Epidermal leaf structures in species of Asystasieae, Pseuderanthemeae, Graptophylleae and Odontonemeae (Acanthaceae)

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Epidermal leaf structures on the upper and lower epidermis (cell structure, stomata, non-glandular and glandular hairs, cystoliths) of five species of Asystasieae (*Asystasia* Bl., *Chamaeranthemum* Nees), five species of Pseuderanthemeae (*Pseuderanthemum* Radlk.), four species of Graptophylleae (*Pachystachys* Nees, *Ruspolia* Lindau, *Anisacanthus* Nees), and fifteen species of Odontonemeae (*Peristrophe* Nees, *Hypoestes* R. Br., *Ballochia* Balf. f., *Clinacanthus* Nees, *Ruttya* Harv., *Ecbolium* Kurz, *Mackaya* Harv., *Odontonema* Nees, *Rhinacanthus* Nees, *Schaueria* Nees) were studied. Most of the material originated from plants cultivated in greenhouses. Additional observations have been made on herbarium specimens. The tribes Asystasieae, Graptophylleae and Pseuderanthemeae were found to be homogeneous groups as regards leaf epidermal structures. The subtribes Odontonemeae-Diclipterinae and Odontonemeae-Monotheciinae are tolerably homogeneous groups. They are distinctly separated from each other and from the third subtribe of the Odontonemeae, i. e. Odontoneminae, which is a heterogeneous group regarding leaf epidermal structures.

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Bremekamp (1965) united the typical representatives of Lindau's Asystasieae, Graptophylleae, Pseuderanthemeae and Odontonemeae in a single subtribe Odontoneminae of the tribe Justicieae. The present studies were made in order to find out whether or not epidermal characters might be helpful in the delimitation of the tribes Asystasieae, Graptophylleae, Pseuderanthemeae and Odontonemeae of Lindau (1895).

Material and Methods

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 position 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: *Asystasia gangetica* (L.) T. Anders. (2 plants), *A. laticapsula* C. B. Cl. ex Karlström (3 pl.), *A. travancorica* Bedd. (6 pl.), *Chamaeranthemum beyrichii* Nees (3 pl.), *Pseuderanthemum alatum* (Nees) Radlk. (2 pl.), *P. cinnabarinum* (Wall.) Radlk. (3 pl.), *P. indicum* (Nees) Cowan (4 pl.), *P. tuberculatum* (Hook. f.) Radlk. (3 pl.), *P. tunicatum* (Afzel.) Milne-Redhead (3 pl.), *Pachystachys lutea* Nees (3 pl.), *Ruspolia seticalyx* (C. B. Cl.) Milne-Redhead (3 pl.), *R. hypocrateriformis* (Vahl) Milne-Redhead (3 pl.), *Anisacanthus virgularis* Nees (2 pl.), *Ballochia rotundifolia* Balf. f. (3 pl.), *Ruttya fruticosa* Lindau (3 pl.), *Clinacanthus siamensis* Bremek. (1 pl.), *Peristrophe speciosa* Nees (3 pl.), *Hypoestes antennifera* S. Moore (6 pl.), *H. aristata* (Vahl) Soland. ex Roem. et Schult. (2 pl.), *H. verticillaris* (L. f.) Soland. ex Roem. et Schult. (2 pl.), *Odontonema schomburgkianum* (Nees) O. Kuntze (5 pl.), *O. strictum* (Nees) O. Kuntze (4 pl.), *Mackaya bella* Harv. (3 pl.), *Schaueria calicotricha* Nees (3 pl.), *Rhinacanthus communis* Nees (6 pl.), and *Ecbolium revolutum* C. B. Cl. (3 pl.).

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Additional observations were made on herbarium material of the following species: *Asystasia laticapsula* C. B. Cl. ex Karlström (4 specimens), *A. gangetica* (L.) T. Anders. (2 sp.), *A. schimperi* T. Anders. (6 sp.), *Ruttya fruticosa* Lindau (2 sp.), *Ecbolium amplexicaule* S. Moore (1 sp.), *E. hamatum* C. B. Cl. (1 sp.), and *E. revolutum* C. B. Cl. (4 sp.).

Voucher specimens are deposited at GB.

Observations

Cell structure

Intervenous areas. The epidermal cells are irregular with sinuous or slightly sinuous walls (Fig. 1 A, B, Table 1). When there is a difference in the degree of undulation between the two surfaces of the leaves, the cells of the lower epidermis have walls more undulated than those of the upper epidermis. In *Anisacanthus virgularis, Hypoestes aristata* and *H. antennifera* the degree of cell wall undulation is most pronounced (Fig. 1 C), while in *Chamaeranthemum beyrichii, Odontonema strictum, Ballochia rotundifolia, Ecbolium revolutum,* and *E. amplexicaule* the cell walls of the upper epidermis are straight (Fig. 1 D).

No important size differences between intervenous cells from the lower and the upper epidermis were found. The cells in *Ballochia rotundifolia* and *Odontonema strictum* are markedly larger than those of the other species (Fig. 1 D).

On veins. The costal cells are straight-walled, mostly elongated, and arranged end to end in parallel rows, in all species studied (Fig. 1 E–G). The cells on the lower and upper epidermis are almost equal in size in most species (Table 1). In *Peristrophe speciosa, Hypoestes aristata, Pseuderanthemum tunicatum, Chamaeranthemum beyrichii,* and *Ruttya fruticosa* the cells of the lower epidermis are markedly longer than those of the upper one (Table 1). The most elongated costal cells are found in *Peristrophe speciosa* and *Hypoestes aristata*. The shortest costal cells are found in *Clinacanthus siamensis*.

Stomata

Stomata are scattered in intervenous areas in the lower epidermis in all species studied. They belong to the diallelocytic type as defined by Payne (1970). Stomatal size and frequency and stomatal indices are shown in Table 1.

Among the species grown under greenhouse conditions stomata were present and sparsely scattered in intervenous areas of the upper epidermis in *Asystasia laticapsula, Ecbolium revolutum* and *Hypoestes verticillaris*. The frequencies were lower than those of the lower epidermis. In *Asystasia gangetica, A. travancorica, Peristrophe speciosa, Hypoestes antennifera, H. aristata, Clinacanthus siamensis, Odontonema strictum,* and *Rhinacanthus communis* stomata occurred very sparsely in the upper epidermis and were restricted to areas in close vicinity of the midrib. No great differences in stomatal size (i. e. the size of guard cells) between the lower and upper epidermis were found in most of those species which have stomata on both surfaces of the leaves. In *Clinacanthus siamensis* and *Hypoestes aristata*, however, stomata of the upper epidermis were markedly larger than those of the lower epidermis (Table 1). In *Hypoestes antennifera* and *Rhinacanthus communis* the stomata in the upper epidermis were longer than those of the lower one.

In *Odontonema strictum* stomata occur on the midrib of the lower epidermis (Fig. 1 H). In *Asystasia laticapsula, Peristrophe speciosa, Hypoestes antennifera, H. verticillaris,* and *Rhinacanthus communis* stomata occur on the midrib of the upper epidermis. The frequencies are very low. In *Odontonema strictum* and *Hypoestes* spp. the occurrence of stomata on midribs seems to be regular, while in the other mentioned species it seems to be occasional. In *Asystasia gangetica* stomata occur sparsely on the midrib of both leaf surfaces. In all species where stomata occurred on the midribs the guard cells were predominantly oriented parallel to the

Fig. 1. Epidermal cells from intervenous areas and costal cells. — A, C: Cells with sinuous walls (int, le). — B: Cells with slightly sinuous walls (int, ue). — D: Cells with straight walls (int, ue). — E–H: Costal cells (le). Notice stomata in H. — The dotted lines in B, D, F indicate the outlines of cystoliths. — A: *Pseuderanthemum indicum*. — B, G: *Clinacanthus siamensis*. — C: *Anisacanthus virgularis*. — D, H: *Odontonema strictum*. — E: *Peristrophe speciosa*. — F: *Pseuderanthemum alatum*. — int intervenous area, le lower epidermis, ue upper epidermis.

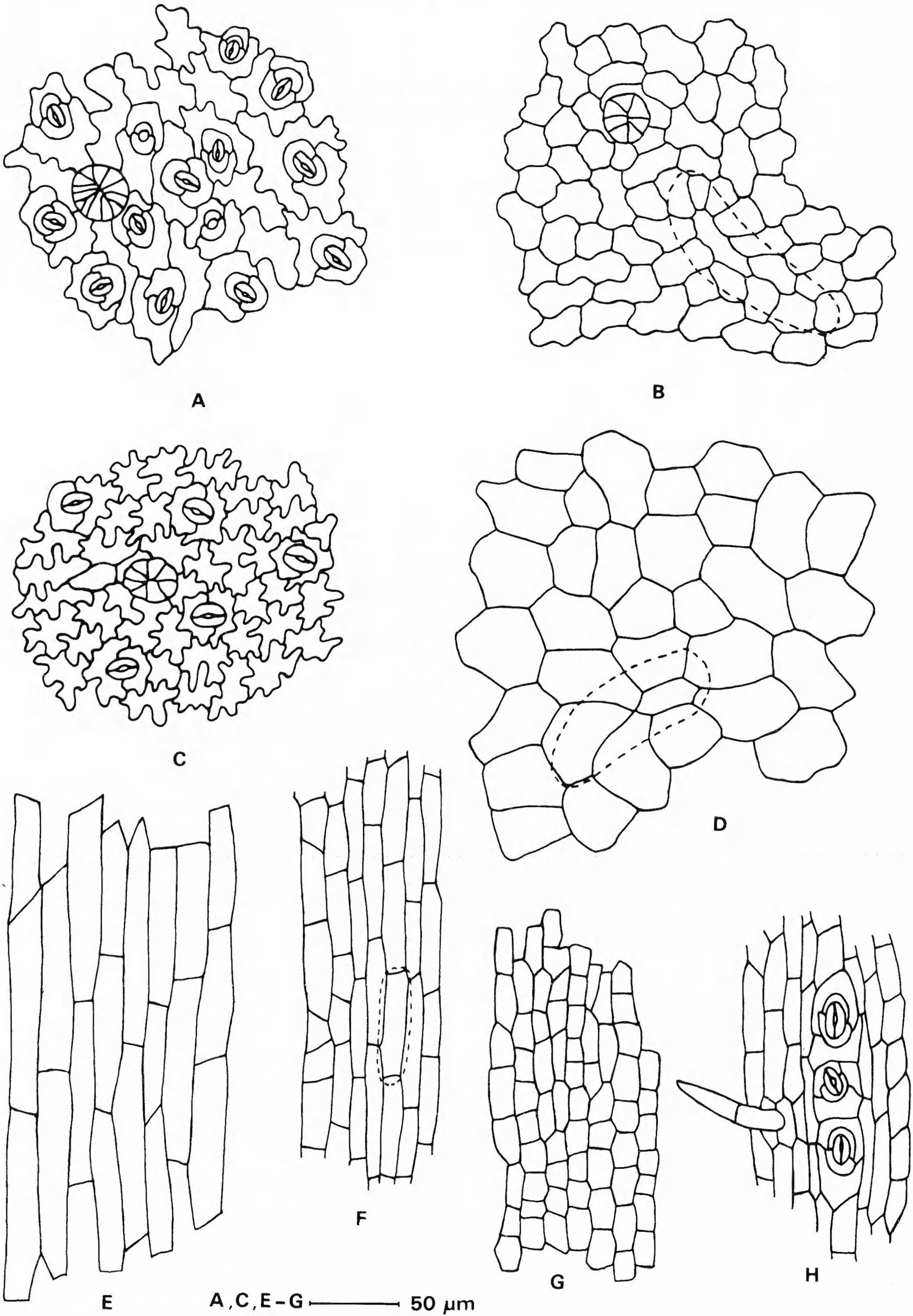
A
B
C
D
E
F
G
H
A,C,E-G 50 µm
B,D,H 50 µm

