* DC. is discussed and presented. Both genera belong to the Compositae-Inuleae-Athrixiinae.

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Recently I revised the genus *Leysera* and the plant known as *L. montana* was excluded (Bremer 1978). It is here described as a new monotypic genus, *Oreoleysera*. The related monotypic genus *Antithrixia* is little known and it is here presented in some detail. *Oreoleysera* is confined to the mountains of the southwestern Cape and *Antithrixia* occurs in Namaqualand (Fig. 1). Both genera belong to the Compositae-Inuleae-Athrixiinae. They are illustrated in Figs. 2 and 3, respectively.

I have examined material from a number of herbaria, listed under the distribution of each genus and abbreviated according to Holmgren & Keuken (1974). A complete list of examined specimens is kept at the Museum of Natural History, Section for Botany, Stockholm.

Generic delimitation

The circumscription of genera as well as that of other supraspecific categories is partly natural, partly artificial. In a phylogenetic system it is natural so far that the group must be monophyletic, i.e. its members must be descended from a common ancestor and it must include all the descendants of that ancestor. The size of the group circumscribed as e.g. a genus, or in other words the taxonomist's choice between one genus or a number of smaller genera, is artificial, however. Most of the genera recognized today were defined in the nineteenth century, when the demand for monophyly was not recognized or when the criteria for establishing monophyletic taxa were still inadequate. Monophyletic as well as non-monophyletic (paraphyletic or polyphyletic) genera were established. Non-monophyletic genera must always be abandoned, since they do not represent natural groups. It may be preferable to split also monophyletic genera, however, if their circumscription, i.e. their artificially chosen size, is too wide for a practicable definition to be made.

The monophyletic genus *Leysera* is defined by its derived (apomorphous) pappus features; the disc-floret pappus consists of scales and a few bristles and the ray-floret pappus consists of scales only. In the new genus *Oreoleysera* the pappus consists of several bristles and no scales, a comparatively primitive (plesiomorphous) condition. Thus *O. montana* (=*Leysera montana*), lacking the derived pappus features (a synapomorphy) of true *Leysera* species, had to be excluded from *Leysera* (Bremer 1978 p. 371); if not, *Leysera* cannot convincingly be demonstrated as monophyletic. *O. montana* has solitary capitula on long peduncles, a derived feature shared with the *Leysera* species, but retaining *O. montana* within *Leysera* because of this single alleged synapomorphy would make a practicable definition of the genus difficult; the pappus fea-

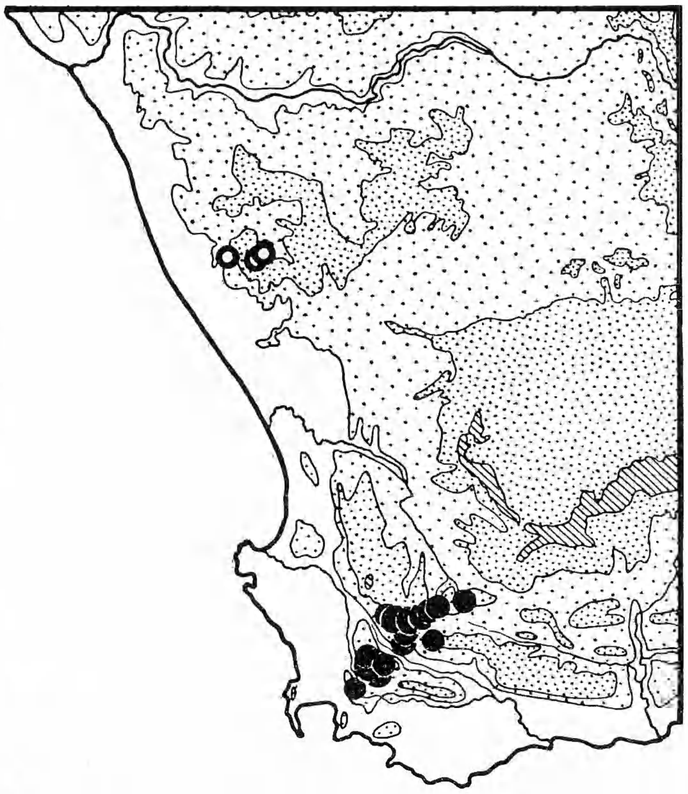

Fig. 1. Known distribution of *Oreoleysera montana* (●) and *Antithrixia flavicoma* (○).

tures, which define related genera, could not be used.

Oreoleysera is monophyletic as a monotypic genus and it is defined by the specialized montane habit and the pedunculate capitula, two derived (apomorphous) features.

Bolus (1905), who described *Leysera montana* (=*O. montana*), erroneously interpreted the pappus as consisting of both scales and bristles. There are no scales, however, although a few bristles might be rather short, but they are not flat like the true scales of the *Leysera* species.

Both *Oreoleysera* and *Leysera* belong to the *Athrixia* group (Merxmüller et al. 1977 p. 597) of the Inuleae-Athrixiinae. Within this group *Relhania, Rosenia,* and *Antithrixia* are genera related to *Oreoleysera* and *Leysera* Bremer 1976 a p. 9). *Relhania* and *Rosenia* were recently revised (Bremer 1976 a, 1976 b) and the delimitations of these genera are discussed in the revisions. *Antithrixia* was described by De Candolle (1838) with one species only, *A. flavicoma*. As a monotypic genus it is monophyletic, but it has no obvious derived (apomorphous) features. The pappus consists of many bristles and no scales, the primitive (plesiomorphous) condition shown also by *Oreoleysera* within this group of genera. *Antithrixia* and *Oreoleysera* can of course not be united on account of this symplesiomorphy in pappus structure, since it cannot indicate a monophyletic group.

Two Ethiopian species have erroneously been referred to *Antithrixia*. These two species, *A. abyssinica* (Sch. Bip.) Vatke and *A. angustifolia* Oliv. & Hiern have recently been transferred to *Macowania* (Burtt & Grau 1972).

Oreoleysera Bremer, gen. nov.

Typus: *O. montana* (Bolus) Bremer.

Fruticulus compactus caulibus brevibus, robustis, dense foliosis. *Folia* integra, costata, oblanceolata–anguste spathulata, dense cano-tomentosa glandulosaque. *Capitula* heterogama, solitaria in pedunculis longis et glandulosis. *Involucrum* campanulatum. Bracteae involucri pluriseriatae, imbricatae, glabrae; interiores apice scariosae patentesque. *Receptaculum* epaleaceum. *Flores radii* feminei, fertiles, ligulati. Lamina flava, apice triloba. Stylus bifidus; rami styli lineares, obtusi–rotundati. Achaenia ut in floribus disci. *Flores disci* multi, perfecti. Corolla flava, quinqueloba. Antherae lineares, basi caudatae; caudae steriles, subulatae. Stylus bifidus; rami styli anguste oblongi, apice penicillati, rotundati–truncati; areae stigmaticae in vittis duabus distinctis. *Achaenia* teretia, pilosa. Pappus setis multis, barbellatis, distinctis vel basaliter parum connatis, indistincte uniseriatis.

Oreoleysera montana (Bolus) Bremer, comb. nov.

Basionym: *Leysera montana* Bolus 1905 p. 138 – Holotype: Bolus 6367 (BOL).

A low, compact, densely branched shrublet with short, robust, densely leafy stems, basally clothed with dry leaf-bases. *Leaves* crowded on the branches, entire, flat or somewhat concave, mid-ribbed, oblanceolate–narrowly spatulate, 7–20 × 1–4 mm, densely greyish-tomentose and glandular, obtuse. *Capitula* heterogamous, solitary on 10–75 mm long, glandular peduncles. *Involucre* campanulate, 10–16 mm wide. Involucral bracts 40–75, in several rows, imbricated, entire, glabrous, yellowish brown, acute; outer small and ovate; inner gradually longer and narrowly elliptic-oblong, apically scarious and spreading, 7–11 × 0.8–2.5 mm. *Receptacle* epaleate, flat–convex. *Ray-florets* 12–25, female, fertile. Tube cylindrical, glabrous or with a few hairs similar to those of the disc-florets. Lamina elliptic-oblong, 5–9 × 1.2–3 mm, yellow, 4-veined, apically 3-lobed. Style terete, bifid;

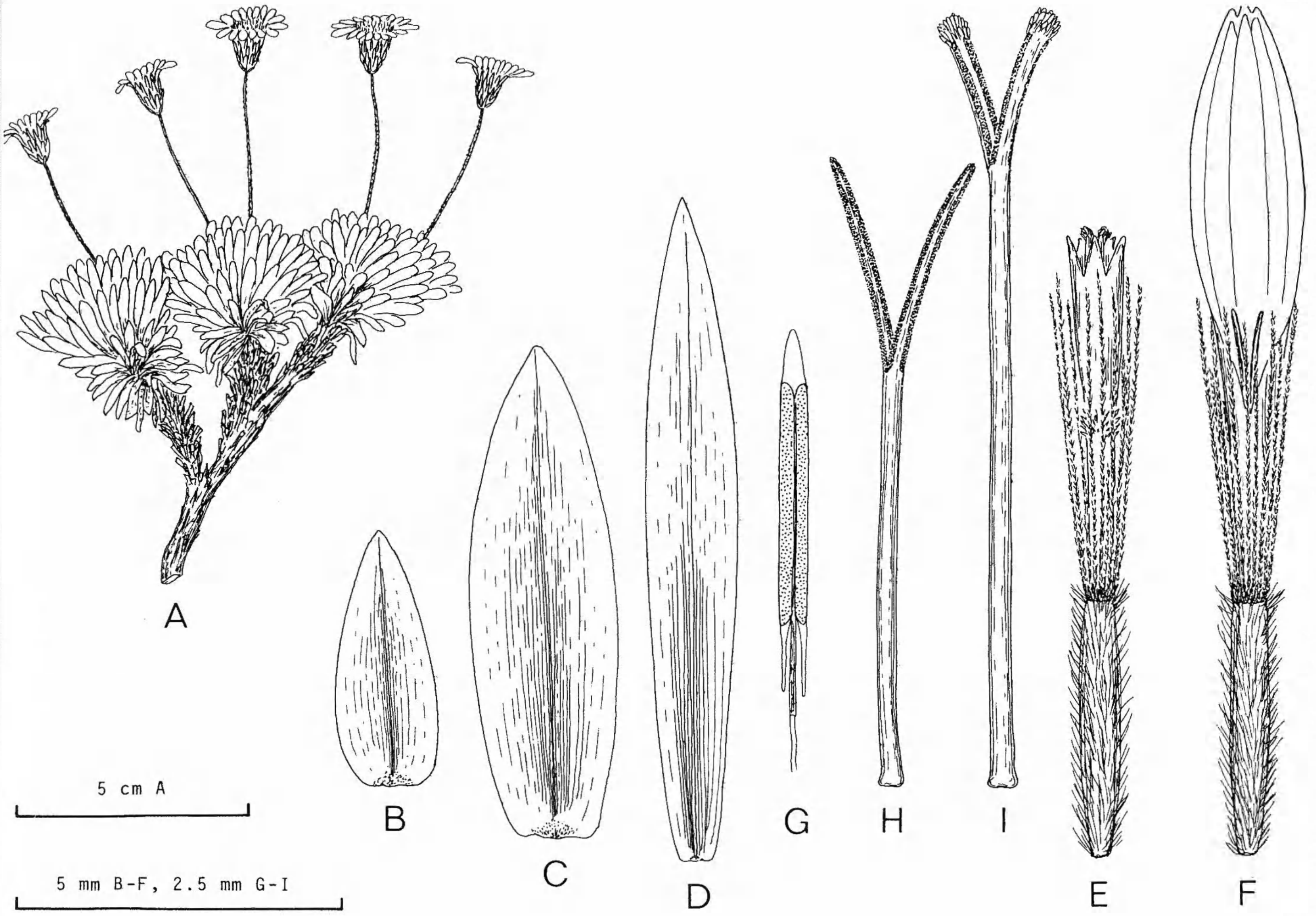

Fig. 2. *Oreoleysera montana*. – A: Habit. – B–D: Involucral bracts. – E: Disc-floret. – F: Ray-floret. – G: Stamen. – H: Style of ray-floret. – I: Style of disc-floret. – A–I: Esterhuysen 9874 (BOL).

style-branches linear, obtuse–rounded, 1/4–1/2 of the style length. Achenes as in disc-florets. *Disc-florets* 40–125, perfect. Corolla indistinctly divided into a lower cylindrical tube and an upper cyathiform limb, 4.5–6.7 mm long, with a collar of slender, multicellular hairs (probably reduced glands) just below the limb, yellow, 5-lobed; corolla lobes narrowly ovate-triangular. Anthers linear, with a sterile, flat, obtuse–rounded apical appendage and sterile, subulate tails, 1/6–1/4 of the anther length. Style terete, bifid, slightly longer than corolla; style-branches semiterete, narrowly oblong, apically penicillate, rounded–truncate; stigmatic areas in two discrete lines. *Achenes* terete, narrowly elliptic-oblong in outline, 3.5–5.4 mm long, densely covered with slender, tricellular hairs (twin hairs with two parallel, elongated cells and a basal, lateral cell). Pappus of several, free or basally somewhat connate, barbellate bristles in one indistinct row.

Flowering period November–January.

Distribution (Fig. 1). *O. montana* grows in rock crevices above 1000 m in the mountains of the southwestern Cape. Most of the collections are from Hex River Mts (Matroosberg, Milner Peak, Buffelshoek Peak, Buffels Dome, Mt Brodie, Shale Peaks, Brandwacht Peak, and Waaihoek Mtn) in Worcester Division, where it is also known from Keeromsberg and Du Toits Peak. In Paarl Division it has been collected at Seven Sisters Mtn, Wellington Sneeuwkop, and Wemmershoek Mts (April Peak) and in Stellenbosch Division it is known from Jonkershoek Ridge Peaks. Esterhuysen made 20 of the 23 collections, all housed at the Bolus Herbarium (BOL) except for one collection, which is at Kirstenbosch (SAM).

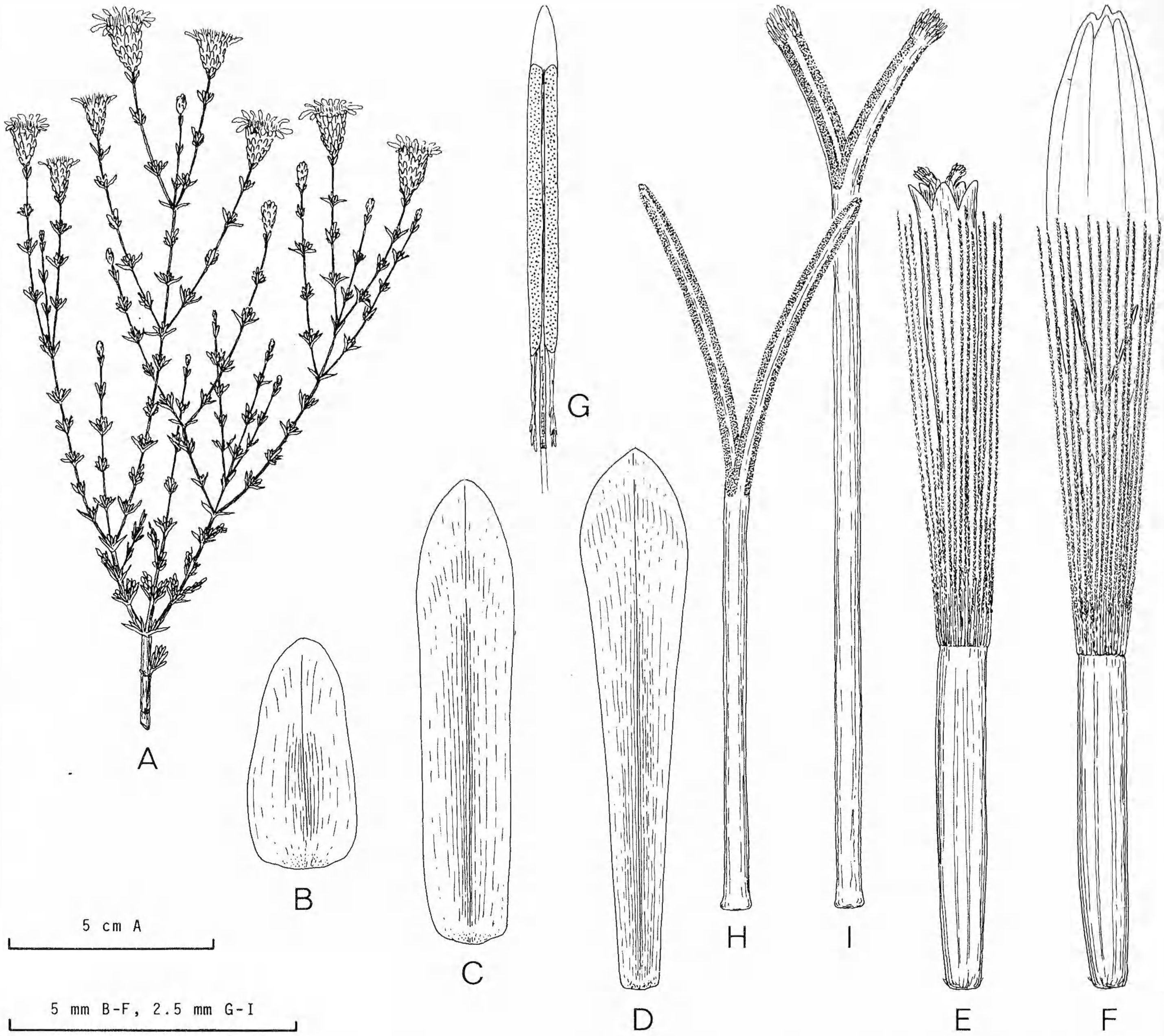

Fig. 3. *Antithrixia flavicoma*. – A: Portion of plant. – B–D: Involucral bracts. – E: Disc-floret. – F: Ray-floret. – G: Stamen. – H: Style of ray-floret. – I: Style of disc-floret. – A–I: Bremer 401 (S).

Antithrixia DC.

De Candolle 1838 p. 277 – Type species: *A. flavicoma* DC.

A moderately branched shrub. *Leaves* decussate and crowded on lateral brachyblasts, entire, mid-ribbed, linear, dorsally glabrous or laxly tomentose, ventrally furrowed and tomentose. *Capitula* heterogamous, solitary, almost sessile, terminal. *Involucre* cyathiform–campanulate. Involucral bracts in several rows, imbricated, glabrous; inner with a scarious and somewhat bulging apical limb. *Receptacle* epaleate. *Ray-florets* female, fertile, ligulate. Lamina yellow, apically 3-lobed. Style bifid; style-branches linear, obtuse. Achenes as in disc-florets. *Disc-florets* perfect. Corolla yellow, 5-lobed. Anthers linear, basally caudate; tails sterile, subulate, slightly branched. Style bifid; style-branches narrowly oblong, apically penicillate, truncate; stigmatic areas in two discrete lines. *Achenes* terete, glabrous or with a few basal hairs. Pappus of many, free or basally somewhat connate, barbellate bristles in c. 2 indistinct rows.

Antithrixia flavicoma DC.

De Candolle 1838 p. 278 – Lectotype: Drège (G-DC, seen in microfiche only).

A moderately branched, up to c. 0.5 m high shrub with ascending–erect, brown–greyish, puberulous stems. *Leaves* decussate and semiamplexicaul, mostly crowded on lateral brachyblasts, entire, almost triquetrous with projecting mid-rib dorsally, linear, 2–9 × 0.4–1.5 mm, dorsally glabrous or laxly tomentose and sometimes with a few conical glands, ventrally furrowed and tomentose, greyish green, acute–obtuse and somewhat mucronate. *Capitula* heterogamous, solitary, almost sessile and terminal on the upper stems. *Involucre* cyathiform–campanulate, 7–11 mm wide. Involucral bracts 25–60, in several rows, imbricated, entire, glabrous, yellowish brown, obtuse–rounded; outer small and ovate; inner gradually longer and oblong–somewhat spatulate with a scarious and somewhat bulging apical limb, 11–14 × 1–3.5 mm. *Receptacle* epaleate, flat–convex. *Ray-florets* 7–18, female, fertile. Tube cylindrical, glabrous. Lamina elliptic-oblong, 6–10 × 1.3–2 mm, yellow and sometimes dorsally brownish purple, 4-veined, apically 3-lobed. Style terete, bifid; style-branches linear, obtuse, 1/3–1/2 of the style length. Achenes as in disc-florets. *Disc-florets* 12–35, perfect. Corolla indistinctly divided into a lower cylindrical tube and an upper narrowly cyathiform limb, 6.5–9.5 mm long, glabrous, yellow, 5-lobed; corolla lobes ovate–triangular. Anthers linear, with a sterile, flat, obtuse–rounded apical appendage and sterile, subulate, slightly branched tails, 1/5–1/3 of the anther length. Style terete, bifid, slightly longer than corolla; style-branches semiterete, narrowly oblong, apically penicillate, truncate; stigmatic areas in two discrete lines. *Achenes* terete, narrowly oblong in outline, 5–8 mm long, smooth or somewhat ribbed, glabrous or with a few, basal, tricellular hairs (twin hairs). Pappus of many, free or basally somewhat connate, barbellate bristles in c. 2 indistinct rows.

Flowering period October–November.

Distribution (Fig. 1). *A. flavicoma* is a karoo shrub, confined to the Kamiesberg region in Namaqualand. The original collection was made by Drège between Pedroskloof and Leliefontein (specimens at BM, G, G-DC, L, MO, S, and W). Subsequently it has been collected twice only, by Acocks at Grootvlei west of Kamieskroon (Acocks 19587 at M and PRE) and by myself midway between Bovlei and Draaiklip (Bremer 401 at S).

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Cyphia (Lobeliaceae) in tropical Africa

Mats Thulin

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The tropical African species of the genus *Cyphia* Berg. (Lobeliaceae) are revised. Sixteen species are recognized, four of which, *C. brevifolia* Thulin, *C. nyikensis* Thulin, *C. decora* Thulin and *C. brachyandra* Thulin are described for the first time. Typification, synonymy, notes on distribution and habitat, maps and keys are provided for all taxa. The isolated taxonomic position of this entirely African genus in the Campanulaceae–Lobeliaceae alliance is emphasized.

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The genus *Cyphia* Berg. is confined to southern and tropical Africa. There are some 60 species in all, the majority in South Africa, and a decreasing number towards the north and west. Ethiopia, in the northernmost part of the range, has two species and West Africa none. The principal aim of this revision of the tropical African members of the genus is to provide the necessary background information for its treatment in Flora Zambesiaca, Flora of Tropical East Africa and Flore d'Afrique Centrale.

The study is based on herbarium material and the following herbaria have been consulted, either by material obtained on loan or by personal visits: B, BM, BR, BRLU, COI, EA, FI, G, K, LD (in part), LISC, LISU, PRE, S, SRGH, UPS, W. Under the heading Additional collections a list is given for each species of all collections examined which have previously not been cited in any of the works given in the literature references for the species. For the more common species this is done in a very abbreviated form if the collections are not of particular importance.

Taxonomic position

Cyphia is a very distinct genus in the Campanulaceae–Lobeliaceae alliance and was given family rank, as Cyphiaceae, by de Candolle (1839 a, b). Walpers (1852) placed it along with the small American genera *Cyphocarpus* Miers (Chile) and *Nemacladus* Nutt. (mainly California) in a subfamily of Lobeliaceae. Schönland (1889), essentially following Bentham & Hooker (1876), treated these three genera plus *Parishella* A. Gray (California) as a subfamily, Cyphioideae, placed between Campanuloideae and Lobelioideae in his widely circumscribed Campanulaceae. This system was followed by Wimmer (1968), but at that time also *Pseudonemacladus* Mc Vaugh (Mexico) had been added. These four American genera thus included in Cyphioideae are all very different from *Cyphia* and some of them are also very different inter se and the subfamily is obviously a very heterogeneous group. Consequently, both *Nemacladus* and *Cyphocarpus* have been considered families of their own (Nuttall 1843 and Miers 1848 respectively). The heterogeneity of Cyphioideae is also well illustrated by the profound differences in pollen morphology present between some of the genera (Dunbar 1975).

Cyphia is particularly characterized by its style which has no free stigma, but instead a stigmatic cavity filled with a slimy fluid and communicating with the air by a small lateral aperture. At the mouth of the aperture there is a drop of this slimy substance, to which the pollen grains may stick and within which they germina-

Fig. 1. Pollen grain of *Cyphia decora* (SEM), × c. 1450. From Jackson 2167 (SRGH).

te. Often the pollen grains are even drawn into the stigmatic cavity, probably by occasional contraction of the slime. For more detailed descriptions of the style of *Cyphia* see Schönland (1890) and Marloth (1932), who both made observations on South African members of the genus. Marloth (1932 p. 212) remarks about *C. volubilis* (Burm. f.) Willd. that it is visited by smaller kinds of hawk-moths, but the pollination mechanism has not been studied in detail. The curious smooth pollen grains in the genus (Fig. 1) should also be considered in this context. They were described and depicted as prolate by Dunbar (1975), but in several species checked by me the grains were constantly found to be more or less spheroidal.

The stylar structure of *Cyphia* has often been compared with, or considered homologous to, the pollen-cup (indusium) of Goodeniaceae and a close affinity to this family has often been implied. Several early authors also included *Cyphia* in Goodeniaceae. Recently Goodeniaceae has been found to contain iridoids, in contrast to the rest of Campanulales (Jensen, Nielsen & Dahlgren 1975), and the family was subsequently removed from this order. *Cyphia* does not contain iridoids (Dahlgren in litt.). Laticiferous vessels are present in the genus (Schönland 1890) and the roots contain inulin (Marloth 1932).

For the present I find it most convenient to regard *Cyphia* with its zygomorphic flowers, racemose inflorescences and colporate pollen grains as a marginal member of Lobeliaceae. The differences from subfamily Lobelioideae, however, are considerable. So, for example, apart from the stylar difference, the anthers are free, the pollen grains are almost completely smooth, and the root ends in a usually subglobose tuber (Fig. 3). Certainly a much better rounding-off of Lobeliaceae is obtained if *Cyphia* is treated as a monogeneric family as proposed by de Candolle, but such an action should not be taken without considering also the American genera mentioned above.

Historical outline

The genus *Cyphia* was proposed by Bergius (1767) to accommodate the South African *Lobelia bulbosa* L., one of the two Linnaean *Lobelias* now referred to it. The second, *L. phyteuma* L., was transferred to *Cyphia* by Willdenow (1798) along with four other *Lobelias*, all from the Cape. During the first half of the 19th century several additional species from South Africa were described, e.g. by Ecklon & Zeyher and Presl. Presl (1837, 1838) also distinguished the three subgenera *Cyphia ("Eucyphia"), Isomeria* and *Cyphiella,* although in 1837 without indicating their rank. Sonder (1865) made a summing up of the genus for South Africa with 20 species. The first species to be described from outside South Africa was *C. stheno* Webb (1849) from Angola (hitherto the type has been believed to be from the Cape Verde Islands, see under the species) followed in 1851 by *C. glandulifera* Hochst. ex A. Rich. from Ethiopia. This was the only species in the genus recorded in Flora of Tropical Africa (Hemsley 1877). In the 1890's *C. lasiandra* Diels and *C. lobelioides* Welw. ex Hiern were described from Angola, and *C. nyasica* Bak. from Malawi. A further 10 species from tropical Africa were added by various authors during the first half of this century. Phillips (1917) revised the South African members of the genus (25 species) and in 1968 Wimmer's treatment of the whole genus appeared in Pflanzenreich. Eighty species were recognized, 25 of which occurring in tropical Africa. Numerous species and infraspecific taxa were described by Wimmer, but unfortunately many of his names are invalid as

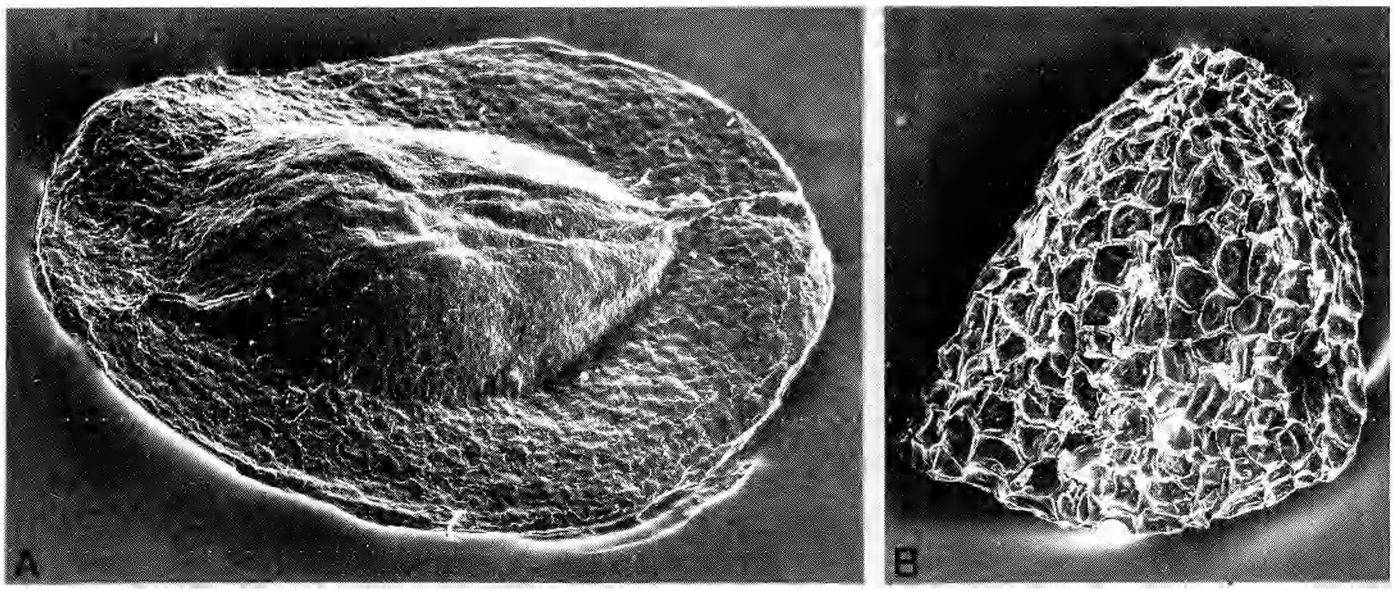

Fig. 2. Seeds (SEM). – A: *Cyphia reducta*. Broadly winged, not reticulate. From Loveridge 1357 (SRGH). – B: *C. brachyandra*. Unwinged, coarsely reticulate. From Pawek 3423 (K). Both × c. 40.

he often failed to designate types properly. Wimmer recognized Presl's groups *Cyphia* and *Cyphiella* as sections and also made a further subdivision, describing five subsections and three series, the names of which are all invalidly published.

Infrageneric subdivision

The present work indicates that Wimmer's (1968) subdivision of the genus (see also under Historical outline) in many cases is unnatural. Several times I found it necessary to unite ''species'' which had been placed by Wimmer in different subsections. This regional revision, however, does not provide a sufficient background for an infrageneric rearrangement to be made, but a few notes may be given.

Wimmer's two sections, *Cyphiella* with a tubular corolla and *Cyphia* with the corolla split to the base into two lips are usually easily distinguished, although *C. mazoensis* S. Moore is a somewhat intermediate case. Normally the corolla is tubular in this species, but sometimes it is split more or less to the base. In this account I have followed Wimmer and placed the species with a tubular corolla first, although I sometimes find this sequence disputable (see under *C. stenopetala*).

The characters used by Wimmer for his subdivision into subsections and series are: stem erect or twining, leaves crowded at the base or spread out on the stem, leaf shape, stamens short or long compared to the length of the corolla and anthers glabrous or hairy on the back. All these characters vary considerably in the genus, also within single species. Other, potentially more useful characters in this context are presence or absence of a wing around the seeds (Fig. 2 A, B) and connate or free filaments. Winged seeds and connate filaments seem to be correlated in the tropical African species, but too little is known about the South African ones for any conclusions to be made. A major problem is that seeds are not known in many of the species. There seems to be a comparatively long interval between flowering and fruiting in the genus (already observed by de Candolle 1839 b p. 153) and when in fruit the plants apparently are too inconspicuous to be regularly collected.

Key to the species

1. Corolla tubular with a 5-lobed limb 2
– Corolla split to the base into 2 lips, the upper lip 3-lobed and the lower lip consisting of 2 free petals 6
2. Leaves up to 25 × 1.5 mm, erect; plants erect or almost so 3
– Leaves larger, spreading; plants erect or twining 4
3. Inflorescence rhachis shortly crisped pubescent; leaves at least up to 10 mm long; petals 8–10 mm long, densely pubescent on the inside in their entire length .... 1. *C. stheno*
– Inflorescence rhachis glabrous; leaves less than 4 mm long; petals 5–6 mm long, pubescent on the inside in the lower half only .... 2. *C. brevifolia*
4. Plant erect; raceme short, dense, long-pedunculate; corolla c. 8 mm long .... 3. *C. nyikensis*
– Plant twining to suberect; raceme long, ± lax; corolla 8–21 mm long 5
5. Corolla glabrous outside; inflorescence rhachis practically glabrous; seeds not winged, irregularly angular, 0.8–1 mm long .... 4. *C. stenopetala*
– Corolla crisped pubescent outside; inflorescence rhachis crisped pubescent at least towards the apex; seeds broadly winged, flat, c. 2.4–3.2 mm long .... 5. *C. mazoensis*
6. Plant twining; corolla 3.5–4 mm long .... 8. *C. reducta*
– Plant erect or twining; corolla at least 5 mm long 7
7. Hairs on the back of the connectives up to c. 0.1–0.3 mm long or absent; filaments free to the base; seeds broadly winged, flat 8
– Hairs on the back of the connectives up to c. 0.8–1.5 mm long; filaments ± connate at the base; seeds (not known in *C. richardsiae, C. ubenensis, C. rupestris*) not or scarcely winged, coarsely reticulate 12
8. Anthers glabrous on the back of the connective, penicillate at the tip; plant erect or somewhat twining; leaves ± in a rosette at the base; inflorescence rhachis glabrous; corolla glabrous outside .... 9. *C. glandulifera*
– Anthers ± pubescent on the back of the connectives, or, if occasionally glabrous, other characters not as above 9
9. Stem twining; inflorescence rhachis glabrous; corolla glabrous outside .... 10. *C. eritreana*
– Stem erect or twining, if twining inflorescence rhachis and outside of corolla pubescent 10
10. Stems usually several from the base, ± erect; inflorescence rhachis practically glabrous; corolla 6.5–7.5 mm long, papillose mainly along the sutures outside .... 7. *C. decora*
– Stem single, erect or twining; inflorescence rhachis crisped pubescent at least towards the apex; corolla short pubescent outside 11
11. Plant ± erect; corolla 5–6.5 mm long .... 6. *C. alba*
– Plant ± twining; corolla 8–18 mm long .... 5. *C. mazoensis*
12. Stamens 2.5–3.2 mm long; upper petals not or scarcely saccate at the base 13
– Stamens 4–8 mm long; upper petals usually markedly saccate at the base 14
13. Plant erect or somewhat twisting, 20–50 cm; inflorescence fairly dense, up to c. 15 cm .... 11. *C. richardsiae*
– Plant twining, usually much longer; inflorescence lax, up to 100 cm .... 13. *C. brachyandra*
14. Petals densely pubescent on the inside near the tip; leaves linear .... 12. *C. ubenensis*
– Petals glabrous or almost so on the inside near the tip; leaves various 15
15. Plant erect; hairs on the back of the connectives less than 1 mm long; anthers not apically connate .... 14. *C. rupestris*
– Plant erect or twining, if erect the other characters not as above 16
16. Plant usually erect; inflorescence dense to rather lax with a sulcate rhachis; anthers with a tuft of c. 0.5 mm long hairs at the tip by which the anthers are firmly united apically, at least in young flowers .... 15. *C. erecta*
– Plant usually twining; inflorescence usually very lax with a ribbed rhachis; anthers with a tuft of 0.2–0.5 mm long hairs at the tip, not or very loosely united apically .. 16. *C. lasiandra*

1. C. stheno Webb

Webb 1849 p. 148; Schmidt 1852 p. 207; Chevalier 1935 p. 888; Wimmer 1968 p. 937, Fig. 38 A. – Orig. coll.: Angola (see under Distribution and habitat), unknown collector, probably da Silva (P holotype, not seen).

C. lobelioides Welw. ex Hiern 1898 p. 628. – Orig. coll.: Angola, Huila, between Lopollo and Morro de Quilengues, Welwitsch 1135 (BM holotype, BR, COI, G, K, LISU).

Distribution and habitat. The country of origin of the type specimen of *C. stheno* is not indicated on the sheet (see below) but was said to be the Cape Verde Islands by Webb at the original description of the species. Considering the general distribution of the genus this is a very unlikely locality and the plant was mentioned by Chevalier (1935 p. 813) as one of the phytogeographically most remarkable members of the flora of these islands. From the preface of Webb's paper (Webb 1849 p. 93) it is evident that the type specimen is part of a Portuguese collection which was taken as a war-trophy from Lisbon to Paris in 1808 by M. G. St. Hilaire and which ''was accompanied by no written document by which the native country of the plants could be ascertained''. This collection is now attributed to the Portuguese J. da Silva Fejó, who collected on the Cape Verde Islands in 1784–87 (Chevalier 1935 p. 888, Barbosa 1962 p. 84). Wimmer (1968) correctly placed the Angolan *C. lobelioides* as a synonym of *C. stheno* but did not question the Cape Verde Islands as the origin of the type of the latter name, although the species has never been recollected there. As all subsequent material of *C. stheno* has been collected in the highlands of Angola it seems reasonable to suppose that this is the area of origin also for the type specimen and that this specimen somehow came to be among Fejó's collection on its removal from Lisbon. The true collector was then most probably J. J. da Silva, another important early Portuguese collector, who collected in Angola in the 1780's, and whose collection was also brought from Lisbon to Paris during the Napoleonic war in 1808. According to Mendonça (1962 p. 113), da Silva collected precisely in the highland areas of Angola where *C. stheno* is known to occur today. Fig. 7 A.

C. stheno seems always to grow in more or less swampy ground, such as damp wooded meadows and depressions in grasslands; alt. 1400–1500 m.

Additional collections. Angola. Benguela, Cuiva R.–Catumbela R., Babaéra, XII.1932, Gossweiler 9683 (BM). Huila, Huila, 31.I.1956, Mendes 1509 (LISC); 7.9 km on the Sá da Bandeira–Chibia road, 30.XII.1969 Mendonça 151 (LISC, SRGH); Cunene, 54 km on the Cuvelai–Bambi road, 16.II.1973, Menezes, Barroso & Sousa 4667 (SRGH). Bié, Ganguelas, Vila Artur de Paiva, 27.XII.1959, Mendes 1814 (LISC); Menongue, Vila Serpa Pinto, 15.II.1960, Mendes 2625 (LISC).

2. C. brevifolia Thulin, sp. nov. – Fig. 3

Orig. coll.: Angola, Bié, Andulo, Catetula, 9.XI.1965, Teixeira et al. 9305 (COI holotype, LISC).

Species nova, *C. sthenonis* Webb affinis, a qua inflorescentia glabra, foliis tantum 2–4 mm longis, et floribus minoribus corolla 5–6 mm longa et intus sursum glabra differt.

Erect or somewhat twining herb, up to c. 40 cm, from a subglobose root-tuber c. 1–1.5 cm in diameter. *Stem* not or sparsely branched, ribbed, glabrous in its entire length. *Leaves* scale-like, few, erect, widely scattered on the stem, 2–4 × 0.6 mm, linear, acute at the apex, denticulate, glabrous. *Raceme* moderately dense, up to 10 cm; pedicels up to 2.5(–4.8) mm, glabrous; bracts linear-lanceolate, up to 2.8 mm; bracteoles linear, c. 1 mm. *Hypanthium* broadly obconical, 10-nerved, glabrous. *Calyx*-lobes narrowly triangular, erect, up to c. 1 mm, glabrous, usually with a pair of teeth at the margin. *Corolla* 5–6 mm, rose, tubular with 5 subequal lobes c. 2.5 mm long, at least the 2 lower petals with slits along their sutures at the base, glabrous outside, finely pubescent in a zone on the lower half inside. *Stamens* c. 2.4 mm; filaments linear, free, slightly dilated at the base, sparsely pubescent on the inside in the upper part; anthers elliptic-oblong, c. 1.2 mm, pubescent with short hairs on the back of the connective and with a short tuft of hairs at the tip. *Style* c. 2 mm. Capsule and seeds not known.

Distribution and habitat. Only known from the type collection (Fig. 7 A). The habitat of the plant was not recorded, but it was collected at c. 1650 m altitude.

Notes on taxonomy. C. brevifolia is closely related to *C. stheno*. Although known only from a single collection, of which I have seen 4 individuals, I have no doubts about its being a distinct species. The variation within *C. stheno* is now fairly well known and *C. brevifolia* differs clearly

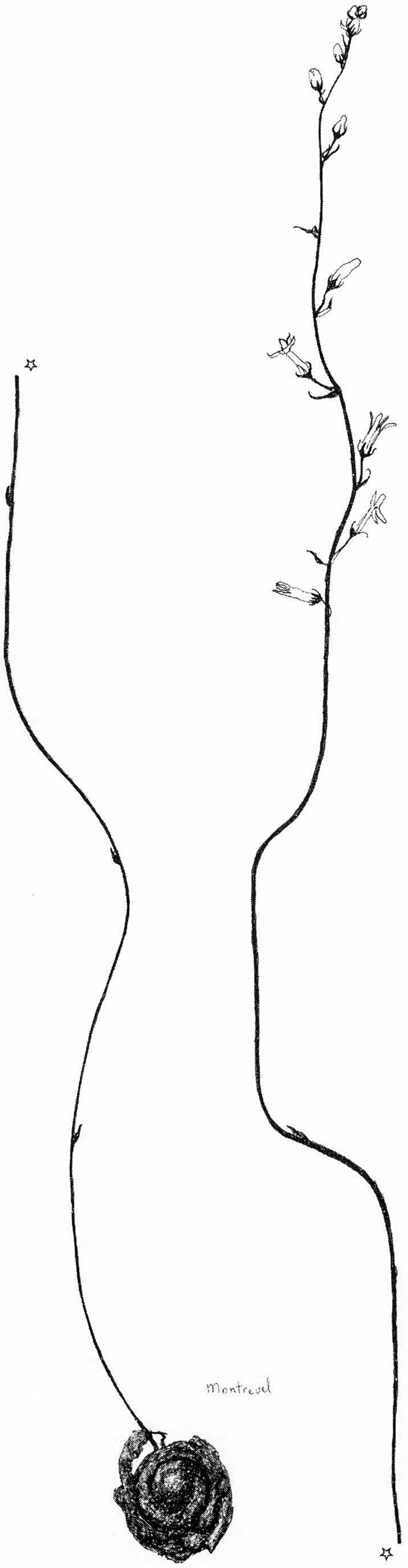

Fig. 3. *Cyphia brevifolia,* × 0.75. From Teixeira et al. 9305 (COI).

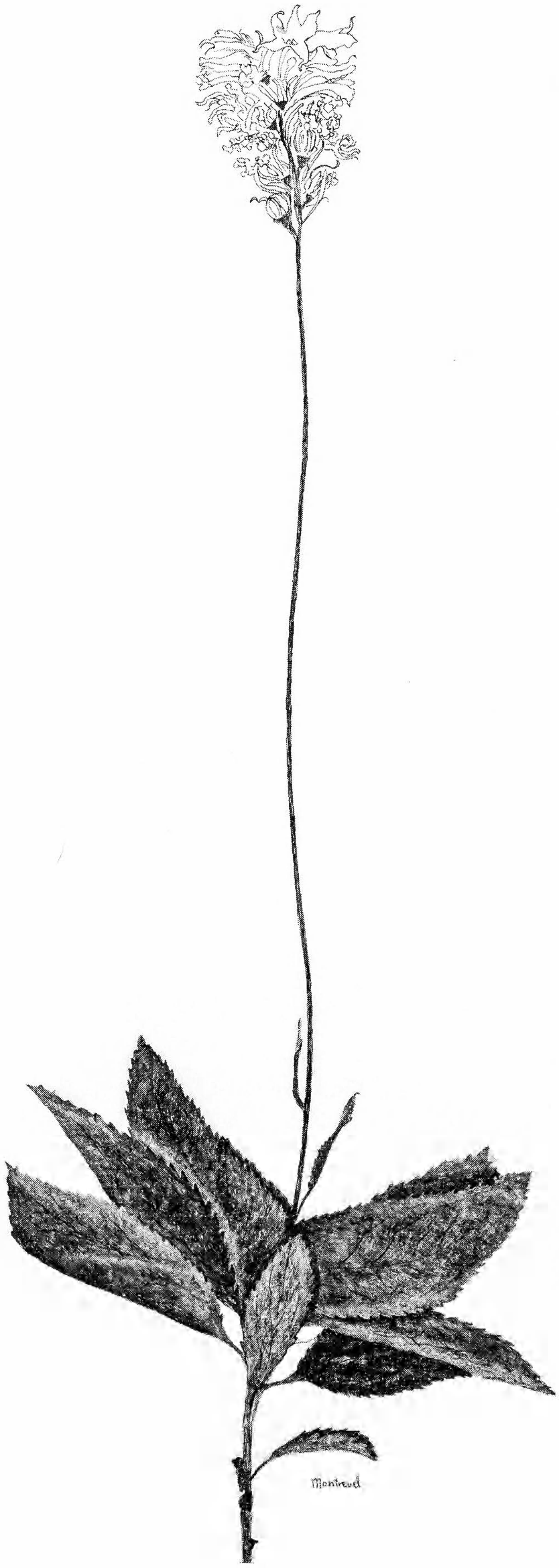

Fig. 4. *Cyphia nyikensis,* × 1. From Robinson 4515 (SRGH).

in several respects: the inflorescence rhachis, pedicels and hypanthia are glabrous (shortly crisped pubescent in *C. stheno*); the leaves are shorter (less than 4 mm versus at least up to 10 mm); the flowers are smaller (corolla 5–6 mm versus 8–10 mm, calyx-lobes c. 1 mm versus c. 1–2 mm) and the petals are finely pubescent on the inside in the lower half only (densely pubescent on the inside in their entire length in *C. stheno*). Furthermore, the apical tuft of hairs on the anthers is shorter in *C. brevifolia* and the anthers are shortly pubescent on the back of the connectives, while in *C. stheno* the anthers are usually glabrous on the back.

Seeds are known neither in *C. brevifolia* nor in *C. stheno*.

3. C. **nyikensis** Thulin, sp. nov. – Fig. 4

Orig. coll.: Malawi, Nyika Plateau, 14.III.1961, Robinson 4515 (SRGH holotype).

Species nova, propter caulem erectum, folia 20–45 × 7–18 mm et basin versus aggregata, inflorescentiam densam longi-pedunculatam, corollam tubulosam circa 8 mm longam, et stamina libera antheris dorsaliter brevi-pubescentibus distinctissima.

Erect herb, 15–23 cm. *Stem* unbranched, ribbed, papillose at the base, shortly pubescent in the inflorescence region, otherwise glabrous. *Leaves* subsessile to shortly petiolate, crowded towards the base of the stem, 20–45 × 7–18 mm, usually with 1–2 smaller leaves further up on the stem, lanceolate to elliptic, acute at the apex, cuneate at the base, glabrous; margin serrate-crenate, slightly revolute; veins prominent beneath, papillose. *Raceme* dense, up to 3 cm, long-pedunculate; pedicels up to 2 mm, shortly pubescent; bracts up to 10 mm, dentate; bracteoles up to 5 mm, lanceolate-acuminate. *Hypanthium* broadly obconical, 10-nerved, shortly pubescent. Calyx-lobes narrowly triangular, erect, 3.2–5.6 mm, glabrous, with 1–2 pairs of teeth at the margin. *Corolla* c. 8 mm, pale pink, tubular with 5 subequal lobes c. 4 mm long, at least the 2 lower petals with slits along their sutures at the base, tube shortly pubescent on the outside and on the inside towards the base, lobes papillose on both sides. *Stamens* c. 3.2 mm; filaments linear, free, slightly dilated at the base, sparsely pubescent; anthers narrowly elliptic-oblong, c. 1.5 mm, shortly pubescent on the back and with a short tuft of hairs at the tip. *Style* c. 1.8 mm. Capsule and seeds not known.

Distribution and habitat. Only known from the type collection (Fig. 7 A). Growing in shallow soil over rock; alt. 2400 m.

Notes on taxonomy. *C. nyikensis* is a very distinct species and it is indeed difficult to tell where its affinities are in the genus. By its almost rosulate leaves and long peduncle it is suggestive of some of the species in Wimmer's subsect. *Scaposae* but these all have a 2-lipped, non-tubular corolla. The holotype consists of 5 individuals.

4. C. **stenopetala** Diels

Diels 1898 p. 112; Wimmer 1968 p. 945, Fig. 42 A. – Orig. coll.: South Africa, Transvaal, Blinkwaater and Hellsgate, between Lydenburg and Spitzkop, II.1888, Wilms 894 (B holotype †, BM lectotype, selected here, G not seen, K).

C. bechuanensis Bremekamp & Obermeÿer 1935 p. 437. – Orig. coll.: Botswana, Metsimaklaba R., near Gaberones, 15.III.1930, van Son in HTM 28788 (PRE holotype, not seen, BM).

C. stenopetala Diels var. *johannesburgensis* Wimmer 1968 p. 946. – Orig. coll.: Transvaal, Johannesburg Distr., Witpoortje Kloof, 12.III.1920, Moss 3561 (J holotype, not seen).

Distribution and habitat. *C. stenopetala* is distributed mainly in Transvaal and NE Cape Province and is included in this account because of the type collection of *C. bechuanensis* from SE Botswana, which is part of the Flora Zambesiaca area. Only a few collections from Transvaal and none from Cape Province have been studied and the map (Fig. 7 A) is mainly based on Wimmer's list of collections (Breyer in Rogers 23992 is *C. rogersii* S. Moore and has been excluded). The species occurs in grassland and rocky places.

Notes on taxonomy. I follow Wimmer and place *C. stenopetala* together with the other species with a tubular corolla, but it may well prove to be more closely related to the ''*C. lasiandra* group'' instead. It agrees with this group mainly by having connate filaments and unwinged, reticulate seeds (see also under Infrageneric subdivision).

5. C. **mazoensis** S. Moore

Moore 1907 p. 46; Wimmer 1968 p. 949, Fig. 42 B. – Orig. coll.: Rhodesia, Mazoe, I.1906, Eyles 231 (BM holotype, SRGH).

C. rivularis Wimmer 1952 p. 145, 1968 p. 942, Fig. 37 A, synon. nov. – Orig. coll.: Rhodesia, Inyanga Distr., Inyangombi R. above Nyamziwa Falls, 18.I.1948, Chase 590 (W holotype, BM, SRGH).

C. mazoensis S. Moore var. *stellaris* Wimmer 1952 p. 144. – Orig. colls.: Rhodesia, Umtali Distr., Stapleford, 17.V.1944, Hopkins in GHS 12477 (W syntype, SRGH); ibid., Cecil Heights Commonage, 22.IV.1950, Chase 2139 (W syntype, BM, LISC, SRGH); Inyanga Distr., Pungwe Valley, 17.VII.1948, Chase 894 (W syntype, BM, LISC, SRGH).

?*C. gamopetala* Duvigneaud & Denaeyer-De Smet 1963 p. 133, synon. nov. – Orig. coll.: Zaire, Katanga, Swambo, 28.XII.1959, Duvigneaud 4806 C (BRLU, not found).

C. subscandens Wimmer 1968 p. 949, Fig. 40 B, nom. invalid. – Orig. coll.: Zambia, Sunzu Mt., 6.I.1950, Bullock 2184 (K, W).

C. mazoensis S. Moore f. *angustior* Wimmer 1968 p. 950, nom. invalid. – Orig. colls.: Rhodesia, Umtali Distr., Banti Forest, 4.XI.1955, Exell, Mendonça & Wild 210 (BM, SRGH); Melsetter Distr., Iona Farm, 15.III.1953, Chase 4860 (SRGH).

C. rogersii S. Moore subsp. *rogersii* sensu Wimmer 1968 p. 947, Fig. 39, pro parte, quoad specim. ex Zambia.

Distribution and habitat. C. mazoensis was only known by Wimmer (1968 p. 950) from Rhodesia and Zambia, but is here also recorded from Malawi and Mozambique. *C. gamopetala,* described from Katanga, most probably belongs to this species too, but the type seems to be lost and no other material from Katanga has been seen. It was said to have glabrous anthers, and in this and other respects its description best matches specimens from N Zambia which Wimmer placed in *C. rogersii*. Fig. 7 B.

Growing usually on rocky ground in woodland and grassland; alt. 850–2100 m.

Notes on taxonomy. C. mazoensis normally has a tubular corolla, but sometimes it is ± split to the base also in young flowers (e.g. Norlindh & Weimarck 4862). Specimens from E Rhodesia with branched inflorescences, where the flowers are 2–5 together in the leaf-axils have been called *C. rivularis* or *C. mazoensis* var. *stellaris*. However, there are too many intermediates for this distinction to be maintained, at least on the specific level.

C. mazoensis is very closely related to *C. rogersii* S. Moore (1918) in Transvaal, which differs mainly by being glabrous on the outside of the corolla and by always being glabrous on the back of the connectives. They might perhaps be treated as subspecies.

Additional collections. Zambia. N Prov., Bock 34 (PRE); Fanshawe 1973 (K); Gamwell 2 (BM); Ricardo 146 (BM); Richards 8412 (K, SRGH), 10695 (SRGH), 12056 (K, SRGH); Robinson 4316 (SRGH). C Prov., Fanshawe 9177 (K, SRGH), 11169 (SRGH); Hamlyn 9 (EA); Noak 98 (SRGH); White 2293 (K). S Prov., White 6826 (K). *Malawi.* C Prov., Kongwe Mt, near Dowa, 18.II.1959, Robson 1655 (K, LISC, SRGH); Dedza Distr., Chiwao Hill, 3.II.1967, Salubeni 544 (LISC, SRGH); ibid., Chongoni Forest, 11.II.1969, Salubeni 1261 (K, SRGH). *Rhodesia.* N Prov., Wild 5784 (SRGH). C Prov., Eyles 3261, 4765 (SRGH); Godman 190 (BM); Mavi 1293 (COI, SRGH); Norlindh & Weimarck 4902 (LD); Wild 5997 (K, LISC, SRGH). E Prov., Bamps et al. 774 (BR, SRGH); Burrows 346 (SRGH); Chase 3680 (BM, SRGH), 6398 (K, SRGH); Ferrar 3938, 3942 (PRE); Norlindh & Weimarck 4681, 4862, 5024 (LD). S Prov., Biegel 3085 (B, K, SRGH); Biegel et al. 4295 (K, LISC, SRGH); Pope 990 (SRGH). *Mozambique.* Manica e Sofala, Martins Falls, 6.II.1958, Hall 390 (SRGH); Chimanimani Mts, near St George's Cave, 12.IV.1967, Grosvenor 394 (K, LISC, SRGH); Gorongosa Mt, Gogogo Summit Area, IV.1972, Tinley 2519 (SRGH).

6. C. **alba** N. E. Br.

Brown 1906 p. 165; Wimmer 1968 p. 973, Fig. 56 A. – Orig. coll.: Rhodesia, Manika, N of Umtali, XII.1899, Cecil 163 (K holotype).

C. alba N. E. Br. f. *purpurea* Wimmer 1968 p. 973. – Orig. coll.: Rhodesia, Inyanga Distr., Mt Inyangani summit ridge, Whellan & Davies 987 (K holotype, SRGH).

Distribution and habitat. C. alba is only known from some mountains in E Rhodesia (Fig. 7 C). In upland grassland; alt. 1700–2450 m.

Additional collections. Rhodesia. E Prov., Bamps et al. 223, 421, 424 (BR); Biegel 4128 (SRGH); Chase 8120 (K, SRGH); Fries, Norlindh & Weimarck 3439, 3460, 3855 (LD); Gilliland 969 (BM, K, SRGH); Goodier 497 (SRGH); Miller 4733 (SRGH); Norlindh & Weimarck 4516, 4965 (LD); Obermeyer 2115 (BM); Vanden Berghen 71 (BR); Wild 4889 (K, SRGH).

7. C. **decora** Thulin, sp. nov. – Figs. 1, 5

Orig. coll.: Malawi, Mt Mlanje, Chambe Plateau, 22.III.1958, Jackson 2167 (K holotype, SRGH).

Species nova *C. albae* N. E. Br. affinis, a qua imprimis caulibus e basi plerumque pluribus, inflorescentia glabra vel papillosa, petalis 6.5–7.5 mm longis, et antheris dorsaliter dense brevi-pubescentibus sed apice plerumque glabris differt.

Erect or ascending, sometimes somewhat twining herb, 7–45 cm, from a root-tuber c. 2 cm thick. *Stems* usually several from the base, ribbed, entirely glabrous or sparsely papillose in the inflorescence region only. *Leaves* sessile or

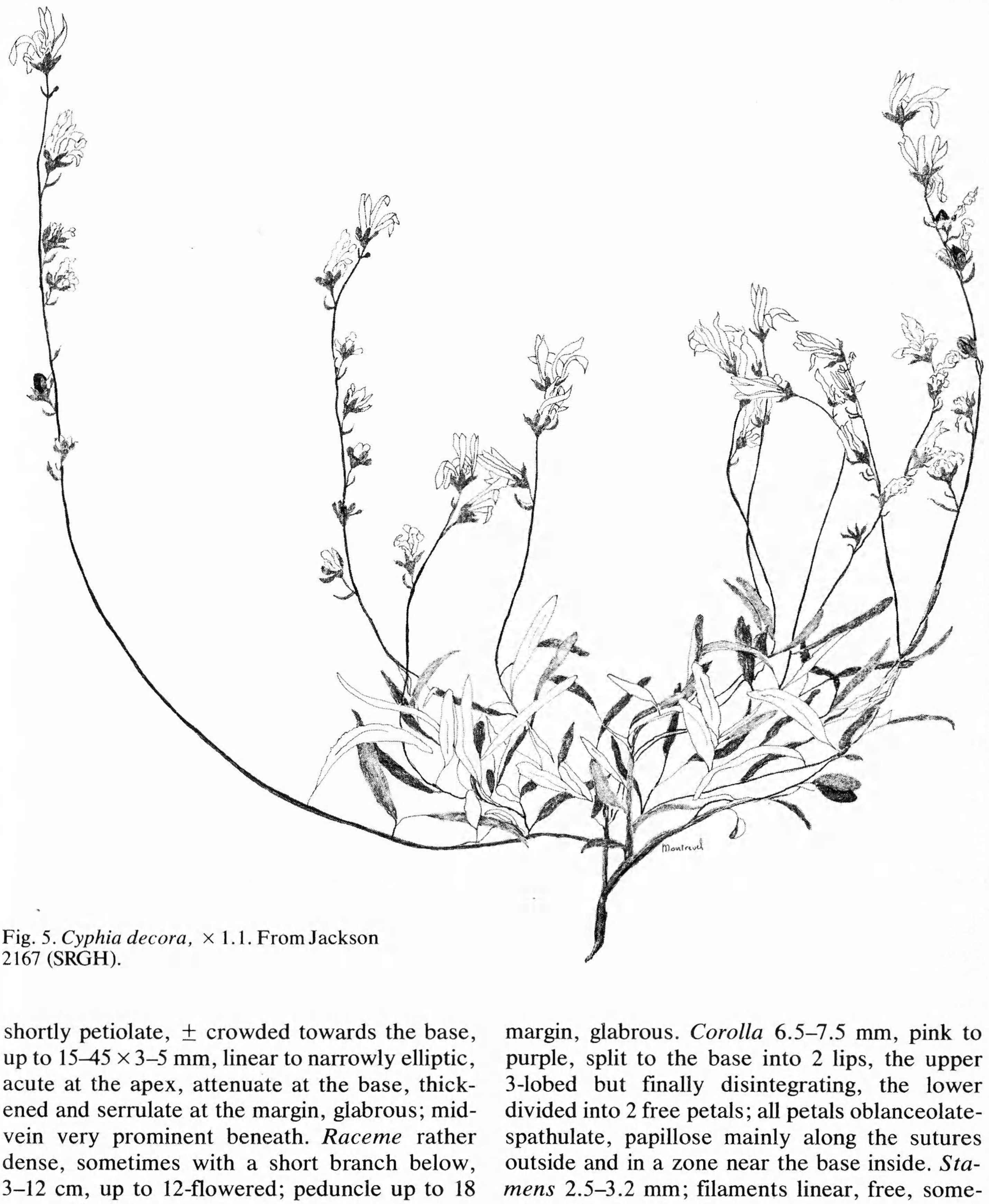

Fig. 5. *Cyphia decora,* × 1.1. From Jackson 2167 (SRGH).

shortly petiolate, ± crowded towards the base, up to 15–45 × 3–5 mm, linear to narrowly elliptic, acute at the apex, attenuate at the base, thickened and serrulate at the margin, glabrous; midvein very prominent beneath. *Raceme* rather dense, sometimes with a short branch below, 3–12 cm, up to 12-flowered; peduncle up to 18 cm; pedicels 1–2.5 mm, papillose to subglabrous; bracts linear-lanceolate, up to 5 mm, often denticulate; bracteoles ±1.5 mm. *Hypanthium* cup-shaped, 10-nerved, sparsely papillose to subglabrous. *Calyx*-lobes narrowly triangular, ± erect, 1.5–2.2 mm, with 1–2 pairs of teeth at the margin, glabrous. *Corolla* 6.5–7.5 mm, pink to purple, split to the base into 2 lips, the upper 3-lobed but finally disintegrating, the lower divided into 2 free petals; all petals oblanceolate-spathulate, papillose mainly along the sutures outside and in a zone near the base inside. *Stamens* 2.5–3.2 mm; filaments linear, free, somewhat dilated at the base, pubescent; anthers elliptic-oblong, 1.2–1.4 mm, densely and shortly pubescent (hairs c. 0.2–0.3 mm) on the back of the connective but usually glabrous at the very tip. *Ovary* semi-inferior; style c. 2 mm. Capsule subglobose, with 10 distinct nerves connected by weak transversal nerves; valves 2–3 mm long, about as long as inferior part of capsule. Seeds ± broadly elliptic in outline, flat, broadly winged, 2–2.4 × 1.2–1.8 mm.

Distribution and habitat. C. decora is endemic on Mt Mlanje in S Malawi (Fig. 7 C). In upland grassland, often in rock cracks; alt. 1820–2150 m.

Notes on taxonomy. C. decora is allied to *C. alba* from which it differs mainly as follows: stems usually several from the base (versus always single), inflorescence rhachis glabrous or sparsely papillose (versus shortly crisped pubescent); pedicels and hypanthia papillose to subglabrous (versus shortly crisped pubescent); petals 6.5–7.5 mm, papillose mainly along the sutures outside (versus 5–6.5 mm, ± densely short pubescent all over on the outside); anthers 1.2–1.4 mm, densely pubescent with hairs c. 0.2–0.3 mm long on the back of the connective but usually glabrous at the very tip (versus 0.9–1.2 mm, usually pubescent with hairs c. 0.1–0.2 mm long on the back of the connective, always so at the tip).

Collections (besides the type). *Malawi.* S Prov., Mt Mlanje, head of Great Ruo Valley, 20.VII.1956, Newman & Whitmore 123 (BM); ibid., without precise locality, 12.II.1958, Chapman 500 (SRGH); ibid., Sombani Plateau, 12.V.1963, Wild 6210 (SRGH); ibid., Chambe basin, 23.I.1967, Hilliard & Burtt 4591 (K, SRGH); ibid., near Sombani hut, 16.VI.1978, Iwarsson s. n. (UPS).

8. C. **reducta** E. Wimm. – Fig. 2 A

Wimmer 1952 p. 144, 1968 p. 1001, Fig. 72 C. – Orig. coll.: Rhodesia, Domboshawa, 16.II.1947, Wild 1662 (W lectotype, selected here, K, SRGH isolectotypes).

Distribution and habitat. Only known from a small area in C Rhodesia (Fig. 7 C). Twining among grasses; alt. 1520–1680 m.

Additional collection. Rhodesia. C Prov., Domboshawa, Ngomakurira, 14.III.1965, Loveridge 1357 (SRGH).

9. C. **glandulifera** Hochst. ex A. Rich.

Richard 1851 p. 8, t. 64; Hemsley 1877 p. 471; Chiovenda 1916 p. 109 as *"C. glandulosa"*; Cufodontis 1965 p. 1056; Wimmer 1968 p. 956, Fig. 48 A; Agnew 1974, p. 513, 514 (fig.). – Orig. coll.: Ethiopia, Chiré, Quartin Dillon & Petit s. n. (P lectotype, selected here, seen in photo only).

C. glandulifera Hochst. ex A. Rich. f. *obovatifolia* Wimmer 1968 p. 956. – Orig. coll.: Kenya, N Frontier Prov., Dandu, 9.V.1952, Gillett 13148 (W holotype, EA, FI, K).

C. glandulifera Hochst. ex A. Rich. f. *subcuspidata* Wimmer 1968 p. 957. – Orig. coll.: Kenya, Thika R., Fort Hall Road, 24.VI.1909, Battiscombe 141 (K holotype).

Distribution and habitat. C. glandulifera was recorded by Wimmer from Ethiopia, Uganda, Kenya, Tanzania and Malawi, but the records for Uganda and Malawi are erroneous and all specimens cited from there are actually from Kenya. I have not seen any other collections from these two countries, but the species also occurs in Somalia as already reported by Chiovenda (1916) and Cufodontis (1965). Fig. 7 C.

In grassland or woodland, often in wet depressions; alt. 450–2200(–2900) m, but some of the specimens from Somalia appear to be from lower altitudes.

Notes on taxonomy. The species is very variable in habit and leaf shape and two of the extremes were recognized as forms by Wimmer. Different forms may occur together as shown by Faden 67/240 and 67/247 from Kenya. The latter has narrow leaves, as the type race, and is said to be common in the area, while the former has broad leaves and is said to be occasional.

Additional collections. Ethiopia. Eritrea, Beccari 179 (FI); Bellini 465 (FI); Corradi 112 (FI); Gandussio 26 (FI); Hildebrandt 383 (BM); Mooney 8029 A (K); Pappi 94, 1345, 7034 (FI); Ragazzi 17 (FI); Steudner 1378 (K, S). Begemdir, Schimper 1376 (P). Sidamo, Corradi 7389, 7390 (FI); Eriksson 687 (S); Friis et al. 780 (BR); Ruspoli & Riva 1393 (FI); Thesiger 2030 (BM); Vatova 174 (FI). *Somalia,* Glover & Gilliland 248 (EA, BM); Hemming 2311 (EA, K); Popov 1054 (EA, K). *Kenya,* N Frontier Prov., Magogo 1362 (BR, EA, K). Turkana Prov., Symes 383 (EA, K); Tweedie 3813 (K); Wilson 2027 (EA). Rift Valley Prov., Bally 1015 (EA, K); Gillett 17294 (EA, FI, K); Kerfoot 340 (EA). C Prov., Adamson in Bally 4335 (EA, G, K); Ament & Magogo 311 (EA); Bally 8462 (EA, K); Christensen 105 (EA); Coryndon s. n. (EA); Faden 67/240 (EA, K); Fries & Fries 23 (UPS); Gilbert & Thulin 1756 (UPS); Gitau & Okwaro F × 4 (EA); Hale 14 (G, K); Hansen 787 (EA); Kibue K 150 (EA, K); Lucas & Polhill 60 (EA); Magius in Polhill 220 (K); Mathew 6047 (EA, FI, K); Mbuvi 335 (EA); Mearns 214 (BM); Newbould 2981 (K); Ossent 297 & 531 (EA); Polhill 380 (BR, EA, K); Robertson 1940 (EA); Scott Elliott 6698 (BM); Starzenski 8 (BR); Verdcourt 463 (BR, EA, FI, K), 1954 (EA, K, UPS). Masai Prov., Bally 5030 (EA, G, K) Coast Prov., Gilbert 1520 (EA); Hucks 1204 (EA). *Tanzania,* Lake Prov., Tanner 488 (K), 1341 (BR, K). N Prov., Beesley 110 (K); Bigger 2348 (EA, K); Carmichael 1380 (BR, EA, K); Greenway & Kirrika 11142 (EA, K); F.A.O. 17 (EA); Gilbert 2105 (EA); Green 1700 (EA); Haarer 1229 (EA, K); Herlocker 324 (EA); Leippert 6452 (BR, EA, K); Moore in EA 14375 (EA); Mosha 1899 (EA); Richards 20327 (K), 20801 (K), 24884 (BR, K), 25426 (BR, K); Robson 200 (EA); Shabani 216 (EA); Welsh 536 (EA). C Prov., Hammond 189 (EA).

10. **C. eritreana** E. Wimm.

Wimmer 1968 p. 989, Fig. 67 B. – Orig. coll.: Ethiopia, Eritrea, Ghinda, 7.II.1891, Schweinfurth 150 (K holotype, G).

Distribution and habitat. C. eritreana is endemic in Ethiopia and was previously only known from the type. Several additional collections from Eritrea have now been seen and the species has also been collected in the Shoa Region (Fig. 7 D). In grassland; alt. 950–1700 m.

Notes on taxonomy. The seeds of *C. eritreana* have not previously been described. In the flowering and fruiting collection Pappi 59, they were found to be flat, broadly winged and c. 1.6 × 1.2 mm. In the seeds as well as in the free filaments, the 2-lipped corolla, glabrous outside, and its entirely glabrous stem, it agrees with the second Ethiopian species, *C. glandulifera,* to which it is apparently closely related. *C. eritreana* differs mainly in its always clearly twining stem with ± scattered, non-rosulate leaves, and its dorsally pubescent anthers.

Additional collections. Ethiopia. Eritrea, Ghinda–Baresa, 17.II.1893, Pappi 59 (FI); Dongollo, 17.II.1902, Pappi 3811, 3822 (FI), II–III.1903, Tellini 1630 (FI); Pianura di Sabarguma, 2–10.III.1902, Pappi 3980 (FI); Ghinda–Dongollo, 25.I.1909, Fiori 1727 (FI); Embatcalla, 1.II.1909, Fiori 1728 (FI). Shoa, 48 km W of Ghedo, 11.IX.1975, Gilbert & Thulin 617 (K, UPS).

11. **C. richardsiae** E. Wimm.

Wimmer 1968 p. 973, Fig. 57. – Orig. coll.: Tanzania, Mpanda Distr., Silkcub Highlands, 3.XII.1956, Richards 7123 (K holotype).

Distribution and habitat. Wimmer cited two collections from Zambia, but they are actually from the W Province of Tanzania and I have seen another specimen from the same area. A single specimen from Katanga apparently belongs here too, as well as some specimens from N Malawi and the adjacent part of the S Highlands Province of Tanzania. In grassland or rocky places; alt. 1050–2600 m. Fig. 7 D.

Notes on taxonomy. The plants from N Malawi and S Tanzania differ slightly from the rest in that the petals are longer (6.5–9.5 mm versus 5–6.5 mm), the inflorescence is somewhat denser and the leaves are more numerous. Also the pubescence on the inside of the petals shows some differences. In typical *C. richardsiae* from W Tanzania this pubescence is dense and confined to a zone on the lower half of the petals, while in the plants from N Malawi it is more sparse and nearer to the base of the petals. In the material from S Tanzania, finally, the petals are sparsely pubescent more or less in their entire length. Possibly the plants from N Malawi and S Tanzania will eventually prove to be a distinct taxon, but the present evidence is too weak and more material is needed.

Capsules and seeds are not known in *C. richardsiae,* but its affinities most probably are with the species with unwinged, reticulate seeds. Habitually it is most similar to *C. ubenensis,* but differs markedly in its much shorter stamens and style, smaller flowers and not or scarcely saccate bases to the upper petals.

Additional collections. Tanzania. W Prov., 32 km on the Mpanda–Ikola road, 31.X.1959, Richards 11672 (K). S Highlands Prov., Umalila, Ilembo, II.1972, Leedal 983 (EA); ibid., Ibaba, Leedal 1339 (EA); ibid., Iriji, 31.I.1978, Leedal 4879 (EA). *Zaire.* Katanga, 2 km E of Niembe, 25.XI.1969, Lisowski, Malaisse & Symoens 8044 (BR). *Malawi.* N Prov., Nyika Plateau, 14.II.1961, Robinson 4507 (SRGH); ibid., Nganda Peak, 16.IV.1975, Pawek 9282 (SRGH).

12. **C. ubenensis** Engl.

Engler 1901 p. 419; Wimmer 1968 p. 973, Fig. 58 B. – Orig. coll.: Tanzania, W Ubena, Livingstone Mts, Lugara Mt, 30.III.1899, Goetze 821 (B holotype †, BR lectotype, selected here, BM).

Distribution and habitat. Only known from the type collection from S Tanzania (Fig. 7 D). In upland grassland; alt. 2300 m.

Notes on taxonomy. Seeds are not known in *C. ubenensis,* but the basally connate filaments and the dorsally lanate anthers indicate a relationship with the "*C. lasiandra* group". The species is characterized by its linear leaves, long-pedunculate inflorescence and by having the inside of the petals densely pubescent at the tips.

Fig. 6. *Cyphia brachyandra,* flowering portion, × 1.2. From the type locality.

13. C. **brachyandra** Thulin, sp. nov. – Fig. 2 B, 6

Orig. coll.: Tanzania, S Highlands Prov., Mufindi area, Lugoda tea estate, valley between the superintendent's house and Lugoda tea factory, 17.VI.1978, Thulin & Mhoro 3261 (UPS holotype, DSM, EA, K, MO, WAG).

Species nova, a *C. lasiandra* Diels staminibus brevioribus et petalis basi vix saccatis, a *C. richardsiae* E. Wimm. caule volubili longo et inflorescentia laxa differt.

Twining, slender herb, up to 2 m, from a subglobose or elongated root-tuber, up to 3 cm. *Stem* not or sparsely branched (in upper part only), ribbed, glabrous or very sparsely and finely crisped pubescent in the inflorescence region. *Leaves* sessile or shortly petiolate, up to 35–85 × 2–30 mm, linear to ovate, acute at the apex, attenuate to cuneate at the base, serrate or crenate at the margin, glabrous; venation prominent beneath; petiole up to 12 mm, often curved. Raceme lax, up to 100 cm long and c. 20–30-flowered; pedicels up to 3–13 mm, shortly crisped pubescent; bracts ± leaf-like, diminishing in size upwards; bracteoles 1–2 mm. *Hypanthium* broadly obconical, 10-nerved, glabrous or sparsely pubescent at least towards the base. *Calyx*-lobes narrowly triangular, ± erect or spreading, becoming reflexed in fruit, 2.4–4 mm, with 1–3 pairs of teeth at the margin, glabrous or sparsely ciliate. *Corolla* 9–12 mm, pale pink, pale purple or mauve, split to the base into 2 lips, the upper 3-lobed but finally disintegrating, the lower divided into 2 free petals; all petals linear, glabrous outside, pubescent inside at the base. *Stamens* c. 3 mm; filaments linear, abruptly dilated, ciliate and obscurely connate at the very base; anthers elliptic-oblong, 1.4–1.6 mm, pubescent with up to 0.8–1 mm long, rather straight hairs on the upper 3/4 of the connective and with shorter hairs towards its base, also a small tuft of hairs c. 0.2 mm long at the tip. *Ovary* semi-inferior; style 1.5–2 mm. *Capsule* ovoid, with 10 distinct nerves connected by weak transversal nerves; inferior part cup-shaped, 2.4–4 mm long; valves 2.8–3.2 mm. *Seeds* ± broadly elliptic in outline, ± compressed and irregularly angular, c. 1.2 mm, coarsely reticulate, brown.