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

Species	Cell structure in intervenous areas		Cell size, midrib (μm)		Stomatal frequency per mm²		Stomatal index		Stomatal size (μm)	
	L	U	L	U	L	U	L	U	L	U
Asystasieae										
Asystasia laticapsula	sin	sin	38×15	39×20	74	13	15.4	5.4	20×13	19×11
A. travancorica	sin	sl sin	37×13	41×13	81	*	15.2	–	21×14	19×12
A. gangetica	sin	sin	36×12	45×15	78	*	16.3	–	20×13	22×13
Chamaeranthemum beyrichii	sl sin	str	66×11	48×17	58	0	15.8	0	17×9	0
Pseuderanthemeae										
Pseuderanthemum alatum	sin	sl sin	45×15	54×16	40	0	10.7	0	17×10	0
P. cinnabarinum	sin, sl sin	sl sin	29×18	25×18	39	0	12.7	0	20×12	0
P. indicum	sin	sin	48×11	53×15	111	0	17.5	0	16×9	0
P. tuberculatum	sin	sin, sl sin	32×9	32×15	77	0	10.9	0	19×13	0
P. tunicatum	sl sin	sl sin	65×14	39×16	75	0	15.7	0	18×11	0
Graptophylleae										
Pachystachys lutea	sin, sl sin	sin	33×13	24×13	63	0	9.8	0	16×10	0
Ruspolia hypocrateriformis	sin	sin	43×18	41×12	47	0	9.9	0	23×14	0
R. seticalyx	sin	sl sin	45×10	39×16	69	0	12.9	0	17×12	0
Anisacanthus virgularis	sin	sin	40×19	41×15	48	0	9.1	0	19×14	0
Odontonemeae-Diclipterinae										
Peristrophe speciosa	sin	sin	93×17	48×16	51	*	13.3	–	22×13	22×15
Hypoestes antennifera	sin	sin	35×17	33×13	59	*	14.0	–	19×12	25×14
H. aristata	sin	sin	89×19	57×17	63	*	16.6	–	24×15	30×16
H. verticillaris	sin	sin	57×21	48×15	106	10	15.7	2.8	17×11	18×12
Odontonemeae-Monotheciinae										
Ballochia rotundifolia	sl sin	str	46×12	38×18	77	0	17.8	0	21×14	0
Clinacanthus siamensis	sin	sl sin	22×12	25×15	38	*	8.8	–	21×13	29×17
Ruttya fruticosa	sin	sin	59×17	36×13	36	0	11.8	0	25×14	0
Odontonemeae-Odontoneminae										
Ecbolium revolutum	sl sin	str	34×13	36×11	65	30	10.7	6.5	18×13	19×14
Mackaya bella	sin	sin	36×13	32×17	86	0	16.0	0	19×12	0
Odontonema schomburgkianum	sin	sl sin	43×12	36×12	56	0	12.5	0	20×13	0
O. strictum	sl sin	str	59×20	53×23	43	*	15.3	–	24×13	23×17
Rhinacanthus communis	sin	sin	36×15	48×17	51	*	15.6	–	20×13	24×15
Schaueria calicotricha	sin	sin, sl sin	36×11	36×14	55	0	12.5	0	22×13	0

longitudinal walls of the epidermal cells of the midrib.

Among the species of which herbarium material was studied stomata were present in intervenous areas in the upper epidermis in all species but *Ecbolium amplexicaule* and *Ruttya fruticosa* (Table 2). In *Ecbolium hamatum* and *E. revolutum* stomata were very sparsely scattered in intervenous areas and predominantly restricted to areas in close vicinity of the midrib. In *Asystasia gangetica* stomata were present on the midrib of the upper epidermis.

Non-glandular hairs

Uniseriate, multicellular hairs occur in most of the species studied. The lengths and number of cells of the hairs are presented in Table 3. From the table can be seen that some species lack hairs in intervenous areas, others on the midrib. When there is more than one type of non-glandular hair on a leaf, the types of trichome bases bearing them are often different. The non-glandular hairs may arise from one single epidermal cell or two cells (Fig. 2 A, E, F). In some species the epidermal base cells do not differ or differ slightly from the other epidermal cells (Fig. 2 A, D). In other species these epidermal base cells differ

Table 2. Cell structure and size and stomatal characters of herbarium specimens. — L lower epidermis. U upper epidermis. — sin sinuous walls, sl sin slightly sinuous walls, str straight walls. — * stomata rare, only occurring in close vicinity of the midrib.

Species	Cell structure in intervenous areas		Cell size, midrib (μm)		Stomatal frequency per mm^2		Stomatal index		Stomatal size (μm)	
	L	U	L	U	L	U	L	U	L	U
Asystasia gangetica	sl sin	sl sin	54×13	60×16	123	11	–	–	17×11	19×12
A. laticapsula	sl sin	sl sin	51×13	52×17	67	40	23.2	17.3	25×17	24×15
A. schimperi	sin, sl sin	sin, sl sin	75×17	52×16	71	49	17.8	16.9	23×12	24×14
Ruttya fruticosa	sin	sin	50×12	36×14	77	0	16.7	0	23×14	0
Ecbolium amplexicaule	str	str	41×22	47×15	44	0	16.3	0	22×15	0
E. hamatum	sin	sin	56×16	51×16	40	*	14.9	–	21×13	23×13
E. revolutum	sin	str	48×15	43×20	66	*	13.0	–	22×14	22×14

Table 3. Length (in μm) and number of cells of non-glandular hairs on midrib and from intervenous areas (int a). Plants growing under greenhouse conditions. — L lower epidermis. U upper epidermis. — [1] Cells lack ornamentation, [2] rare, [3] very rare, only in close vicinity of veins, [4] basal cells red-coloured.

Species	Hair length Midrib		int a		Number of cells Midrib		int a	
	L	U	L	U	L	U	L	U
Asystasieae								
Asystasia laticapsula	309	213	285	233	3–5	3–5	3–5	3–5[1]
	1093	974	1177	902	8–11	6–9	6–9	6–8
A. travancorica	192	288	0	79	2–4	3–5	0	1–2
A. gangetica	268	104	82	120[2]	3–5	3–4	2–3	2–3
Chamaeranthemum beyrichii	364	348	292	265	3	3	3	3
			47	37			1	1
Pseuderanthemeae								
Pseuderanthemum alatum	307	0	0	482	5–7	0	0	5–6
P. cinnabarinum	196	214	0	0	4–5	3–6	0	0
P. indicum	198	165	0	433	5–7	6–8	0	–7
P. tuberculatum	157	55	0	0	3–4	1–2	0	0
P. tunicatum	212	268	0	314	5	5–8	0	3–7
Graptophylleae								
Pachystachys lutea	235	356	0	254	4–6	5–6	0	5–6
Ruspolia hypocrateriformis	249	304	0	0	3–8	3–4	0	0
R. seticalyx	267	251	0	230	3–4	4–5	0	3–4
Anisacanthus virgularis	180	211	0	133	3–4[2]	4–5	0	2–4
Odontonemeae-Diclipterinae								
Peristrophe speciosa	201	260	0	67	2–6	3–6	0	3–4
Hypoestes antennifera	666	149	395[3]	225	6–8[1]	2–4[1]	4–5[1]	3–4[1]
	195				3–5			
H. aristata	662	296	0	303	3–5	3–5	0	3–4
		526				5		
H. verticillaris	195	290	0	865	3–5	3–5	0	5–6
Odontonemeae-Monotheciinae								
Ballochia rotundifolia	201	48	0	0	2–4	1–2	0	0
Clinacanthus siamensis	164	218	0	0	2–3[2]	2–3	0	0
Ruttya fruticosa	341	326	0	0	4–5	3–4	0	0
Odontonemeae-Odontoneminae								
Ecbolium revolutum	223	151	150	161	2–4	2–3	2–3	1–4
Mackaya bella	263	0	0	0	8–9[4]	0	0	0
Odontonema schomburgkianum	238	360	0	438	4–7	4–8	0	6–7
O. strictum	114	0	0	0	3–5	0	0	0
Rhinacanthus communis	140	153	0	111	2–4	2–3	0	2–3[2]
Schaueria calicotricha	204	208	0	0	3–5	3–6	0	0

from the other epidermal cells in size and shape and in the pattern in which they are arranged (Fig. 2 B, D). If the normal epidermal cells are sinuous-walled, the walls of the trichome base cells are very often straight-walled (Fig. 2 B). Sometimes the non-glandular hairs are so numerous, that almost every epidermal cell is a trichome base cell.

The cell walls of the non-glandular hairs are ornamented in most species studied. The type of ornamentation is more or less the same in all species. The degree of ornamentation, however, varies. In some species the basal cells are more densely ornamented than the apical ones, while the opposite condition is true for other species. The only species, where the non-glandular hairs totally lack ornamentation is *Hypoestes antennifera* (Fig. 2 A, C). In *Asystasia laticapsula* the non-glandular hairs in intervenous areas of the upper epidermis lack ornamentation, while the hairs in other areas are ornamented. The hairs in *Hypoestes aristata* and hairs in the upper epidermis in *Anisacanthus virgularis* are sparsely ornamented.

The cell walls of the non-glandular hairs are normally thin. *Pseuderanthemum tuberculatum, Ecbolium revolutum, Ballochia rotundifolia*, and *Clinacanthus siamensis* differ in having hairs with markedly thick walls (Fig. 2 G, H).

The apices of the non-glandular hairs are normally tapering and pointed. In *Pseuderanthemum indicum* the apices are, however, blunt.

There are no marked differences in the size and shape of cells of a non-glandular hair in most species. The exception is true for the apical cell, which often is longer than the other cells. This is most pronounced in *Chamaeranthemum beyrichii*, where the hairs consist of 1 or 2 very short, basal cells and 1 long, apical cell (Fig. 2 E). In intervenous areas in the upper epidermis in *Hypoestes antennifera* the non-glandular hairs consist of 3–4 cells, where the basal one differs in size and shape (Fig. 2 C). In intervenous areas in *Pseuderanthemum indicum* the hairs are provided with apical cells, which are markedly shorter than the basal ones (Fig. 2 B). This seems to be normal and not to be due to that length stretching of the cells has not been completed, since I have not observed hairs, where all cells are equal in size.

Short, 1-celled hairs occur in intervenous areas on both surfaces of the leaves in *Chamaeranthemum beyrichii* (Fig. 2 F).

In most species the non-glandular hairs are straight, but in *Chamaeranthemum beyrichii* and *Ruttya fruticosa* they are markedly curved (Fig. 2 E, I).

Normally the non-glandular hairs are uniseriate, but in *Pseuderanthemum tunicatum* branched hairs frequently occur on the midrib of the lower epidermis (Fig. 2 L). In *Hypoestes antennifera* I have at one occasion observed a branched hair. Since I have observed only one branched hair in this species, I conclude that it was an abnormality. In *Peristrophe speciosa*, on the midrib of the upper epidermis, I have at one occasion found a branched hair, and at another occasion a hair with a tendency to branching (Fig. 2 K). Probably branched hairs is an abnormality in this species too.