Distribution and habitat. In the highlands of N Malawi and S Tanzania (Fig. 7 C). At forest margins, in scrub or rocky places; alt. 1880–2280 m.

Notes on taxonomy. The variation in leaf-shape is considerable within *C. brachyandra*. Thus Pawek 2169 and 3423 from Malawi have linear leaves (although the lower ones are missing) and Eggeling 6542 from Tanzania has ovate leaves. The other material from Tanzania, however, is more or less intermediate and within the type collection the leaf-shape varies from narrowly lanceolate to ovate.

C. brachyandra is habitually very similar to *C.*

lasiandra which is sympatric but usually occurs at lower altitudes. The shorter stamens with shorter anthers and only obscurely connate filament-bases, and the not or scarcely saccate bases to the upper petals seem to be the only reliable distinguishing characters for *C. brachyandra,* but as these characters are constant and no intermediates have been seen I consider it specifically distinct. In the size and shape of the stamens as well as in the shape of the petal-bases, *C. brachyandra* instead agrees with the likewise sympatric *C. richardsiae* which, however, is a small erect plant with a much denser and shorter inflorescence.

Collections (besides the type). Tanzania. S Highlands Prov., Mufindi area, Lugoda tea estate, 10.V.1968, Renvoize & Abdallah 2076 (EA, K), 5.V.1969, Paget-Wilkes 526 (EA); Livingstone Mts., Upangwa, V.1953, Eggeling 6542 (EA). *Malawi.* N Prov., Nyika Plateau, Chelinda R. Bridge, 12.IV.1969, Pawek 2169 (K), 29.III.1970, Pawek 3423 (K).

14. C. **rupestris** E. Wimm.

Wimmer 1968 p. 972, Fig. 55. – Orig. coll.: Tanzania, Njombe Distr., Elton Plateau, 7.I.1957, Richards 7561 (K holotype, BR, W).

Distribution and habitat. Only known from the highlands N of Lake Malawi in S Tanzania (Fig. 8 A). In upland grassland, usually in rocky places; alt. 2400–2900 m.

Notes on taxonomy. C. rupestris is closely related to *C. lasiandra* and *C. erecta* and has connate filament-bases like these species. Together they form a taxonomically difficult complex, "the *C. lasiandra* group", and the three species recognized here are all rather ill-defined. Seeds are not known in *C. rupestris* and may provide additional differential characters. *C. rupestris* in its erect stem and condensed inflorescence agrees with *C. erecta* which is allopatric and occurs at lower altitudes. *C. rupestris* differs in its more compact habit, shorter, less than 1 mm long (c. 1.5 mm long in *C. erecta*) hairs on the back of the connectives, not apically connate anthers, and in its usually longer pedicels (up to 5–15 mm versus 1–6 mm). *C. lasiandra,* on the other hand, is sympatric with *C. rupestris* and on Mbeya Mts they have even been collected at what appears to be the same place (Kerfoot 1664 and 1718 respectively), although the altitude, 2600 m, is rather exceptional for *C. lasiandra.* Both the plants are said to be common there. *C. rupestris* differs from *C. lasiandra* mainly in its short, non-twining stem, condensed inflorescence and usually almost sessile leaves.

Additional collections. Tanzania. S Highlands Prov., Njombe Distr., above Matamba, II.1961, Procter 1793 (EA, K), 21.I.1978, Leedal 4864 (EA); Mbeya Distr., Mbeya Range, 16.III.1960, Kerfoot 1718 (EA, K), 17.III.1960, Kerfoot 1782 (EA), 11.II.1978, Leedal 4920 (EA).

15. C. **erecta** De Wild.

De Wildeman 1903 p. 162, t. 38/5-8; Milne-Redhead 1951 p. 378; Wimmer 1968 p. 974, Fig. 59. – Orig. coll.: Zaire, Katanga, Lukafu, XII.1899, Verdick 345 (BR holotype).

C. scandens De Wildeman 1903 p. 163; Wimmer 1968 p. 974, Fig. 74 C. – Orig. coll.: Zaire, Katanga, Lukafu, II.1900, Verdick 368 (BR holotype).

C. erecta De Wild. f. *minor* De Wildeman 1914 p. 444. – Orig. coll.: Zaire, Katanga, Shinsenda, III.1912, Ringoet in Homblé 481 (BR holotype).

C. regularis Wimmer 1952 p. 143, 1968 p. 975, Fig. 48 C, synon. nov. – Orig. coll.: Zambia, upper Loangwa River, 14.I.1897, Nicholson s. n. (K holotype).

C. erecta De Wild. var. *ufipana* Wimmer 1968 p. 975, nom. invalid. – Orig. colls.: Tanzania, Ufipa Distr., Chapota, 5.XII.1949, Bullock 2061 (K); Malawi, Kota-Kota, Benson 693 (PRE, not seen).

C. rhodesiaca Wimmer 1968 p. 975, Fig. 58 C, synon. nov. – Orig. coll.: Zambia, Mwinilunga Distr., Kalanda Dambo, 10.XII.1937, Milne-Redhead 3593 (BR holotype, BM, K).

15 A. C. **erecta** De Wild. var. **erecta**

Inflorescence ± elongated; corolla 9–16 mm; plant usually glabrous or pubescent on inflorescence only.

Distribution and habitat. In S Tanzania, Zaire (Katanga), Zambia and Malawi (Fig. 8 A). In grassland, woodland and thickets; alt. 560–2000 m.

Notes on taxonomy. C. erecta is a variable species, not always easily distinguished from *C. lasiandra* and *C. rupestris.* I have followed Milne-Redhead (1951) in considering the type specimen of *C. scandens* as conspecific, although the plants are more twining than usual. Var. *witteana* is a large-flowered, usually pubescent form in Katanga, which seems worthy of recognition. Seeds are not known in this variety.

Additional collections. Tanzania. W Prov., Richards 11871 (K); Robinson 4769 (K, SRGH); Sanane 1519 (K). S Highlands Prov., Björnstad 2175 (EA, K, UPS);

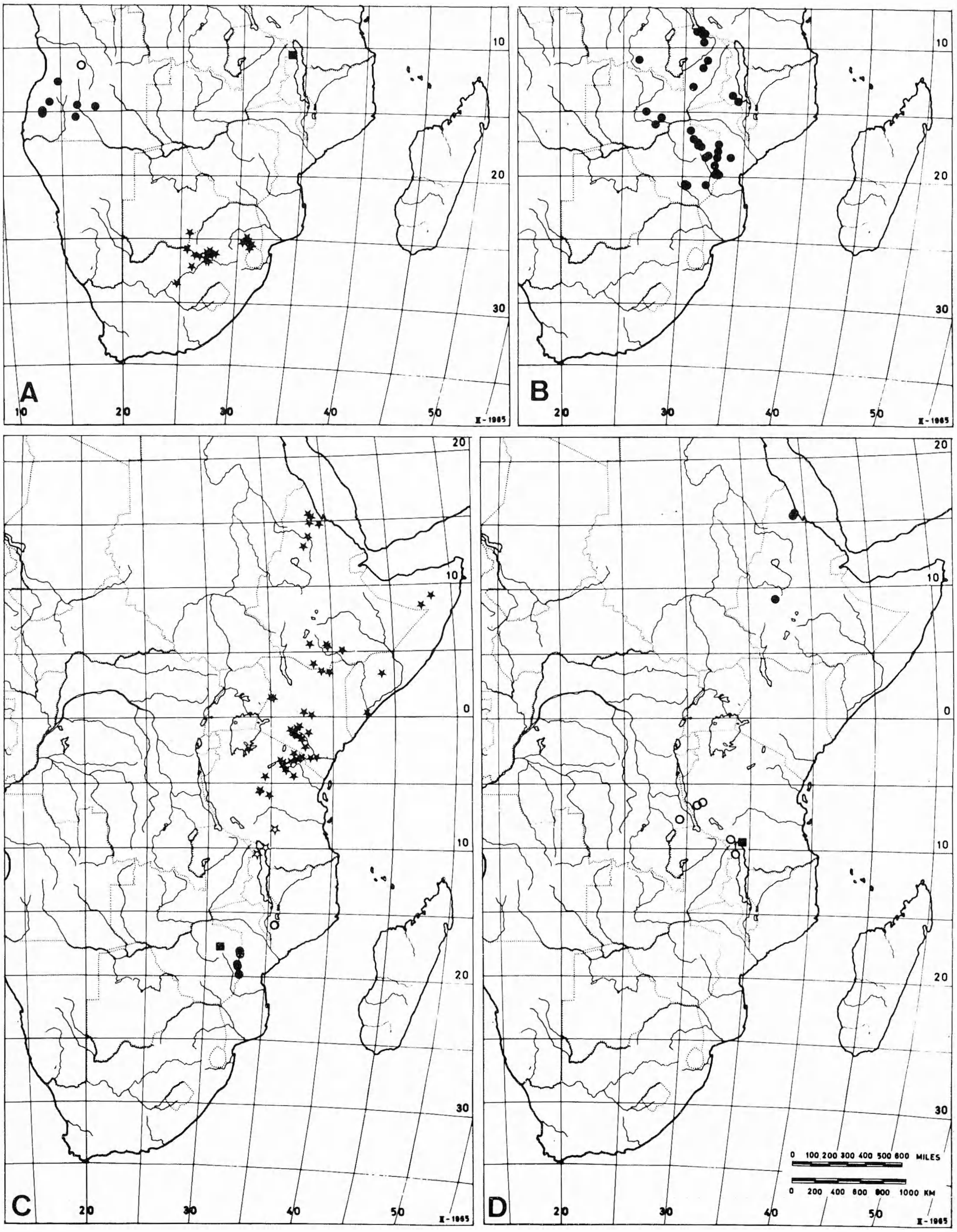

Fig. 7. Known distribution of species of *Cyphia*. – A: *C. stheno* (●), *C. brevifolia* (○), *C. nyikensis* (■) and *C. stenopetala* (★). – B: *C. mazoensis*. – C: *C. alba* (●), *C. decora* (○), *C. reducta* (■), *C. glandulifera* (★) and *C. brachyandra* (☆). – D: *C. eritreana* (●), *C. richardsiae* (○) and *C. ubenensis* (■).

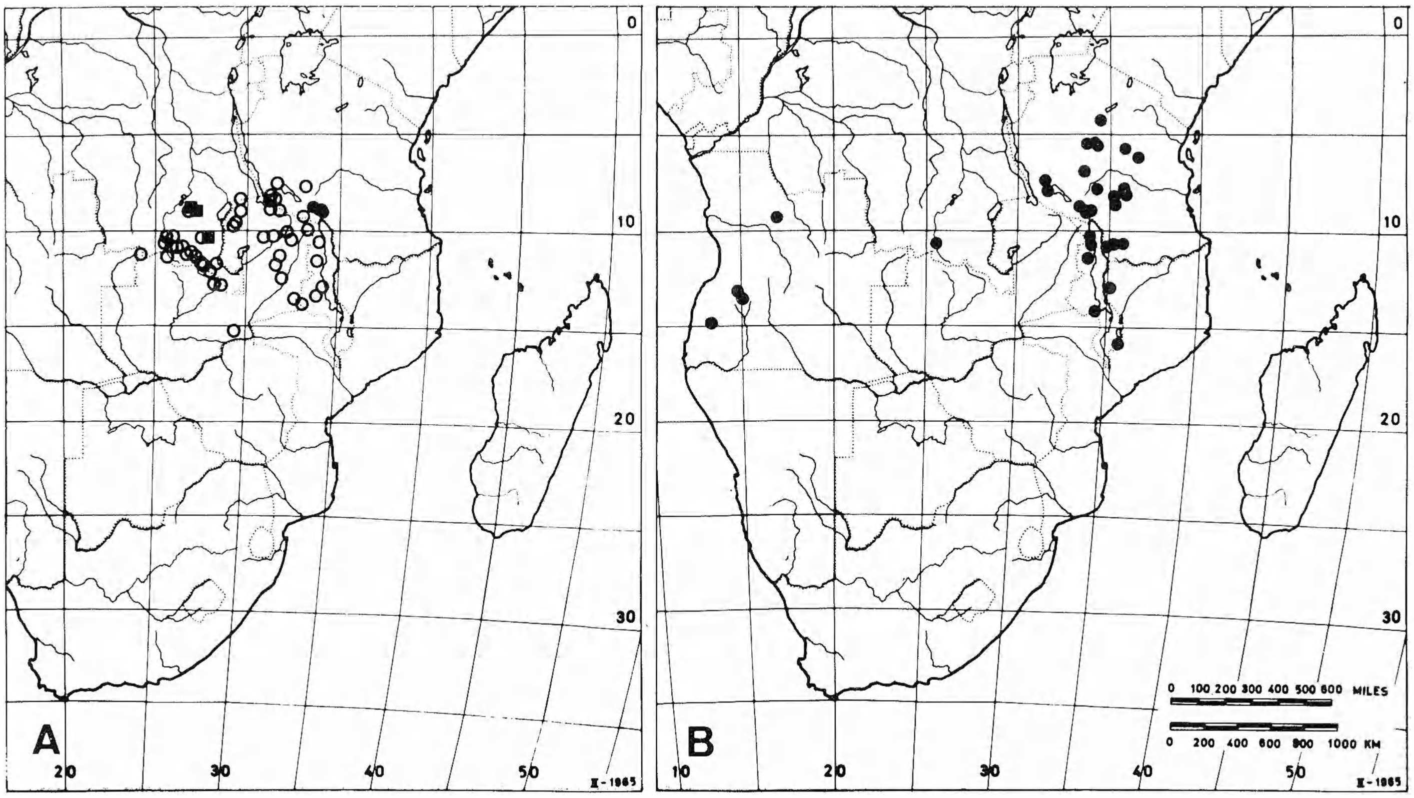

Fig. 8. Known distribution of taxa of *Cyphia*. – A: *C. rupestris* (●), *C. erecta* var. *erecta* (○) and *C. erecta* var. *witteana* (■). – B: *C. lasiandra*.

Leedal 827, 931, 4746 a (EA). *Zaire*. Katanga, Briart s. n. (BR); Brynaert 564, 588, (BR); Detilleux 162, 228, 354 (BR); Duvigneaud 4102 E, 4142 E, 4412 E, 4413 E, 4423 E, 4424 E, 4429 E, 4430 E, 4593 E, 4715 E (BRLU); Hock s.n. (BR); Kalenda 5 (BR); Malaisse 6220 (BR, UPS), 6711 (UPS), 7671 bis (UPS), 7999 (BR), 8379 (BR), 8408 (UPS), 9200 (BR); Poelman 117 (BR); Quarré 4961 (BR); Salésiens 542 (BR); Schmitz 8182 (BR); Symoens 14022 (BR, K, UPS); de Witte 3033 (BR). *Zambia*. N Prov., Astle 1184 (K, SRGH), 1257 (SRGH); Bock 78, 167, 213 (PRE); Fanshawe 1964, 4012 (K); Ricardo 102 (BM); Richards 6 (K), 212 (K), 3719 B (K, SRGH), 11994 (K), 13698 (K, SRGH), 15408 (K); Robinson 4177 (EA, SRGH), 4360 (K); Walter 16 (K). W Prov., Fanshawe 572 (K), 695 (BR, K, SRGH); Linley 34 (SRGH); Mutimushi 125 (SRGH); Robinson 6040 (K); Shepherd 105, 106 (K); Wilberforce 10 (K). C Prov., Astle 4401 (SRGH); Robinson 6187 (K. SRGH). E Prov., King 447 (SRGH); Pawek 6156(K SRGH). *Malawi*. N Prov., Chapman 364 (BM); Pawek 8034 (SRGH); Robinson 4507 (K). C Prov., Benson 278 (PRE); Robinson 4507 (K); Robson 1070 (BM, K, LISC, SRGH).

15 B. **C. erecta** De Wild. var. **witteana** E. Wimm.

Wimmer 1968 p. 975, as "*wetteana*". – Orig. coll.: Zaire, Katanga, Lukafu, XII.1930, de Witte 49 (BR holotype).

Inflorescence strongly contracted, 1–5 cm; corolla 15–20 mm; plant often shortly pubescent in all parts.

Distribution and habitat. Only known from Katanga (Fig. 8 A). In grassland up to 1900 m altitude.

Additional collections. *Zaire*. Katanga, Mubale R., 16.I.1948, de Witte 3244 (BR); Mukana–Kabwe Kanono, 7.XII.1948, de Witte 4760 (BR).

16. **C. lasiandra** Diels

Diels 1898 p. 111; Wimmer 1968 p. 991, Fig. 66 D. – Orig. coll.: Angola, Huila, Antunes s.n. (B holotype †, COI lectotype, selected here).

C. nyasica Baker 1898 p. 157, synon. nov.; Wimmer 1968 p. 1010, Fig. 77. – Orig. coll.: Malawi, between Kondowe and Karonga, VII.1896, Whyte s.n. (K holotype).

?*C. antunesii* Engler 1902 p. 147, synon. nov.; Wimmer 1968 p. 983. – Orig. coll.: Angola, Huila, Monyno, IV.1899, Antunes 175 (B holotype †).

C. cacondensis Good 1927 p. 68, synon. nov.; Wimmer 1968 p. 991, Fig. 66 B. – Orig. coll.: Angola, between Kaconda and Bissapa, 5.III.1907, Gossweiler 4302 (BM holotype).

C. zernyana Wimmer 1968 p. 1006, Fig. 74 D, synon. nov. – Orig. coll.: Tanzania, Matengo Highlands, Litembo, 15.II.1936, Zerny 432 (W holotype).

C. exelliana Wimmer 1968 p. 1010, Fig. 76 E, synon. nov. – Orig. coll.: Malawi, Dedza Mt, 20.III.1955, Exell, Mendonça & Wild 1080 (SRGH holotype, BM).

C. peteriana Wimmer 1968 p. 1010, Fig. 78, 79 E, synon. nov. – Orig. coll.: Tanzania, Unyanyembe at Malongwe, 8.I.1926, Peter 34472 (B holotype).

C. floribunda Wimmer 1968 p. 1013, Figs. 67 C, 83, synon. nov. – Orig. coll.: Tanzania, Bwanye, Mwagoye, 16.II.1914, Stolz 2521 (B holotype, BM, BR, K, UPS). According to Wimmer isotypes are present also in P, PRE, W and Z.

Note on typification. No original material of *C. lasiandra* was found by Wimmer (1968 p. 991), who neotypified with another specimen from Angola (Herb. Bolus 12513, not seen). As an isotype is present in COI, this takes precedence and is here selected as a lectotype.

Distribution and habitat. In Tanzania, Zaire (Katanga), Malawi, Mozambique and Angola (Fig. 8 B). The species (and its synonyms) has not previously been reported from Zaire and Mozambique. In grassland, woodland and thickets; alt. 840–2200(–2900) m.

Notes on taxonomy. The name *C. lasiandra* has hitherto been used only for the type collections, but as it was published in May 1898 it antedates the more well-known *C. nyasica* which appeared in July the same year.

The species is usually a twining and climbing herb, more than one m, and up to several m, long with a very lax and long inflorescence, but shorter and ± erect specimens with more contracted inflorescences may occur, which approach *C. erecta* in habit. The most extreme collection in this respect is Teixeira et al. 9765 from Angola, and also the lectotype is unusually short and compact. A similar specimen from Tanzania is Licky 4550.

The many species recognized by Wimmer and now included here were said to differ mainly in leaf-shape and relative length of corolla and stamens. In the larger material now available no clear distinctions could be made, however, and I prefer to treat it as a single variable species. The specimens from Mt Mlanje have narrower leaves and longer pedicels than the other material from Malawi, but they are matched in these characters by some specimens from Tanzania (Richards 8662) and Zaire.

The type of *C. antunesii* is lost and the description deviates on two points from that of *C. lasiandra:* the calyx-lobes are said to be strongly unequal, two small and three long, and the petals glabrous inside and pilose outside. Probably these statements are due to erroneous observations. The two short calyx-lobes may have been the bracteoles and the petals may have been twisted. One more specimen is known from the type locality of *C. antunesii*, namely Dekindt 1201 (P, not seen), a photograph of which was published by Wimmer (1968 Fig. 83, as *C. floribunda*). This specimen, which like the type of *C. antunesii* was collected in April 1899, agrees with *C. lasiandra*.

Additional collections. Tanzania. W Prov., Bullock 2563 (K); Richards 8662 (BR, K). C Prov., Hammond 292 (EA, K); Hornby 908 (EA, K); Richards 19934 (BR, EA, K). S Highlands Prov., Björnstad 2631 (EA); Edong in C.A.W.M. 4455 (EA); Fuller 123 (K); Githiaka in C.A.W.M. 4146 (EA); Kawede in C.A.W.M. 4352 (EA); Kerfoot 1664 (EA, K); Leedal 1049 & 1851 (EA); Licky in C.A.W.M. 4550 (EA); Nicholson 100 (EA); Paget-Wilkes 780 (EA); Pedersen 762 (EA); Polhill & Paulo 1377 (B, BR, EA, K, SRGH); Prins 325 (EA); Procter 1798 (EA); Richards 13992 (K); Watermeyer AW 40 (K). S Prov., Milne-Redhead & Taylor 8889 (K), 9605 (B, BR, EA, K). *Zaire.* Katanga, Kolwezi, Dikuluwe, 21.I.1960, Duvigneaud 5141 E, 5146 E (BRLU). *Malawi.* N Prov., Chapman 128 (SRGH); Pawek 940 (SRGH), 2348 (K), 5109 (SRGH), 6834 (PRE). C Prov., Jeke 168 (SRGH). S Prov., Caulfield in GHS 86313 (SRGH); Chapman 487 (BM, SRGH); Iwarsson 827 (UPS); Jackson 2170 (K, SRGH); Robinson 5384 (SRGH); Wild 6222 (SRGH). *Mozambique.* Niassa, Maniamba, Jéci Mts, Mt Chicungulo, 2.III.1964, Torre & Paiva 10978 (LISC). *Angola.* Malange, Quela, II.1922, Nolde 683 (BM).

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Pyrrolizidine alkaloids – occurrence and systematic importance in angiosperms

C. C. J. Culvenor

Culvenor, C. C. J. 1978 12 15: Pyrrolizidine alkaloids – occurrence and systematic importance in angiosperms. *Bot. Notiser 131:* 473–486. Stockholm. ISSN 0006-8195.

The structure and biosynthesis of pyrrolizidine alkaloids is reviewed, and their occurrence in the angiosperm system is tabulated. Aliphatic monocarboxylic acids are characteristic for the Boraginaceae, macrocyclic diesters are common in the Senecioneae (Compositae) and *Crotalaria* (Leguminosae), esters of aryl and aralkyl acids occur mainly in the tribe Kerosphaereae of Orchidaceae. In addition, there are scattered occurrences within a further 8 families. The occurrence of pyrrolizidine alkaloids does not seem very useful for taxonomy above the level of family; by contrast, it is important for delimitation of the tribe Senecioneae and in the infrageneric taxonomy of *Crotalaria.*

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The pyrrolizidine group of alkaloids has received extensive chemical and biological study mainly because they are the cause of considerable poisoning of livestock (Bull et al. 1968) and to a lesser extent of humans (Khanin 1956, Bras et al. 1957, De Waal 1940). Their effects include characteristic liver and lung lesions and they are mutagenic and carcinogenic (Bull et al. 1968, McLean 1970, International Agency for Research on Cancer 1976). This toxicity is restricted essentially to alkaloids which are esters of aminoalcohols based on 1-hydroxymethyl-1,2-dehydropyrrolizidine with branched chain acids of a unique type. Biogenetically related alkaloids which have no chronic toxicity are also found. Moreover, there are a number of simple and complex alkaloids containing a pyrrolizidine ring which are possibly of a different biogenetic origin.

This review is concerned with occurrences at the genus level and higher, and with the implications for taxonomy and phylogeny. Occurrences at the species level have been detailed by Bull et al. (1968) and Warren (1955, 1966). The tabulated data on alkaloid distribution is referenced as far as possible to these reviews. The chemistry and molecular structures of the alkaloids are treated by the same authors and by Klásek & Weinbergová (1975), and toxicology and other biological effects by Bull et al. (1968), McLean (1970) and Mattocks (1972).

Structural groups, biosynthesis and distribution

The pyrrolizidine aminoalcohols and non-ester alkaloids

The main groups of pyrrolizidine alkaloids are based on aminoalcohols which are diastereoisomers or simple derivatives of 1-hydroxymethyl-pyrrolizidine. They may have 1, 2 or 3 hydroxyl groups and a 1,2-double bond, and are known in many of the possible stereochemical forms (Fig. 1).

The aminoalcohols with a 1,2-double bond, supinidine, heliotridine, retronecine, otonecine and crotanecine (Fig. 1 E–H), when appropriately esterified, form the classical liver-damaging alkaloids of the family Boraginaceae and the genera *Senecio* and *Crotalaria*. Stereochemistry is less variable in this group, the C8 H-atom being always α-oriented with only one known exception

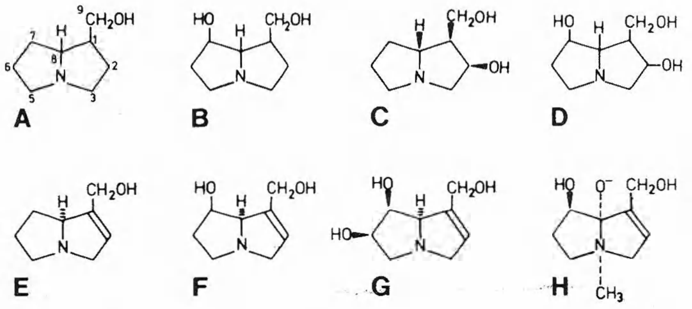

Fig. 1. The pyrrolizidine aminoalcohols. Dotted and thickened lines denote α- and β-orientation of bonds, respectively; α meaning orientation away from the observer, β towards the observer. – A: Isoretronecanol, 1β-CH_2OH, 8α-H; lindelofidine, 1α-CH_2OH, 8β-H; trachelanthamidine, 1α-CH_2OH, 8α-H; laburnine, 1β-CH_2OH, 8β-H. – B: Platynecine, 1β-CH_2OH, 7β-OH, 8α-H; turneforcidine, 1α-CH_2OH, 7β-OH, 8α-H; hastanecine, 1β-CH_2OH, 7β-OH, 8β-H. – C: Macronecine. – D: Rosmarinecine, 1β-CH_2OH, 2α-OH, 7β-OH, 8α-H; croalbinecine, 1α-CH_2OH, 2β-OH, 7β-OH, 8α-H. – E: Supinidine. – F: Heliotridine, 7α-OH; retronecine, 7β-OH. – G: Crotanecine. – H: Otonecine.

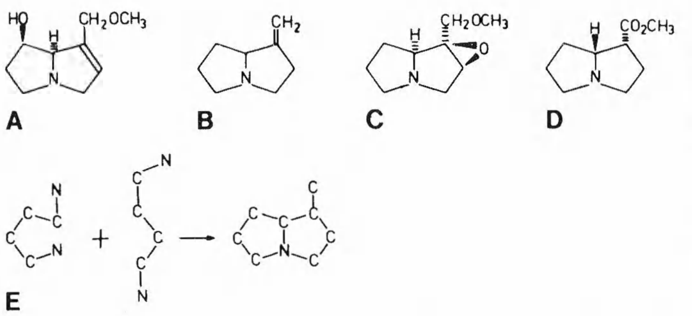

Fig. 2. A–D: Non-ester pyrrolizidine alkaloids. – E: Biosynthesis of pyrrolizidine aminoalcohols from putrescine-type precursors.

(α- and β-orientation are defined in Fig. 1 caption). It has not yet been determined whether this exception, an ester of (+)-supinidine from *Cynoglossum australe,* is hepatotoxic.

The aminoalcohols have been isolated as such only occasionally, and to a limited extent also as methyl ethers or anhydro derivatives (Table 1, Fig. 2 A–C). They appear to occur occasionally in the genera which are predominantly sources of the ester alkaloids. For example, the methoxy and 1-methylene derivatives are characteristic to some extent of certain subseries of the genus *Crotalaria*. Biogenetic studies favour ornithine, arginine or an equivalent such as putrescine as the precursor of the aminoalcohols (Fig. 2 E) (Bottomley & Geissman 1964, Bale & Crout 1975).

Some of the simple derivatives may be products of further metabolism of ester alkaloids. Thus an organism in sheeps' rumen, *Peptococcus heliotrinreducans,* has the capability for converting hepatotoxic ester alkaloids into 1-methylenepyrrolizidine (Fig. 2 B) derivatives (Dick et al. 1963, Lanigan 1976).

Laburnine acetate and 1-carboxypyrrolizidine methyl ester (Fig. 2 D) found in *Vanda* and *Chysis,* Orchidaceae, have been included here although they are strictly not "non-esters". In the present context, acetic acid is probably best regarded as an adventitious esterifying acid while the 1-carboxypyrrolizidine ester does not fit elsewhere and is also probably without systematic significance.

Table 1. Distribution of pyrrolizidine aminoalcohols and non-ester alkaloids. [1]Bull et al. 1968, [2]Lüning 1974, [3]Sasaki & Hirata 1970, [4]Borges Del Castillo et al. 1970.

Family/subfamily	Tribe	Genus
Apocynaceae		
Echitoideae	Ecdysantherae	*Anodendron*[3]
	Parsonsieae	*Urechites (Fernaldia)*[4]
Boraginaceae		
Heliotropioideae		*Heliotropium*[1]
Compositae		
Tubuliflorae	Eupatorieae	*Eupatorium*[1]
Leguminosae		
Papilionoideae	Genisteae	*Crotalaria*[1]
		Cytisus[1]
Orchidaceae		
Monandrae	Kerosphaereae	*Chysis*[2]
		Liparis[2]
		Vanda[2]
		Vandopsis[2]
Santalaceae		
		Thesium[1]

Esters of pyrrolizidine aminoalcohols with aliphatic acids

Esters of monocarboxylic acids (Fig. 3). The alkaloids in this group may be mono- or diesters. Both categories typically have a hydroxylated or methoxylated α-isopropylbutyric acid esterifying the C9-OH of the aminoalcohol. The diesters have angelic acid (or sometimes its isomer, tiglic acid) esterifying a C7-OH of the aminoalcohol. In a small number of alkaloids, this C_5 acid esterifies a hydroxyl group of the larger acid instead. The acids based on the α-isopropylbutyric acid skeleton have an α-OH group as a constant feature. In the alkaloid, latifoline (Fig. 3 C), from *Cynoglossum latifolium,* one of the isopropyl methyls is oxidised to carboxyl and lactonised. All four optically-active forms of the acid shown in indicine have been found to occur; these are (+)- and (−)-trachelanthic acid and (+)- and (−)-viridifloric acid. [(+)-viridifloric acid is a recent finding in an alkaloid of *Heliotropium curassavicum* (Mohanraj et al. 1978).]This variability in stereochemistry, combined with the additional asymmetry present in the aminoalcohols, makes purification and complete structural identification difficult in this type of alkaloid. Free hydroxyl groups in either the aminoalcohol or the acid parts of the molecule are sometimes acetylated.

Angelic and tiglic acids are derived from isoleucine or its precursors, threonine and 2-oxobutyric acid (Fig. 4 A) (Crout et al. 1966). One of the α-isopropylbutyric acids, echimidinic acid in heliosupine, has been shown to incorporate labelled valine. The valine or its equivalent, 3-methyl-2-oxobutyric acid, is thought to combine with "active" acetaldehyde derived from pyruvate (Fig. 4 B) (Crout 1966). Two alkaloids from *Heliotropium* species are interesting variants. The acid part of the recently isolated curassavine (Fig. 5 C) (Mohanraj et al. 1978) appears to be derived in a similar way from isoleucine in place of valine. The acid part of strigosine (Fig. 5 D) has the carbon skeleton of isoleucine and differs from curassavine in lacking the additional C_2 unit.

Other atypical alkaloids of this group are shown in Fig. 5. Sarracine and macrophylline (Fig. 5 A, B) have angelic acid or its hydroxylated derivative, sarracinic acid, esterifying the C9-OH of the aminoalcohol. Both are from *Senecio* species, a genus in which the macrocyclic diester alkaloids are highly characteristic. It is hard to avoid the inference that they are biogenetically related to the macrocyclic diesters.

Planchonelline (Fig. 5 E), from *Planchonella* (Sapotaceae), and cornucervine (Fig. 5 F), from *Phalaenopsis* (Orchidaceae), contain the unusual esterifying acids, methylthioacrylic and 3-hydroxy-3-methoxycarbonyl-5-methylhexanoic acid, respectively. These acids show a resem-

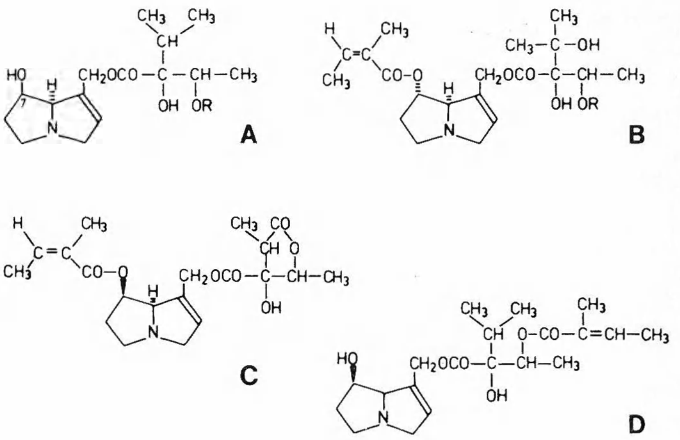

Fig. 3. Typical esters of aminoalcohols with monocarboxylic aliphatic acids. – A: Indicine, 7β-OH, R = H; rinderine, 7α-OH, R = H; heliotrine, 7α-OH, R = CH_3. – B: Lasiocarpine, R = CH_3; heliosupine, R = H. – C: Latifoline. – D: Anadoline.

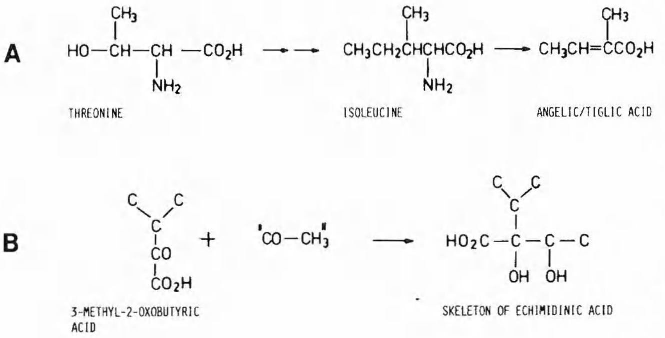

Fig. 4. Biosynthetic pathways. – A: Angelic and tiglic acids. – B: Echimidinic acid.

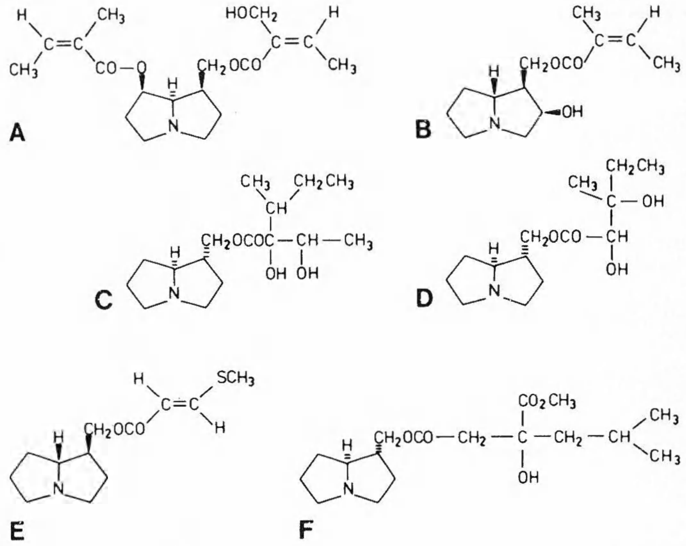

Fig. 5. Some atypical esters of monocarboxylic aliphatic acids. – A: Sarracine. – B: Macrophylline. – C: Curassavine. – D: Strigosine. – E: Planchonelline. – F: Cornucervine.

Table 2. Distribution of esters of pyrrolizidine aminoalcohols with aliphatic monocarboxylic acids. [1]Edgar & Culvenor 1975, [2]Bull et al. 1968, [3]Man'ko & Marchenko 1971, [4]Pedersen 1975, [5]Man'ko & Vasil'kov 1968, [6]Furuya & Araki 1968, [7]Culvenor & Smith unpubl., [8]Lüning 1974.

Family/subfamily	Tribe	Genus
Apocynaceae		
Echitoideae	Parsonsieae	*Parsonsia*[1]
Boraginaceae		
Heliotropioideae		*Heliotropium*[2]
		Tournefortia[2]
Boraginoideae	Cynoglosseae	*Cynoglossum*[2]
		Lindelofia[2]
		Paracaryum[2]
		Paracynoglossum[3]
		Rindera[2]
		Solenanthus[2]
		Trachelanthus[2]
		Trichodesma[2]
	Eritrichieae	*Amsinckia*[2]
		Asperugo[4]
		Lappula[5]
	Anchuseae	*Anchusa*[4]
		Symphytum[6]
	Lithospermeae	*Lithospermum*[4]
		Macrotomia[2]
		Myosotis[7]
	Echieae	*Echium*[2]
Celastraceae		*Bhesa*[2]
Compositae		
Tubuliflorae	Eupatorieae	*Eupatorium*[2]
	Senecioneae	*Senecio*[2]
Orchidaceae		
Monandrae	Kerosphaereae	*Phalaenopsis*[8]
Sapotaceae		*Mimusops*[2]
		Planchonella[2]

blance to the more typical acids of the group which may be superficial but is yet thought-provoking. The impression is gained that they originate from different precursors but that an evolutionary process (such as the maximisation of biological potency) has brought them to a form close to that of the typical acids.

Members of this group are found in 6 families – the Apocynaceae, Boraginaceae, Celastraceae, Compositae, Orchidaceae and Sapotaceae (Table 2). However they are characteristic only of the Boraginaceae and of the tribe Eupatorieae of the Compositae, with a possible extension to the genus *Parsonsia* (Apocynaceae).

The occurrence in *Parsonsia* is noteworthy. Although the Apocynaceae are characterised more by complex indole alkaloids (Plumerioideae) and aminosteroids and cardenolides (Echitoideae and Cerberoideae), three other occurrences of pyrrolizidine derivatives in the Apocynaceae are known. Two are atypical alkaloids in *Alafia* (Echitoideae, tribe Nerieae) (Païs et al. 1971) and *Anodendron* (Echitoideae, tribe Ecdysanthereae) (Sasaki & Hirata 1970), but the compound from *Urechites* (or *Fernaldia*; cf. Woodson 1936) (Echitoideae, tribe Parsonsieae) (Borges Del Castillo et al. 1970) is a non-basic oxidation product of the alkaloids found in *Parsonsia*. It seems likely that further exploration will reveal a higher incidence of pyrrolizidine alkaloids in the Echitoideae and in the tribe Parsonsieae in particular.

In the Boraginaceae, the α-isopropylbutyric ester alkaloids have been found in 17 genera of the Heliotropioideae and Boraginoideae and may well be present in nearly all species of these subfamilies.

In the Compositae, only *Eupatorium* is at present known to contain α-isopropylbutyric ester alkaloids. However there is evidence from insect feeding behaviour that they may occur in some other genera of the tribe Eupatorieae. The only monocarboxylic acid ester alkaloids found in the tribe Senecioneae are sarracine and macrophylline (Fig. 5 A, B). A group of non-basic, pyrrolic compunds closely related to sarracine have recently been isolated from *Senecio cissampolinus* (Bohlmann et al. 1977). The same authors isolated a similar derivative of a macrocyclic diester alkaloid from another *Senecio* species and this type of compound may occur more widely in the genus.

Macrocyclic diester alkaloids. The macrocyclic diesters are formed from dicarboxylic acids which are glutaric, adipic or pimelic derivatives (Fig. 6) and resemble the acids based on α-isopropylbutyric acid in being branched and hydroxylated. The aminoalcohols are 7,9-diols, with or without an additional OH or the 1,2-double bond, but heliotridine (Fig. 1) is excluded, probably because a 7α-OH creates too large a space between hydroxyls for cyclisation to be possible. Esterification is usually at the C7- and C9-OH groups forming 11-, 12- and 13-membered rings. Some crotanecine diesters have a C6- rather than

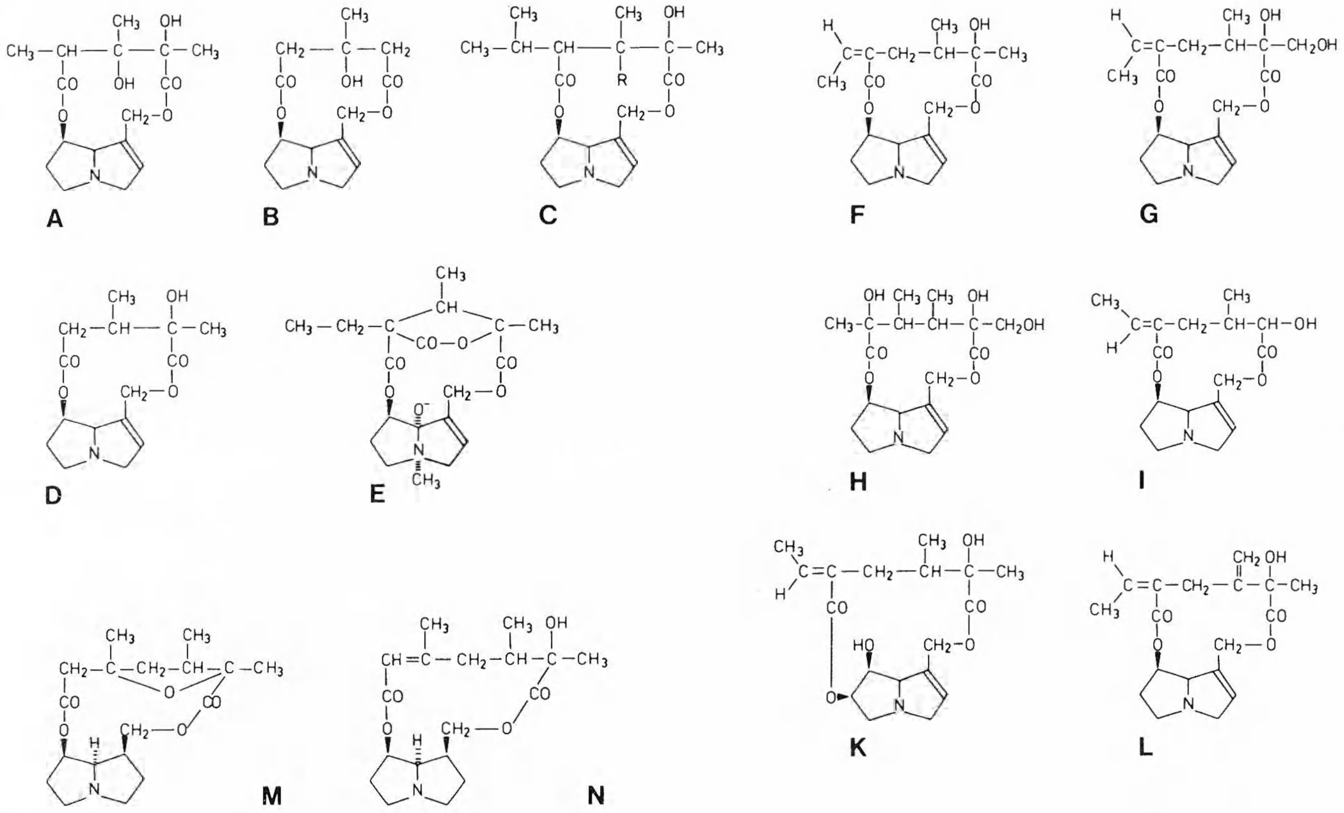

Fig. 6. Pyrrolizidine macrocyclic diester alkaloids. – A–E: Glutaric acid types. – F–L: Adipic acid type. – M, N: Pimelic acid type. – A: Monocrotaline. – B: Dicrotaline. – C: Trichodesmine, R = OH; incanine, R = H. – D: Crobarbatine. – E: Retusamine. – F: Senecionine. – G: Retrorsine. – H: Sceleratine. – I: Nilgirine. – K: Madurensine. – L: Seneciphylline. – M: Nemorensine. – N: Bulgarsenine.

a C7-OH esterified, as in madurensine, which also has a 13-membered ring (Fig. 6 K).

The glutaric acids are commonly C_8 as in monocrotaline or C_{10} as in trichodesmine (Fig. 6 C), but they can also be C_9 as in crobarbatine (Fig. 6 D) and C_6 as in dicrotaline (Fig. 6 B). The acid in retusamine has an unusual carbon skeleton as well as a γ-lactone ring (Fig. 6 E).

Representative adipic diesters are shown in Fig. 6 F–L. Most of the adipic acids have the same C_{10} carbon skeleton as senecionine (Fig. 6 F), differing mainly in oxygenation pattern, configuration of the double bond and presence or absence of an additional double bond. A different C_{10} skeleton occurs in sceleratine (Fig. 6 H), while in nilgirine a methyl group has been lost from the senecionine-type skeleton (Fig. 6 I). Diesters of substituted pimelic acids (Fig. 6 M, N) have been reported recently from *Senecio* spp. (Klásek et al. 1973, Nguyen Thi Nghia et al. 1976).

The macrocyclic diesters occur typically in the tribe Senecioneae (Compositae) and in the genus *Crotalaria* (Leguminosae) (Table 3). In 10 genera of the Senecioneae, including about 90 *Senecio* species, the alkaloids which have been isolated are nearly all diesters of the adipic acid type. The macrocyclic diesters occur in no other tribe of the Compositae and so, within the Compositae, they are truly characteristic of the Senecioneae.

In the genus *Crotalaria,* both the glutaric and adipic type of macrocyclic diester occur in significant number – 22 species are known to contain the glutaric type and 14 species the adipic type. There are isolated occurrences of glutaric diesters in two genera of the Boraginaceae; furthermore, the recent, remarkable finding of senecionine, an adipic diester, in the genera *Caltha* (Ranunculaceae) and *Castilleja* (Scrophulariaceae) (Stermitz & Adamovics 1977, Stermitz, personal communication) must be mentioned.

The biogenesis of the macrocyclic diesters is complex and still only partly understood. The pyrrolizidine moiety is presumably formed from the normal aminoalcohol precursors – two molecules of ornithine or an equivalent. Attention has been concentrated on determining the origin of the unusual dicarboxylic acids and the sequence of events in forming the macrocyclic ring.

The dicarboxylic acids may be classified into four types of carbon skeleton, three having vari-

Table 3. Distribution of macrocyclic diesters of pyrrolizidine aminoalcohols. – In the column to the right, the type of esterifying acid is given (cf. Fig. 7). – [1]Bull et al. 1968, [2]Pimenov et al. 1975, [3]Alieva et al. 1976, [4]Furuya et al. 1971, [5]Klásek et al. 1971, [6]Klásek et al. 1973, [7]Nguyen Thi Nghia et al. 1976, [8]Hikichi & Furuya 1974, [9]Culvenor et al. 1976, [10]Stermitz & Adamovics 1977, [11]Stermitz pers. comm.

Family/subfamily	Tribe	Genus	Acid
Boraginaceae			
Heliotropioideae		*Heliotropium*[1]	A
Boraginoideae	Cynoglosseae	*Trichodesma*[1]	A
Compositae			
Tubuliflorae	Senecioneae	*Adenostyles*[1,2]	C
		Brachyglottis[1]	C
		Cacalia[1]	C
		Doronicum[3]	C
		Emilia[1]	C
		Erechtites[1]	C
		Farfugium[4]	C
		Ligularia[5]	C
		Petasites[1]	C
		Senecio[1,6,7]	C D
		Syneilesis[8]	C
		Tussilago[9]	C
Leguminosae			
Papilionoideae	Genisteae	*Crotalaria*[1]	A B C
Ranunculaceae		*Caltha*[10]	C
Scrophulariaceae		*Castilleja*[11]	C

ations in addition to the common form (Fig. The pimelic acids (type D) are probably best regarded as another variation of the adipic acids (type C), leaving three commonly occurring skeletons. Types A, C and D are C_{10} acids and may be seen to contain two C_5 units. Type B has one such unit. Although superficially isoprenoid, these C_5 units are not derived from the acetate-mevalonate pathway.

Following on earlier work on the synthesis of seneciphyllic acid in *Senecio douglasii,* in which the specific incorporation of isoleucine into the right-hand C_5 unit was recognised (Crout et al. 1966), a study of the formation of senecionine in *Senecio magnificus* has shown that both C_5 units of senecic acid (type C) are derived from isoleucine (Fig. 8) (Crout et al. 1972). Threonine is incorporated, but apparently after conversion into isoleucine. β-methylenenorvaline is also specifically incorporated whereas C_5 intermediates derived from isoleucine are not (Bale et al. 1978).

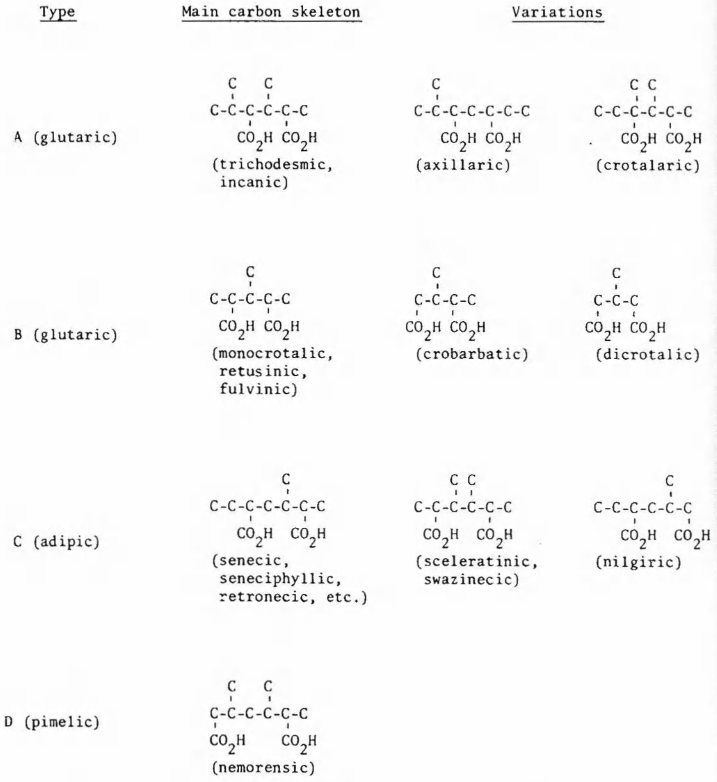

Fig. 7. Carbon skeletons of the dicarboxylic acids.

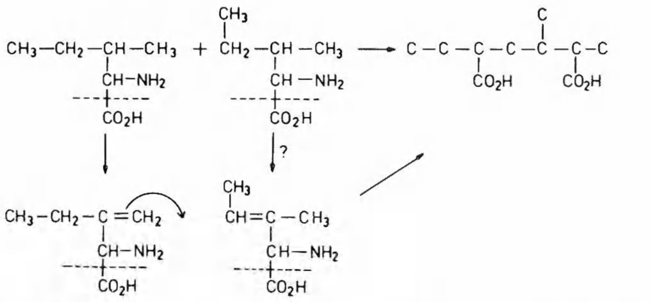

Fig. 8. Biosynthesis of senecic acid from isoleucine.

These authors have proposed an attractive scheme for the linking of the C_5 units in which β-methylenenorvaline is activated as a pyridoxal derivative and reacts with an electrophilic carbon of the right-hand C_5 unit. The latter may undergo linking as the isomeric $\beta\gamma$-dehydroisoleucine, $CH_3CH=C(CH_3)CH(NH_2)CO_2H$ (Crout, personal communication).

The acids of types A and B have not been investigated to the same extent. Both appear to have the right-hand C_5 unit of type C and the specific incorporation of threonine and isoleucine into monocrotalic acid (type B) has been demonstrated (Robins et al. 1974). The other three carbons of monocrotalic acid were thought at first to be propionate derived but propionate is

Table 4. Distribution of esters of pyrrolizidine aminoalcohols with aryl and aralkyl acids. [1]Lüning 1974, [2]Bull et al. 1968, [3]Païs et al. 1971.

Family/subfamily	Tribe	Genus
Apocynaceae		
Echitoideae	Nerieae	*Alafia*[3]
Orchidaceae		
Monandrae	Kerosphaereae	*Doritis*[1] *Hammarbya*[1] *Kingiella*[1] *Liparis*[1] *Malaxis*[1] *Phalaenopsis*[1] *Trichoglottis*[1] *Vanda*[1] *Vandopsis*[1]
Santalaceae		*Thesium*[2]
Sapotaceae		*Planchonella*[2]

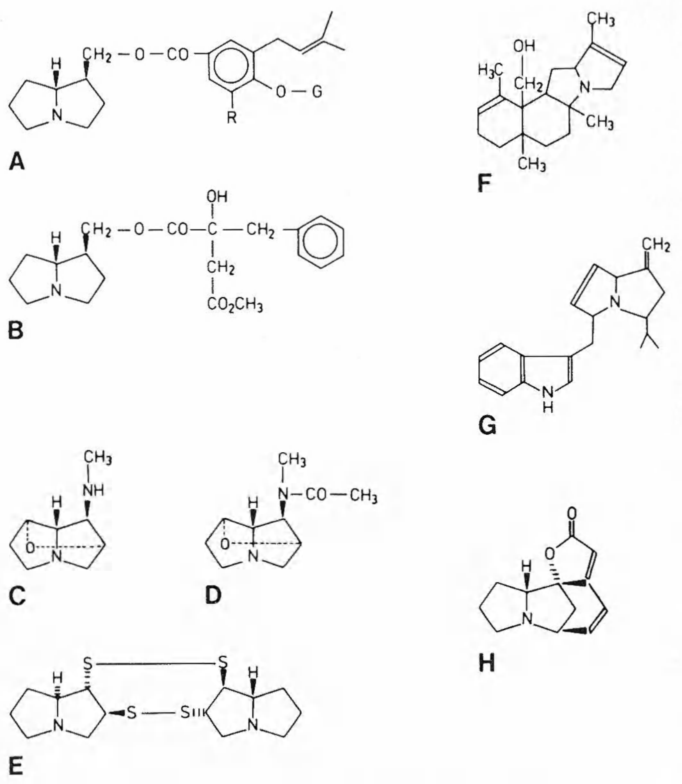

Fig. 9. A–B: Esters of aminoalcohols with aryl and aralkyl acids. – C–E: 1-amino-pyrrolizidine alkaloids and cassipourine. – F–H: Miscellaneous pyrrolizidine alkaloids of different origin. – A: Malaxine, R = H, G = glucosyl; grandifoline, R = $-CH_2CH=C(CH_3)_2$, G = 2-O-(glucopyranosyl)-arabinopyranosyl; keitaoine, R = OCH_3, G = glucosyl; auriculine, R = $-CH_2CH=C(CH_3)_2$, G = glucosyl. – B: Phalaenopsine-La. – C: Loline. – D: Lolinine. – E: Cassipourine. – F: Thelepogine. – G: Peduncularine. – H: Norsecurinine.

now known to be non-specifically incorporated (Crout, personal communication). In trichodesmine, the asymmetric carbon atoms in the right hand C_5 unit have the same configuration as in monocrotaline (Robins & Crout 1969), leading to an expectation that the C_5 unit in this alkaloid, with a type A acid, has the same origin. Crout's present view is that the acids of type A and B are derived from leucine (left-hand C_5 unit) and isoleucine (right-hand C_5 unit) and that those of type B have undergone removal of some of the carbon atoms. Dicrotalic acid (type B) is β-hydroxy-β-methylglutaric acid, an intermediate on the pathway to mevalonic acid, and so has a possible alternative origin.

So far there is no firm knowledge of the time sequence of formation of the acids in relation to the esterification of the aminoalcohols and formation of the macrocyclic ring. Until recently, opinion has favoured the preliminary formation of a diester with two separate C_5 units. Ring closure would then occur by linking the C_5 units. Sarracine (Fig. 5 A), an atypical alkaloid in a genus rich in macrocyclic alkaloids, has seemed to be a model for the intermediate diester. There is also an obvious relationship with the diesters typical of the Boraginaceae (Fig. 3), for which the different right-hand esterifying acid may prevent macro-ring formation. The occurrence in the Boraginaceae of strigosine and curassavine with their apparent isoleucine origin (Fig. 5), as well as that of the macrocyclic alkaloids trichodesmine and incanine (Fig. 6 C), strengthen the suggestion of a similarity in origin of these two main groups of pyrrolizidine alkaloids. Although the variations in carbon skeletons of the dicarboxylic acids imply a measure of flexibility in the coupling of the C_5 units, the recent evidence and views of Crout require that the C_{10} skeleton is assembled before the left-hand ester link at least. Further evidence on the complex origins of these alkaloids must be awaited.

Esters with aryl and aralkyl acids. Apart from laburnine benzoate and thesinine and its dimer, thesine, which are isolated occurrences in the Sapotaceae and Santalaceae respectively, this group consists of benzylsuccinic and substituted benzoic esters unique to the Orchidaceae (Table 4, Fig. 9 A, B). The acids are frequently combined with sugars to form glycosides. The benzyl-succinic acid which occurs in phalaenopsine-

Table 5. Distribution of 1-aminopyrrolizidine derivatives. [1]Bull et al. 1968.

Family/subfamily	Tribe	Genus
Gramineae	Festuceae	*Festuca*[1]
	Triticeae	*Lolium*[1]
Leguminosae		
Papilionoideae	Genisteae	*Adenocarpus*[1]
		(*Cytisus*)[1]
Rhizophoraceae		*Cassipourea*[1]

Table 6. Distribution of fused ring pyrrolizidine derivatives. [1]Bull et al. 1968, [2]Bick et al. 1971, [3]Rouffiac & Parello 1969, [4]Saito et al. 1965.

Family	Tribe	Genus
Gramineae	Andropogoneae	*Thelepogon*[1]
Elaeocarpaceae		*Aristotelia*[2]
Euphorbiaceae		*Phyllanthus*[3]
		Securinega[4]

La is probably derived from phenylalanine and acetate (Lüning 1974).

1-aminopyrrolizidine derivatives. This group consists basically of several N-alkyl and N-acyl derivatives of 1-amino-2,7-epoxypyrrolizidine (Fig. 9 C, D) which are found in *Lolium* and *Festuca* (Gramineae) and in *Adenocarpus*, possibly also *Cytisus*, of the Leguminosae (Table 5). The *Cytisus* alkaloid is a pyrrolizidine derivative of similar type but whether the point of attachment of the amino grouping is at C1 or C2 has not been definitely settled (Neuner-Jehle et al. 1965). They are generally regarded as having a different origin from the other pyrrolizidine alkaloids but it is possible that they are derived from the ordinary aminoalcohols by a specific pathway. The case for the latter suggestion is strengthened by their occurrence in *Adenocarpus*, a member of the same tribe (Genisteae) as the main pyrrolizidine source, *Crotalaria*.

The alkaloid cassipourine (Fig. 9 E), from the genus *Cassipourea* (Rhizophoraceae), has also been included in this group. Although not a 1-aminopyrrolizidine derivative, it has sulphur atoms substituted at C1 and C2 where the loline alkaloids have nitrogen and oxygen. The functionality is thus of similar type and suggests a similar biogenetic origin.

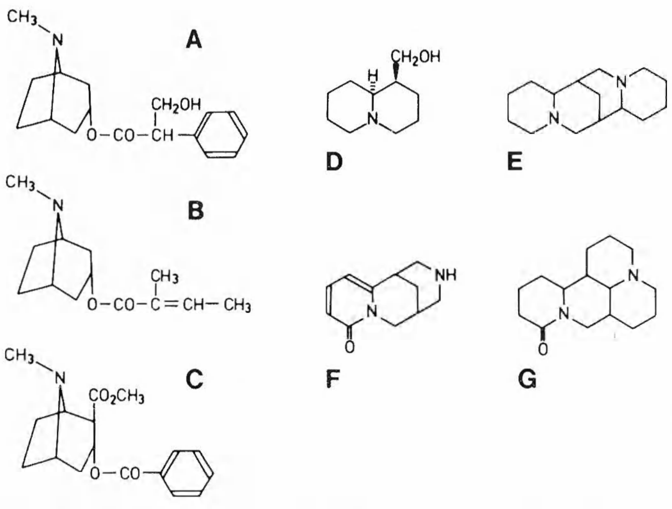

Fig. 10. A–C: Some typical tropane alkaloids. – D–G: Quinolizidine alkaloids structurally related to the pyrrolizidine group. – A: Hyoscyamine. – B: Tigloidine. – C: Cocaine. – D: Lupinine. – E: Sparteine. – F: Cytisine. – G: Matrine.

Miscellaneous pyrrolizidine derivatives. Several occurrences are known of unusual pyrrolizidine derivatives in the Gramineae, Elaeocarpaceae and Euphorbiaceae: thelepogine (Fig. 9 F), in *Thelepogon elegans,* peduncularine (Fig. 9 G) in *Aristotelia peduncularis,* norsecurinine (Fig. 9 H) and dihydronorsecurinine in *Securinega virosa* and the enantiomer of norsecurinine in *Phyllanthus niruri* (Table 6). The presence of a pyrrolizidine ring in these alkaloids appears to be a chance event and the group is regarded as biogenetically unrelated to the other pyrrolizidine alkaloids.

Relationships between the pyrrolizidine group and other alkaloids

Tropane alkaloids. The tropane alkaloids (Fig. 10 A–C) have a ring system closely related to pyrrolizidine and have other points of resemblance to pyrrolizidine alkaloids in that the ring is usually hydroxylated and esterified. Some of the esterifying acids are of the type derivable from isoleucine and valine as in the pyrrolizidine alkaloids. However the experimental evidence points to formation of the tropane ring from one ornithine unit and acetoacetate with subsequent esterification (Liebisch 1969, Leete 1972). The tiglic acid present in some alkaloids is derived as in pyrrolizidine alkaloids from isoleucine. Tropic acid, as shown by incorporation experiments, may be fully derived from phenylalanine or from tryptophane and is also derivable from phenylacetic acid plus a C_1 unit (Herbert 1974). The tropane alkaloids are found almost entirely in the Solanaceae, with occurrences also in *Convolvulus* (Convolvulaceae), *Erythroxylum* (Erythroxylaceae) and *Bruguiera* (Rhizophoraceae) (Boit 1961, Loder & Russell 1969), and some other taxa (Romeike 1978).

Quinolizidine alkaloids. The quinolizidine alkaloids also show a formal relationship to the pyrrolizidines in having a nitrogen atom at a bridgehead position and, in the case of lupinine and epilupinine, a similar side-chain CH_2OH.

A recent review of chemotaxonomic aspects of this alkaloid group (Schwarting 1974) points out that it is diverse structurally and in its precursor substances. Only the alkaloids such as lupinine, sparteine and matrine (Fig. 10 D, E, G), typical of the Leguminosae (tribes Sophoreae, Podalyrieae and Genisteae) and occurring also in isolated genera of the Berberidaceae, Chenopodiaceae and Solanaceae, show relationship with the pyrrolizidine group. They are derived from lysine, cadaverine or an equivalent (Schütte 1960, 1961), and are in this sense homologues of the pyrrolizidines.

Pyrrolizidine alkaloids and taxonomy

Boraginaceae. There are no instances in the Boraginaceae known to the author in which problems of taxonomy would be assisted by use of the currently known alkaloid data. However the very widespread, possibly almost universal, occurrence of the pyrrolizidine ester alkaloids in this family (as restricted to the subfamilies, Heliotropioideae and Boraginoideae) may be of value in considering the classification of some genera.

Compositae. The very high, possibly universal, incidence of pyrrolizidine ester alkaloids in the tribe Senecioneae, is of value in deciding to which tribes of the Compositae certain genera belong (Robins 1977 pp. 840–842). There appear to be current differences of opinion about the limits of the Senecioneae (e.g. Herout 1974, Powell & Turner 1974, Seigler et al. 1974) and it seems important that a character which has previously been uniform and consistent should be taken into account along with the other two chemical markers known for this tribe – the presence of furanoeremophilane sesquiterpenes (Herout 1974) and the absence of acetylenic compounds which characterise other tribes of the Compositae (Sörensen 1963, 1974).

The genus *Adenostyles* was classified at one time in the Eupatorieae whereas the chemical evidence indicates that it should be in the Senecioneae. Herout (1974) has reported that it contains furanoeremophilane derivatives found in the Senecioneae but not in the Eupatorieae. The presence of pyrrolizidine alkaloids in the genus is evident from the recent re-naming of *Senecio rhombifolius* (Willd.) Sch. Bip., which contains typical macrocyclic diesters, as *Adenostyles rhombifolia* (Willd.) M. Pimen. (Pimenov et al. 1975). Fortunately, it seems that taxonomists are also agreed that *Adenostyles* is properly classified in the Senecioneae (Merxmüller 1974).

Arnica is currently in the Senecioneae but its position has been questioned. Merxmüller (1974) has quoted serological incompatibility and Sörensen (1974) has pointed to the presence of acetylenic compounds which are extremely rare in the Senecioneae. On the other hand, Turner (1974) supported its retention for reasons relating to a broader view of the morphological boundaries of the tribe. The presence of alkaloids of unknown structure in *Arnica montana* was reported some years ago by the present author (Bull et al. 1968). A recent re-examination has shown that the alkaloids are not pyrrolizidine derivatives and they differ also from N-ethoxycarbonyl-L-prolinamide reported to occur in this species by Holub et al. (1977). Thus in this instance, the chemical evidence is fully consistent with transfer of *Arnica* to another tribe.

The classification of *Tussilago* in the Senecioneae was queried by Herout (1974) because of the absence of furanoeremophilanes. However it was recognised that one negative finding carried little weight and the present author has since found a pyrrolizidine diester typical of the Senecioneae in *Tussilago farfara* (Culvenor et al. 1976). The position of *Tussilago* can therefore be regarded as satisfactory.

Powell & Turner (1974) have proposed the transfer of the subtribe Peritylinae from the Helenieae to the Senecioneae, on mainly morpho-

Table 7. Pyrrolizidine alkaloid occurrences at the level of order and superorder in the system of Dahlgren (1975).

Superorder	Order	Family
Dicotyledons		
Asteranae	Asterales	Compositae
Celastranae	Celastrales	Celastraceae
	Santalales	Santalaceae
Gentiananae	Gentianales	Apocynaceae
Lamianae	Scrophulariales	Scrophulariaceae
Myrtanae	Myrtales	Rhizophoraceae
Primulanae	Ebenales	Sapotaceae
Ranunculanae	Ranunculales	Ranunculaceae
Rosanae	Fabales	Leguminosae
Solananae	Solanales	Boraginaceae
Monocotyledons		
Commelinanae	Poales	Gramineae
Lilianae	Orchidales	Orchidaceae

logical grounds. An examination of the alkaloids and other secondary metabolites of the genera concerned should be made before reaching decision on the transfer. Seigler et al. (1974) investigated *Hulsea,* at present classified in the tribe Helenieae, and *Arnica,* said to show an affinity with *Hulsea,* by means of alkaloid precipitation tests and obtained negative results. Unfortunately, such simple tests are an unreliable guide to the presence of alkaloids of the pyrrolizidine group and a more sophisticated study is required.

Leguminosae. The genus *Crotalaria* is another prolific source of pyrrolizidine alkaloids. Although there is a greater degree of structural diversity than in the alkaloids of the Boraginaceae and Senecioneae, the presence of pyrrolizidine alkaloids derived from the aminoalcohols is highly characteristic of this genus within the Leguminosae. Alkaloids of the loline-type occur in *Adenocarpus* and *Cytisus,* genera in the same tribe, Genisteae, but not in *Crotalaria.* Virtually all *Crotalaria* species which have been investigated contain pyrrolizidine alkaloids and no other type of alkaloid has been isolated from the many species studied in detail.

The alkaloids are of value in considering affinities between *Crotalaria* species. The series *Simplicifoliae* contains mostly glutaric-type macrocyclic diesters, some adipic-type macrocyclic diesters and in one species *(C. verrucosa,* subseries *Eriocarpae),* 1-methylenepyrrolizidine. In the series *Unifoliolatae,* only glutaric-type macrocyclic diesters have been recorded. The series *Digitatae,* subseries *Dispermae,* is characterised by methyl ether alkaloids. The subseries *Polyspermae* of the *Digitatae* is rather diverse and contains both types of macrocyclic diester and the 1-methylenepyrrolizidine alkaloids.

Phylogenetic significance

The pyrrolizidine alkaloids have a scattered distribution in the plant kingdom. Excluding the fused-ring group which is regarded as probably irrelevant, the 12 plant families in which they have been found are in 12 different orders. In the system of Dahlgren (1975), the 12 orders are in 11 different superorders (Table 7), indicating the tenuous relationship between the families concerned. In Fig. 15, the orders in which these alkaloids occur are marked on a pictorial representation of the Dahlgren classification of angiosperms. Two of the orders are in the superorder Celastranae but little significance attaches to this because both occurrences are isolated instances in a single genus. The only point which can be made is that the orders of two of the families which contain many pyrrolizidine alkaloids, the Boraginaceae (Solanales) and Compositae (Asterales) are adjacent in Fig. 11 even though in different superorders. It seems that at the level of the superorders, little significance can be drawn from pyrrolizidine alkaloid occurrences.

In the classifications of Cronquist (1968) and Takhtajan (1969), the plant orders are arranged in subclasses which are only 10 in number compared with Dahlgren's 34 superorders. In these larger groupings, the pyrrolizidine occurrences show a recognisable pattern. Although the pyrrolizidine-containing families are again in different orders, the orders come under two main subclasses, the Rosidae and Asteridae (Table 8). The table includes the occurrence of the four significant structural types of alkaloids at family level and it is seen that the two principal types, the aliphatic monocarboxylic esters and the macrocyclic diesters are concentrated in the Asteridae. The other main occurrence of these esters is in the Rosidae (Leguminosae), for which, in Cronquist's opinion, there is increasing evidence of an ancestral relationship with the Asteridae.

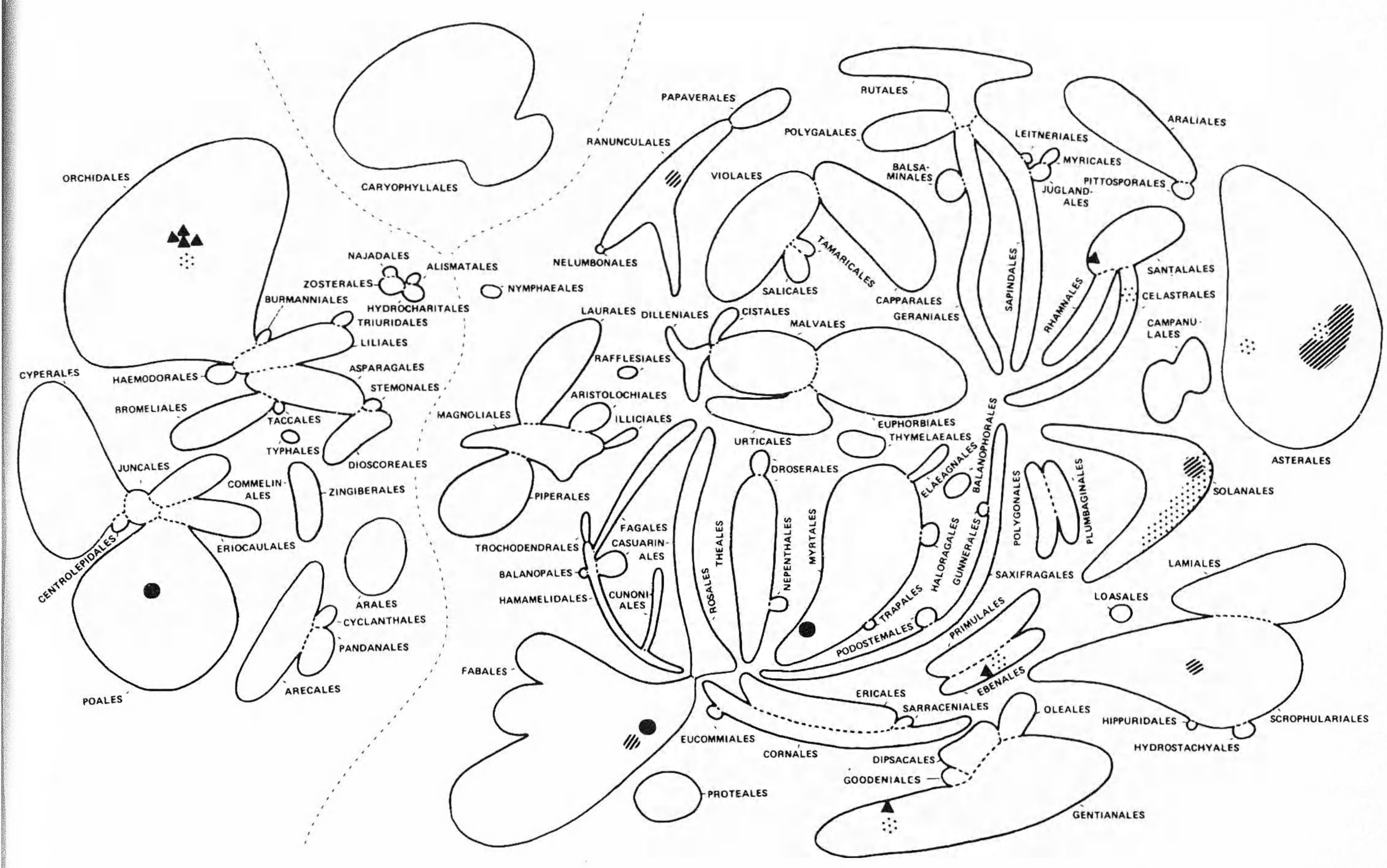

Fig. 11. Pictorial representation of pyrrolizidine alkaloid occurrences in the Dahlgren classification of angiosperms. – Dotted areas: esters with aliphatic monocarboxylic acids. – Hatched areas: macrocyclic diesters. – Triangles: esters with aryl and aralkyl acids. – Solid black areas: 1-aminopyrrolizidine derivatives.

Table 8. Pyrrolizidine alkaloid occurrences at the level of order and subclass in the system of Cronquist (1968). – (a) aliphatic monocarboxylic esters, (b) macrocyclic diesters, (c) esters of aryl and aralkyl acids, (d) 1-aminopyrrolizidine derivatives.