The orientation of the transverse cell walls in the hairs in *Ruttya fruticosa* and to some extent in *Ecbolium revolutum* differ from those of the other species (Fig. 2 I). In *Ruttya fruticosa* the apical cell of the hair has markedly thicker walls than the basal cells.

On the midrib of the upper epidermis in *Peristrophe speciosa* non-glandular hairs with another type of transverse cell walls occur occasionally (Fig. 2 K).

Among the species of which herbarium material was studied *Ecbolium amplexicaule* is the only one which totally lacks non-glandular hairs (Table 4). In *E. hamatum, Ruttya fruticosa* and

Fig. 2. Non-glandular hairs. — A: Uniseriate hairs arising from a single epidermal cell and one hair with two epidermal base cells. Cell wall ornamentation is lacking (midrib, le). — B–D: Uniseriate hairs with several epidermal base cells, differing in shape from the other epidermal cells (B, C int, ue; D midrib, le). — E: Uniseriate, curved hair with two very short basal cells (midrib, le). — F: Very short, 1-celled hairs (int, ue). — G, H: Uniseriate, thick-walled hairs (midrib, le). — I: Uniseriate hair with oblique transverse walls (midrib, le). — K: Uniseriate hairs with normal transverse cell walls and one oblique wall (midrib, ue). — L: Branched hair (midrib, le). — The wall ornamentation is not marked in F, G, I, K, L. — A, C: *Hypoestes antennifera.* — B, D: *Pseuderanthemum indicum.* — E, F: *Chamaeranthemum beyrichii.* — G: *Ballochia rotundifolia.* — H: *Pseuderanthemum tuberculatum.* — I: *Ruttya fruticosa.* — K: *Peristrophe speciosa.* — L: *Pseuderanthemum tunicatum.* — int intervenous area, le lower epidermis, ue upper epidermis.

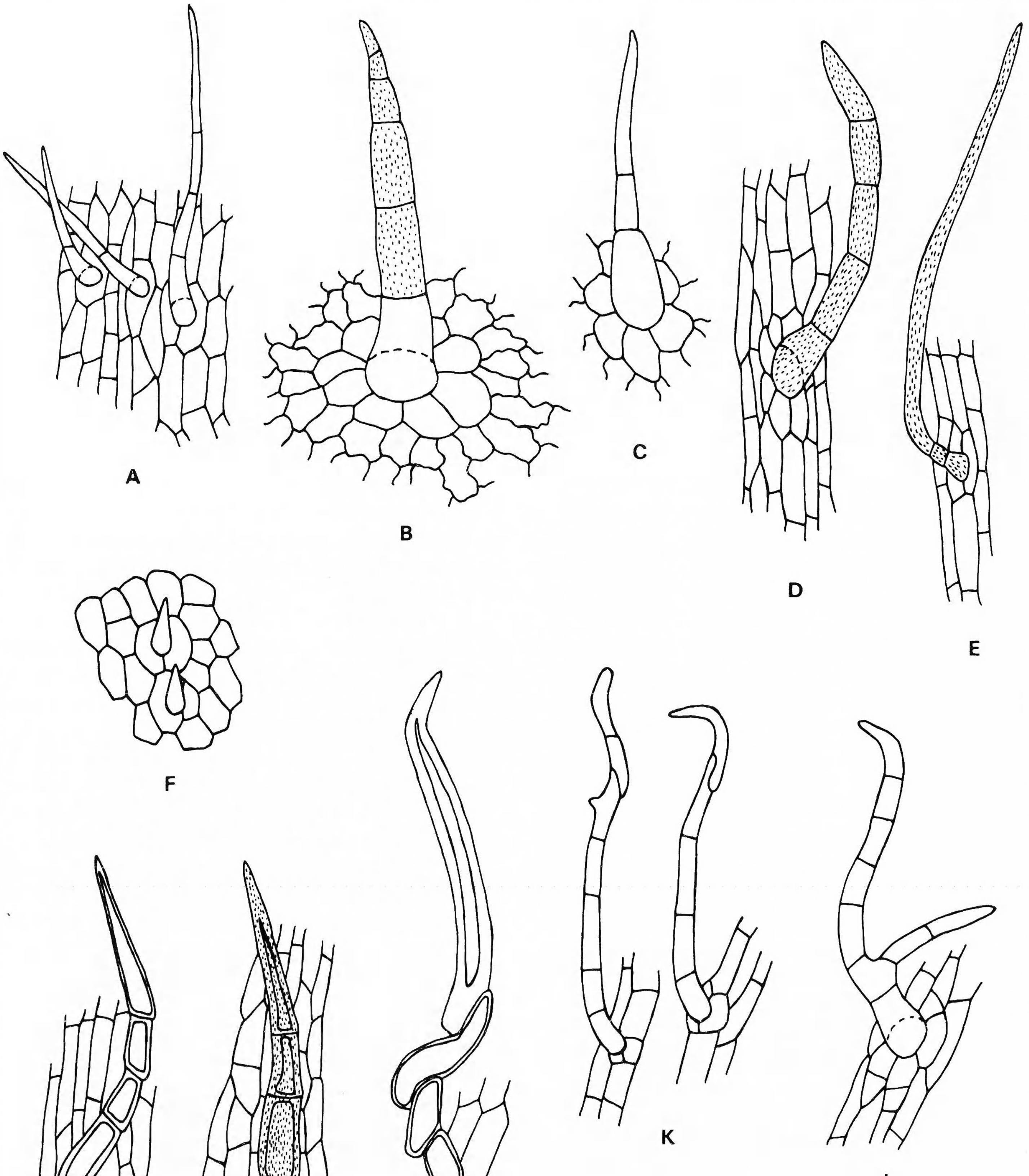
A
B
C
D
E
F
G
H
I
K
L
A – C, E, K 50 μm
D, F – I, L 50 μm

Table 4. Length (in μm) and number of cells of non-glandular hairs on midrib and from intervenous areas (int a) of herbarium specimens. — L lower epidermis. U upper epidermis. — [1] rare.

Species	Hair length				Number of cells			
	Midrib		int a		Midrib		int a	
	L	U	L	U	L	U	L	U
Asystasia gangetica	159	243	0	0	3–4	3–5	0	0
A. laticapsula	196	243	239	228	–3	3–5	2–4	2–3
	650	671		534	6–7	5–8		5–6
A. schimperi	819	650	339	308	6	4–7	3–5	2–5
	286	194			3–4	3–4		
Ruttya fruticosa	284[1]	179	0	0	3	2–4	0	0
Ecbolium amplexicaule	0	0	0	0	0	0	0	0
E. hamatum	278	310	0	0	3–5	3–5	0	0
E. revolutum	271	406	122	157	3–5	5–6	2–3	2–3

Asystasia gangetica non-glandular hairs are absent in intervenous areas of the upper epidermis. In the other species of which herbarium material was studied, non-glandular hairs of the same type as those of the cultivated material occur.

Glandular hairs

Subsessile glandular hairs are common among the species studied. They occur on the midrib, on veins and in intervenous areas on both surfaces of the leaves. The frequencies, however, vary. These hairs consist of a globular head, normally composed of 4 or 8 cells, and a single-celled stalk. The walls of the head cells are thin. The outlines of the head cells in *Anisacanthus virgularis* differ somewhat from the condition in the other species. In this species the cell walls are somewhat bulging (Fig. 3 G).

In some species the number of cells of the heads seems to be constant, while in other species the number varies. The subsessile glandular hairs in the species studied of *Peristrophe* and *Hypoestes* are always provided with 4-celled heads (Fig. 3 A). In *Pseuderanthemum* the heads are normally 8-celled or sometimes more than 8-celled. The studied species of Odontonemeae-Monotheciinae, i. e. *Ballochia rotundifolia, Ruttya fruticosa* and *Clinacanthus siamensis*, have 8-celled heads. In *Clinacanthus siamensis* the heads sometimes are 6-celled (Fig. 3 B). In the other tribes and subtribes the number of the head cells varies. In *Asystasia laticapsula, A. gangetica* and *Rhinacanthus communis* the heads are 4-celled, while in *A. travancorica* and *Ecbolium revolutum* the numbers vary. The greatest variation in the number of head cells occurs in *Pachystachys lutea*, where the heads may be 4-, 6-, 8-, or many-celled (Fig. 3 D, H). The head cells in *Odontonema schomburgkianum, Mackaya bella, Schaueria calicotricha*, and *Asystasia travancorica* contain small hyaline drops (Fig. 3 F).

Stalked glandular hairs occur in a few species. In *Rhinacanthus communis* these hairs consist of 1–3 stalk cells and a 4- or 8-celled globular head (Fig. 3 I, K). They occur sparsely on the midrib of the lower epidermis. In *Hypoestes antennifera* the stalks are longer, consisting of 8–9 cells. The heads are 4-celled (Fig. 3 L). These hairs occur sparsely on the midrib of the upper epidermis. On the midribs in *Peristrophe speciosa* another type of stalked glandular hairs occurs. These hairs consist of 2–5 stalk cells and a few-celled head (Fig. 3 N–T). In this species there is no sharp distinction between non-glandular hairs and stalked glandular hairs as regards cell wall ornamentation. The cell walls of the non-glandular hairs are always ornamented, while the short, stalked glandular hairs sometimes lack ornamentation (Fig. 3 N, R). However, stalked glandular hairs with ornamented cell walls (Fig. 3 O, S, T) occur together with those which lack ornamentation. Stalked glandular hairs with 2 or 3 stalk cells, the basal one longer, and a somewhat elliptic head occur in *Ecbolium revolutum* and *E. hamatum* (Fig. 3 M).

Cystoliths

Cystoliths occur epidermally or subepidermally on the midrib, on veins and in intervenous areas.