Subclass	Order	Family	Alkaloid type			
			a	b	c	d
DICOTYLEDONS						
Magnoliidae	Ranunculales	Ranunculaceae		+		
Dilleniidae	Ebenales	Sapotaceae	+		+	
Rosidae	Rosales	Leguminosae		++		+
	Cornales	Rhizophoraceae				+
	Santalales	Santalaceae			+	
	Celastrales	Celastraceae	+			
Asteridae	Gentianales	Apocynaceae	+		+	
	Lamiales	Boraginaceae	++	+		
	Scrophulariales	Scrophulariaceae		+		
	Asterales	Compositae	+	++		
MONOCOTYLEDONS						
Liliidae	Orchidales	Orchidaceae	+		++	
Commelinidae	Cyperales	Gramineae				+

However the genus *Crotalaria* (Leguminosae) is quite distant from the other main pyrrolizidine-producing taxa with little morphological evidence for a closer relationship and thus for a common origin.

Within the Asteridae, the occurrence of the same α-isopropylbutyric ester alkaloids in the Boraginaceae, the Eupatorieae (Compositae) and the Parsonsieae (Apocynaceae, subfamily Echitoideae) has a significance enhanced by the use made of these alkaloids by insects (Edgar et al. 1974). The alkaloids concerned are the source of a mating pheromone for adult male Danaid butterflies which, although living as larvae on plants containing cardenolides (mainly in the Asclepiadaceae), must seek out pyrrolizidine-containing plants and ingest the alkaloids before they become capable of mating. This dual chemical requirement led to the suggestion that the genera or families concerned are derived from a common ancestor which contained the same type of alkaloid as well as the cardenolides, and the double dependency of the Danaids arose as the ancestral genus split into two lines, each containing one of the required chemical constituents. The Apocynaceae are a key element in this suggestion because the family is closely related to the Asclepiadaceae and the subfamily Echitoideae in which the pyrrolizidine alkaloids occur is known to contain cardenolides also. The Apocynaceae has a greater resemblance to the ancestral genus than the Boraginaceae and Compositae and certain of its genera such as *Parsonsia* and *Urechites (Fernaldia)* probably elaborate both the requirements of the Danaid butterflies. However, the genetic capability for producing pyrrolizidine alkaloids of this type in the Apocynaceae has apparently been retained or expressed only in the subfamily Echitoideae and there not consistently. In the system of Dahlgren, the Boraginaceae and Compositae are in orders which are adjacent although in different superorders, but the Apocynaceae is regarded as being at a distance in the order Gentianales. A relationship between the three families is not suggested.

Considerable interest attaches also to the co-occurrence of adipic-type macrocyclic diester alkaloids in *Crotalaria* and in the Senecioneae (Compositae) and of glutaric-type diesters in *Crotalaria* and the Boraginaceae. A high degree of coincidence is involved in alkaloids which combine the pyrrolizidine aminoalcohols and such biogenetically complex and unusual acids. Have the sympetalous families retained a genetic capability present already in common ancestors with the Leguminosae, or has the capability been developed independently in the Leguminosae and the sympetalous groups? There can be no conclusive answer to this question at the present time. However, one must recognise that with alkaloids as biologically active as the esters of the 1,2-unsaturated aminoalcohols (they produce chronic hepatotoxic and pneumotoxic effects and are mutagenic and carcinogenic), natural selection could exert a powerful directing influence in biosynthesis.

Little significance can be read into the pyrrolizidine occurrences in the monocotyledon families, Orchidaceae and Gramineae, because any suggested links with dicotyledon families may stretch credulity from a morphological viewpoint. However the formation of pyrrolizidine esters is a well-established trait among genera of the Orchidaceae and this takes its place alongside pollination mechanisms as a second point of similarity between the Orchidaceae and the Apocynaceae-Asclepiadaceae complex (or an immediate ancestor). The formation of the unusual loline-type alkaloids in both the Gramineae and the Leguminosae is another intriguing coincidence.

The distribution of pyrrolizidine alkaloids sheds only a meagre light on the phylogeny of angiosperms at the present time but there are obviously areas in which useful contributions may be expected in the future. Perhaps they may come with attempts to explain in evolutionary terms the characteristic appearance of the same complex alkaloid structures in one or two genera of single families of morphologically distant orders.

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Embryology of Ursinia (Compositae)

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The genus *Ursinia* Gaertn. has a monosporic, 8-nucleate embryo sac of the Polygonum type. A synergid haustorium is always present. The upper antipodal cell is binucleate, the lower one uninucleate; a secondary nuclear division may take place. Both antipodes or more often the upper one alone, grow considerably with age. They are supposed to function as haustoria. The cells of the integumentary tapetum become strongly elongated radially. The endosperm is of the Nuclear type. The results point to affinities with the Anthemideae, or possibly the Heliantheae, rather than with the Arctoteae, in which the genus has been placed previously. The chromosome number for *U. cakilefolia* DC. and *U. chrysanthemoides* (L.) Poir. var. *geyeri* (Bolus & Hall) Prassler is n = 8.

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The genus *Ursinia* Gaertn. occurs mainly in the Cape Province of S Africa. A few species reach S Namibia, and one species occurs in Ethiopia (Prassler 1967).

There has been a great deal of uncertainty about the correct systematic position of the genus. Hoffmann (1894) thought that *Ursinia* was definitely anthemideous in habit and in style shape, although he followed Bentham & Hooker (1873) and referred it to the tribe Arctoteae, partly owing to its well developed pappus. So too did Small (1919), who considered that *Ursinia* forms a link to the Senecioneae. On a basis of the gross morphological and anatomical characters, Beauverd (1915) united *Ursinia* with the Anthemideae. Recent studies of fruit characters (Reitbrecht 1974) and of pollen morphology (Stix 1960) have lead to the same conclusion. However, Skvarla et al. (1977) state that the pollen of *Ursinia* is of Senecioid type, though they discuss the genus in connection with the Arctoteae. Greger (1977), Hegnauer (1977), Mabry & Bohlmann (1977) and Valadon (1977) all report that *Ursinia,* together with six other S African genera, lacks polyacetylenes but contains characteristic furansesquiterpenes; this makes their placement in Anthemideae uncertain. Cronquist (1955) regarded the peripheral flowers of the heads of *Ursinia* as true ray florets and discussed possible relationships to both Anthemideae and Arctoteae; while Carlquist (1976) regards them instead as ligulate disc florets and consequently refers *Ursinia* to the tribe Arctoteae (Cichorioideae).

Robinson & Brettell (1973) consider that *Ursinia* is fairly closely related to the Anthemideae. Nevertheless, they preferred to create a new, monogeneric tribe, the Ursinieae, because of the very specialised anther appendages and its pappus and pollen structures. Taking into account the resemblances in the microcharacteristics of the ligule cells, fruit characters, pollen morphology and chemical constituents, Baagøe (1977 a) expanded the Ursinieae to include seven other African Compositae genera. Baagøe (1977 a, b) thinks that *Ursinia* finds a more natural place near to the Arctoteae-Calenduleae than it does with the Anthemideae.

Like Stapf (1933) some authors recognize two distinct genera, *Ursinia* and *Sphenogyne* R. Br. for the species concerned here. Prassler (1967) treats *Sphenogyne* as a subgenus of *Ursinia*, owing to the absence of good diagnostic characters.

Ursinia anthemoides has been studied embryologically by Dahlgren (1924) and Schürhoff (1926). Both authors noted the presence of a synergid haustorium and of a giant antipode, and a Nuclear type of endosperm formation; Schürhoff (1926) supposed that the giant antipode functions as a haustorium.

The chromosome number is n = 8 in all taxa of *Ursinia* investigated, except for *U. anthemoides* ssp. *anthemoides*, for which n = 7 was found (Haesler 1967, Nordenstam 1967, 1969).

In the present investigation macrosporogenesis, development of the embryo sac and to some extent the endosperm formation of some *Ursinia* species were studied. The purpose was to find out whether or not embryological characters could shed new light on the classification problems. Of the species investigated, *U. anthemoides* (L.) Poir. belongs to subgen. *Sphenogyne* (R. Br.) Prassler, *U. cakilefolia* DC. and *U. chrysanthemoides* (Less.) Harv. to subgen. *Ursinia*.

Material and methods

Material was grown in Göteborg in 1967 from achenes originating from the Botanical Gardens of Bonn and Uppsala *(Ursinia anthemoides* subsp. *anthemoides)* and from the National Botanic Gardens, Kirstenbosch, S Africa *(U. anthemoides* subsp. *versicolor, U. cakilefolia).* Material from flowering plants in the Botanical Garden at Copenhagen (*U. anthemoides* subsp. *anthemoides* and subsp. *versicolor;* 1967), in the Bergius Botanical Garden, Stockholm (*U. anthemoides* subsp. *anthemoides, U. chrysanthemoides;* 1967) and the Royal Botanic Gardens, Kew (*U. chrysanthemoides;* 1966) was also fixed.

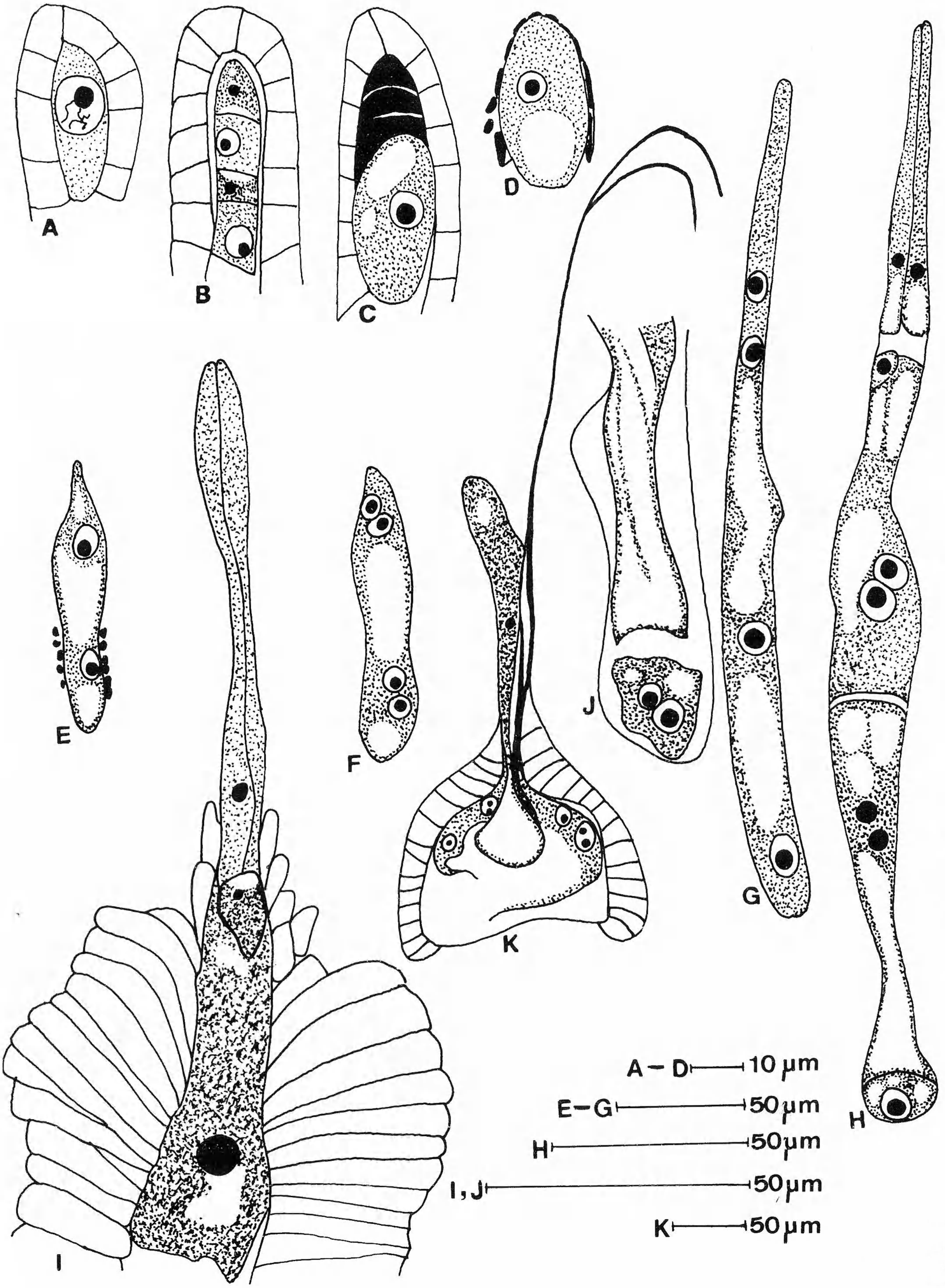
The specimens were identified by Dr Maria Prassler, München. Voucher specimens, as well as the slides studied, are deposited at the Department of Systematic Botany, University of Göteborg.

Buds and flower heads were trimmed to rectangular shape with a razor blade and prefixed in Carnoy's solution for ten seconds at most. The final fixation was made in Navashin-Karpeschenko's fluid. After dehydration and infiltration the material was embedded in paraffin wax and cut by a microtome into sections 10–16 μm thick (varying according to the developmental stage of the flowerheads). Staining was in Fast Green–Safranin–Gentian Violet.

Ursinia anthemoides subsp. anthemoides

The archespore is 1-celled (Fig. 1 A). The meiotic divisions give rise to a linear tetrad of megaspores (Fig. 1 B), of which the chalazal one develops into an embryo sac, while the others degenerate (Fig. 1 C). Embryo sac development is monosporic, of the Polygonum type. The nucellar epidermis begins to degenerate already during the tetrad stage and very little remains when the embryo sac reaches the 2-nucleate stage (Fig. 1 D, E). The embryo sac now begins to increase in length and becomes narrowed apically when the micropyle is penetrated. Large vacuoles occur at this stage (Fig. 1 E). The 2 + 2-position of the nuclei in the early 4-nucleate stages (Fig. 1 F) always changes to a 2 + 1 + 1-position in later ones (Fig. 1 G). In the organized embryo sac, the two antipodes invariably lie one above the other. The upper antipode is primarily 2-nucleate and much larger than the 1-nucleate, lower one (Fig. 1 H). At the time of fusion of the polar nuclei the upper antipode usually undergoes a conspicuous vacuolization, in connection with an increase in length in the chalazal direction (Fig. 1 H). Meanwhile the basal antipode seems to penetrate through the surrounding tissue, often obliquely in relation to the length-axis of the embryo sac. In consequence, the basal antipode gets a very winding course and the surrounding tissues have a disrupted look. Many serial sections have to be studied in order to discover the basal antipode and its nucleus. In later stages the upper antipode increases enormously in length, and sometimes one or both of its nuclei divide. The basal antipode sometimes becomes 2-nucleate and partially vacuolized (Fig. 1 J). The unfertilized egg cell is not very conspicuous (Fig. 1 H, 1 I). The synergids are very long and narrow and extend well up into the micropyle. When the egg cell has been fertilized, one of the synergids seems to degenerate, while the other one extends half-way

Fig. 1. *Ursinia anthemoides* subsp. *anthemoides*. – A: Megaspore mother cell. – B: Tetrad. – C: Old tetrad with functional megaspore. – D: 1-nucleate embryo sac. – E: 2-nucleate embryo sac. – F, G: 4-nucleate embryo sacs. – H: 8-nucleate embryo sac. – I: Upper part of an 8-nucleate embryo sac with elongated synergids; integumentary tapetum. – J: Lowermost part of an 8-nucleate embryo sac with the basal antipode in a two-nucleate stage. – K: Upper part of an embryo sac with free endosperm nuclei in the endosperm chamber and a synergid haustorium.


A
B
C
D
E
F
G
H
I
J
K
A – D 10 µm
E – G 50 µm
H 50 µm
I, J 50 µm
K 50 µm

up the micropyle and later penetrates the surrounding tissues on the side facing the funiculus (Fig. 1 K). The basal part of the synergid is then bladderlike. The synergid obviously has an haustorial function. The endosperm is Nuclear (Fig. 1 K). The integumentary tapetum is well-developed by the time the embryo sac has become organized (Fig. 1 I, K).

Ursinia anthemoides subsp. **versicolor** (DC.) Prassler

The archespore is usually 1-celled, but in a few cases tetrads with degenerating cells adjacent to the megaspores have been observed; this may indicate that the archespore sometimes consists of more than one cell. The embryo sac development is similar to that of subsp. *anthemoides*. There are always two antipodes; the upper one is the larger and is 2-nucleate. A division of both the nuclei of this antipode may occur before fusion of the polar nuclei occurs (Fig. 2 A). The upper antipode becomes vacuolized and increases in size, while the basal one remains small, 1-nucleate (Fig. 2 A, B) and shows no signs of vaculoization; it is probably displaced by the upper one. During the later stages of endosperm development, both antipodes are displaced towards the chalaza, are pressed together and eventually degenerate. During the initial phases of this process the antipodal nuclei are still present, but later on disappear. The endosperm is Nuclear (Fig. 2 C, D). At first the nuclei lie in narrow plasma strings along the walls of the embryo sac; later on the endosperm chamber lengthens enormously and becomes filled successively with free nuclei. Cell wall formation beings apically, in the vicinity of the proembryo. During endosperm development the surrounding tissue degenerates to yield a confused mass of crowded and disintegrating cells and is probably consumed as nourishment for the endosperm. One of the synergids degenerates, while the other one forms a well-developed haustorium which is closely connected with the proembryo (Fig. 2 C, D).

Ursinia cakilefolia

The archespore is mostly 1-celled (Fig. 3 A) but may sometimes be multicellular, since degenerating tetrads have been observed adjacent to the embryo sacs (Fig. 3 E). The tetrad is linear (Fig. 3 B) and in most cases the chalazal megaspore forms the embryo sac (Fig. 3 C). The development of the embryo sac is monosporic and of the Polygonum type (Fig. 3 C–F). The organized embryo sac has two antipodes, which may be equal in size (Fig. 3 F). The upper one is 2-nucleate but secondary nuclear divisions may occur, resulting in a 4-nucleate antipode. The lower antipode is 1-nucleate but may become secondarily 2-nucleate. Vacuolization of the antipodes, as well as of the endosperm chamber, suggests that a considerable increase in length of the embryo sac occurs. Endosperm stages have not been observed.

The chromosome number n = 8 was determined from pollen mother cells (Fig. 3 G).

Ursinia chrysanthemoides var. **geyeri** (Bolus & Hall) Prassler

The archespore is 1-celled (Fig. 4 A). The first division results in the formation of two dyad cells (Fig. 4 B); thereafter a linear tetrad is formed. The chalazal megaspore develops into the embryo sac (Fig. 4 C); this development is monosporic and of the Polygonum type (Fig. 4 C–F; D and E show early phases, in which the nuclei have not yet reached their final destinations). The organized embryo sac (Fig. 4 F) has two equal-sized antipodes; both are vacuolized. The lower antipode, 1-nucleate, sometimes becomes 2-nucleate (Fig. 4 F); the upper on at times contains four nuclei. In later stages the embryo sacs often show degenerating antipodes. The synergids are elongated, as in the other taxa studied. One of them degenerates, the other one develops a haustorium and may almost fill the micropyle as far up as the funiculus. In young embryo sacs the egg cell is small; in older ones the synergid haustorium is in contact with the proembryo (Fig. 4 G). The endosperm is Nuclear (Fig. 4 G). The integumentary tapetum disintegrates and becomes consumed, except around the uppermost part of the endosperm chamber (Fig. 4 G).

The chromosome number n = 8 was determined from pollen mother cells (Fig. 4 H).

Discussion

Status of Sphenogyne. The antipodes are exceedingly elongate and very dissimilar in size in

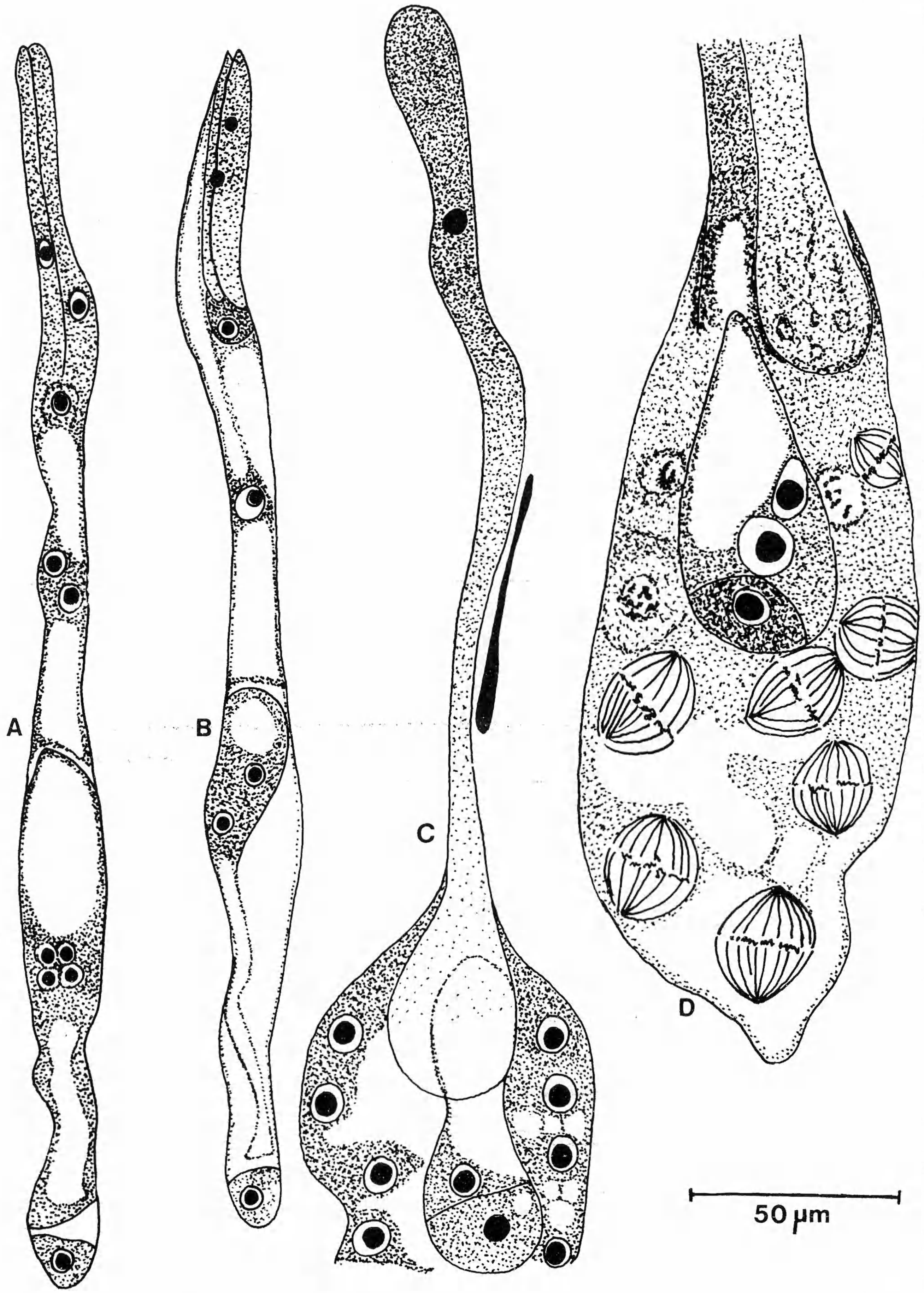


Fig. 2. *Ursinia anthemoides* subsp. *versicolor*. – A, B: Organized embryo sac with two antipodes. – C: Endosperm with proembryo and synergid haustorium. – D: Dividing endosperm nuclei, proembryo and the lowermost parts of the synergids. One of the synergids is degenerating.

Ursinia anthemoides (subgen. *Sphenogyne*), while they are equal in size and do not increase in length to the same extent in *U. cakilefolia* and *U. chrysanthemoides* (subgenus *Ursinia*). This suggests that a difference exists between the two subgenera; however, since a further 29 and 5 species, respectively, exist to be studied, no final conclusion can be drawn. On the other hand, elongate synergid haustoria are very rare in the Compositae and their presence in all the taxa investigated probably indicates a not-too-distant relationship.

Urisinia and Arctoteae-Arctotinae. From its gross morphology Hoffmann (1894) included *Ursinia* in the subtribe Arctotidinae (Arctotinae). The embryo sac development of *Arctotis* L., *Haplocarpha* Less. and *Arctotheca* Wendl. is monosporic and of the Polygonum type (Ahlstrand unpubl.). This represents similarity with *Ursinia;* however, the shape of the embryo sac in these genera is different from that of *Ursinia*. They all have three antipodes, which show no haustorial activity, and their synergids do not develop into haustoria. The Arctotoid pollen type and that of *Ursinia* have very different wall structures (Stix 1960, Skvarla et al. 1977). *Ursinia* contains no acetylenes, but such compounds are frequently present in Arctoteae (Valadon 1977). The basic chromosome numbers for the Arctotinae species hitherto investigated are x = 9 and 15 (Norlindh 1977). Thus, all evidence so far suggests that *Ursinia* should be excluded from the Arctoteae-Arctotinae.

Ursinia and Calenduleae. Synergid haustoria are present in *Calendula* (Schürhoff 1926). However, the young, organized embryo sacs of *Calendula* are much more rounded in shape than those of *Ursinia*. The synergids are short and their haustorial function is not evident until a late stage of development, particularly during endosperm formation. Since both genera are otherwise well separated morphologically, the presence of a synergid haustorium in both probably merely represents a case of parallel evolution. The embryo sac of *Dimorphotheca, Osteospermum* and *Chrysanthemoides* species is of the Polygonum type (Ahlstrand unpubl.); but there are primarily three antipodes present and no synergid haustoria. Stix (1960) found four different spinuloid pollen types in Calenduleae, three of which had holes in the spine-tips as in *Ursinia*. Skvarla et al. (1977) emphasize the thickened foot layer (nexine-1) of *Ursinia* pollen; this layer is thinner in Calenduleae (Stix 1960). Moreover, a nexine-2 layer is usually absent in *Ursinia,* but always present in Calenduleae, and is often furrowed internally. The basic chromosome numbers in the Mediterranean genus *Calendula* are x = 7, 8, 9, 11 and 15 (Ammal & Sobti 1962, Meusel & Ohle 1966). The remaining genera of Calenduleae have x = 8, 9, 10 and 12; x = 10 is the most usual number in the S African members (Norlindh 1963, 1977). Thus there is no evidence of any close relationship between *Ursinia* and any of the Calenduleae genera.

Ursinia and Anthemideae. The genera *Ormenis, Achillea, Anacyclus, Cladanthus, Lasiospermum* and *Lonas* of the subtribe Anthemidinae resemble *Ursinia* in having a Polygonum type of embryo sac development. However, there are generally three antipodes in these genera. A 1-celled archespore, which is the most common condition in the *Ursinia* species studied, is found only in a few *Anthemis* species and in *Lasiospermum radiatum* (Harling 1950, 1960). In the subtribe Chrysantheminae, some species of *Chrysanthemum* and all *Matricaria* species have a 1-celled archespore. The embryo sac development of the latter two genera is either mono-, bi- or tetrasporic. More than half of the species so far investigated have a monosporic embryo sac development of the Polygonum type. Some species have two antipodes, like *Ursinia*. The upper one is then 2-nucleate and secondary nuclear division, without cell wall formation, occurs (Harling 1951). However, in most of these species the basal antipode is larger than the upper one, whereas in *Ursinia* they are equal in size or the upper one is larger. These similarities do not necessarily indicate a true relationship, since they are rather generalized and both the number and shape of the antipodes are very variable within the Compositae as a whole (Schnarf 1931 p. 220).

Like *Ursinia, Cotula turbinata* develops a synergid haustorium and its embryo sac development is of the Polygonum type. It differs from *Ursinia* in possessing a many-celled archespore, three antipodes and a Cellular type of endosperm formation (Dahlgren 1924, Harling 1951, Davis 1966). Their relationship does not therefore appear to be a very close one.

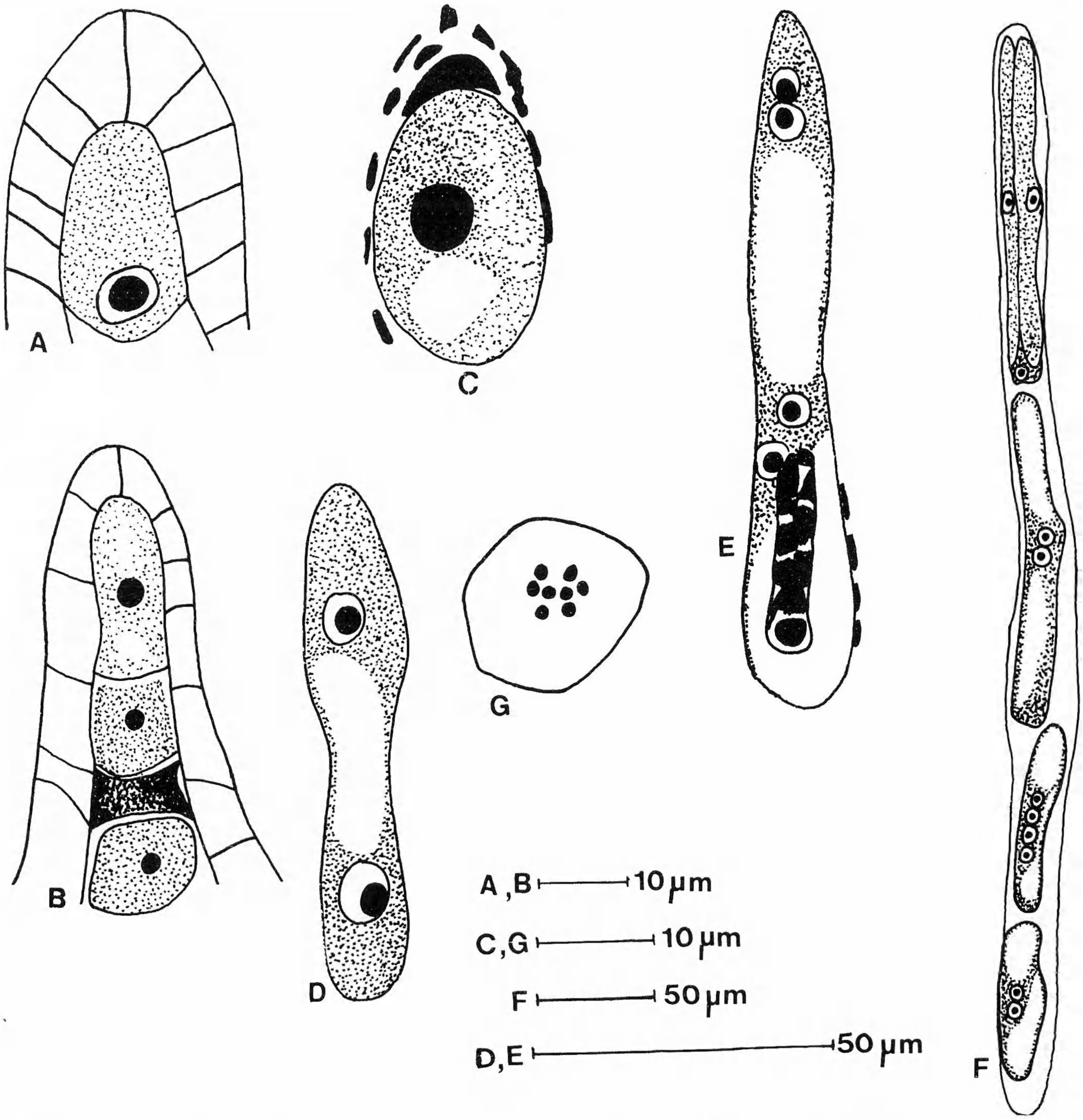


Fig. 3. *Ursinia cakilefolia.* – A: Megaspore mother cell. – B: Tetrad. – C: 1-nucleate embryo sac; degenerating cells of the nucellar epidermis and of the tetrad. – D: 2-nucleate embryo sac. – E: 4-nucleate embryo sac and remainders of a tetrad. – F: Embryo sac with secondarily divided antipode nuclei. – G: Pollen mother cell, metaphase, n = 8.

The Anthemideae can be divided into two groups on the epidermal cell structure of the corolla ligules (Baagøe 1977 a). One group, with papillose cells, roughly corresponds to the genera embryologically studied by Harling. *Ursinia* and *Lasiospermum* belong to the second group, with tabular epidermis cells and sessile, 1-celled glands on ligules and corollas (Beauverd 1915, Baagøe 1977 a). Possession of a polarized endothecial tissue is another similarity between these two genera (Nordenstam 1976). Except for the number of antipodes they have the same type of embryo sac development. Both genera contain sesquiterpenes, but no polyacetylenes, which are otherwise characteristic for the Anthemideae (Greger 1977). Probably they are interrelated.

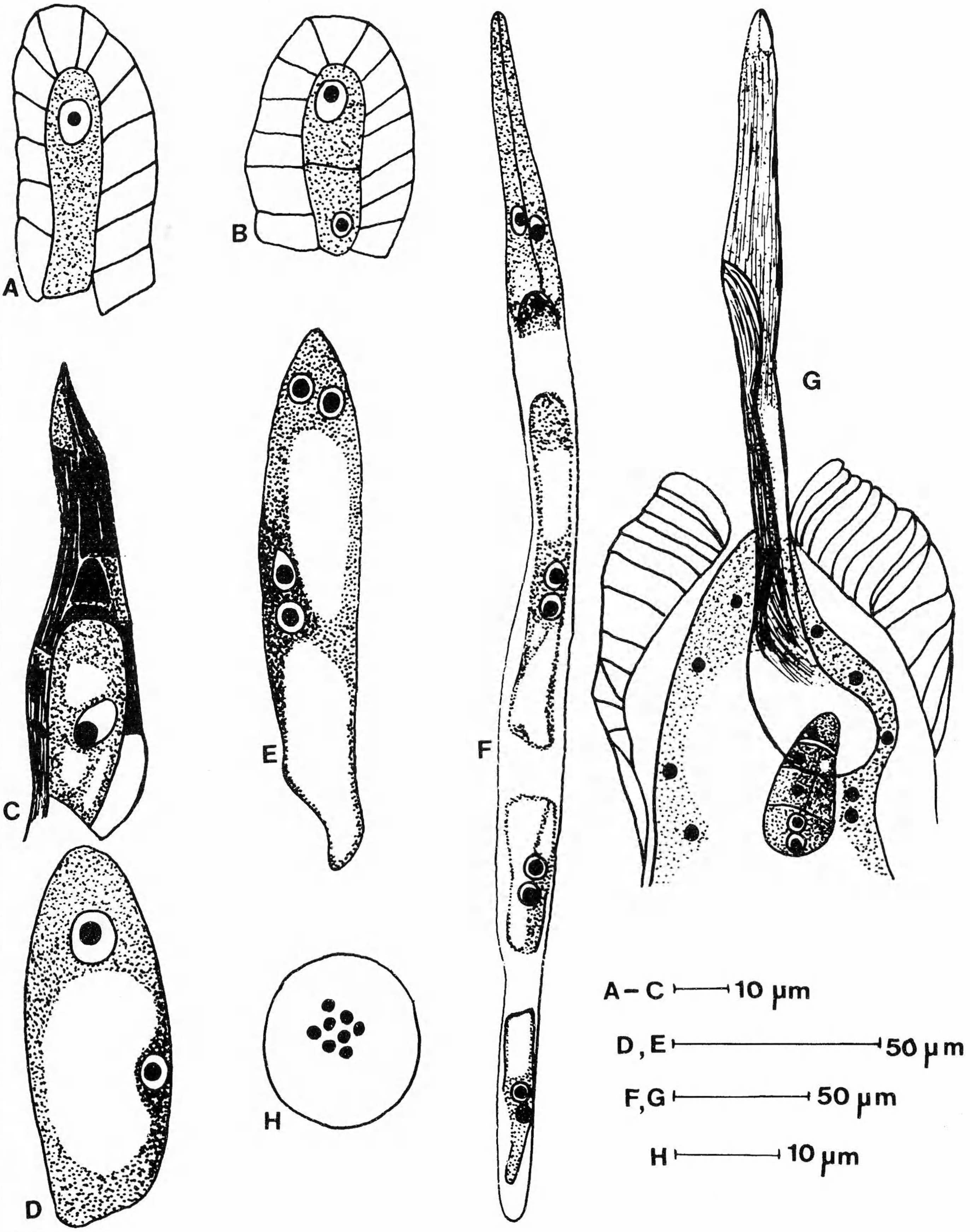


Fig. 4. *Ursinia chrysanthemoides* var. *geyeri*. – A: Megaspore mother cell. – B: Dyad. – C: 1-nucleate embryo sac; degenerating tetrad cells and nucellar epidermis cells. – D: 2-nucleate embryo sac. – E: Young 4-nucleate embryo sac. – F: Embryo sac with two antipodes, the basal one with the nucleus secondarily divided. – G: Endosperm, proembryo, synergid haustorium and the unchanged remainder of the integumentary tapetum. – H: Pollen mother cell, metaphase, n = 8.

Except near the pollen apertures the pollen wall of Anthemideae, like that of *Ursinia,* lacks the innermost exine layer, the nexine-2 (Stix 1960).

The most common basic chromosome number in Anthemideae is x = 9 but x = 8, 10, 13 and 17 have also been reported (Heywood & Humphries 1977). *Lasiospermum* has x = 9 and 10 (Harling 1950, Nordenstam 1967); among the genera listed in Darlington & Wylie (1955) only three *Artemisia* species have x = 8. *Pentzia* is reported to have x = 6, 7 and 8; *Cotula* has 2n = 16, 18 and 20 (Nordenstam 1967, 1969).

The inclusion of *Ursinia* in Anthemideae is usually based on exomorphic characters; however, its well-developed pappus sets it apart and its chromosome number is also exceptional for that tribe. On embryological grounds, however, there is no contradiction for a relationship with the Anthemideae.