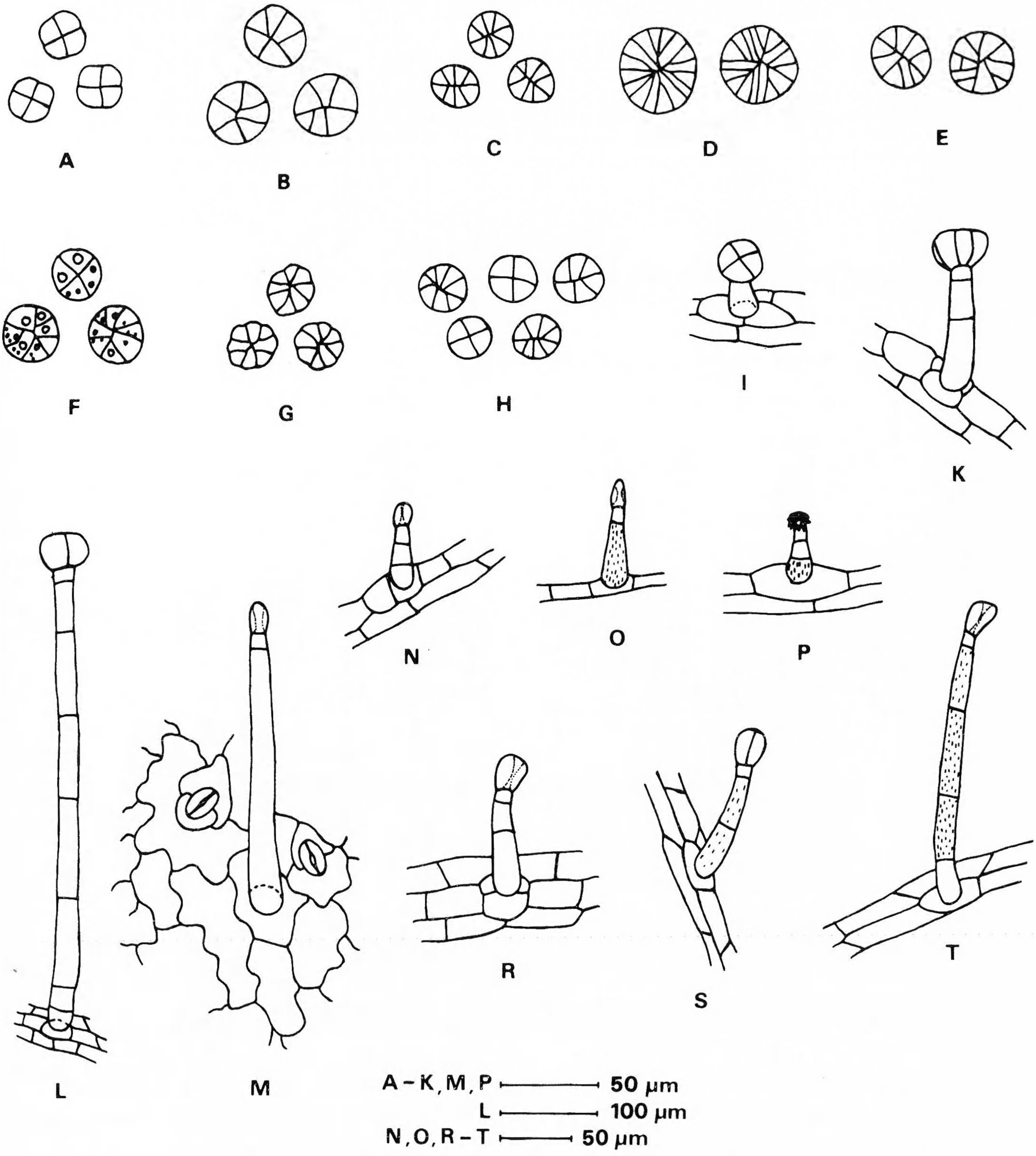

Fig. 3. Glandular hairs. — A–H: Subsessile glandular hairs, seen from above (A, C, D, F, G, int, le; B, E int, ue; H midrib, le). — I, K: Short, stalked glandular hairs with globular heads (midrib, le). — L: Long, stalked glandular hair with a globular head (midrib, ue). — M: Long, stalked glandular hair with a somewhat elliptic head (int, le). — N–T: Stalked glandular hairs. N, R without cell wall ornamentation; O, P, S, T with ornamentation (N, O, R–T midrib, ue; P midrib, le). — A, L: *Hypoestes antennifera*. — B: *Clinacanthus siamensis*. — C: *Ruspolia seticalyx*. — D, H: *Pachystachys lutea*. — E: *Ruttya fruticosa*. — F: *Asystasia travancorica*. — G: *Anisacanthus virgularis*. — I, K: *Rhinacanthus communis*. — M: *Ecbolium hamatum*. — N–T: *Peristrophe speciosa*. — int intervenous area, le lower epidermis, ue upper epidermis.

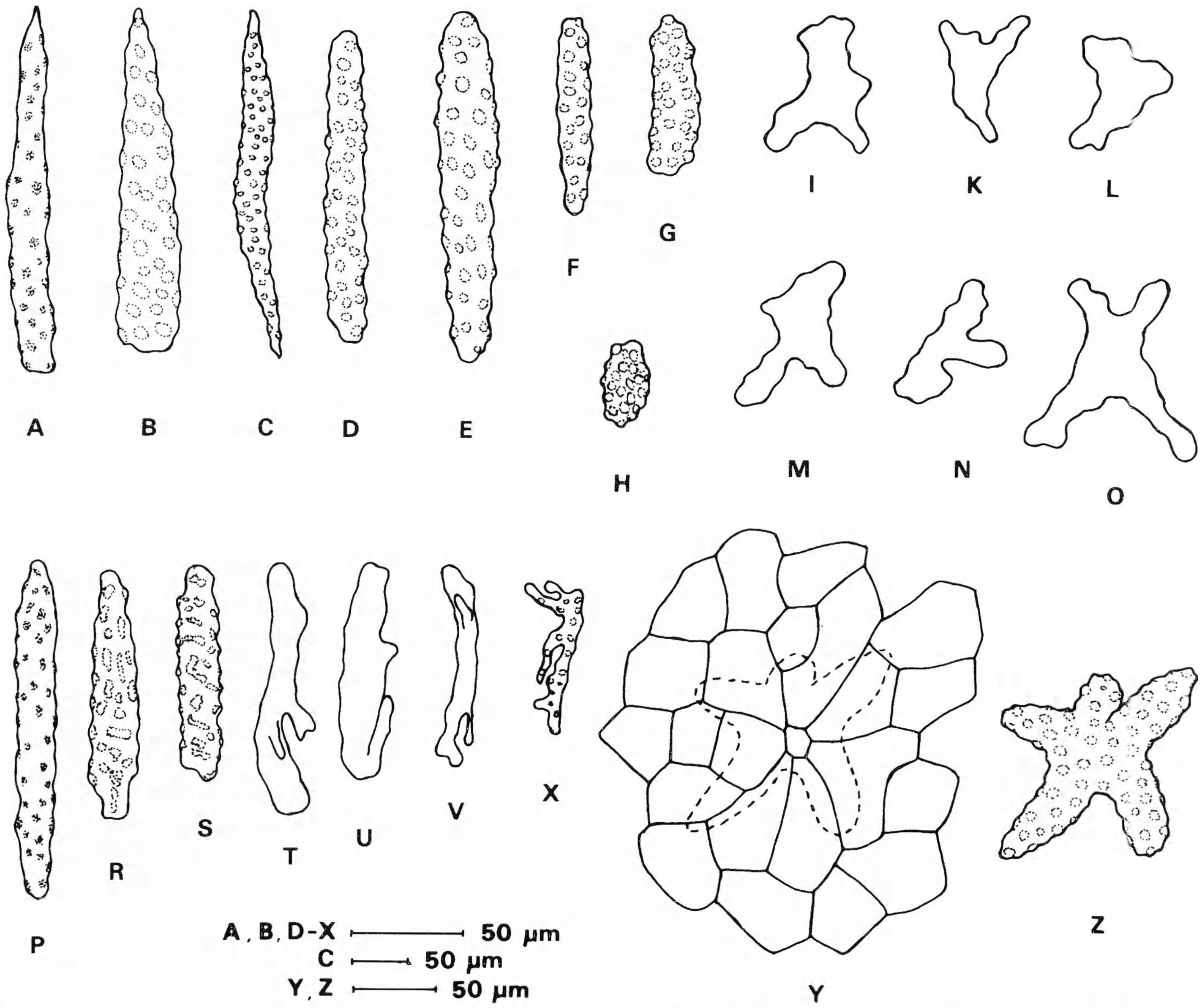

Fig. 4. Cystoliths. — Elongated, narrow, tapering at one end, type (1) (int, le). — B: Elongated, broad, tapering at one end, type (2) (int, le). — C: Elongated, tapering at both ends, type (3) (int, ue). — D: Elongated, narrow, blunt at both ends, type (4) (midrib, ue). — E: Elongated, broad, blunt at both ends, type (5) (midrib, le). — F: Short, narrow, blunt at both ends, type (6) (midrib, ue). — G: Short, broad, blunt at both ends, type (7) (int, le). — H: Rounded, type (8) (int, le). — I–O: Irregular, type (9). The tubercles are not marked (int, le). — P: Cystolith with sparsely distributed tubercles a (midrib, ue). — R, S: Cystoliths with irregular tubercles (midrib, le). — T–X: Irregular cystoliths. The tubercles are marked in X (int, ue). — Y: Subepidermal cystolith. The dotted lines correspond to the outlines of the cystolith (int, ue). — Z: The cystolith indicated in Y. — A, T–X: *Rhinacanthus communis*. — B: *Pseuderanthemum tunicatum*. — C, F: *Ecbolium revolutum*. — D: *Ruspolia seticalyx*. — E: *Mackaya bella*. — G: *Asystasia laticapsula*. — H: *Asystasia travancorica*. — I–O, Y, Z: *Ballochia rotundifolia*. — P: *Ruttya fruticosa*. — R: *Clinacanthus siamensis*. — S: *Odontonema schomburgkianum*. — int intervenous area, le lower epidermis, ue upper epidermis.

In most species cystoliths occur on both surfaces of the leaves. Cystoliths are, however, absent in intervenous areas of the lower epidermis in *Pseuderanthemum alatum, P. indicum, Ruttya fruticosa, Mackaya bella*, and *Odontonema strictum*. Cystoliths are very sparsely distributed on the midrib of the lower epidermis in *Asystasia travancorica, Pseuderanthemum indicum* and *Ruttya fruticosa*, and in intervenous areas of the lower epidermis in *Asystasia gangetica*. The cystoliths are normally simple, but double cystoliths are common in *Asystasia, Chamaeranthemum, Pseuderanthemum, Ruspolia seticalyx, Hypoestes antennifera, Mackaya bella*, and *Odontonema*. On the midrib the cystoliths are always straight. This is also true for in-

Table 5. Length and breadth (in μm) and type of cystoliths on midribs and from intervenous areas. Plants growing under greenhouse conditions. — l length, b breadth. — [1] very sparsely distributed.

Species	Midrib, lower epidermis				Midrib, upper epidermis				Intervenous areas lower epidermis				Intervenous areas upper epidermis			
	l	b	l/b	type	l	b	l/b	type	l	b	l/b	type	l	b	l/b	type
Asystasieae																
Asystasia laticapsula	58	17	3.5	7	61	21	2.9	7	54	14	4.0	7	51	17	3.1	7
A. travancorica	60	27	2.2	7[1]	79	29	2.7	7	27	19	1.5	8	66	29	2.8	7
					43	25	1.7	8	39	17	2.3	7				
A. gangetica	34	21	1.6	8	42	26	1.7	8	34	20	1.7	8[1]	49	33	1.5	8
	51	19	2.7	7	69	24	2.8	7					69	27	2.5	7
Chamaeranthemum beyrichii	64	19	3.4	7	89	23	3.8	5	137	23	6.0	5	121	23	5.3	5
								8								
Pseuderanthemeae																
Pseuderanthemum alatum	68	19	3.6	7	82	22	3.8	5	absent				84	21	4.0	5
P. cinnabarinum	88	23	3.8	5	108	30	3.7	5	105	31	3.4	5	120	38	3.2	5
P. indicum	55	19	2.8	7[1]	56	17	3.2	7	absent				57	18	3.2	7
P. tuberculatum	197	18	11.4	1	135	14	9.7	1	131	15	8.5	1	232	31	7.6	1
P. tunicatum	87	27	3.2	5	105	29	3.6	5	127	31	4.1	2	143	34	4.2	2
Graptophylleae																
Pachystachys lutea	131	22	6.0	2	106	24	4.2	5	81	21	3.9	5	88	21	4.0	5
	60	20	3.0	7												
Ruspolia hypocrateriformis	78	29	2.7	7	48	19	2.5	7	69	28	2.5	7	61	27	2.2	7
R. seticalyx	88	21	4.2	5	81	15	5.4	4	80	17	4.7	4	61	20	3.1	7
Anisacanthus virgularis	80	14	5.6	4	107	17	6.5	4	29	9	3.5	–	80	15	5.4	4
Odontonemeae-Diclipterinae																
Peristrophe speciosa	123	18	6.9	1	156	22	6.9	2	134	16	9.0	1	143	18	7.8	1
Hypoestes antennifera	73	18	4.0	1	111	21	5.3	1	64	18	3.7	7	40	14	2.9	7
					52	17	3.1	7								
H. aristata	136	22	6.2	2	68	22	3.1	7	100	18	5.5	1	98	22	4.7	2
					154	28	5.5	2								
H. verticillaris	61	13	4.7	1	122	21	5.8	1	182	24	7.7	2	146	22	6.7	5
									103	15	6.7	1				
									62	10	6.2	6				
Odontonemeae-Monotheciinae																
Ballochia rotundifolia	168	20	8.2	1	196	28	6.9	5	–	–	–	9	–	–	–	9
Clinacanthus siamensis	110	24	4.5	5	103	23	4.5	5	140	31	4.5	5	133	32	4.2	5
Ruttya fruticosa	82	23	3.6	5[1]	95	17	5.5	4	absent				83	21	3.9	5
Odontonemeae-Odontoneminae																
Ecbolium revolutum	115	19	6.1	1	57	9	6.2	6	106	11	10.0	4	432	36	12.3	3
Mackaya bella	112	28	4.1	5	123	30	4.1	5	absent				105	27	3.8	5
Odontonema schomburgkianum	85	18	4.9	4	122	19	6.5	4	96	24	4.0	5	100	29	3.5	5
O. strictum	95	28	3.5	5	82	29	2.9	5	absent				123	21	6.1	1
					162	30	5.4	1								
Rhinacanthus communis	107	16	6.7	1	99	20	5.0	1	99	10	9.9	1	115	14	8.5	4
Schaueria calicotricha	163	18	9.0	1	182	20	9.2	1	93	15	6.2	4	92	18	5.2	4

tervenous areas in most of the species. In *Peristrophe speciosa* they are markedly curved.

On the basis of the size and shape of the cystoliths occurring in the species studied they may be classified as follows: (1) elongated, narrow, tapering at one end (breadth: $\leqslant 21\ \mu$m, length/breadth: $\geqslant 4.0$; Fig. 4 A); (2) elongated, broad, tapering at one end (b: $\geqslant 22\ \mu$m, l/b: $\geqslant 4.0$; Fig. 4 B); (3) elongated, tapering at both ends (l/b: $\geqslant 4.0$; Fig. 4 C); (4) elongated, narrow, blunt at both ends (b: $\leqslant 20\ \mu$m, l: $\geqslant 80\ \mu$m; Fig. 4 D); (5) elongated, broad, blunt at both ends (b: $\geqslant 21\ \mu$m, l: $\geqslant 80\ \mu$m; Fig. 4 E); (6) short, narrow, blunt at both ends (l: $\leqslant 80\ \mu$m, l/b: $\geqslant 5.0$; Fig. 4 F); (7) short, broad, blunt at both ends (l: $\leqslant 80\ \mu$m, l/b: 2.1–4.0; Fig. 4 G); (8) rounded (l/b: $\leqslant 2.0$; Fig. 4 H); (9) irregular (Fig. 4 I–O). The sizes and types of the cystoliths are shown in Table 5. In *Anisacanthus virgularis* in intervenous areas of the lower epidermis very short and narrow cystoliths occur. They correspond to the type (7), but the breadth of the cystoliths is markedly less than that of the species characterized by the type (7). In intervenous areas of the upper epidermis in *Rhinacanthus communis* another type of cystolith sometimes occurs. It is irregular and provided with short protuberances (Fig. 4 T–X). In most species the sizes of the cystoliths are much the same in intervenous areas and on the midrib.

The cystoliths are provided with rounded tubercles, more or less densely distributed over the surface (Fig. 4 B–H). In *Ruttya fruticosa* and *Rhinacanthus communis* the tubercles are sparsely distributed (Fig. 4 A, P). *Clinacanthus siamensis* and *Odontonema* differ in having irregular tubercles (Fig. 4 R, S).

Discussion

Epidermal cells, intervenous areas. In most of the species studied the cell shape is different on the two surfaces of the leaves. The degree of undulation is the chief varying factor. The use of cell wall undulation as a taxonomic character calls for the utmost caution (Stace 1965). However, it is interesting to compare the findings of De (1967 b) with the results of the present study. De found that the epidermal cells in intervenous areas of both surfaces of the leaves were straight-walled in *Odontonema strictum*. This is in agreement with my own findings. In *Asystasia gangetica* and *Rhinacanthus nasuta* (L.) Kurz (= *R. communis*) the cell walls were found to be "wavy". This is also in agreement with my findings. It is inappropriate to compare the results from the other species studied by De with my own findings, since we have not studied the same species. However, De found that in *Pseuderanthemum bicolor* Radlk. the cells were straight-walled, while they in *Ecbolium viride* (Forsk.) Merrill were said to be slightly wavy. The cell walls in the species of *Pseuderanthemum* studied by me are either sinuous or slightly sinuous, while in *Ecbolium revolutum* they are slightly sinuous or straight.

Costal cells. The difference in size of the costal cells of the lower and upper epidermis is probably of little value taxonomically, since differences were found between the species in one and the same genus. This is most prominent in *Pseuderanthemum*.

Stomata. The frequency of stomata is often stated as the number of stomata per mm^2. Since the stomatal frequency often varies on different parts of one single leaf, and on different leaves of one plant, it is better to use the stomatal index (Salisbury 1927). The variations in stomatal frequency then can be almost cancelled.

From Table 1 can be seen that the studied species of Asystasieae show values for the stomatal index which differ only slightly from each other. The same is true for the stomatal frequencies, with the exception for *Chamaeranthemum beyrichii.* The species of Graptophylleae show conformity as regards the stomatal index, with the exception for *Ruspolia seticalyx.* On the other hand there are great differences in both stomatal frequency and stomatal index between the genera, as also between the species in one and the same genus, in the other tribes. The greatest variation occurs in *Pseuderanthemum.* Therefore I conclude that the stomatal frequency and the stomatal index is of little value taxonomically in the species examined.

More important is the presence or absence of stomata in the upper epidermis. No stomata were found in the upper epidermis in *Pseuderanthemum.* This is in agreement with the findings of Ahmad (1974), who studied 6 species of *Pseuderanthemum* and did not find stomata in the upper epidermis. Stomata are also absent in the upper epidermis in the species studied belonging to the Graptophylleae. In the other tribes some species have stomata in the upper epidermis, others have not. De (1967 b) reported stomata occurring in the upper epidermis in *Rhinacanthus nasuta.*

The occurrence of stomata on the midrib of the upper epidermis is restricted to *Asystasia, Peristrophe, Hypoestes* and *Rhinacanthus.* The only species in which stomata occur on the midrib of the lower epidermis are *Asystasia gangetica* and *Odontonema strictum.* In all species, where stomata occur on the midrib, these stomata are greater than those occurring in intervenous areas. The only exception is *Odontonema strictum.*

The same phenomenon as described for *Dyschoriste perrottetii* (Nees) O. Kuntze (Karlström 1978) regarding modification of stomatal frequency, was found in *Asystasia laticapsula.* Leaves from herbarium specimens of this species collected in Kenya in 1971 were studied to provide comparison with those of the cultivated material (cuttings from the same stand). Stomata were present in the upper epidermis both on the herbarium specimens and the fresh, cultivated material. However, great differences in the stomatal indices were found. It seems clear that the stomatal frequencies have diminished during the period of cultivation.

Non-glandular hairs. The size of the non-glandular hairs is of less value taxonomically compared with trichome structure. I found that the size variation in some species may be considerable within the species. This is in agreement with Ahmad (1978). The occurrence of different types of non-glandular hairs, the number of cells of the hairs, and the differences in the ornamentation of the cell walls certainly are more important as taxonomic aids.

Ahmad (1974) reported that non-glandular hairs are absent in *Pseuderanthemum atropurpureum* (Bull.) Bailey, *P. kewense* Bailey and *P. variabile* (R. Br.) Radlk., sparsely occurring in *P. bicolor* (Schrank.) Radlk. and common in *P. malaccense* Lindau and *P. grandiflorum* Domin.

In *Odontonema strictum* non-glandular hairs occur only on the midrib of the lower epidermis. In other areas they are lacking. Ahmad (1978) found no non-glandular hairs at all in *O. nitidum* O. Kuntze and *O. strictum*.

In most of the species studied non-glandular hairs are absent in intervenous areas of the lower epidermis, while they occur in corresponding areas of the upper epidermis. This is true for most of the species studied in Pseuderanthemeae, Graptophylleae and Odontonemeae-Odontoneminae. In Odontonemeae-Monotheciinae non-glandular hairs are absent in intervenous areas on both leaf surfaces. In the third subtribe of Odontonemeae, i.e. Diclipterinae, non-glandular hairs are absent in intervenous areas of the lower epidermis in *Peristrophe speciosa, Hypoestes aristata* and *H. verticillaris*. In *H. antennifera* non-glandular hairs are rare and restricted to areas in close vicinity of veins.

De (1967 b) reported 2–3-celled, thick-walled non-glandular hairs with the basal cell wider in *Rhinacanthus nasuta*.

Ahmad (1974) found branched hairs rarely occurring in *Pseuderanthemum bicolor*. Unicellular hairs were reported as common in *Asystasia dalzelliana* Santapau, *Rhinacanthus nasuta, Pseuderanthemum grandiflorum*, and *P. malaccense* (Ahmad 1978).

Hairs with the apical cell lying at right angles to the basal part and with thicker walls than the basal cells occur in *Ruttya speciosa* (Hochst.) Engl. (Ahmad 1978). This type of hair corresponds to that found by me in *R. fruticosa*.

Glandular hairs. The occurrence of different types of glandular hairs is a character of taxonomic value. In the species studied five main types could be recognized: subsessile hairs with 4-celled globular heads; subsessile hairs with 8-celled globular heads; subsessile hairs with many-celled heads; stalked hairs with 4-or 8-celled globular heads; and stalked hairs with 1- or 2-celled heads and sometimes with ornamented cell walls. None of the tribes or subtribes were found to be characterized by only one type of glandular hairs. However, in the species studied belonging to the Odontonemeae-Diclipterinae the subsessile glandular hairs always were provided with 4-celled heads. Together with these hairs stalked glandular hairs occur in *Peristrophe speciosa* and *Hypoestes antennifera*. Subsessile glandular hairs with 2–4-celled globular heads were reported in *Peristrophe tinctoria* Nees, with globular 4-celled heads in *P. acuminata* Nees, *P. bicalyculata* (Retz.) Nees, *Rungia pectinata* Nees, and *Dicliptera roxburghiana* Nees (Ahmad 1978). In this latest mentioned species stalked glandular hairs similar to those of *Peristrophe speciosa*, as described above, also occur. Thus this subtribe shows great conformity as regards glandular hairs.

Subsessile hairs with 4-celled heads also occur in the Asystasieae, but here together with hairs with 8- or 10-celled heads. Subsessile hairs with 4–8-(mostly 4-)celled globular heads were found in *Asystasia* spp. (Ahmad 1978).

In the other tribes and subtribes subsessile hairs with 4-celled heads do not occur, with the exception for *Ecbolium revolutum* and *Pachystachys lutea*. In these species, however, the heads may also contain 6, 8, or more than 8 cells. Ahmad (1978) reported 8-celled globular heads in *Graptophyllum pictum* Griff, 4-celled globular heads in *Pachystachys coccinea* Nees and *Rhinacanthus nasuta*, and 4–8-celled globular heads in *Odontonema*. Thus in Graptophylleae and Odontonemeae-Odontoneminae different types of glandular hairs occur.