Ursinia and Heliantheae. An 8-nucleate, Polygonum type, embryo sac and an integumentary tapetum which is very elongate radially has been found in *Dahlia, Cosmidium, Cosmos* and *Bidens* (Palm 1915, Täckholm 1916, Dahlgren 1920). The species of the cited genera and of *Helianthus* (Dahlgren 1924) also have two antipodes, which are very large in many Heliantheae genera (Dahlgren 1920 p. 498). An antipodal haustorium has been found in *Bidens* (Davis 1966 p. 90). In *Helianthus* the synergids lengthen considerably during development, but their function as haustoria is not evident (Schnarf 1931 p. 219). In species of *Dahlia, Helianthus, Bidens, Galinsoga* and *Glossocardia* the endosperm is of the Nuclear type (Palm 1915, Dahlgren 1924, Davis 1966). Thus there are great embryological similarities between *Ursinia* and some Heliantheae genera. Cronquist (1955) regarded the Heliantheae as the most primitive tribe in Compositae, to which all other tribes are related, directly or indirectly. The possible relationship between *Ursinia* and the Heliantheae, not previously stressed, deserves further investigation, taking into account a greater array of characteristics.

Acknowledgements. My sincere thanks are due to Dr Maria Prassler, München, who helped with the identification of my voucher material, to Professor Gunnar Harling, Göteborg, for valuable advice and criticism of the manuscript, and to Dr Bo Peterson, Göteborg, for bringing me in contact with specialists at several institutes.

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New species of Taraxacum from Denmark

Hans Øllgaard

Øllgaard, H. 1978 12 15: New species of Taraxacum from Denmark. *Bot. Notiser 131:* 497–521. Stockholm. ISSN 0006-8195.

The distribution types of species of *Taraxacum* in Denmark are discussed. 26 new species of sect. *Taraxacum,* occurring in Denmark, are described and their distribution types given. 11 of these species are also known from neighbouring countries. 21 species have been studied in cultivation. *T. inops* is unique in lacking pollen and in having pure yellow styles and stigmas.

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Our present knowledge of the *Taraxacum* flora of Denmark, although incomplete, is still considerable, such that some species are known to be widespread and common over the whole country, while others are only common in limited areas. The reasons for these differences in distributions and frequencies are uncertain. If one supposes that the commonest species are frequent because they are 'old', i.e. long-established and therefore have had a very long time in which to produce seed and spread, then one could further assume that the local species have either arisen later or been introduced later. According to this theory the local species ought to be in process of spreading. To prove or disprove this theory accurate data of distribution for the local species are necessary, so that future differences can be detected.

Cultivated *Taraxacum* species grow well both on clayey and sandy soils. It is instructive to observe which species are able to spread and thrive as ruderals outside cultivation. In my garden in Filskov (C Jutland) I cultivated about 150 Danish and alien *Taraxacum* species for 5 years. Seeds from these plants were inevitably spread by the wind into the surrounding countryside. Their offspring became naturalized at very different frequencies. Only c. 5 species became naturalized in any great numbers and all were previously known from C Jutland (perhaps being presently expanding), viz. *T. canoviride* Lindb. fil., *T. inarmatum* M. P. Chr., *T. pronilobum* H. Øllg. *T. subhuelphersianum* M. P. Chr., and *T. tanyphyllum* Dahlst. The 4 distribution maps in Fig. 1 are examples of *Taraxacum* species which have mainly eastern, western, northern or southern distributions in Denmark. These species may be in process of extending their distribution areas or are perhaps dependent on the somewhat different climates of the 4 regions, or on differences in soil conditions.

In order to survive any *Taraxacum* species must continuously find new localities because of crop rotation, the modern use of herbicides in agriculture, and loss of habitats due to building on the outskirts of towns and villages. In permanent pasture the *Taraxaca* become crowded out by tall grasses. Possibly the factors which determine whether or not a new species becomes widespread and numerous, are those which affect the seedling stages.

In this paper 26 species of Taraxacum new to science are described. They all belong to sect. *Taraxacum.* The species (except for *T. barbatulum, lilaceum, paeninsulae, ruptifolium* and *wiinstedtii*) have been cultivated experimentally, together with closely related species, and therefore the specific differences were readily observed.

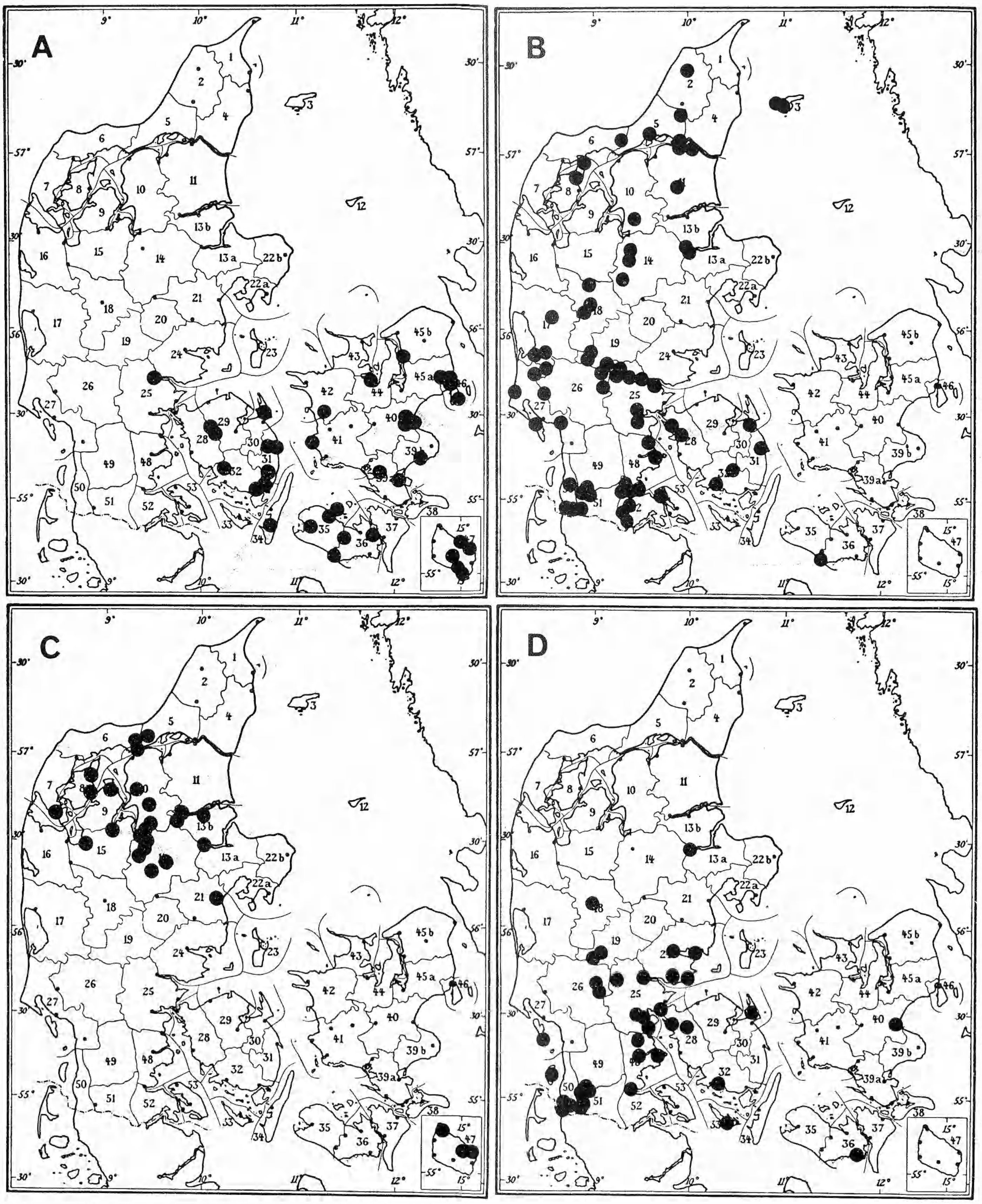

Fig. 1. Distribution within Denmark of four species of *Taraxacum*. – A: *T. semiglobosum* Lindb. fil. (eastern). – B: *T. subdahlstedtii* M. P. Chr. (western). – C: *Taraxacum speciosiflorum* M. P. Chr. (northern). – D: *Taraxacum aequisectum* M. P. Chr. (southern).

Fig. 2. *T. acre.*

All specimens here designated as isotypes are parts of the holotype individual. All the habit drawings were made from the holotypes, at ¼ natural size. The achenes are drawn 5 × natural size.

I have consulted the herbaria of the Botanical Institute, University of Århus (AAU), the Botanical Museum, University of Copenhagen (C), and the Section for Botany, Swedish Museum of Natural History, Stockholm (S), as well as the personal herbaria of C.-F. Lundevall, T. Brandt-Pedersen, A. Pedersen and E. Wessberg. C. I. Sahlin (CIS), J. L. van Soest, A. Hagendijk, H. Zevenbergen, R. Bäck, A. Railonsala and A. Richards sent much material from their personal herbaria. Most Danish material of the new species originates from my own field studies (c. 340 localities in different parts of the country have been visited).

A complete list of all the Danish localities for the new species will be deposited at Botanisk Museum, Gothersgade 130, DK-1123 Copenhagen, Denmark, and copies will be sent on request.

Taraxacum acre H. Øllgaard, sp. nov. – Fig. 2

Typus: Denmark, Jutland, distr. 14, Kjellerup, roadside at the ring road, near the Bøgildgård road, 5.V.1975, HØ 75–72 (C holotype).

Planta mediocris, patens. *Folia* late lanceolata, obscure subglaucescenti-viridia, parce araneosa–fere glabra; lobi laterales numerosi, valde approximati, deltoidei, acuti, dorso convexo, integro; lobus terminalis parvus, triangularis, lateribus rectis vel raro convexis, apicibus acutis; interlobia ± plicata, interdum leviter piceata; petioli alati, lucide purpurei. *Scapi* ± brunnescentes, superne ± dense araneosi. *Involucrum* magnitudine mediocre, sat obscure glaucescentiviride, leviter pruinosum; squamae exteriores c. 4 mm latae, c. 14 mm longae, irregulariter reflexae vel retroflexae, apicibus interdum leviter corniculatis, non marginatae, supra irregulariter et sordide rubescentes. *Calathium* c. 45 mm diametro, convexum, radians, luteum; ligulis marginalibus extus stria cano-violacea ornatis; antherae polliniferae; stigmata virescentia. *Achenium* fusco-stramineum, c. 4.5 mm longum (pyramide inclusa), superne spinulis sat distantibus, pervalidis instructum, spinulis summis nihilominus longis, conspicue decurvatis, pyramide c. 0.9 mm longa, subcylindrica, valida, inferne plerumque leviter spinulosa, sat abrupte abiente; rostrum c. 9 mm longum.

Taraxacum acre is similar to *T. pachylobum* Dahlst., both species having densely lobate leaves and brightly coloured petioles with rather broad wings. *T. acre,* however, has more regularly lobed leaves. The acute and entire lobes are longer and less reflexed than the lobes of *T. pachylobum,* which are very often obtuse and ± toothed. The outer bracts of *T. acre* are reflexed and irregular, not spreading and regular as in *T. pachylobum.*

T. acervatum Hagl. unpubl., a species known from Sweden and Finland, differs from *T. acre* in having narrower petioles and ± contracted end lobes.

Denmark, distr. 8, 10, 13 b–15, 18, 19. Common in the Viborg region.

Taraxacum aethiopiforme H. Øllgaard, sp. nov. – Fig. 3

Typus: Denmark, Jutland, distr. 11, Ålborg, Bygade, small site near Skelagervej, 4.V.1974, HØ 74–129 (C holotype).

Planta magnitudine mediocris, sat gracilis. *Folia* lanceolata, sat obscure viridia, parce vel in foliis interioribus sat manifesto araneosa; lobi laterales 4–5 utrimque, deltoidei, recurvi vel in foliis interioribus sat patentes, sensim angustati, acuti vel singuli apice rotundati, dorso integro vel nonnumquam uno dente acuto instructo, in foliis interioribus plerumque subulato-dentato, margine inferiore loborum foliorum interiorum uno dente praedito vel subulato-dentato; interlobia leviter plicata plerumque dentata vel subulato-den-

Fig. 3. *T. aethiopiforme.*

tata, saepe piceata; lobus terminalis mediocris vel (in foliis interioribus) sat magnus, sagittato-hastatus, lateribus integris vel incisis; petioli non alati, cum nervo mediano brunnescenti-purpurei. *Involucrum* atroviride, leviter pruinosum; squamae exteriores virides, acutae languidae, retroflexae, c. 13 mm longae, c. 2.5 mm latae. *Calathium* mediocre, flores marginales subtus stria cano-violacea notati; antherae polliniferae; stigmata virescentia. *Achenium* fusco-stramineum, sat alte sulcatum, c. 4.4 mm longum (pyramide inclusa), superne spinulis validis instructum, ceterum ± verrucosum, pyramide leviter conica, c. 0.7 mm longa, plerumque spinulis paucis et parvis instructa; rostrum c. 13 mm longum.

Fig. 4. *T. asperatilobum.*

Taraxacum aethiopiforme is a medium-sized, rather slender plant, with dark grey-green and glabrescent leaves with brownish-purple petioles and midribs. The petioles of the outer leaves are only faintly coloured or quite pale. The heads are dark green, with reflexed, narrow, green, unbordered outer bracts. Pollen is produced. The stigmas are distinctly discoloured. The achene is long (> 4 mm incl. cone).

Because of its slender growth, frequently rounded, lateral leaf lobes, and dark heads with narrow, reflexed outer bracts, *T. aethiopiforme* greatly resembles *T. aethiops* Hagl. However, the latter has a more strongly coloured, pure purple petiole and a green midrib in the upper half of the leaf. The stigmas of *T. aethiops* are very light-coloured, almost yellow. The lobation of the outer leaves of the two species also differs.

Denmark, Jutland, widely distributed but uncommon (distr. 11, 13 a, 14, 15, 21, 24, 25).

Taraxacum asperatilobum H. Øllgaard, sp. nov. – Fig. 4

Typus: Denmark, Jutland, distr. 7, Thisted, roadside at A 11 (main road no. 11), 3 km NE of the town, 10.V.1975, HØ 75–135 (C holotype) – Paratypus fructi-

Fig. 5. *T. barbulatum.*

fer: specimen grown from the root of HØ 75–136 (part of orig. coll.; C).

Planta mediocris–sat magna. *Folia* lanceolata, pure viridia, subnitida, parce vel (in foliis interioribus) sat manifesto araneosa; lobi laterales 5–6 utrimque, deltoidei, in foliis exterioribus et intermediis e base sat lata in apicem ± longum, tenuem, acutum subsensim angustati, marginibus superioribus dentibus longis et linearibus instructis, inferioribus integris, in foliis interioribus sensim angustati, dorso subulato-dentato; interlobia plana vel leviter crispa, viridia vel (in speciminibus expositis) parce piceata; lobus terminalis sagittato-hastatus, foliorum exteriorum et intermediorum acuminatus, incisus et plerumque dentatus, interiorum lateribus convexis, subulato-dentatis; petioli ± alati, foliorum exteriorum pallidi, intermediorum et interiorum ± colorati, nervo mediano pallido. *Involucrum* viride, leviter pruinosum, maxime inferne; squamae exteriores c. 17 mm longae, c. 4.5 mm latae, ± recurvae, extremis angustioribus, sensim angustatae, virides, apicibus plerumque leviter brunnescentibus, subtus atrovirides et nitidae, non (vel inconspicue) marginatae. *Calathium* luteum, convexum, radians; ligulae marginales subtus stria obscure caesio-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* (non holotypi, sed speciminis collectionis originalis culti) fusco-stramineum, c. 4 mm longum (pyramide inclusa), superne spinulosum, ceterum verrucosum vel fere laeve, pyramide subcylindrica, 0.8–0.9 mm longa, manifesto definita.

Taraxacum asperatilobum is related to *T. praeradians* Dahlst., which has a similar leaf lobation. *T. asperatilobum,* however, has less hairy, lighter green leaves, less broadly winged petioles, far more dentate lateral and incised and dentate terminal leaf lobes. The cone of the achene is also longer (only c. 0.5 mm in *T. praeradians*). The outermost involucral bracts of *T. praeradians* are broad (4.5–6 mm), whereas in *T. asperatilobum* they are linear or somewhat narrower than the other outer bracts.

Denmark, distr. 2, 7, 14, 20, 34, 39 a. Local and rare.

Taraxacum barbatulum H. Øllgaard, sp., nov. – Fig. 5

Typus: Denmark, Jutland, distr. 15, Mønsted, roadside at the chalk-pit, 3.V.1974, HØ 74–105 (C holotype).

Planta magnitudine mediocris. *Folia* obscure viridia, manifesto araneosa, exteriora et intermedia lanceolata, lobis lateralibus c. 5 utrimque, deltoideis, subacutis, in dorso uno dente magno et lato instructis, lobo terminali sat parvo, triangulari, integro vel interdum inciso, interiora late lanceolata, valde araneosa, lobis lateralibus approximatis, magis dentatis–denticulatis, dorso convexo, lobo terminali magno, lateribus dentatis vel incisis; interlobia integra vel denticulata, plerumque leviter piceata; petioli sat lati, angustissime alati vel non alati, conspicue purpurei, toto nervo mediano in foliis interioribus colorato. *Scapi* manifesto araneosi. *Involucrum* c. 14 mm longum, c. 11 mm latum, sat obscure viride, leviter pruinosum; squamae exteriores c. 4 mm latae, c. 15 mm longae, non marginatae, supra sordide virides et saepe irregulariter sordide rubescentes, reflexae. *Calathium* obscure luteum, convexum, radians; flores marginales subtus stria cano-violacea ornati; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 3.8 mm long-

Fig. 6. *T. bellum.*

um (pyramide inclusa), superne spinulis validis et latis instructum, ceterum fere laeve, pyramide subconica, 0.3–0.5 mm longa; rostrum c. 12 mm longum.

Taraxacum barbatulum is distinguished by its dark green, hairy leaves with rather strongly coloured petioles and midribs (especially those of the inner leaves). The scapes are conspicuously woolly. The outer bracts are rather long and broad, unbordered, recurved–reflexed, usually reddish-tinged. The cone of the achene varies somewhat in length.

T. barbatulum has much in common with *T. semiglobosum* Lindb. fil., but is distinguished by the different shape of the outer leaves, and by having less acute lateral leaf lobes and much darker coloured leaves and heads. The outer bracts of *T. semiglobosum* are as a rule slightly bordered. In leaf shape *T. triangularidentatum* v. Soest (1975 p. 148) is even more similar to *T. barbatulum,* but the former has almost smooth leaves with pale or pink petioles, and patent–recurved outer bracts.

Denmark, Jutland, distr. 9, 10, 13 b–15, 18, 21. Locally very common; probably expanding.

Taraxacum bellum H. Øllgaard, sp. nov. – Fig. 6

Typus: Denmark, Jutland, distr. 14, Bjerringbro, outskirts towards Hobro, storage yard at Bjerringbro Byggecenter, 10.V.1974, HØ 74–159 (C holotype).

Planta alta. *Folia* late lanceolata, laete canescenti-viridia, interiora manifesto, cetera parce araneosa; lobi laterales sat numerosi (4–7 binilobi); pars basalis lobi lata saepe lobulato-dentata, margine inferiore plerumque dentato, pars apicalis linearis–clavata, integra, subobtusa, in foliis exterioribus et intermediis plerumque erecta; interlobia subcrispa, subulata vel valde dentata, viridia vel in foliis interioribus subtus piceo-marginata; lobus terminalis foliorum exteriorum et intermediorum mediocris sagittato-hastatus, marginibus lateralibus integris vel rarius incisionibus instructis, foliorum interiorum major, lobulato-incisus; petioli subangusti vel interdum anguste alati, roseo-violacei. *Scapi* longi, tantum sub involucro araneosi. *Involucrum* c. 15 mm longum, c. 11 mm latum, viride, non pruinosum; squamae exteriores ovato-lanceolatae–lanceolatae, c. 5 mm latae, planae, conspicue albomarginatae, supra virides vel aequaliter et levissime rubescentes, patentes vel leviter recurvae. *Calathium* c. 55 mm diametro, leviter radians, leviter convexum, ligulae apicibus luteis, marginales subtus stria canoviolacea ornatae; antherae polliniferae; stigmata leviter virescentia. *Achenium* fusco-stramineum, c. 3.8 mm longum (pyramide inclusa), c. 1.1 mm latum, superne spinulis brevibus et validis instructum, saepe squamuloso-spinulosum, ceterum leviter verrucosum vel laeve, pyramide c. 0.7 mm longa; rostrum c. 11 mm longum.

Taraxacum bellum is a tall species, recognizable by its light grey-green leaves with rather numerous lateral lobes. The lobes of the outer and middle leaves have a broad inner part, which merges fairly abruptly into a linear or club-shaped, rather obtuse, often erect, apex. The petioles are reddish, wingless or only narrowly winged. The involucres have broad, patent or slightly recurved outer bracts with a distinct white margin.

Fig. 7. *T. curtifrons*.

T. bellum somewhat resembles *T. altissimum* Lindb. fil., but has light-coloured leaves, the lateral lobes of which are often club-shaped and more obtuse than those of *T. altissimum* and with more and longer teeth on the lower margins of the lobes. The outer bracts of *T. bellum* have broader margins than those of *T. altissimum* and the ligules are not red-tipped as in the latter species.

Denmark, Jutland, distr. 11, 13, 14, 21, 22 a. Common where it occurs.

Taraxacum curtifrons H. Øllgaard, sp. nov. – Fig. 7

Typus: Denmark, Jutland, distr. 24, Horsens, grass field at Bævervej, 17.V.1972, HØ 1864 (C holotype, AAU isotype).

Planta mediocris. *Folia* lanceolata vel linguata, sat brevia, laete canescenti-viridia; petioli alati, alis 2–5 mm latis, pallidi, nervo mediano sursum saepe brunnescente vel sordide violascente; folia exteriora parce pilosa; lobi uniformes, densissimi, integri, dorsis concavis, marginibus inferioribus convexis, interlobiis angulis acutis constantibus, lobo terminali curto, parvo, obtuso–acuto; folia intermedia foliorum exteriorum similia, longiora, magis pilosa, lobis pluribus; folia interiora ± araneosa, petiolis longis angustis, lobis lateralibus paucis, sat parvis, apicibus longis tenuibus acutis, interlobiis rotundatis. *Scapi* longiores quam folia. *Involucrum* c. 13 mm longum, c. 11 mm latum, viride, supra nigrescens, leviter pruinosum; squamae exteriores ovato-lanceolatae, mucronatae, supra ± valde colore rubro-violaceo tinctae, subtus fusco-virides, c. 12 mm longae, c. 4 mm latae, patentes–leviter recurvae, apicibus incurvis. *Calathium* 40–45 mm diametro, leviter convexum, sat obscure luteum; ligulae marginales subtus stria cano-violacea instructae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* c. 3.5 mm longum (pyramide inclusa), c. 1 mm latum, superne spinulis brevibus validis densis instructum, inferne verrucosum–fere laeve, pyramide c. 0.4 mm longa, subconica.

Taraxacum curtifrons has green, winged petioles and short, bright green, erect leaves with closely set, broad, entire, lateral lobes. The midrib is greenish or brownish. The inner leaves are rather hairy and differ from the outer and intermediate leaves in having incompletely developed lateral lobes and wide, rounded interlobes. The terminal lobe is large and sagittate to hastate. The outer involucral bracts are fairly broad and slightly recurved, with erect tips, clearly violet-coloured above.

T. curtifrons can be confused with *T. cyanolepis* Dahlst. and *T. excellens* Dahlst., which also have green petioles and violet outer bracts. *T. cyanolepis*, however, has more obtuse lateral lobes, with more convex upper edges and longer, more rounded interlobes; in addition *T. cyanolepis* has narrower and more intensely coloured outer bracts. The inner leaves of *T. curtifrons* are quite different from those of *T. cyanolepis*. The achene of *T. curtifrons* is more sharp-

Fig. 8. *T. distinctilobum.*

ly-shouldered than that of *T. cyanolepis. T. excellens* has more elongate leaves, with more lateral lobes and a strongly coloured midrib.

Denmark, distr. 13 a, 21, 22 a, 24, 39 a, 42. Here and there between Randers and Horsens in Jutland. – Germany, Nordrhein-Westfalen, Brilon, Bredelar, 4.V.1973, CIS 63135 (herb. CIS).

Taraxacum distinctilobum H. Øllgaard, sp. nov. – Fig. 8

Typus: Denmark, Jutland, distr. 25, Fredericia, grass area at Industrivej, 18.V.1969, HØ 1315 (C holotype).

Planta mediocris. *Folia* sat obscure viridia, oblonge lanceolata, parce araneosa, multilobata, lobis ± approximatis; petioli ± alati, purpurei, nervo mediano sordide rubro-violaceo; lobi laterales deltoidei, uniformes, subhamati, subobtusi, margine superiore integro vel (in foliis interioribus vel in speciminibus senibus) ± subulato-dentato vel interdum parce dentato; interlobia rotundata, integra vel parcissime dentata, ± piceata; lobus terminalis in foliis exterioribus parvus, in foliis intermediis et interioribus sat magnus, cordato-sagittatus, subobtusus vel mucronatus, lateribus saepe rotundato-incisis. *Involucrum* obscure viride, non pruinosum; squamae exteriores lanceolatae, c. 12 mm longae, c. 3 mm latae, virides vel paulatim leviter rubescentes, reversae, tortiusculae, apicibus saepe sub involucro inflexis, non marginatae. *Calathium* c. 45 mm diametro, luteum, convexum, radians; ligulae marginales subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4 mm longum (pyramide inclusa) superne spinulosum, ceterum verrucosum vel fere laeve, pyramide sat valida, subcylindrica, c. 0.4 mm longa; rostrum c. 11 mm longum.

This medium-sized species is especially recognizable from its leaves, which have a rather large number of lateral lobes, and rounded, mostly entire, tar-coloured interlobes, and usually subobtuse terminal lobes. The petioles are broad and ± winged, distinctly purple. The involucres are dark-coloured, with rather small, mostly irregularly reflexed, somewhat twisted, green outer bracts. Pollen is produced, and the styles and stigmas are discoloured.

The leaves of *T. distinctilobum* somewhat resemble those of *T. distinctum* Lindb. fil. and less strongly those of *T. rhodopodum* Dahlst. *T. distinctilobum* differs from *T. distinctum* in having winged petioles and dark green involucres with reflexed outer bracts. *T. rhodopodum* is more robust, with paler green leaves, larger involucres, and almost horizontally extended, coloured outer bracts, c. 4 mm broad.

Denmark, distr. 17, 20, 23–25, 28–31, 45 a. Common in Jutland near the Little Belt, and in Funen.

Taraxacum fioniae T. Brandt-Pedersen ex H. Øllgaard, sp. nov. – Fig. 9

Typus: Denmark, Funen, distr. 30, Kerteminde, meadow at the restaurant "Pax", 5.V.1972, leg. T. Brandt-Pedersen 72–1 (C holotype). – Paratypus fructifer: Denmark, Funen, distr. 31, Sdr. Højrup, 1.V.1971 leg. T. Brandt-Pedersen HØ 1567 (C).

Planta mediocris–sat alta. *Folia* late lanceolata, obscure canescentia, saepe manifesto araneosa, 5–6 binilobi, lobis deltoideis, sat patentibus, acutis, dorso convexo, plerumque integro, sed interdum subulis instructo, margine inferiore recto vel leviter concavo; interlobia sat longa, distincta, crispa, ± subulato-dentata, piceata; lobus terminalis triangularis, marginibus lateralibus concavis–convexis, in foliis intermediis et interioribus plerumque incisis, saepe rotundato-incisis; petioli ± alati, pallidi vel levissime rubescentes. *Involucrum* c. 14 mm longum, c. 10 mm latum, viride; squamae exteriores lanceolatae, c. 17 mm longae, c. 3.5 mm latae, olivaceo-virides, ± reflexae, saepe tortiusculae. *Calathium* c. 45 mm diametro; ligulae marginales extus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, 4.0–4.4 mm longum (pyramide inclusa), superne dense spinulosum, ceterum verrucosum vel fere laeve, pyramide c. 0.7 mm longa, plerumque leviter spinulosa.

Taraxacum fioniae has dark, grey-green, ± pilose leaves with winged, pale or very faintly coloured petioles. The lateral leaf lobes are sharp and rather narrow. When opposite, two lobes from a crescent which merges abruptly into the interlobe, which is distinctly tar-coloured, with either entire or faintly subulate-dentate margins which are parallel to the midrib.

T. fioniae resembles *T. araneosum* Dahlst., *T. huelphersianum* Dahlst. and *T. undulatiflorum* M. P. Chr. All four have ± winged, pale to rather pale-coloured petioles and hairy leaves with tar-coloured interlobes. In shape and colour the leaves are almost the same as those of *T. sublongisquameum* M. P. Chr. The differences between *T. fioniae* and these other four species are listed in Table 1. *T. fioniae* has been discovered and named by T. Brandt-Pedersen, at whose kind request I described it.

Denmark, Funen, several localities in distr. 30 and 31, besides 1 locality in distr. 34.

Taraxacum gesticulans H. Øllgaard, sp. nov. – Fig. 10

Typus: Denmark, Jutland, distr. 4, Tylstrup, at the main road crossroads, 5.V.1972, HØ 2176 (C holotype).

Planta magnitudine mediocris. *Folia* late lanceolata, laete canescenti-viridia, parce vel in foliis interioribus manifestius araneosa; lobi laterales foliorum exteriorum et intermediorum deltoidei, plerumque integri, e base lata et gibberosa in apicem linearem, patentem–porrigentem abrupte abientes, interiorum ± regulariter hamati, plerumque sensim angustati; interlobia plicata, viridia, plerumque uno dente instructa, foliorum interiorum minus dentata; lobus terminalis foliorum exteriorum et intermediorum parvus, late hastatus, subacutus, interiorum mediocris, breviter sagittatus; petioli alati, pallidi. *Involucrum* viride, leviter pruinosum; squamae exteriores c. 15 mm longae, c. 4 mm latae, supra laete, subtus obscure virides, planae, firmulae, alte recurvae, marginatae. *Calathium* luteum, convexum, radians; ligulae marginales extus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 3.8 mm longum (pyramide inclusa), superne spinulis sat gracilibus, densis, patentibus instructum, ceterum leviter verrucosum vel laeve, pyramide 0.3–0.4 mm longa, conica, sat abrupte abiente, saepe spinulosa.

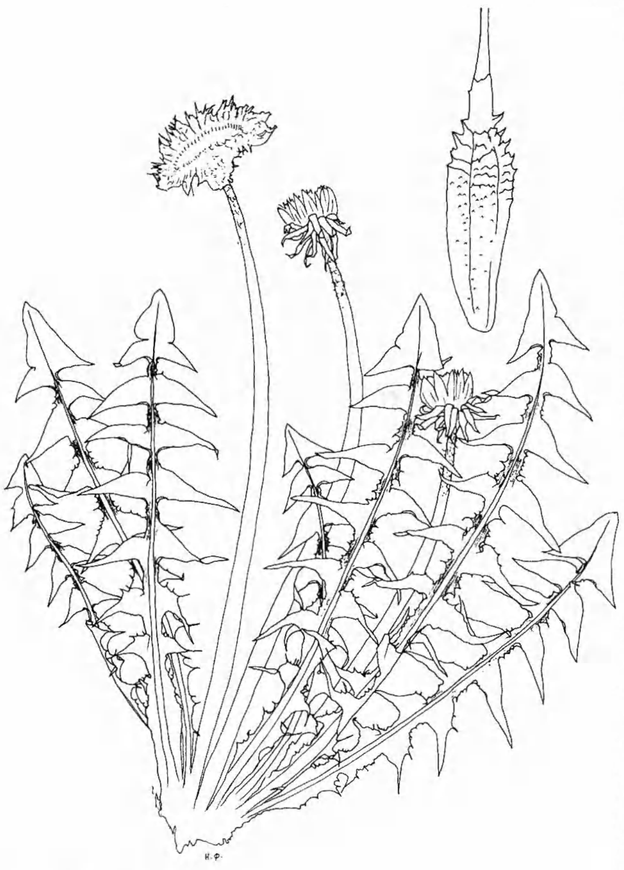

Fig. 9. *T. fioniae*.

Taraxacum gesticulans is recognizable by its pale, winged petioles and crisp, light green, leaves with crowded, deltoid, patent lateral lobes, of which at least those of the middle leaves are falcate, the basal part being often strongly convex along the upper edge while the outer part is broadly linear, patent to erect, and subacute. The terminal lobe is short, broad and hastate. The inner leaves have hamate lateral lobes and a medium-sized, shortly sagittate, terminal lobe. The outer bracts are recurved and bordered.

T. gesticulans is related to *T. corynodiforme* H.S.Z., *T. corynodes* Hagl., *T. percrispum* M. P. Chr., *T. subaurosulum* M. P. Chr., *T. undulatiforme* Dahlst. and *T. undulatum* Lindb. fil. & Markl. All have green, winged, petioles and

Table 1. Differences between *Taraxacum fioniae* and some related species.

Taraxacum fioniae	**Taraxacum araneosum**
Lower margin of leaf lobes entire	Lower margin often with a conspicuous tooth
Taraxacum fioniae	**Taraxacum huelphersianum**
Leaf lobes rather distant	Lobes crowded
Interlobes entire or subulate-dentate	Interlobes of outer leaves mostly with a large tooth
Terminal lobe often with rounded lateral processes and incisions	Terminal lobe never with rounded incisions
Outer bracts at least 16 mm	Outer bracts usually shorter than 14 mm
Taraxacum fioniae	**Taraxacum sublongisquameum**
Terminal lobe often incised	Terminal lobe entire
Interlobes of middle leaves often subulate-dentate	Interlobes mostly entire
Leaves hairy	Leaves smooth or sparsely hairy
Taraxacum fioniae	**Taraxacum undulatiflorum**
Margins of interlobes parallel to the midrib and faintly subulate-dentate	Interlobes of outer leaves rounded or acute-angled; those of middle and inner leaves often with a large tooth
Outer bracts at least 16 mm	Outer bracts less than 15 mm
Cone of the achene longer than 0.5 mm	Cone shorter than 0.5 mm

broad outer bracts. The differences are given in the key in Table 2.

Denmark, Jutland, distr. 1, 2, 4. Rare. – Germany, Niedersachsen, Steinhude am Meer, 9.V.1969, CIS 69122 (herb. CIS); Nordrhein-Westfalen, Pivitsheide (9 km E of Detmold), 9.V.1969, CIS 69165, 69203, 69204 (herb. CIS).

Taraxacum inops H. Øllgaard, sp. nov. – Fig. 11

Typus: Denmark, Jutland, distr. 25, Mørkholt Hage, grass field at the road S of the weekend cottages, 28.V.1970, HØ 70–20 (C holotype).

Planta mediocris. *Folia* sat obscure viridia, leviter pilosa, crispula; petioli sat lati, sordide rosei, alati, alis 1–3 mm latis inferne etiam sordide roseis; interlobia plerumque piceata; folia exteriora late lanceolata, binilobis 3–4, lobis deltoideis, leviter hamatis, integris vel parce dentatis, lobo terminali parvo, triangulari, integro, vel mediocri, marginibus lateralibus incisis, apice contracto; folia intermedia c. 4 binilobis instructa, lobis sat approximatis, hamatis, integris vel parce denta-

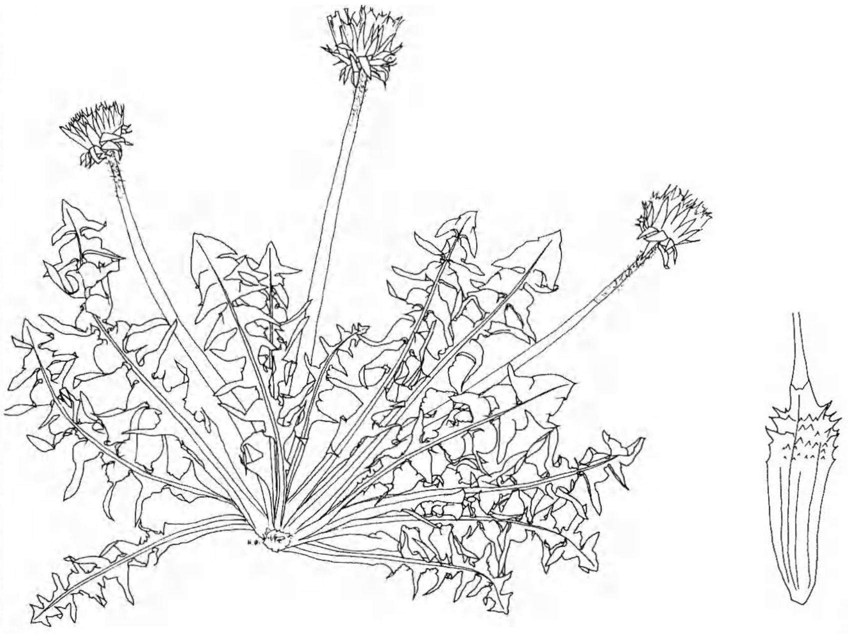

Fig. 10. *T. gesticulans*.

Table 2. Differences between *Taraxacum gesticulans* and some related species.