Odontonemeae-Monotheciinae shows great conformity as regards the glandular hairs. Hairs with 8-celled heads dominate. The dominating type occurring in Pseuderanthemeae is subsessile hairs with 8-celled, globular heads. This is in agreement with Ahmad (1974, 1978).

References

Ahmad, K. J. 1974: Cuticular and epidermal structures in some species of Eranthemum and Pseuderanthemum (Acanthaceae). *Bot. Notiser 127:* 256–266.

Ahmad, K. J. 1978: Epidermal hairs of Acanthaceae. *Blumea 24:* 101–117.

Bhoj Raj 1961: Pollen morphological studies in the Acanthaceae. *Grana Palynologica 3:* 1–108.

Bremekamp, C. E. B. 1965: Delimitation and sub-division of the Acanthaceae. *Bull. Bot. Surv. India 7:* 21–30.

De, A. 1966: Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. I. Cytological studies. *Trans. Bose Res. Inst. 29:* 139–175.

De, A. 1967 a: Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. II. Floral anatomy. *Trans. Bose Res. Inst. 30:* 27–43.

De, A. 1967 b: Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. III. General anatomy. *Trans. Bose Res. Inst. 30:* 51–67.

De, A. 1968: Cytological, anatomical and palynological studies as an aid in tracing affinity and phylogeny in the family Acanthaceae. IV. Palynology and final conclusion. *Trans. Bose Res. Inst. 31:* 17–29.

Karlström, P.-O. 1973: Embryological studies in the Acanthaceae. II. The genera Pseuderanthemum Radlk., Ruspolia Lindau, Eranthemum L. and Lankesteria Lindl. *Svensk Bot. Tidskr. 67:* 257–280.

Karlström, P.-O. 1974: Embryological studies in the Acanthaceae. IV. The genera Asystasia Bl. and Chamaeranthemum Nees. *Svensk Bot. Tidskr. 68:* 315–328.

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

Lindau, G. 1895: Acanthaceae. *In* A. Engler & K. Prantl, *Die natürlichen Pflanzenfamilien, IV: 3 b.* Leipzig.

Payne, W. W. 1970: Heliocytic and allelocytic stomata: unrecognized patterns in the Dicotyledonae. *Amer. J. Bot. 57:* 140–147.

Salisbury, E. J. 1927: On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Phil. Trans. R. Soc. London, Ser. B, 216:* 1–65.

Stace, C. A. 1965: Cuticular studies as an aid to plant taxonomy. *Bull. Brit. Mus. Nat. Hist., Bot. 4:* 3–78.

Daphne pontica (Thymelaeaceae), new to the flora of Iran, and new records for Stelleropsis (Thymelaeaceae)

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Peterson, B. 1980 03 17: Daphne pontica (Thymelaeaceae), new to the flora of Iran, and new records for Stelleropsis (Thymelaeaceae). *Bot. Notiser 133:* 17–19. Stockholm. ISSN 0006-8195.

Daphne pontica L. (Thymelaeaceae) has been found in the Central Elburz Mountains. It is new to the flora of Iran. A short description with figures and a map of distribution are given. Additional records for some species of *Stelleropsis (Thymelaeaceae)* are given for the Flora Iranica.

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Until now four species and one subspecies of *Daphne* have been known for the flora of Iran, viz., *D. mezereum* L., *D. rechingeri* Wendelbo, *D. mucronata* Royle, *D. stapfii* Bornm. & Keissl., and *D. oleoides* Schreb. subsp. *kurdica* (Bornm.) Bornm. (Peterson 1972).

Daphne pontica L.

During a botanical trip in July 1974 to the Sang-Deh area (Prov. of Mazandaran) about 30 km SE Pol-e Sefid on the northern slopes of the Central Elburz Mountains, J. Renz and M. Iranshahr collected some specimens (n. 16822) that proved to be a species of *Daphne,* previously not recorded from Iran, viz. *D. pontica* L. During another visit to the same area in May 1975 it was possible for J. Renz to collect specimens in flower. The collections were made at an altitude of 2400 m. Specimens (Renz in Rechinger n. 52684) are preserved in EVIN, GB, TARI, and W.

Daphne pontica is found in SE Bulgaria, Turkey (along the Black Sea coast in both European and Asiatic parts) and Gruziya (Georgia) in Western Transcaucasia. The range of distribution of the species is shown by Czeczott (1937, Fig. 9) and Grossheim (1962, Map 253). There is a large gap of 500–900 km between the Iranian localities and the nearest one in the Western Caucasus (Fig. 1). This kind of disjunction is not unusual. Other good examples are found in the distributional patterns of e. g. *Erythronium caucasicum* G. Woron., *Paeonia wittmanniana* Hartwiss ex Lindl. and *Vaccinium arctostaphylos* L. There is good reason to assume that the gap in distribution in the Caucasus is real as this region seems to be well investigated. On the other hand the Caspian forest of Iran are still undercollected and species new to the region are found by several collectors. Thus a subspecies of *Cortusa matthioli* was reported as new to Iran by

Fig. 1. Known distribution of *Daphne pontica*. ● = Iran. Mazandaran, Sang-Deh. ✖ = Iran. Gilan, Arbustan, Yehlah (exact locality not known). Hatching indicates areas where the species is fairly common.

Iranshahr and Renz from the same locality where they found *Daphne pontica* (Iranshahr & Wendelbo 1976). Other forest species recently found are *Pyrola secunda* (Frey & Probst 1977), *P. rotundifolia* and *Orobanche flava* (Assadi & Wendelbo 1977).

According to specimens at the British Museum and Kew *D. pontica* was collected in Iran (Arbustan, Yehlah) already in 1936 by Miss N. Lindsay. It has not been possible to find the geographic position of this locality, but, according to other collections by Miss Lindsay at the same time, it must be situated somewhere in the province of Gilan. The species does not seem to have been recollected in this area.

Daphne pontica (Fig. 2; also Brickell & Mathew 1976: 164) belongs to the section *Laureola*. The flowers appear at the base of the current year's leaves thus differing from *D. mezereum* and *D. rechingeri* of the section *Mezereum* with flowers arising from the axils of the previous year's leaves. The flowers of *D. pontica* are glabrous and vary in colour from pale yellow to greenish whereas *D. mezereum* and *D. rechingeri* have white, cream or pink flowers, sometimes hairy. The calyx lobes of *D. pontica* are about as long as the tube, 5–11 mm, and usually recurved.

The very closely related *D. albowiana* G. Woron. ex Pobed. (syn.: *D. pontica* subsp. *haematocarpa* G. Woron.) differs from *D. pontica* in having smaller and thinner leaves and in smaller, bright red to red berries. *D. albowiana* is recorded from about the same area of the Western Caucasus as *D. pontica*.

Description. An erect, sparingly branched *shrub* up to 1 m. *Branches* brownish, glabrous; young shoots greenish. *Leaves* clustered at the ends of the branches, (30–)45–72(–90) mm long, (15–)23–33(–38) mm wide, obovate or obovate-oblong, acute, tapering to the base, subsessile or sessile, glabrous, glossy. *Flowers* generally in pairs, sometimes 1 or 3; peduncles 15–25 mm long, in the axils of bracts at the base of the current year's leaves; pedicels 5–8 mm long; hypanthium 6–12 mm long, slender, smooth, greenish-yellow or pale yellow; lobes 5–11 mm long, narrowly lanceolate, acute, spreading. *Ovary* glabrous. *Berry* black or bluish black, 5–6 mm long, 3–4 mm wide.

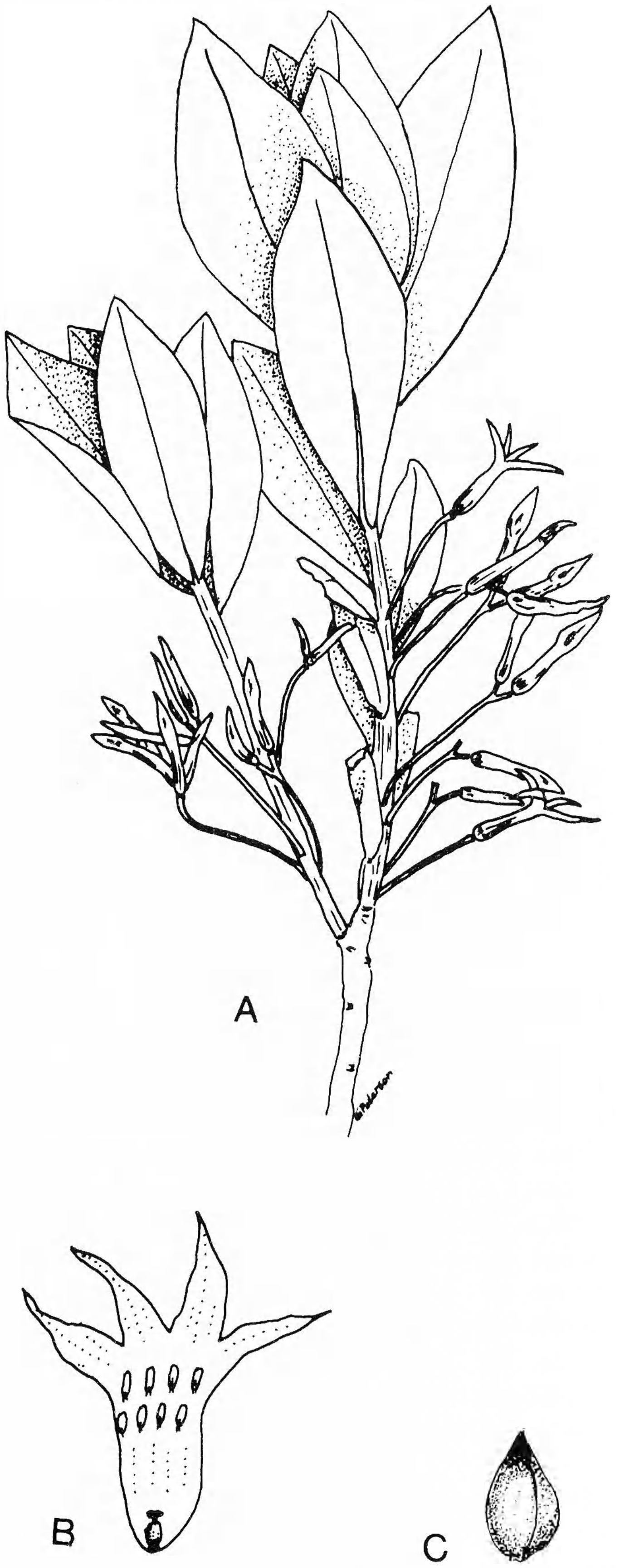

Fig. 2. *Daphne pontica*. — A: Flowering branch, × 0.9. — B: Dissected flower, × 2.7. — C: Fruit, × 2.7.—A & B from Renz in Rechinger 52684 (GB), C from Renz & Iranshahr 16822 (GB). Drawing: Gunnel Peterson.

I will take this opportunity to report a few new records for some other species of *Thymelaeaceae* for the Flora Iranica:

Stelleropsis antoninae Pobed.

Persia. E: Khorasan: In collibus argillosis inter Shahabad et Bojnurd, 36 km a Bojnurd occidentem versus, 800 m, 23.V.1977, K. H. Rechinger 55547 (G). — C: Damghan-Semnan: In montibus prope Tuweh a Damghan boreo-occidentalem versus, 1900–2500 m, 7.VI.1977, K. H. Rechinger 56469 (G); 33 km NE Semnan versus Damghan, 1600–1700 m, 25.IV.1975, K. H. Rechinger 50248 (G, GB); 43 km SW Damghan, 1300 m, K. H. Rechinger 50265 (G, GB). Tehran: Nimrud W Firuzkuh, 1600–1700 m, 29.V.1975, Renz in Rechinger 53997 (G, GB).

S. iranica Pobed. subsp. **iranica**

Persia. E: Khorasan: In montibus serpentinicis prope Robat-e-Safid inter Mashhad et Torbat-e Heydariyeh, 1800–2000 m, 29.V.1977, Renz & Runemark in Rechinger 55991 (G).

S. iranica subsp. **pilosa** B. Peterson

Afghanistan. E: Ghazni: Col, 15 à 20 km au N de Ghazni, 2250–2400 m, 18.IV.1958, Pabot A 606 (G).

References

Assadi, M. & Wendelbo, P. 1977: New and interesting plant records from NW Iran. *Iran. Journ. Bot. 1:* 97–108.

Brickell, C. D. & Mathew, B. 1976: *Daphne. The genus in the wild and in cultivation.* The Alpine Garden Society. Woking.

Czeczott, H. 1937: The distribution of some species in Northern Asia Minor and the problem of Pontide. *Mitt. königl. naturwiss. Inst. Sofia 10:* 43–68.

Frey, W. & Probst, W. 1977: Pyrola secunda (Pyrolaceae), new to Iran. *Iran. Journ. Bot. 1:* 121–122.

Grossheim, A. A. 1962: *Flora Kavkasa 6.* Moskva & Leningrad.

Iranshahr, M. & Wendelbo, P. 1976: A new subspecies of Cortusa matthioli (Primulaceae) from N Iran. *Iran. Journ. Bot. 1:* 57–60.

Peterson, B. 1972: Thymelaeaceae. *In* K. H. Rechinger (ed.), *Flora Iranica 95.* Graz.

Announcements from the Hunt Institute

Nominations for Lawrence Memorial Award

The Award Committee of the George H. M. Lawrence Memorial Fund solicits nominations for the 1980 Lawrence Memorial Award. The Fund and Award have been established on a permanent basis to honor the memory of Dr. Lawrence, founding Director of the Hunt Institute for Botanical Documentation at Carnegie-Mellon University. The purpose of the Award is to support *travel for doctoral dissertation research* in systematic botany or horticulture, or their history, including literature and exploration. It is expected that the 1980 Award will amount to $1,000, which will be available to the recipient for expenditure during the two-year period from date of award. Award funds will not be applicable to research travel accomplished prior to the date of award.

Major professors and other relevant faculty are urged to submit letters of nomination for outstanding doctoral students who have achieved official candidacy for their degrees, will be conducting dissertation research in one of the above fields during the coming two years, and whose work would benefit significantly from the travel the Award would allow. The Committee will consider nominations only—no direct applications will be entertained. A potential candidate who wishes to be considered should request his/her major professor to submit a nomination in his/her behalf. This may take the form of a letter of nomination and endorsement which covers supporting materials prepared by the candidate.

A nomination (or supporting materials) should describe briefly but clearly the candidate's program of research and how the travel enabled by the Award would contribute significantly to its quality. Letters of nomination, together with any supporting materials, should be received by the Committee no later than 1 April 1980. The awardee will be selected and the decision announced by 1 May 1980. Nominations and supporting materials, requests for further information, and any other communication regarding the Fund and Award should be directed to: Dr. Robert W. Kiger, Director, Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA 15213. Tel. (412) 578-2434.

Post-graduate Fellowship

The Hunt Institute for Botanical Documentation (Carnegie-Mellon University, Pittsburgh, PA) invites applications for 1980–81 appointments in its continuing program of post-graduate research fellowships for junior scholars (i.e., those with recent Ph. D. or other appropriate terminal graduate study). Normally, fellowship tenure is limited to one year, but renewal for an additional year may be possible in exceptional cases. Fellowships are tenable in any of the Institute's field of research, principally the History of Botany, Botanical Biography and Iconography, Botanical Bibliography, and History of Botanical Art & Illustration. Fellows undertake research projects of their own choice, working closely with and directly under the supervision of senior Institute faculty.

One Hunt Fellowship will be awarded for academic year 1980–81 (10-month period), commencing September, with a stipend of $10,000. Applicants should submit a curriculum vitae, names of at least three persons familiar with their academic qualifications who will provide recommendations on request, and reprints or copies of published work, if any. A brief but specific description of the applicant's proposed research project must accompany the application; projects must be susceptible of completion, ready for publication, within the fellowship period. Potential applicants having a strong interest in botanical documentation but no specific project in mind are encouraged to contact the Institute for further information about its facilities, collections and research program, and for consultation on possible projects. Applications deadline: 1 April 1980. Selection and notification by 1 May 1980. Direct inquiries, letters of application, and supporting materials to Dr. Robert W. Kiger, Director, Hunt Institute, Carnegie-Mellon University, Pittsburgh, PA 15213.

The inflorescence of Calceolaria

LENNART ANDERSSON and ULF MOLAU

Andersson, L. & Molau, U. 1980 03 17: The inflorescence of Calceolaria. *Bot. Notiser 133:* 21–32. Stockholm. ISSN 0006-8195.

The variation in inflorescence organization in *Calceolaria* is conveniently described using an architectural model with a pair-flowered cyme as the fundamental module. The basic growth habit is that of a low-growing shrub or subshrub. The flowering shoots are hapaxanthic and have a decussate phyllotaxy. From the axils of the upper leaf pairs cymes arise, and the two uppermost cymes seem to be branches from a dichotomy. The dichotomy is interpreted as a pseudo-dichotomy. The flower pair, which occurs at each branching of the cyme, consists of flowers with the same orientation and takes the position of terminal flowers in normal cymes. It is interpreted as a terminal flower and the flower from its reduced bracteole. A number of variations on this basic theme are found in the genus. Through the formation of lateral branches, which repeat the pattern of the main axis, polytelic synflorescences arise. In short-lived herbaceous species, the major part of the aerial plant body is made up of a few cymes with the capacity of much prolonged growth. In the rosulate perennial herbs, the number of cymes and of flowers per cyme is much reduced, this ultimately leading to one-flowered inflorescences. In the section *Zygophylla*, the dichotomy is often replaced by a short sterile shoot segment. This is interpreted as a derived condition. Interpretations are based on data from ontogeny and comparative morphology.

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Calceolaria is the largest genus of the Scrophulariaceae in South America, and ranges from S Mexico to Cape Horn. It comprises at least 300 species, which all have an inflorescence organized in the same basic manner, though often much modified. When initiating a taxonomic revision of the *Calceolaria* species occurring in NW South America, Molau (1978 a) proposed a descriptive terminology for inflorescences and flowers. At the same time a morphological interpretation of the inflorescence was suggested, based mainly on studies of herbarium material. In the customary colleaguial manner, we had discussed several possible interpretations and agreed on what appeared to be the simplest one. The purpose of that interpretation was to define clearly the terms applied to taxonomically important structures, terms which were used in previous treatments of the genus (e.g. Pennell 1951, Edwin 1971). The taxonomic literature consulted did not give any further information on the inflorescence of *Calceolaria* or related genera with similar organizational patterns.

Later Molau had the opportunity of gathering seeds from wild plants in Ecuador and comparatively ample cultivated material became available. Studies of this material revealed that development and orientation of the flowers deviated from that expected from our interpretation. Therefore, we found ourselves compelled to reconsider the case. Focusing on more purely morphological problems, some German literature (too often neglected in American taxonomy) was consulted (e.g. Goebel 1931, Weber 1973, Ritterbusch 1976) and as a result another and more complex interpretation appeared more probable. We therefore decided to test our hypothesis in an investigation based on the cultivated material, the results being here presented.

Material and methods

The material used was grown from seeds gathered from wild material and cultivated at approximately 12°C. Flowering was induced by adjusting day length to 12 hours. Ten species representing all major organizational patterns were used for the basic study, which was supplemented by a scoring of some fifty species in the herbarium. It was observed that although branching patterns remain constant in cultivation, cultivated specimens usually have fewer flowers than specimens gathered in the field.

The general patterns of organization were studied in branches with mature or nearly mature flowers and the entire flowering branch was analyzed in order to ascertain the relationship between flowering and vegetative parts of the plant body.

Development of the inflorescence was studied in *C. helianthemoides* and (less extensively) *C. trilobata*. About 100 actively growing shoots were dissected but about two thirds were found to be in a vegetative phase. In order to lessen the refractive disturbances caused by glands or hairs, dissection was usually carried out in a drop of 70 % ethanol. Dissections were made under a stereo microscope at magnifications up to 50×, and all drawings were made with the aid of a camera lucida.

The internal structure of 10 inflorescence buds (3 spp.) was studied in serial sections. The buds were cut off when c. 5 mm long, fixed in Karpechenko's fluid and cut on a rotation microtome at c. 10 μm.

Fundamental patterns of inflorescence organization

To illustrate the fundamental patterns of inflorescence organization, we have chosen *C. helianthemoides* H. B. K. (Figs. 1 D, 2, 3). The reasons are that (1) it has a rather small and perspicuous inflorescence which illustrates well the basic features (2) it is readily cultivated and flowers continuously without a pronounced period of dormancy and could therefore provide ample material for investigation (3) it is essentially glabrous, which lessens the refractive disturbances at high magnifications. The species was treated taxonomically by Molau (1978 b).