1. Outer bracts unbordered or very faintly bordered 2
– Outer bracts distinctly bordered 5
2. Lateral lobes recurved; outer bracts reflexed .... *T. percrispum*
– Lateral lobes patent or erect; outer bracts horizontal or somewhat recurved 3
3. Distal (linear) part of lateral lobes about 6 times as long as broad .... *T. subaurosulum*
– Distal part of lateral lobes c. 3 times as long as broad 4
4. Lobes obtuse; interlobes very short .... *T. corynodes*
– Lobes acute–subacute: interlobes not conspicuously short .... *T. undulatiforme*
5. Lateral lobes gradually narrowed, obtuse, hamate; leaves hairy; lower edge of lateral lobes mostly with a large tooth .... *T. undulatum*
– Distal part of lateral lobes of the middle leaves well-defined, linear 6
6. Distal part of lateral lobes of the midle leaves short, obtuse; leaves strongly hairy; lower edge of lateral lobes often with a large tooth .... *T. corynodiforme*
– Distal part of lateral lobes of the middle leaves long–very long, subacute; leaves faintly hairy; lateral lobes mostly entire .... *T. gesticulans*

tis, interlobiis plicatis, integris–parce dentatis, inferne longioribus, magis dentatis, lobo terminali mediocri, apice contracto; lobi laterales foliorum interiorum latiores magis dentati, lobo terminali majore–maximo, valde dentato vel inciso. *Involucrum* c. 15 mm longum, c. 11 mm latum, obscure caesio-viride, leviter pruinosum; squamae exteriores c. 15 mm longae, c. 4.5 mm latae, irregulariter reflexae, apicibus ± corniculatis, supra laete virides vel fortuito leviter rubescentes. *Calathium* c. 50 mm diametro, convexum, luteum; ligulae marginales ad c. 2.7 mm latae, dentibus terminalibus nudis, extus stria fusco-purpurea ornatae; antherae polline carentes; stylus et stigmata lutea. *Achenium* fuscum, pervalidum, c. 4.3 mm longum (pyramide inclusa), c. 1.5 mm latum, alte sulcatum, superne dense et pervalide spinulosum, ceterum ± manifesto verrucosum vel fere laeve, pyramide cylindrica, c. 0.9 mm longa, semper manifesto spinulosa, abrupte abiente.

Taraxacum inops is unique, since it produces no pollen and has pure yellow styles and stigmas. Very few other *Taraxacum* species show these characters, only *T. speciosum* Raunk., *T. peramplum* Railonsala, and possibly *T. subhuelphersianum* M. P. Chr. *T. speciosum* has darker yellow flowers, less strongly coloured petioles, and the inner leaves do not have large, dentate, terminal lobes. *T. peramplum* has more dentate side-lobes to the middle leaves and petioles with narrower wings. *T. subhuelphersianum* has light green leaves, with no tar-coloration, and its outer involucral bracts are more regular and often bordered. *T. inops* is easily separated from the above-mentioned species by its very robust and deeply furrowed achene, which is very strongly spinulose apically and has a cylindric, spinulose, 0.7–1.0 mm long cone.

T. inops flowers early in the season. When I cultivated this species in 1969–1972 it flowered each year about a week before all the other 147 *Taraxacum* species, excepting *T. planum* Raunk.; Øllg.

Denmark, Jutland, distr. 9, 10, 14, 15, 17, 24–26. Rather rare. – Germany, Schleswig, Dorpstedt, 2.V.1973 CIS 63084 (herb. CIS); Stormarn, Bad Oldersloe, Retwischfeld, 2.V.1973, CIS 63099 (herb. CIS).

Fig. 11. *T. inops*.

Fig. 12. *T. lilaceum.*

Taraxacum lilaceum H. Øllgaard, sp. nov. – Fig. 12

Typus: Denmark, Jutland, distr. 9, Oddense, roadside at Kåstrupvej (towards Jebjerg), 22.V.1976, HØ 76–158 (C holotype).

Planta mediocris. *Folia* lanceolata–late lanceolata, laete canescenti-viridia, parce vel (in foliis interioribus) sat araneosa; lobi laterales c. 5 utrobique, deltoidei, subacuti, dorso convexo, integro vel (in foliis interioribus) ± dentato; interlobia mediocriter longa, crispula, superiora integra, cetera dentata, viridia; lobus terminalis foliorum exteriorum et intermediorum sat parvus, cordatus, apice subobtuso; petioli anguste alati, pallidi, in nervum medianum ± coloratum abientes. *Scapi* folia superantes, superne colorati, ceterum pallidi, sub involucro dense araneosi. *Involucrum* c. 16 mm longum, c. 13 mm latum, viride, pruinosum; squamae exteriores c. 16 mm longae, c. 5 mm latae, supra laete lilaceae, subtus obscure brunnescenti-virides, valde pruinosae, anguste denticulato-marginatae, aliae adpressae, aliae patentes, ceterae recurvae. *Calathium* sat obscure luteum, radians, ligulis marginalibus subtus stria cano-violacea ornatis; antherae polliniferae; stigmata leviter virescentia. *Achenium* fusco-stramineum, c. 4 mm longum (pyramide inclusa), superne sat valde spinulosum, spinulis saepe latis–latissimis, in pyramidem c. 0.7 mm longam, cylindricam, inferne interdum spinulosam, sat abrupte abiens.

Taraxacum lilaceum has very conspicuous involucres, rendering the species recognizable some distance away. The outer involucral bracts are long and broad, bright lilac above, brownish-green below. Their tips are bent upwards. The petioles are green, and the midribs ± brownish-purple, especially those of the inner leaves. The flowers produce pollen, and the stigmas are discoloured.

None of the species with green petioles and purplish- or reddish-coloured outer involucral bracts, viz. *T. acutifrons* Markl., *T. cyanolepis* Dahlst., *T. excellens* Dahlst., *T. piceatum* Dahlst., and *T. subcyanolepis* M. P. Chr. have bright lilac-coloured outer bracts. However, the colour is difficult to preserve in dried plants, and determination of herbarium specimens must be based on the larger outer bracts and the leaf shape, which is rather invariable.

Denmark, Jutland, distr. 9, only known from the type locality, where it was abundant. – Sweden, Gothenburg, Änggårdsplatsen, 1 plant, 18.V.1975, HØ 75–231 (herb. HØ).

Taraxacum mirum H. Øllgaard, sp. nov. – Fig. 13

Typus: Denmark, Jutland, distr. 14, Kjellerup, pit at the river, near the road towards Viborg, 2.V.1973, HØ 1914 (C holotype).

Planta mediocriter alta. *Folia* late lanceolata, sat canescenti-viridia, plerumque sat manifesto araneosa; lobi laterales c. 6 utrimque, deltoidei, plerumque patentes, lingulati, subacuti, foliorum intermediorum plerumque e base ± gibbera subabrupte in apicem late linearem abientes, dorso integro vel interdum dente magno instructo, interiorum sensim angustati, integri; interlobia plerumque bene definita, dentibus paucis validis instructa, ± piceata; lobus terminalis brevis, hastatus,

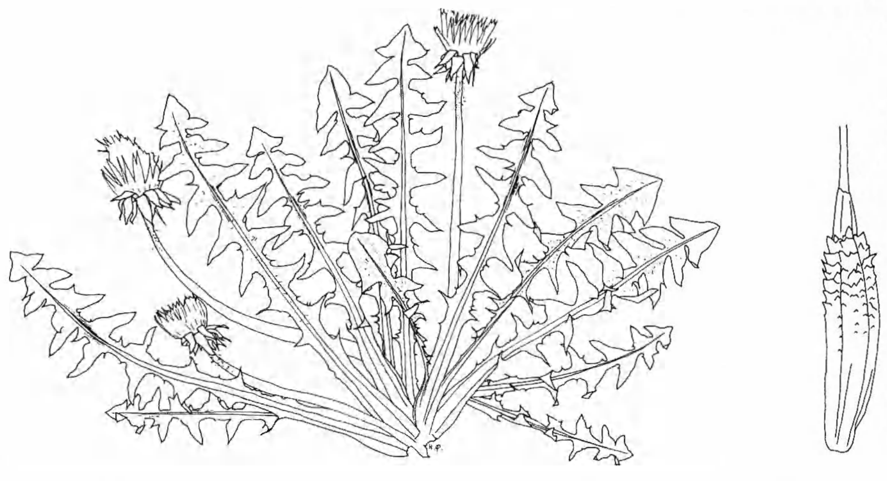

Fig. 13. *T. mirum.*

marginibus lateralibus saepe rotundato-incisis, foliorum interiorum paulo major, sagittato-cordatus; petioli anguste alati, pallidi (vel saepe levissime rosei). *Involucrum* c. 17 mm longum, c. 11 mm latum, viride, levissime pruinosum; squamae exteriores reversae–retroflexae, c. 15 mm longae, c. 4 mm latae, saepe leviter sinuosae, virides, non marginatae. *Calathium* c. 45 mm diametro, luteum, radians; ligulae marginales subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4.2 mm longum (pyramide inclusa), superne spinulis sat brevibus et tenuibus instructum, ceterum leviter verrucosum et laeve, pyramide subconica, c. 0.7 mm longa, sensim abiente.

Taraxacum mirum has rather hairy, greyish-green, leaves, usually with patent lateral lobes, of which those of the middle leaves often have a broad basal part which merges ± abruptly into a short, broadly linear, outer part, the upper edge of which is either entire or has a single, large tooth. Nearly all the lobes are subacute. The interlobes are well defined, often tar-coloured, with a few conspicuous teeth. The terminal lobe is small, usually with rounded incisions along the upper margins. The petioles are only faintly coloured or quite pale. The outer involucral bracts are green, reflexed and unbordered. The achenes are long and slender, their spines short and rather thin. The cone is usually very indistinct, about 0.7 mm long.

Like *T. lingulatum* Markl., *T. mirum* has lingulate lateral lobes, but its leaves are more regular in shape and the terminal lobe is different. The achenes are also different.

Denmark, Jutland, distr. 2, 11, 14, 15, 17, 18, 25, 26. Rather uncommon. – Sweden, Scania, Svalöv, 24.V.1937, G. Haglund (S); Blekinge, Ronneby, Möljerud, 8.VI.1939, G. Haglund (S).

Taraxacum necessarium H. Øllgaard, sp. nov. – Fig. 14

Typus: Denmark, Jutland, distr. 14, Bjerringbro, meadow at the Gudenå bridge, 10.V.1974, HØ 74–164 (C holotype, AAU isotype).

Planta mediocris. *Folia* laete canescentia, sat manifesto araneosa, dense lobata; lobi laterales deltoidei, leviter hamati vel recti, marginibus integris (vel raro parce dentatis), interlobiis colore fusco-violaceo ± tinctis; folia exteriora aequaliter lobata, lobis obtusiusculis, lobo terminali parvo, cordato, obtuso; intermedia lanceolata, lobis sat acutis, lobo terminali late sagittato-cordato, marginibus lateralibus integris; interiora manifesto araneoso-pilosa, lobis lateralibus imperfectis; petioli alati, pallidi. *Scapi* araneosi. *Involucrum* curtum, sat laete viride; squamae exteriores reflexae, virides, leviter pruinosae, c. 14 mm longae, c. 4 mm latae. *Calathium* 40–45 mm diametro, convexum, sat laete luteum, ligulis marginalibus extus stria cano-violacea ornatis; antherae polliniferae; styli sordide lutei, stigmata virescentia. *Achenium* c. 3.4 mm longum (pyramide inclusa), c. 1 mm latum, superne dense et breviter spinulosum, ceterum leviter verrucosum vel fere laeve, pyramide c. 0.5 mm longa, subconica; rostrum 10–12 mm longum.

Taraxacum necessarium has pale, winged petioles and densely lobate, ± hairy leaves. The interlobes are often tar-coloured. The inner leaves are less deeply lobed than are the outer and middle leaves. The scapes are usually densely hairy. The involucres are short, light green, with recurved–reflexed, light green outer bracts. The flowers produce plenty of pollen. The styles and stigmas are discoloured. The achene is short, 3.0–3.5 mm (incl. cone).

T. necessarium resembles *T. pachymerum* Hagl., *T. pallescens* Dahlst., *T. privum* Dahlst. and *T. pycnolobum* Dahlst., but all these species have longer achenes. *T. pachymerum* has coloured, wingless or only narrowly winged petioles, dark involucres with somewhat narrower,

Fig. 14. *T. necessarium.*

often coloured outer bracts. *T. pallescens* has acute lateral leaf lobes, some of the upper ones however being quite obtuse. The interlobes are not tar-coloured. *T. privum* is almost glabrous, with longer involucres and more patent outer bracts than *T. necessarium*. It has quite yellow styles and stigmas and as a rule it produces no pollen. *T. pycnolobum* has patent outer bracts and inner leaves different from those of *T. necessarium*.

Denmark, distr. 1, 3, 5–11, 13–15, 18–21, 22 a, 24–26, 29, 31, 34, 37–38, 39 a, 40, 41, 44–46, 51. Widespread but scattered. – Finland, LK, Sodankylä, 28.VI.1961, C.-F. Lundevall, cult. in Norrköping, cult. no. 6, 10.VI.1965, C.-F. Lundevall; CIS 17702, 17722 (herb. CIS) – Germany, Schleswig-Holstein, Rendsburg, Plötzenbrok, 30.V.1947, W. Christiansen (S); Fehmarn, Petersdorf, 9.V.1974, CIS 63907 (herb. CIS) – Sweden, Scania, Lackalänga, 7.V.1910, E. L. Ekman (S); Ven, 17.V.1935, E. Nyholm (S); Borrby, 20.V.1946, G. Haglund (S).

Taraxacum notabile H. Øllgaard, sp. nov. – Fig. 15

Typus: Denmark, Jutland, distr. 25, Mørkholt Hage, grass field at "Tulip camping", 11.V.1971, HØ 1520 (C holotype).

Planta mediocris. *Folia* lanceolata, obscure canescenti-viridia, crispula, sat araneosa, petiolis anguste alatis, levissime roseis; lobi laterales deltoidei, lati, plerumque valde reflexi, extra medium ± contracti, apice late lineari, margine superiore integro vel (in lobis inferioribus) ± dentato; interlobia ± dentata, saepe leviter piceata; lobus terminalis mediocris, cordato-sagittatus, subobtusus, marginibus lateralibus convexis, integris vel rarius rotundato-incisis. *Scapi* virides, araneosi. *Involucrum* sat laete viride, leviter pruinosum; squa-

Fig. 15. *T. notabile.*

Fig. 16. *T. paeninsulae.*

mae exteriores ovato-lanceolatae, c. 11 mm longae, c. 3.5 mm latae, distendenti-patentes, laete virides, plerumque albo-marginatae. *Calathium* c. 45 mm diametro, luteum, convexum, radians, ligulis marginalibus subtus stria cano-violacea ornatis; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4.2 mm longum (pyramide inclusa) superne spinulosum, ceterum fere laeve; pyramis sat valida, subconica, c. 0.5 mm longa, subsensim abiens; rostrum c. 11 mm longum.

Taraxacum notabile has faintly coloured, rather narrow petioles, fairly narrow, grey-green, somewhat hairy leaves with reflexed lobes. The involucres are light green, with patent, rather short, light-coloured, mostly narrowly bordered outer bracts. Pollen is produced and the stigmas are discoloured.

In leaf shape and lobe type it resembles *T. haematopus* Lindb. fil., but the petioles are never strongly coloured and the achene is less verrucose. *T. calamistratum* Hagl. has broader, quite pale petioles and larger, unbordered outer bracts (c. 13 × 4.5 mm).

Denmark, SE Jutland, distr. 19, 24, 25, 27, 48, 51, 52. Rather rare.

Taraxacum paeninsulae H. Øllgaard, sp. nov. – Fig. 16

Typus: Denmark, Jutland, distr. 15, Mønsted, roadside at the chalk-pit, 3.V.1974, HØ 74–110 (C holotype).

Planta mediocris–sat magna. *Folia* lanceolata–late lanceolata, crispa, sublutescenti-viridia, subcanescentia, interiora sat araneosa; lobi laterales 6–7 utrimque, superioribus plerumque valde approximatis, deltoidei, sensim angustati, acuti, reflexi, plerumque integri; interlobia viridia, plicata; lobus terminalis foliorum exteriorum et intermediorum parvus, acutus, triangulari-sagittatus, interiorum parvus, acutus, triangulari-sagittatus, interiorum fere rotundatus, obtusus; petioli anguste alati, roseo-purpurei. *Involucrum* sat laete viride, c. 14 mm longum, c. 11 mm latum, parce pruinosum; squamae exteriores sat numerosae (20–25), c. 17 mm longae, c. 5.5 mm latae, in eodem involucro et erectae et patentes et recurvae, laete virides, non marginatae. *Calathium* c. 45 mm diametro, luteum, convexum, radians; ligulae marginales c. 2 mm latae, subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 3.6 mm longum (pyramide inclusa), superne breviter et dense spinulosum, ceterum verrucosum vel fere laeve, pyramide conica, c. 0.4 mm longa; rostrum c. 13 mm longum.

Taraxacum paeninsulae is distinguished by its crisp, yellowish- or grey-green leaves, with many (6–7), crowded, lateral lobes rather uniform in shape. The inner leaves have a conspicuous, obtuse terminal lobe. The outer bracts are long, broad and spreading and are yellowish-green, both before and after flowering.

The characteristic shape of the inner leaves, with the numerous, crowded, somewhat claw-like, lateral lobes and the rounded terminal lobe, combined with heads of the type described above, serve to separate *T. paeninsulae* from related species such as *T. aequilobum* Dahlst., *T. contractum* Markl., *T. crispifolium* Lindb. fil. and *T. galbanum* Dahlst.

Denmark, Jutland, distr. 8–10, 14, 15. Rather common in the Viborg region.

Fig. 17. *T. polyhamatum.*

Taraxacum polyhamatum H. Øllgaard, sp. nov. – Fig. 17

Typus: Denmark, Jutland, distr. 10, Møldrup, roadside at the road towards Hobro near A 13, 4.V.1973, HØ 1922 (C holotype, AAU, herb. HØ, herb. T. Brandt-Pedersen isotypes).

Planta mediocris. *Folia* lanceolata, laete canescenti-viridia, parce vel in nervo mediano manifesto araneosa; lobi laterales deltoidei, hamati vel in speciminibus magnis subhamati–recti, integri vel interdum dente conspicuo instructi, binilobis 6–7, approximatis vel in foliis exterioribus et intermediis speciminum juniorum sat distantibus; lobus terminalis sat parvus–mediocris, cordato-sagittatus, integer, foliorum interiorum subacutus; interlobia plerumque integra, in foliis exterioribus saepe dente singulari, foliorum exteriorum et intermediorum plerumque conspicue piceata; petioli pallidi vel pallide rosei, non alati, nervo mediano supra ± brunnescente. *Scapi* araneosi, sub involucro valde araneosi. *Involucrum* 13–14 mm longum, c. 10 mm latum, sat obscure viride, pruinosum; squamae exteriores c. 12 mm longae, c. 3.5 mm latae, lanceolatae, arcuato-patentes, supra sordide violaceae, subtus obscure brunneae, roseo-marginatae. *Calathium* mediocre, luteum, radians; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4.2 mm longum (pyramide inclusa), superne sat tenuiter et crebre spinulosum, ceterum laeve vel fere laeve, pyramide c. 0.4 mm longa, subconica, subsensim abiente.

Taraxacum polyhamatum is recognizable by its light-green leaves, faintly coloured petioles, and brownish-purple outer bracts with a pink border. The tar-coloured interlobes of the outer and middle leaves, the brownish midrib, and the almost invariably entire lateral leaf lobes separate it from its nearest relative, *T. pruinatum* M. P. Chr. The latter species also has whitish-green outer bracts and an achene with a much longer and more cylindric cone (0.8–1.0 mm). Young specimens of *T. polyhamatum* much resemble *T. hamatum* Raunk., but differ in having much lighter-coloured and hairier leaves. Older plants of *T. polyhamatum* differ clearly from *T. hamatum,* having crowded, nearly straight, lateral lobes to the inner leaves and less strongly coloured petioles.

Denmark, Jutland, distr. 10, 11, 13–15, 21, 22 a. Common between Viborg, Randers and Hobro, at some places very abundant. Probably expanding. – England, Moray, Wester Greens, Webster 17961 (OXF).

Taraxacum procerisquameum H. Øllgaard, sp. nov. – Fig. 18

Typus: Denmark, Jutland, distr. 14, outskirts towards Hobro, at Bjerringbro Byggecenter, 10.V.1974, HØ 74–165 (C holotype, AAU isotype).

Planta mediocris–sat magna. *Folia* late lanceolata, canescentia, araneosa; folia exteriora et intermedia c. 4 binilobis instructa, lobis lateralibus hamatis, saepe lingulatis, integris, interlobiis viridibus, planis–fere planis, subangulatis, integris vel magno dente instructis, lobo terminali cordato-sagittato, supra medium leviter vel conspicue protracto; folia interiora magis dentata, lobo terminali longiore, magis acuto, marginibus lateralibus saepe incisionibus acutis vel rotundatis instructis; petioli alati, alis 3–5(–10) mm latis, pallidi, nervo mediano saepe brunnescente. *Involucrum* magnum, viride, non pruinosum; squamae exteriores c. 18 mm longae, c. 4.5 mm latae, virides, retroflexae, non marginatae. *Calathium* c. 50 mm diametro, sat obscure luteum, radians, ligulis marginalibus c. 2 mm latis, subtus stria cano-violacea ornatis; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4.1 mm longum (pyramide inclusa),

Fig. 18. *T. procerisquameum.*

superne spinulosum, spinulis sat validis mediocriter longis, ceterum laeve vel leviter verrucosum, pyramide cylindrica, 0.6–0.8 mm longa, sat abrupte abiente; rostrum c. 15 mm longum.

The pale, winged petioles, hairy leaves with oddly-shaped lateral lobes and large heads with unusually long, broad, reflexed, outer bracts all make *Taraxacum procerisquameum* quite unmistakeable. Only *T. procerum* Hagl. has similar outer bracts, and until I had had an opportunity to study Haglund's original collection of *T. procerum,* I regarded them as identical (Øllgaard 1973 p. 82). *T. procerum,* however, differs from *T. procerisquameum* in having distinctly coloured petioles, only slightly hairy leaves, plicate and toothed interlobes, blunt to obtuse terminal lobes, and achenes about 5 mm long (incl. cone c. 0.4 mm).

Denmark, distr. 5, 9–11, 13, 14, 16, 19, 21, 24–26, 29, 31, 47–49. Here and there, mostly on fertile soil – Finland, Ab, Pojo, Skogböle, 1.VI.1961, H. Såltin (as *T. procerum;* CIS 67952; herb. CIS) St, Loimaa köping, 12.VI.1968, H. Såltin 7627, 7630 (as *T. procerum;* herb. HØ) – Germany, Euskirchen, Blankenheim, Alendorf, 9.V.1973, CIS 63295 (herb. CIS). – Sweden, Halland, Lindberg, 16.V.1974, CIS 64111 (herb. CIS).

Taraxacum pronilobum H. Øllgaard, sp. nov. – Fig. 19

Typus: Denmark, Jutland, distr. 26, Ølgod, grass area at Østvej, 3.VI.1969, HØ 1191 (C holotype) – Paratypus fructifer: HØ 1190 (part of orig. coll.; C).

Planta mediocris, sat gracilis. *Folia* lanceolata, erecta, crispula, laete viridia, plerumque fere glabra, rarius sat manifesto araneosa; folia exteriora late lanceolata, lobis lateralibus sat paucis, deltoideis, dorsis convexis, integris vel uno dente instructis, lobo terminali mediocri, marginibus lateralibus incisis; folia intermedia lanceolata–late lanceolata, lobis lateralibus deltoideis, nunc oppositis nunc alternis, parte basali valde hamata, parte apicali recta vel leviter patente, dorsis integris vel ± dentatis, interlobiis rotundatis, integris vel leviter dentatis, viridibus, lobo terminali majore, late sagittato, plerumque lobulato-inciso; folia interiorum intermediorum similia, tamen magis dentata et pilosa; petioli non vel anguste alati, leviter et pallide purpurei. *Scapi* inferne pallidi vel leviter violacei, superne cupreo-colorati. *Involucrum* obscurum, superne sat nitidum; squamae exteriores c. 12 mm longae, c. 3 mm latae, supernae patentes, inferae ± alte recurvae, obscure virides, non marginatae. *Calathium* c. 47 mm diametro, radians, luteum; ligulae marginales planae,

Fig. 19. *T. pronilobum.*

Fig. 20. *T. pulverulentum.*

subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* c. 4 mm longum (pyramide inclusa), superne squamuloso-dentatum, inferne leviter verrucosum vel fere laeve, pyramide cylindrica, c. 0.5 mm longa.

Taraxacum pronilobum has erect, rather crisp, very light yellowish-green, glabrous to slightly hairy leaves and faintly coloured, rather narrow petioles. The basal part of the lateral leaf lobes is hamate, the outer part straight or slightly patent; the lobes are often alternate. The involucre is dark and somewhat lustrous; the outer involucral bracts are dark green. The upper halves of the scapes are a dull brownish-red. The flowers produce pollen. The styles and stigmas are greenish.

T. pronilobum somewhat resembles *T. semiglobosum* Lindb. fil. (*T. approximans* Lindb. fil.) although the latter species has grey-green, always distinctly hairy leaves, more strongly coloured petioles and reflexed outer bracts. *T. lunare* M. P. Chr. has darker leaves, with obviously winged petioles and the lateral leaf lobes are less dentate or even entire. The outer bracts of *T. lunare* are about 16 mm and light green. *T. pronilobum* has a more slender appearance than *T. lunare*.

Denmark, distr. 5, 11, 13 a, 14, 20, 25, 26, 32, 37, 47. Rare.

Taraxacum pulverulentum H. Øllgaard, sp. nov. – Fig. 20

Typus: Denmark, Jutland, distr. 21, Låsby, roadside at A 15, towards Flensted, 10.V.1967, HØ 1155 (C holotype) – Paratypus fructifer: Denmark, Jutland. distr. 21, Galten, grass field W of Gyvelvej, 24.V.1966, HØ 1145 (C).

Planta mediocris. *Folia* late lanceolata, laete canescenti-viridia, plerumque sat manifesto araneosa; lobi laterales pauci, lati, deltoidei, integri vel raro subulato-dentati, acuti vel in lobis superioribus rotundati; interlobia semper crispa, ± dentata vel rarius integra, supra inconspicue subtus manifestius piceata; lobus terminalis foliorum exteriorum et intermediorum mediocris, sagittatus, subobtusus, marginibus lateralibus crispulis et saepe leviter rotundato-incisis, in foliis interioribus major, ovato-sagittatus; petioli ± alati, pallide violacei. *Scapi* manifesto araneosi. *Involucrum* sat magnum, viride, leviter pruinosum; squamae exteriores c. 16 mm longae, c. 5 mm latae, lanceolatae (vel extremae filiformes), semper ± denticulatae, supra laete, subtus obscure virides, laxe reversae. *Calathium* c. 55 mm diametro, convexum, luteum; ligulae marginales subtus stria cano-violacea ornatae; antherae abundanter polliniferae; stylus et stigmata virescentia. *Achenium* (fere maturum) c. 4 mm longum (pyramide inclusa), superne spinulosum, ceterum tuberculatum vel fere laeve, pyramide c. 0.5 mm longa, cylindrica, rostro c. 12 mm longo.

Taraxacum pulverulentum is characterized by its ± pilose, yellowish green leaves with only a few broad, reflexed, lateral lobes, short and crisp, usually ± tar-coloured interlobes, and faintly coloured petioles. The scapes are clearly hairy. The outer involucral bracts are large, numerous and always ± denticulate, the lowest ones often being ± rudimentary. They are yellowish-green or reddish near the apex.

T. pulverulentum can be confused with *T. fasciatum* Dahlst. and *T. sahlinii* Railonsala. *T. fasciatum* has more frequent side-lobes and the outer bracts are always entire. The leaves of *T. pulverulentum* are larger than those of *T. fasciatum* and the interlobes are crisper. Previously (Øllgaard 1973), I had referred to *T. sahlinii* the material here considered as *T. pulverulentum*. However, Mr C. I. Sahlin, who has seen both *T. pulverulentum* and *T. sahlinii* growing in the wild, doubted that they were identical. Closer examination revealed the following differences. The middle and inner leaves of *T. sahlinii* have very long terminal lobes, and the flowers either produce no pollen or only misshaped pollen grains. The inner leaves of *T. pulverulentum* have large, but rounded terminal lobes, and the flowers produce plenty of normal pollen. Furthermore, the scapes and leaves of the latter species are much more hairy.

Denmark, distr. 1, 2, 4, 5, 8–11, 13–15, 17–27, 29, 31, 32, 36, 37, 45 a. Rather common in Jutland, here and there in Funen, rare in Zealand. – Norway, Hordaland: Voss/Granvin, 1.VI.1948 (S).

Taraxacum quadrans H. Øllgaard, sp. nov. – Fig. 21

Typus: Denmark, Jutland, distr. 5, Sønderøkse, meadow at the road towards Øland, 16.V.1971, HØ 1564 (C holotype, AAU isotype).

Planta mediocris. *Folia* obscure viridia, fere glabra, exteriora late lanceolata, binilobis duobus vel tribus hamatis, obtusiusculis, integris vel parce dentatis; intermedia lanceolata, c. 5 binilobis instructa, lobis deltoideis, ± valde reflexis, acutis, sensim angustatis, partibus basalibus valde hamatis, apicalibus ± patentibus, marginibus superioribus ± dentatis, dentibus sat paribus, vel integris; interlobia brevia, angulata, integra vel raro denticulata; lobus terminalis cordato-sagittatus, integer, saepe mucronatus; folia interiora latius lobata, lobis magis dentatis, dentibus sat paribus, lobo terminali majore, marginibus lateralibus in parte inferiore saepe dentatis; petioli plerumque non alati, purpurei; nervus medianus saepe purpurascens, nervis lateralibus sat validis, prope margines inferiores loborum sitis. *Scapi* paulatim valde brunneo-rubescentes, sub involucro ± araneoso-pilosi. *Involucrum* c. 13 mm longum, c. 10 mm latum, valde obscurum, superne nitidum, inferne pruinosum; squamae exteriores ovato-lanceolatae, planae, acutae, c. 11 mm longae, 3–3.5 mm latae, albo-marginatae, distendenti-patentes, supra pallide virides, subtus obscurae, pruinosae. *Calathium* c. 40 mm diametro, sat laxum, leviter convexum, ligulis marginalibus subtus stria obscure cano-violacea ornatis; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4 mm longum (pyramide inclusa), c. 1 mm latum, subnitens, superne spinulosum, spinulis sat paucis, plerumque brevibus, validis, saepe conjunctis, inferne fere laeve, pyramide c. 0.6 mm longa, subcylindrica, abrupte abiente; rostrum c. 9 mm longum.

Taraxacum quadrans is recognizable by its dark, bluish- or grey-green, leaves with coloured petioles and ± coloured midrib. The lateral lobes are usually entire, but are sometimes regularly dentate. The angle between the lobe and interlobe is generally acute. The outer involucral bracts are ± bordered.

T. quadrans is closely related to *T. marklundii* Palmgr. and *T. subhamatum* M. P. Chr. *T. marklundii* most often has very conspicuous teeth along the upper edge of the side-lobes, especially in the upper part of the leaf, whereas *T. quadrans* has entire or (inner leaves) subulate-dentate side-lobes, especially in the lower part of the leaf. The achene of *T. quadrans* tapers more abruptly into the cone than that of *T. marklundii*. The leaves of *T. subhamatum* are lighter in colour, with an almost colourless midrib, and more rounded interlobes. Furthermore, in *T. subhamatum* the involucre is strongly pruinose throughout, making it lustreless. In *T. quadrans* the involucre is blackish-green and lustrous in the upper part (as that of *T. marklundii*). The outer bracts of *T. subhamatum* are unbordered.

Fig. 21. *T. quadrans*.

I cultivated these 3 species for some years and now realise that *T. subhamatum* is more variable than *T. marklundii* and *T. quadrans*. However, the pruinose involucres with unbordered bracts and the light colour of the leaves are invariable.

Denmark, distr. 1, 3–6, 8–11, 13–21, 22 a, 25–27, 31, 38, 48–51. Here and there – France, Dép. des Yvelines, Forêt de Rambouillet, 8.V.1973, de Retz 67373 (herb. HØ) – Germany, Niedersachsen, Kreis Meppen, 2 km S of Herzlake, 3.V.1969, CIS 69359 (herb. CIS); Rheinland-Pfalz, Kreis Altenkirchen, 2 km W of Friesenhagen, 11.V.1972, CIS 62326 (herb. CIS); Hessen, Kreis Waldeck, Arolsen, 4.V.1973, CIS 63144 (herb. CIS); Nordrhein-Westfalen, Kreis Olpe, Kirchhunden, 5.V.1973, CIS 63173 (herb. CIS) – Holland, Zuid-Holland, Valkenburg, 5.V.1967 CIS et al. 67078 (herb. CIS); Leidschendam, Zijdepolder, 11.V.1970, Tarax.

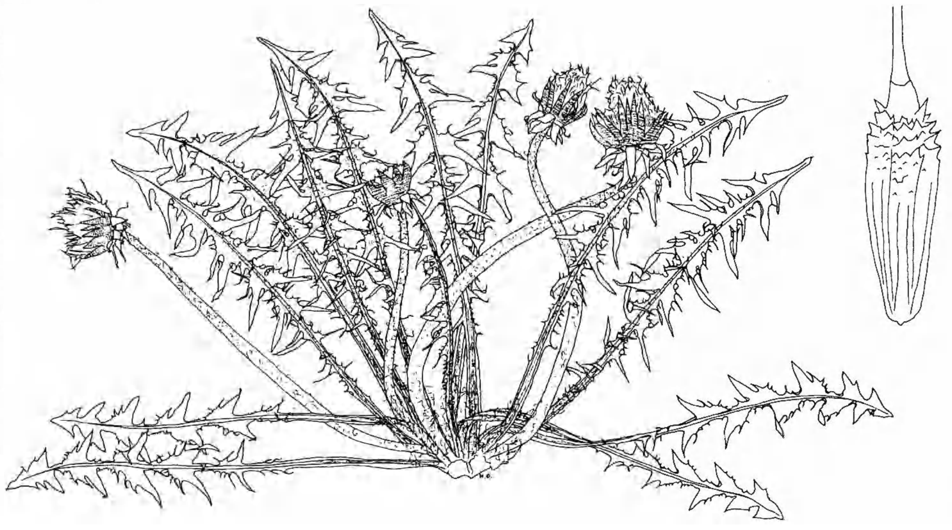

Fig. 22. *T. ruptifolium.*

Neerl. Exs. 150, van Soest (as *T. marklundii* Palmgr.; herb. HØ); Voorburg, Binckhorstpolder, 25.IV.1971, van Soest 53251 (herb. HØ), 25.IV.1973, van Soest 54520 d (herb. Leiden, HØ); The Hague, Van Soutelandelaan, 7.V.1975, van Soest 55579 (herb. HØ).

Taraxacum ruptifolium H. Øllgaard, sp. nov. – Fig. 22

Typus: Denmark, Jutland, distr. 14, Nonbo (4 km S of Viborg), roadside at A 13, 30.IV.1974, HØ 74–96 (C holotype).

Planta magnitudine mediocris. *Folia* lanceolata, lutescentia, canescentia, ± araneosa, adscendentia; lobi laterales deltoidei, c. 5 utrimque, foliorum exteriorum valde dentati, intermediorum et interiorum profunde fissi, partibus (plerumque tribus) omnibus acutis, linearibus, parallelis, margine inferiore lobi integro; interlobia viridia vel leviter piceata, valde dentata et subulato-dentata; lobus terminalis incisionibus ± inconspicuus, in apicem longum, linearem acuminatus, apicibus lobulorum basalium interdum rotundatis; petioli non vel angustissime alati, sordide rubelli vel fere pallidi. *Involucrum* c. 15 mm longum, c. 11 mm latum, viride, non vel levissime pruinosum; squamae exteriores sat paucae (c. 12), c. 14 mm longae, c. 4.5 mm latae, reflexae, sat irregulariter tortiusculae, convexae, virides. *Calathium* luteum, convexum, radians; ligulae marginales extus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata leviter virescentia. *Achenium* fusco-stramineum, c. 3.9 mm longum, superne spinulis validis, sat brevibus instructum, ceterum verrucosum vel fere laeve, in pyramidem latam, subconicam, 0.4–0.5 mm longam subabrupte abiens; rostrum c. 10 mm longum.

Taraxacum ruptifolium is a most characteristic and conspicuous species. The leaves are ascending, yellowish-green, ± hairy, the underside is glabrous and shining. Apart from the outer leaves, almost every detail of the leaf morphology is linear and acute, including the terminal lobes of the inner leaves. This renders the species recognizable some distance away. The petioles are faintly reddish. The outer bracts of the involucre are broad and reflexed, a little twisted and irregular.

T. ruptifolium bears some resemblance to *T. lacerifolium* Hagl., which, however, has clearly winged petioles, less incised leaves and much darker stigmas.

Denmark, distr. 14, 21, 34, 38, 39 b. Abundant at the type locality, elsewhere rare.

Taraxacum subxanthostigma M. P. Chr. ex H. Øllgaard, sp. nov. – Fig. 23

Typus: Denmark, Zealand, distr. 45 a, Farum, roadside at Bregnerødvej, 28.IV.1974, HØ 74–84 (C holotype) – Paratypus fructifer: Denmark, Jutland, distr. 24, Horsens, at the end of Rådmandsvej, 31.V.1970, HØ 1181 (C).

Planta magnitudine mediocris. *Folia* lanceolata, obscure viridia, fluxe araneosa, leviter crispa, sat multilobata; lobi laterales approximati, deltoidei, lati, acuti, sensim angustati, margine superiore convexo, integro (vel in foliis interioribus parce subulato), margine inferiore integro vel uno dente instructo, interlobiis crispis, valde piceatis; lobus terminalis brevis, cordato-sagittatus, marginibus lateralibus convexis, integris vel in foliis interioribus acute vel (raro) rotundato-incisis; petioli anguste vel sat late alati, sat obscure roseo-violacei; nervus medianus sordide ± roseo-violaceus. *Involucrum* obscurum; squamae exteriores lanceolatae, apice contracto, c. 13 mm longae, c. 4 mm latae, obscure virides, interdum leviter violascentes, distendenti-recurvae. *Calathium* convexum, 45–50 mm diametro, radians; ligulae marginales subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* (e progenie radicis paratypi fructiferi cultae lectum) c. 4.4 mm longum (pyramide inclusa), superne sat longe squamuloso-spinu-

Fig. 23. *T. subxanthostigma.*

losum, ceterum fere laeve, pyramide subcylindrica, c. 0.8 mm longa, sat abrupte abiente; rostrum c. 11 mm longum.

Taraxacum subxanthostigma is characterized by its dark green leaves with numerous, broad, sharp, somewhat recurved, lateral lobes, its crisp, tar-coloured interlobes, and its narrowly-winged, rather darkish pink to purple petioles. The involucres are dark with somewhat recurved outer bracts.

It is allied to *T. latissimum* Palmgr. and *T. fasciatum* Dahlst. It differs from the former in having broader, more recurved, lateral leaf lobes, the outer leaves especially, and crisper interlobes. The involucres are darker and the outer bracts shorter. It differs from the latter species in having darker leaves and much more strongly coloured petioles. The leaves of *T. subxanthostigma* usually have more numerous and more heavily crowded lobes. Well-developed specimens of *T. fasciatum* and *T. subxanthostigma* are clearly different, but weak individuals, bad herbarium specimens in particular, are impossible to determine with certainty. If achenes are present, a cylindrical cone, 0.8 mm long, indicates *T. subxanthostigma*.

T. subxanthostigma has been collected by the late M. P. Christiansen since 1944. It did not appear in his last *Taraxacum* work (Christiansen 1971), because he felt uncertain how to separate it from *T. fasciatum* Dahlst. During our last excursion together (1974) we found a very clear *T. subxanthostigma*. He pointed it out as the holotype and asked me to make the description.

Denmark, distr. 7–11, 13 b, 14, 21, 22 a, 24–29, 31, 32, 37, 40, 45–47. Rather rare. – Germany, Nordrhein-Westfalen: Rheinbach, 3.V.1971, CIS 60956 (herb. CIS).

Taraxacum uniforme H. Øllgaard, sp. nov. – Fig. 24

Typus: Denmark, Jutland, distr. 25, Kolding, at Sjællandsgade, 11.V.1972, HØ 1797 (C holotype) – Paratypus fructifer: Denmark, Jutland, distr. 25, Kolding, Tved, roadside, 21.V.1968, HØ 1237 (C, herb. HØ).

Planta alta, ± erecta. *Folia* lanceolata, canescenti-viridia, ± manifesto araneosa; lobi laterales deltoidei, reflexi, acuti, in foliis exterioribus et intermediis integri vel uno dente conspicuo instructi, in foliis interioribus magis dentati; interlobia saepe acuta, parce dentata, maxime in foliis interioribus colore atrocolorata; lobus terminalis in foliis exterioribus et intermediis parvus–mediocris, triangulus, mucronatus, integer, in foliis interioribus magnus–maximus, sagittato-hastatus, lateribus plerumque acute dentatis vel alte incisis; petioli subalati vel (rarius) alati, semper pallidi. *Involucrum* 15–17 mm longum, c. 11 mm latum, viride, non pruinosum; squamae exteriores sat angustae (c. 3 mm) et longae (c. 16 mm), virides vel raro leviter fuscescentes, retroflexae. *Calathium* magnum (55–65 mm diametro), luteum, radians; ligulae marginales extus stria cano-violacea tinctae; antherae polliniferae; stylus et stigmata leviter virescentia. *Achenium* fusco-stramineum, c. 4.3 mm longum (pyramide inclusa), c. 1.1 mm latum (spinulis exclusis), superne spinulis validis sat longis instructum; pyramis c. 0.9 mm longa, subcylindrica.

Fig. 24. *T. uniforme*.

Taraxacum uniforme is rather tall, with ± erect leaves and scapes. The petioles are entirely green. The leaves are hairy, the inner ones with tar-coloured interlobes. The outer involucral bracts are green, long, rather narrow and reflexed.

T. uniforme much resembles *T. macranthum* Dahlst., and for some time I regarded them as identical. However, after finding true *T. macranthum* growing wild, I have changed my opinion. *T. macranthum* has faint-coloured petioles, more dentate middle leaves, with smaller terminal lobes to the inner leaves, the interlobes of which are less (if at all) tar-coloured. The inner involucral bracts of *T. macranthum* are ± connate, whereas those of *T. uniforme* are separate in the normal manner. Finally, the cone of the *T. macranthum* achene is shorter (0.6–0.7 mm) than that of *T. uniforme* (0.8–0.9 mm).

Denmark, Jutland, distr. 25, here and there in the Kolding region.

Taraxacum vanum H. Øllgaard, sp. nov.
– Fig. 25

Typus: Denmark, Jutland, distr. 14, Vium/Lysgård, roadside at A 13, 22.V.1975, HØ 75–300 (C holotype).

A *Taraxaco dahlstedtii* Lindb. fil., cujus simillimum

Fig. 25. *T. vanum*.

est, his notis sejunctum: foliis supra medium latioribus, lutescenti-viridibus, tantummodo interioribus manifesto araneosis; lobis lateralibus supra medium folii densioribus, lobo terminali foliorum intermediorum majore, petiolis pallidius coloratis, minus araneosis; squamis exterioribus latioribus (extimis ad 6 mm latis); achenio latiore, superne crasse et latius spinuloso, in pyramidem modo 0.5 mm longam abrupte abiente.

Taraxacum vanum is easily overlooked. It has no very marked characteristics, but resembles a poorly developed *T. dahlstedtii* Lindb. fil. I have cultivated *T. vanum* since 1967 and compared it with several related species (e.g. *T. laciniosifrons* Wiinst., *T. latisectum* Lindb. fil., *T. christiansenii* Hagl., *T. irritum* Saarsoo, *T. congestum* Hagl. & Saarsoo and *T. dahlstedtii* Lindb. fil.), and have gradually become more and more convinced of its validity as a new species. In addition, I have now observed and collected it from many other localities in Denmark.

It has yellowish-green leaves, of which only the inner ones are conspicuously hairy. The lateral leaf lobes are deltoid, blunt, usually entire, and rather crowded in the upper part of the leaf. The terminal lobes of the inner leaves are generally rather indistinct, being lobulate-incised, the lobes becoming more distinct downwards. The petioles are unwinged, usually only faintly coloured. The holotype represents the maximum degree of colouration. The outer bracts are 4–6 mm broad and reflexed, with the points bent outwards. The achenes are short (c. 3.5 mm, incl. cone) but rather thick; their spines are strong and broad. The cone is very well defined, c. 0.5 mm long.

Most of the above characters serve to separate *T. vanum* from *T. dahlstedtii* Lindb. fil., to which it is very closely related. The latter species has dark green, very hairy leaves, strongly coloured petioles, outer bracts c. 4 mm broad, and the achene has a longer (0.7 mm or more), indistinctly delimited cone. The spines are slender. *T. laciniosifrons* has winged petioles, tar-coloured interlobes, and only rarely has entire lateral lobes. *T. latisectum* has patent, mostly dull-purplish outer bracts, and longer achenes with slender, recurved spines. *T. christiansenii* has somewhat recurved outer bracts with a broad, white, ± crisp border. Its leaves are darker. According to the description (Saarsoo 1963 p. 105) *T. congestum* is a smaller plant with narrower outer bracts and a different kind of achene. *T. irritum* has strongly coloured petioles and the outer involucral bracts are not reflexed.

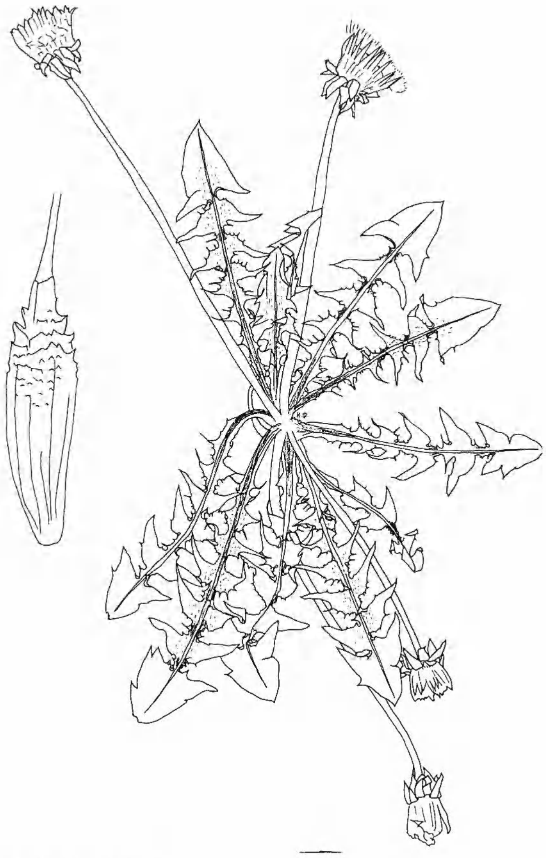

Fig. 26. *T. viridans*.

Denmark, distr. 1–4, 8–11, 13–27, 33, 39 a. Rather common in Jutland.

Taraxacum viridans Hagl. ex H. Øllgaard, sp. nov. – Fig. 26

Typus: Denmark, Jutland, distr. 48, Christiansfeld, roadside at the road towards Sommersted, 300 m from the main road, 18.V.1971, HØ 1556 (C holotype) – Paratypus fructifer: HØ 1619 (part of orig. coll.; C).

Planta mediocris. *Folia* obscure lutescenti-viridia, crispula, fluxe araneosa, exteriora lanceolata, interlobiis plerumque piceatis, parce dentatis; folia intermedia lanceolata–linguata, interlobiis ± subulato-dentatis, duobus dentibus sat validis, oppositis, saepe supra nervum medianum flexis; lobi laterales deltoidei, acuti, marginibus superioribus convexis, integris vel subulato-dentatis, marginibus inferioribus concavis, integris vel interdum dentibus singulis instructis; lobus terminalis magnus, ovato-sagittatus vel hastatus, marginibus lateralibus dentatis vel incisis; folia interiora magis araneosa, lobis lateralibus magis subulato-dentatis, lobo terminali majore; petioli alati, alis 1–5 mm latis, roseo-violacei, nervo mediano praesertim supra brunnescenti-violaceo. *Involucrum* c. 14 mm longum, c. 10 mm latum, obscure canescenti-viride, supra brunneo-violaceum; squamae exteriores ovato-lanceolatae,

Fig. 27. *T. wiinstedtii.*

mucronatae, c. 15 mm longae, c. 5 mm latae, retroflexae, ± marginatae, primum albo-virides, postea leviter et irregulariter rubescentes. *Calathium* 45–50 mm diametro, convexum, radians, sat obscure luteum, ligulis marginalibus subtus stria sat tenui, cano-violacea ornatis; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 4.5 mm longum (pyramide inclusa), superne crasse squamuloso-spinulosum et spinulis singulis brevibus, validis instructum, inferne laeve–leviter verrucosum, pyramide subconica, c. 0.6 mm longa, inferne saepe spinulosa, sensim abiente; rostrum longum (c. 15 mm).

Taraxacum viridans has dark, yellowish green leaves. The interlobes are mostly tar-coloured and dentate. Two of the teeth of the interlobes are often coarser than the rest and are bent upwards, crossing over the midrib. The outer involucral bracts are large, reflexed and narrowly bordered. In the early stages the bracts are whitish-green, like those of *T. pallidipes* Markl., later becoming slightly coloured.

The leaf shape is almost like that of *T. acutifidum* M. P. Chr. and *T. sublongisquameum* M. P. Chr. *T. acutifidum,* however, has a collar of yellowish-green, narrower (c. 3 mm) outer bracts, and the petiole colour is very weakly developed. *T. sublongisquameum* has the same leaf colour and the same brownish midrib, but its interlobes are entire or only faintly subulate-dentate, and the terminal lobe is always entire.

Denmark, Jutland, distr. 13, Randers, 22.5.1973, E. Wessberg (herb. E. Wessberg); distr. 48, around Christiansfeld. Abundant at the type locality. In 1947 G. Haglund found this species in Nr. Tyrstrup N of Christiansfeld, but as his specimens (at S) were not well developed, he just named the plants *T. viridans* but never described them.

Taraxacum wiinstedtii H. Øllgaard, sp. nov. – Fig. 27

Typus: Denmark, Jutland, distr. 14, Vium/Lysgård, roadside at A 13, 22.V.1975, HØ 75-268 (C holotype).

Planta mediocriter alta. *Folia* late lanceolata, sat laete canescenti-viridia, parce–sat manifesto araneosa; lobi laterales c. 5 utrimque, deltoidei, subacuti, superiores hamati, ceteri plerumque lingulati, integri, sensim angustati vel (in speciminibus veteribus) e base lata in apicem late linearem subabrupte abientes; interlobia viridia, plicata, ± valde dentata, dentibus saepe longissimis; lobus terminalis sat parvus, brevis, latus, apice saepe contracto, foliorum interiorum major, marginibus lateralibus saepe late dentatis; petioli lati, anguste roseo-alati, amoene rosei. *Involucrum* c. 14 mm longum, c. 11 mm latum, viride, pruinosum; squamae exteriores c. 15 mm longae, 4–7 mm latae, retroflexae, subsordide laetevirides, ± marginatae, apicibus leviter corniculatis. *Calathium* c. 45 mm diametro, luteum, convexum; ligulae marginales subtus stria cano-violacea ornatae; antherae polliniferae; stylus et stigmata virescentia. *Achenium* fusco-stramineum, c. 3.5 mm longum (pyramide inclusa), superne spinulis sat validis paulum incurvis instructum, ceterum verrucosum vel fere laeve, pyramide c. 0.4 mm longa; rostrum c. 12 mm longum.

Taraxacum wiinstedtii is recognizable by its somewhat greyish-green leaves, usually with a very characteristic lobation, viz. 2 or 3 pairs of lobes at the top of the leaf are hamate, the others being lingulate. The lobes are blunt and entire. The interlobes are green, usually with very conspicuous teeth. The terminal lobes are small, often broader than long and often cuspidate. The petioles are an intense rose-pink colour. The outer involucral bracts are similar to those of *T. retroflexum* Lindb. fil., i.e. light green, broad, reflexed and bordered. The leaf shapes of the two species are quite different. In *T. wiinstedtii* the achene spines have incurved points.

Denmark, Jutland, distr. 6, 10, 13 a, 14, 15, 21, 36, 37. Rare.

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Linnaeus's views on plant classification and evolution

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In *Fundamenta botanica* (1736) Linnaeus presented principles for his concepts of genera, species and varieties. The genera are logically definable according to the arrangement of fructifications. No practical definitions are given for species and varieties, which leaves the genera as the corner-stone of Linnaean taxonomy. A system is natural when it reveals the Creator's great plan. The problem of finding a natural system above generic level occupied Linnaeus from the 1730s onwards. The affinities of genera and natural orders are illustrated in a diagram constructed of circles distributed like territories on a map. A series of papers from the 1740s and 1750s reveal his dissatisfaction with the static, biblical species concept though this did not prevent him from using his classification. The hypothesis of successive hybridization starting from orders to form genera, species and varieties was presented in the 1760s. This new theory of the creation is intimately linked with his theory of a medulla continuing through the generations and cortical substances variously combinable with the medulla.

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It has often been said that in the works published by Linnaeus as a young man in Holland, even in the actual preface to *Systema naturae* (Linnaeus 1735) virtually all he later accomplished is to be found in embryo. As to his botanical classification it is perfectly correct as long as we keep in mind the principles which guided him in the published taxonomic results, but it is equally clear that as he became older he developed new views on the nature of his taxonomic categories. It can hardly be said that this is reflected in his formal taxonomy but can be understood from many of the dissertations defended by his pupils, though as presented by Linnaeus the evidence is often fragmentary and contradictory. The following is a brief outline of a broad subject to which numerous scholars contributed, more recently e.g. Broberg (1975), Eriksson (1969), Frängsmyr (1969), Larson (1971), Lindroth (1967), Ramsbottom (1938), Stafleu (1971), Stearn (1957).

Genus, species and variety

Fundamenta botanica (Linnaeus 1736) which appeared during his second year in Holland, presents his views on the categories he used in the classification. It is remarkable that here only the genus is given a definition that is of practical use: "We admit as many genera as there are different natural species produced by differently built fructifications" i.e. "of which the fructification has the same structure". From a series of other aphorisms it is possible to deduce which the characters of the fructification are and how they should be assessed. This is of course the principle upon which *Genera plantarum* (Linnaeus 1737) builds, a work surprisingly free from vegetative characters. It was also a method of which Linnaeus was openly proud: "... a genus not described according to Linnaeus method is quite imperfect. This sole work [*Genera plantarum*] seems to have required the whole life of a man. The botanists previously complained that the fructification would not be sufficient to distinguish genera, and so (my) predecessors had to go to leaves and facies plantae until Linnaeus showed them otherwise. Hence these genera are accepted by all botanists, who have accomplished anything of importance" (Autobiography III, ed. Malmeström & Uggla 1957 p. 137).

For species and varieties no such concrete rules were given. "We reckon as many species as there were diverse forms created in the beginning" is the famous aphorism which shows that Linnaeus adhered to the dogma of the divine creation of species, already then becoming old-fashioned. It gives no hint of a method for defining the species. He repeated this aphorism in *Philosophia botanica* (Linnaeus 1751 a) and does not add much towards a working definition. "Species are all structures, which do not depend on growth place or other occasional causes". The sentence forms a sort of boundary with the lowest category, the variety, for which *Fundamenta* and *Philosophia* give the following definition: "There are as many varieties as there are plants produced by the seed of the same species". This almost modern touch is purely accidental. Varieties were all sorts of phenotypic divergencies as well as constant cultivars, for example plants with double flowers. Much later, in theses such as *Somnus plantarum* (Linnaeus 1755 b) he was more hesitant asking whether these constant varieties were not after all to be regarded as species. The important point is that unlike earlier systematists he denied the species nature of all kinds of occasional forms, individuals of opposite sexes, abnormities, monstrosities, etc. considering them unimportant and seldom using them in his works. "Varieties which inundated botany he reduced to his species." (Autobiography III, ed. Malmeström & Uggla 1957 p. 151). "Varieties had uselessly increased the number of plants to the double. Linnaeus placed the varieties under his species and thus abolished thousands of names" (Autobiography IV, ed. Malmeström & Uggla 1957 p. 167). With this view a broad species concept is almost inevitable – it would mean a return to Chaos if a new world of variations appeared.

Classes and orders

Another aphorism (No. 162) in *Fundamenta*, and *Philosophia*, summarizes his view of the categories as follows: "The species and genus are always the work of nature. The variety mostly that of cultivation. The class and order are the work of art and of nature". The semantics of the terms "nature" and "natural" are another story, but in this context they must stand for "created by God". It can here be noted in passing that the number of categories is dogmatically set as five. Linnaeus showed an irrational inclination towards the use of the number five, which is also found in the categories of logic philosophy as taught in the schools of his day, and which may form a parallel between natural and logic form just as is expressed more clearly in his generic concept.

The natural genera, which can be defined by means of a clear method, form the corner-stone of Linnaeus's system. In the spirit of Aristotelian logic the essence of the plant is to be revealed and for Linnaeus it is without doubt also to be found, in the fructifications (i.e. the flowers) which were for him the functionally most important parts of the plant, its "perfection". The limited but adequate number of characters and positions also offered added possibilities for logical combinations, but it is often emphasized (e.g. Bremekamp 1952) that the variation on which his taxonomy was based is in itself of little importance biologically (number of carpels, degrees of coalescence, etc.), a fact of which Linnaeus was probably fully aware. For the whole of this scholastic revelation of the created genera and species is offset by the very last line of *Fundamenta* which almost amounts to a word of warning: "In science the fundaments of truth must be confirmed by observation." The fact that the Linnaean genera, in spite of the dogmatic way in which they were defined, have so well stood the test of time must be due to Linnaeus's eminent gift of observation and taxonomic intuition which perhaps unconsciously, so to speak, superseded the dogmatic logic.

The classes and orders "of art and of nature" reveal his conflict between a natural system and an artificial one, his sexual system. For convenience in examination the natural genera were arranged in artificial classes. It seems appropriate here to quote what Elias Fries (1864) said about this system: "Linnaeus's system becomes by its definiteness a short cut to the more scientific, but more undecided natural systems. Like in an index you go from the name to find the thing, in the sexual system (an inverted index) you go from the thing to find the name."

Methodus naturalis

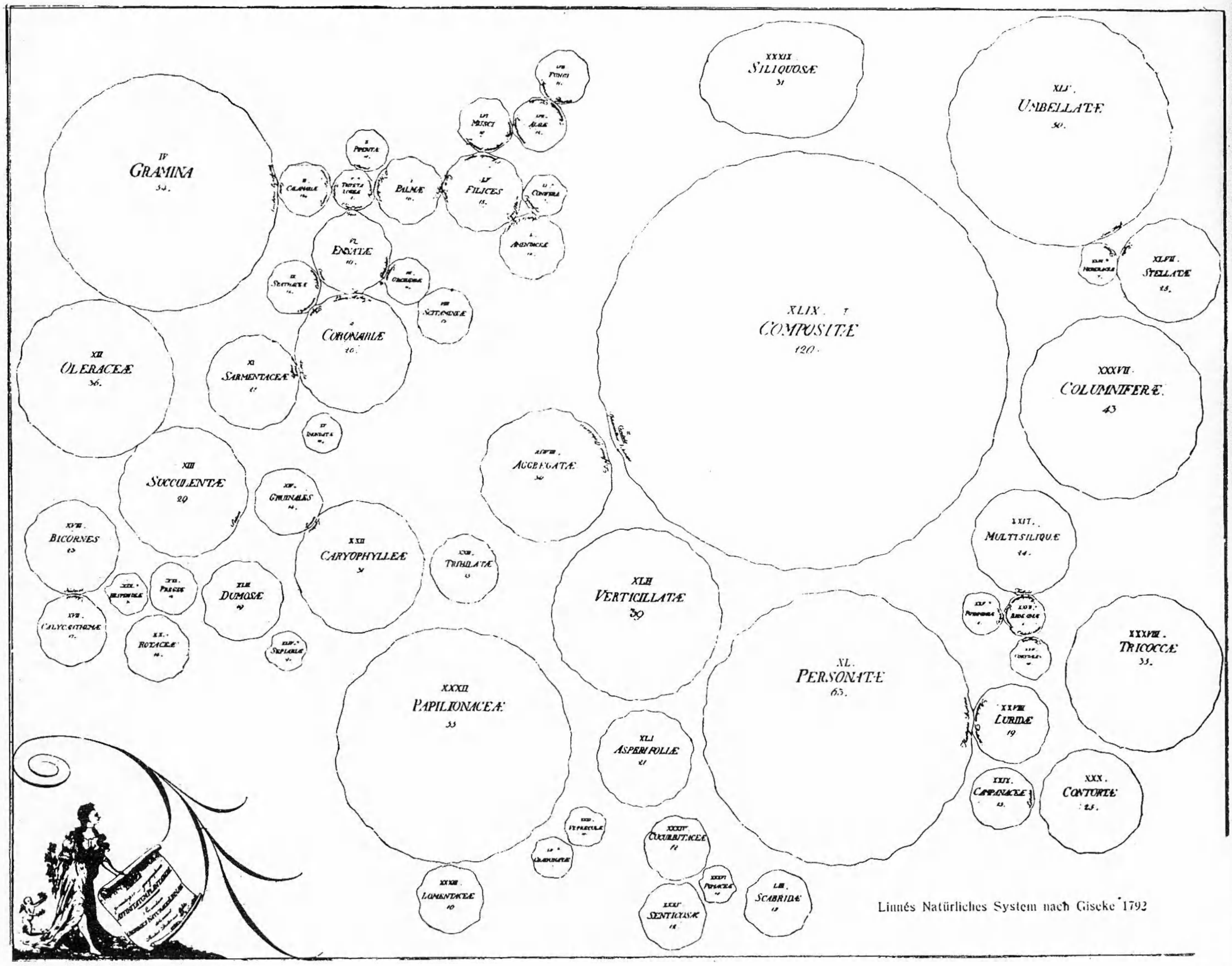
On the other hand a system is said to be natural when it reflects the Creator's great plan for nature. It is for the systematist to reveal this plan, which can be seen as a specialized task when the period of the physico-teological approach was at its height. Man's ultimate raison d'être is to praise the Creator and his plan for the Creation which is purposeful in every detail, a view which imbues much of Linnaeus's writings.

The 77th aphorism in *Fundamenta* runs: "I will myself try to present fragments of a natural method" *(Fragmenta methodi naturalis),* a comparatively modest statement which was reworded in a more impersonal way in *Philosophia*: "fragments of a natural method must be sought with greatest care." Fragments were first presented in *Classes plantarum* (Linnaeus 1738), published during his third year in Holland. In *Philosophia* no less than 63 such natural orders of seed plants are presented largely corresponding to our families, but usually marred by misplaced genera. His orders are found again as an appendix to the sixth edition of *Genera plantarum*. He states no method for distinguishing these orders and we have to presuppose an intuitive comprehension of overall similarity. His thoughts behind the *Fragmenta methodi naturalis* had already been set out in 13 points in *Classes*. From these we learn that to begin with he restricts himself to suggesting the orders. Once these are known they will be simple to arrange in classes. However, Linnaeus never got as far as defining these natural classes but presented the orders in an arbitrary fashion. "System is Ariadne's clew for botany, without which all is chaos" runs aphorism No. 156 in *Philosophia*. "When imitating nature" he wrote in a comment to another aphorism "one must guard against losing Ariadne's clew, as did Morison and Ray" (both of whom had attempted to formulate natural systems) but he is here not much better off himself. "It is, however, impossible to give a key to the (natural) method before all plants have been assigned to their orders" runs the seventh point in *Classes plantarum*. This lack of information may explain why he did not push the matter further. He did not even state explicitly, whether he imagined a definite sequence or other regular plan of arrangement for the natural orders, but the famous statement "Nature makes no leaps" is made in just this connection. Together with this statement, seemingly contradictory to the practical work of classification, may be quoted a passage from a disputation on the question *Cui bono?* (Linnaeus 1752):

"There is, as it were a certain chain of created beings, according to which they seem all to have been formed, and one thing differs so little from the other, that if we fall into the right method we shall scarcely find any limits between them. This no one can so well observe as he who is acquainted with the greatest number of species." This idea of a chain was a commonplace in pre-Darwinistic time (Lovejoy 1936), but in *Philosophia* Linnaeus chose to describe the affinities in another, equally celebrated manner: "All plants show affinities on all sides like the territories on a geographical map." This is an image Linnaeus clung to till the end of his days. He presented it, at least in words, in the lectures given towards the end of his life. From these lectures a *Tabula* (Fig. 1) was constructed and published many years later by his German pupil Giseke (1792; also in Schuster 1928) who spent the summer of 1771 with Linnaeus. The orders are represented as circles and distributed like countries on a map. Of particular interest are the genera whose names appear at the circumference of some circles. Linnaeus regarded them as bridging the gaps between adjacent orders. He said that their names were to be a well-hidden secret which, however, he apparently revealed for Giseke, who in his explanation of the *Tabula* quotes fragments of a discussion with Linnaeus. The diagram is evidence of Linnaeus's never-failing efforts towards finding a "natural method". He ranked "the natural orders" among his master feats although, as he wrote, "many an ignorant would regard (them) to be of little value or use" (Autobiography IV, ed. Malmeström & Uggla 1957 p. 170).

Ambivalence of ideas

The diagram is also of importance as it bears witness to Linnaeus's idea of hybridization as a device for the origin of new forms, for only against that background can it be fully under-



Linnés Natürliches System nach Giseke 1792

Fig. 1. "*Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei*", constructed by P. D. Giseke from Linnaeus's lectures. The numbers of the natural orders (Roman numerals) are the same as in the 6th edition of *Genera plantarum* (1764). The Arabic numerals denote the number of genera, to which the diameters of the circles are approximately proportional. Transitional genera are indicated on adjacent parts of the circumferences. The diagram has been taken from Schuster (1928).

stood. At the same time it shows Linnaeus's adherence to the idea of a continuum in Creation. The empty space between the circles is neither seen as a place where new forms can arise, nor has it been left after forms that are extinct but merely represents unexplored country yet to be discovered. To Linnaeus extinction was something inconceivable, since in Nature's dynamic equilibrium as exemplified in dissertations such as *Oeconomia* (Linnaeus 1749 b) and *Politia naturae* (Linnaeus 1760 b), God created all living beings interdependent and none of them must abandon their role on earth.

Linnaeus's evolutionary ideas build on the concept of hybridization and he finally came to the conviction that its role had been of great importance in the remote past and that hybridization still possibly led to the rise of new forms. Such ideas cannot be traced further back than to the middle of the 1740s. In 1743 he gave a speech *De telluris habitabilis incremento* (Linnaeus 1744 a) with his celebrated description of Paradise. Here the constancy of species is in no way brought into question. Rather it is emphasized in the way he calculates back from the present number of individuals tapering off to a pair of individuals, or one hermaphrodite individual, of each species. "This first among the secondary causes we must presuppose to have been created by God's direct action." The purpose of this speech, the tone of which was somewhat naive, is to give proof of the constancy of species. On this point Linnaeus remains faithful to his Bible.

But in 1744, the same year as this speech was published, he obtained living plants of the celebrated monstrosity, *Peloria, Linaria vulgaris* with regular flowers and discussed it in a dissertation (Linnaeus 1744 b), which is often cited as the prime evidence that Linnaeus was an evolutionist (cf. Gustafsson 1978). Once Linnaeus had become convinced that the plant was not a joke to trap him he became enthusiastic: "It exemplifies something beyond its like in botany", namely that it diverged from its mother genus so far that its fructification necessitated its position in a new genus, yes indeed to another natural order or class. The importance of this extremely drastic case lies in the fact that, quite wrongly, he interpreted it as a hybrid "of greater significance than the hybrids among animals, since there the descendants lack ability of reproduction, as mules and similar creatures". The frequently quoted words with which the dissertation ends are worth repeating: "If *Linaria* does not again arise from *Peloria* a wonderful conclusion will follow, namely that new species may originate among plants; that genera unlike in fructifications may have the same origin and nature, yes that in the same genus there may be different fructifications." Apparently he soon felt some hesitation about *Peloria* and its possible significance, and certainly not only because of objections from theologians. This is understandable since it not only cast doubt over the constancy of species but even of genera, the corner-stone of his system.

The role of hybrids

In *Flora Suecica* (Linnaeus 1745 a) the importance of *Peloria* had already been reduced – it is only mentioned in passing. Six years later, in *Philosophia botanica*, he comments under the aphorism which he still considered to be valid: "We reckon as many species as there were forms created in the beginning ... Evidence against the occurrence of new species is offered by continuous generation, propagation, daily observations, cotyledons", i.e. common experience makes the constancy of species probable. But he does not settle the case. Immediately after the quoted phrase follows: "Doubts have been raised by Marchant, myself in *Peloria* and Gmelin" (who had reported a *Delphinium* hybrid from Russia) and then a number of species are cited, which are as if (i.e. *quasi*) they had fathers from other genera. The numerous species of *Geranium, Mesembryanthemum, Aloë* from Africa, for which in the dissertation *Plantae hybridae* (Linnaeus 1751 b) he presumed a hybrid derivation, are also cited.

Plantae hybridae was published in the same year as *Philosophia* and is an attempt to classify the alleged hybrids so far observed – there are "*bigeneres* (Fig. 2), *congeneres, deformatae, obscurae, suspectae*", but it is perhaps significant that *Peloria* is not among those listed. It is only mentioned in passing in the text among examples that "others may find supra-natural". No evolutionary significance of the hybrids is expressed here, but it should be noted that his observation "constant varieties – almost species" first appeared here. His ambivalence is obvious and he still feels inclined to deny the role of hybridization in evolution.

During this time his *magnum opus, Species plantarum* (Linnaeus 1753), was conceived and many passages reveal that the problems of constancy occupied his mind. "*Affinis*", affinity between species, is often mentioned and it is tempting to attribute this term a deeper meaning than resemblance. The expression "*temporis filia*" is used of certain species with a clear affinity to some other species and he wonders whether all species of a whole genus might not have originated from hybridization. During the ten years that elapsed between the first and second editions of *Species plantarum* such examples multiplied, which reflects Linnaeus's increasing involvement in the problem.

The cortex – medulla theory

During this period some theories that lay behind his observations developed. First the strange idea of medullar and cortical substances which had also been expressed by Caesalpinius but which as elaborated by Linnaeus was the only original Swedish contribution to the many doctrines of reproduction of the day. It matured slowly. Löfling's thesis *Gemmae arborum* (Linnaeus 1749 a) contains the earliest trace, it appears in some pages of *Philosophia* and is fully developed in *Metamorphoses plantarum* (Linnaeus 1755 a) and *Generatio ambigena* (Linnaeus 1759). I need not present these speculations in detail, only make clear that Linnaeus held that a maternal medulla accounted for the gynoecium and also for a mysterious power of life, a vitality, which passes from the mother to the next generation. It is continuous through the ages both backwards and forwards. The paternal cortex accounts for all other organs, the facies of the plant, the other four of the five (N. B.) layers he discerned in the plant. They cover the medulla, which only appears at the final metamorphosis to the flower.

When as in *Generatio ambigena* and the prize paper for the Petersburg Academy, *Disquisitio de sexu plantarum* (Linnaeus 1760 a), this doctrine is combined with the other, namely that all species of a genus have a common medullar substance covered by different cortical substances from various hybrid combinations, an evolutionary doctrine was close at hand. The genera are kept together by that vital maternal medullar substance, which after fertilization by different kinds of pollen develops into different kinds of cortex and different species. Linnaeus's enthusiastic adherence to this doctrine can well be understood agreeing as it does with his idea of stable, natural genera as he had long since difined them. It did not weaken the corner-stone of his system rather it strengthened it and allowed for the confusing affinities noted between species.

To confirm his doctrine in both the above mentioned works he claims that there is an array of hybrids, among them his own successful cross between *Tragopogon porrifolius* and *T. pratensis*. None of them were approved by the great hybrid experimenter Koelreuter on the Petersburg Prize committee, who found his medulla doctrine in its entirety "more ingenious than correct". But in particular the phantastic "*bigeneres*" gave important support to his ideas so that the *Veronica–Verbena* hybrid (Fig. 2) reappears in his paper about ten years after he had as he thought discovered it in his garden in Uppsala.

Fig. 2. "*Veronica* ☿ *hybrida*", as illustrated in the dissertation *Plantae hybridae* (1751). Linnaeus claimed that *Veronica floribus spicatis, foliis ternis* (= *V. maritima* L.) was the mother and *Verbena officinarum* (= *V. officinalis* L.) the father. It has not been identified but could be an abnormal *Verbena* (note the opposite leaves). There is no specimen in the Linnaean herbarium. *Veronica hybrida* L. 1753 is an entirely different plant.

But so far this doctrine had not been linked to the biblical version of the Creation, which had previously been of extreme importance to him. It was inevitable that this problem must be tackled too, and the fruits of his thoughts are to be found in *Fundamentum fructificationis* (Linnaeus 1762) and the preface to the sixth edition of *Genera plantarum* (Linnaeus 1764). Fascinated by his subject he engaged in grandiose speculation increasing the role of hybridization so that it became a three-step process which accounted for all his natural categories. "*Fundamentum fructificationis* had all spoken of but none understood" he says in one autobiography (No. IV, ed. Malmeström & Uggla 1957, p. 166). "The Creator in the beginning covered the medulla with cortex ... from which arose so many different individuals as there are natural *orders*. The Omnipotent mixed those among each other from which arose so many genera from the orders as there were plants" (Linneaus 1762). The genera are thus secondary to the orders but by contrast with the following the Omnipotent was directly involved in their origin, which is of significance. "*Nature* mixed these genera, from which arose so many *species* of the same *genus* as there are today. Chance mixed these species from which arose so many *varieties* as appear here and now. These processes occurred according to the *Creator*'s laws, which run from the simple to the complicated, *Nature*'s law to produce hybrids and *Man*'s laws which are formed by observation and practice'' (Linnaeus 1764).

For an evolutionary theory the question of time is noticeably absent. When and for what duration of time did the events take place? It is surprisingly difficult today to grasp the role of that species-forming hybridization ("... from which arose so many species of the same genus as there are today."). Is it after all a completed process, by contrast with the appearance of varieties? He interpreted the biblical narrative of the Creation but in a manner which was rather conventional for his day and which could not be used to build on. The 6000 years allowed by the Bible he could, however, not accept: "Linnaeus would regard the age of earth older than the Chinese if only Scriptura Sacra permitted'' (Autobiography IV, ed. Malmeström & Uggla 1957 p. 172), and probably much more than so if we are to judge by his exclamations when mentioning the geological phenomena he encountered on his journeys (e.g. Linnaeus 1745 b).

His fascination for evolutionary phenomena never waned and he showed a vivid interest in examples that appeared, as the *Fragariae* discussed with Duchesne in Paris in the 1760s (Hylander 1940). But his evolutionary doctrines are of more interest for what they tell about Linnaeus himself than for their importance to science, his own classification not excepted. If he has had any influence upon the evolutionary ideas that were to come this emanates from works such as *Oeconomia naturae* (Linnaeus 1749 b) and *Politia naturae* (Linnaeus 1760 b) with their exemplifications of a "*bellum omnium inter omnes*'' between not within species to be true, and those of a role for every being in nature (cf. Broberg 1978). Such thoughts, built on observation and numerous other sources, influenced the evolutionists of the following century. It has been said that Linnaeus's greatest significance where the science of evolution is concerned is that he was read by Darwin.

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