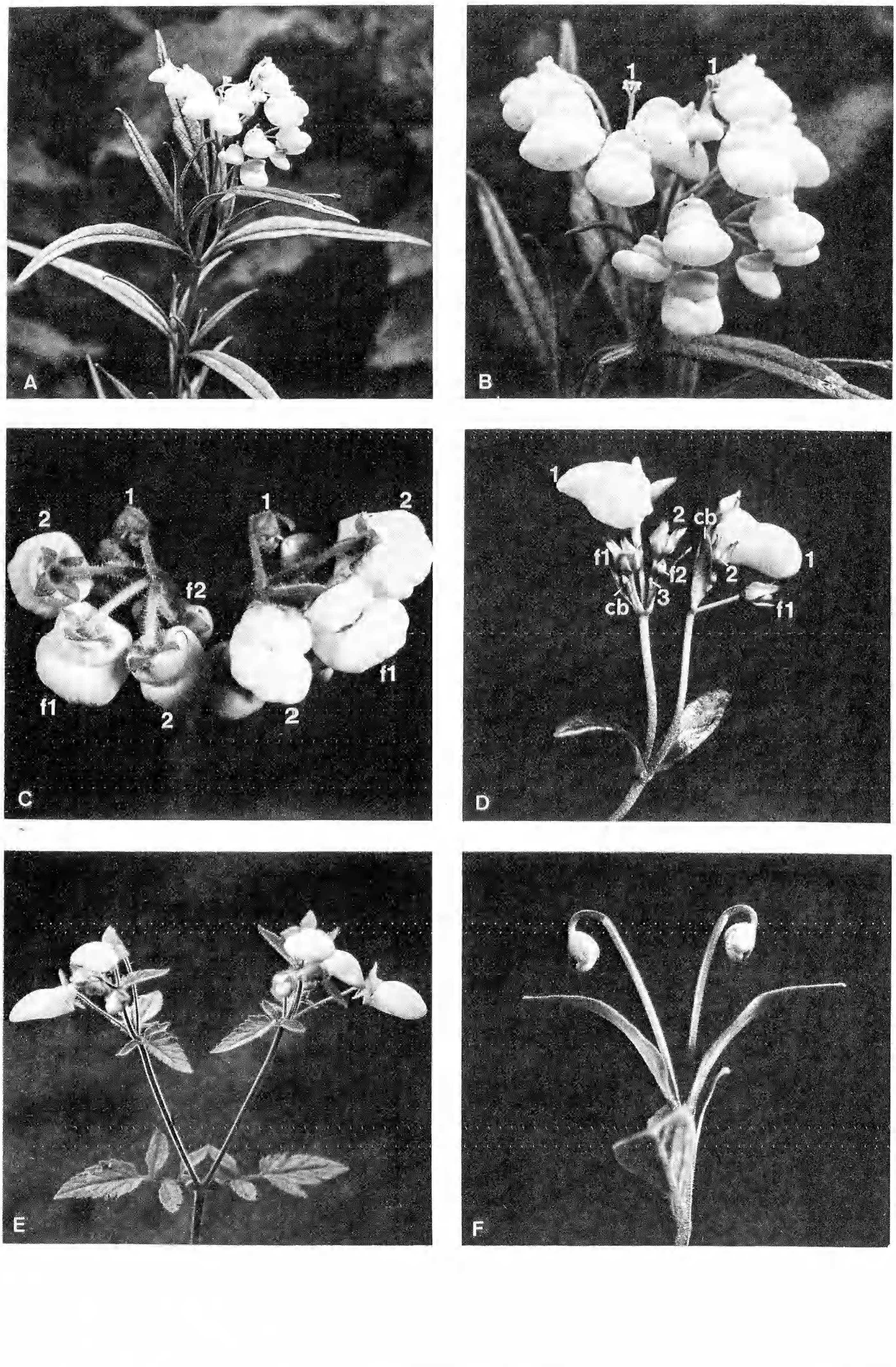
Although it is chosen as a model here, *C. helianthemoides* is by no means a primitive member of the genus. The floral structure is highly specialized and the species possesses several advanced vegetative features, e.g. fasciculate leaves. It is a low-growing subshrub endemic to the highlands of S Ecuador, where it is abundant in relatively dry sites in open mountain scrub and grass páramo. The stems are monopodial in the vegetative phase, woody at base and herbaceous distally. The herbaceous part dies when the fruits are mature and growth is resumed by lateral shoots from the woody proximal part of the stem. In this way the plants soon attain a tufted growth habit. Flowering seems to be fairly continuous also in nature.

The flowering part of the shoot system is conveniently termed a polytelic synflorescence (Troll 1964, Weberling 1965). It is thus made up of a number of more or less equal units, so-called florescences. In the example depicted in Fig. 3, the synflorescence consists of a main florescence (MF) and two co-florescences (CoF). The latter ones are lateral shoots that, more or less perfectly, repeat the pattern of the MF. Each florescence is made up of two cymes, in which the first branching is basically dichasial, although the pattern is complicated by the occurrence of front flowers. The second and subsequent branchings are monochasial and also in these, front flowers complicate the picture.

The two cymes of a florescence are branches from a dichotomy. This dichotomy is topographically important, as in most species of the genus a florescence can be defined as the largest element containing a single dichotomy.

The first branching of a cyme yields four branches, two lateral ones in the plane of the cyme bracts and two central ones decussate to the cyme bracts (Figs. 2 A, 3 B). The two central branches are the pedicels of two flowers with the same orientation. The dorsal one is the terminal flower (1) and the ventral one (flowering somewhat later) is its front flower (f 1). The lateral branches, considerably stouter than the pedicels, continue to branch, but now in a

Fig. 1. Examples of inflorescences in *Calceolaria*. — A–B: *C. rosmarinifolia*, a species characterized by an inflorescence of 3–4 pairs of few-flowered cymes with all flowers flowering almost simultaneously. In B, the faded terminal flowers of the two distal cymes are indicated. — C: *C. crenata*, young inflorescence seen obliquely from above. This species has a prolonged period of flowering and the young buds are concealed by the older flowers. — D: *C. helianthemoides*, terminal part of a flowering shoot, showing two cymes, both with the terminal flower recently unfolded and the others in bud. — E: *C. tripartita*, a vigorous specimen with an inflorescence of two cymes. — F: *C. lanceolata*, a reduced inflorescence of two one-flowered cymes. — A, B, E wild plants from Portete de Tarqui, Azuay province, S Ecuador (photo M. Neuendorf). C, D, F cultivated material. — Vouchers: A–B Harling et al. 14969 (GB), C Harling et al. 14845 (GB), D Harling et al. 15073 (GB), E Harling et al. 14972 (GB), F without voucher. — Abbreviations: 1 terminal flower; 2 lateral flower of the first order, etc.; f1 front flower of the terminal flower, etc.; cb cyme bract.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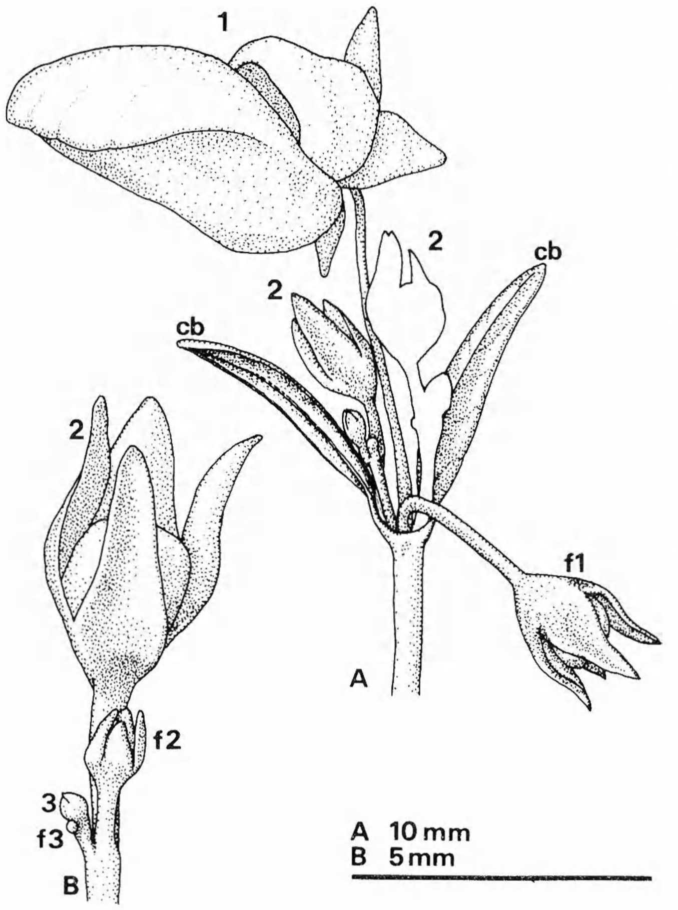

Fig. 2. *Calceolaria helianthemoides*. — A: A young cyme. — B: A lateral branch of the same cyme enlarged. — Abbreviations as in Fig. 1. — Voucher: Harling et al. 15073 (GB).

monochasial manner (Figs. 2, 3 A). Each monochasial branching yields three flowers, viz. a terminal flower, its front flower and a lateral flower. From the pedicel of the lateral flower a tertiary, monochasial branching may occur. In the present example it is incomplete and represented by the front flower f3 only (Fig. 2 B).

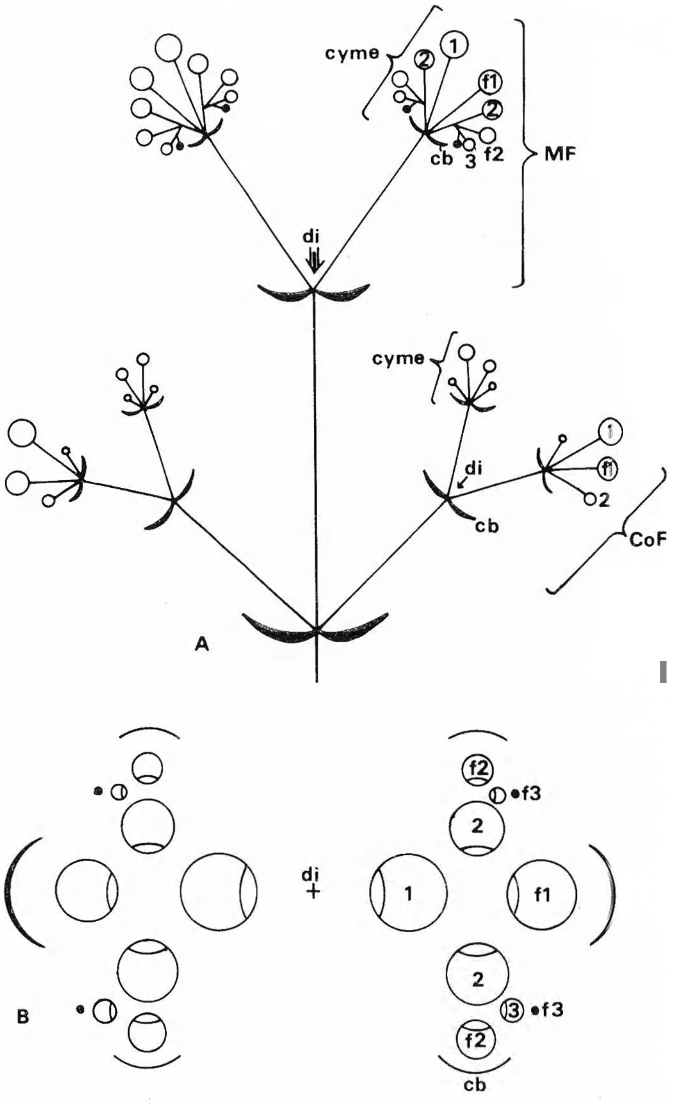

Fig. 3. Diagrammatic representation of a flowering branch of *C. helianthemoides*. — A: showing mainly axes and connections. — B: A projection diagram showing the orientation of the flowers of the distal pair of cymes; the cutting arc indicates the position of the upper lip. — Abbreviations: CoF co-florescence; di (pseudo-)dichotomy; MF main florescence; the others as in Fig. 1.

Interpretations

The dichotomy. The dichotomy is best explained as a pseudo-dichotomy arisen through the abortion of the main shoot apex. The actual evidence for such an interpretation is rather slight, however. Neither necrotic tissues, nor superfluous vascular strands have been found in the nodal region and the vascular system branches in two equal parts (Fig. 4). At the earliest stage at which a dichotomy has been observed (Fig. 5 A–C), two large branch primordia are seen with a minute bulge in between. This bulge soon disappears, it is detectable only in microscopical sections, even at a stage where less than ten flowers have begun to differentiate (Fig. 4 A–B).

At the beginning of a plastochron, the vegetative shoot apex of *Calceolaria* is nearly plane. Due to fusing of the leaf primordia around the axis, it soon appears more or less concave. Therefore, the bulge apparently indicates a slight meristematic activity in the region between the branch primordia, which ceases very soon, however. The cessation of growth apparently occurs so early that the terminal apex does not affect stelar differentiation.

The transition from the vegetative to the flowering phase is marked by a pronouncedly premature formation of axillary buds. In the vegetative phase these are first externally discernible dur-

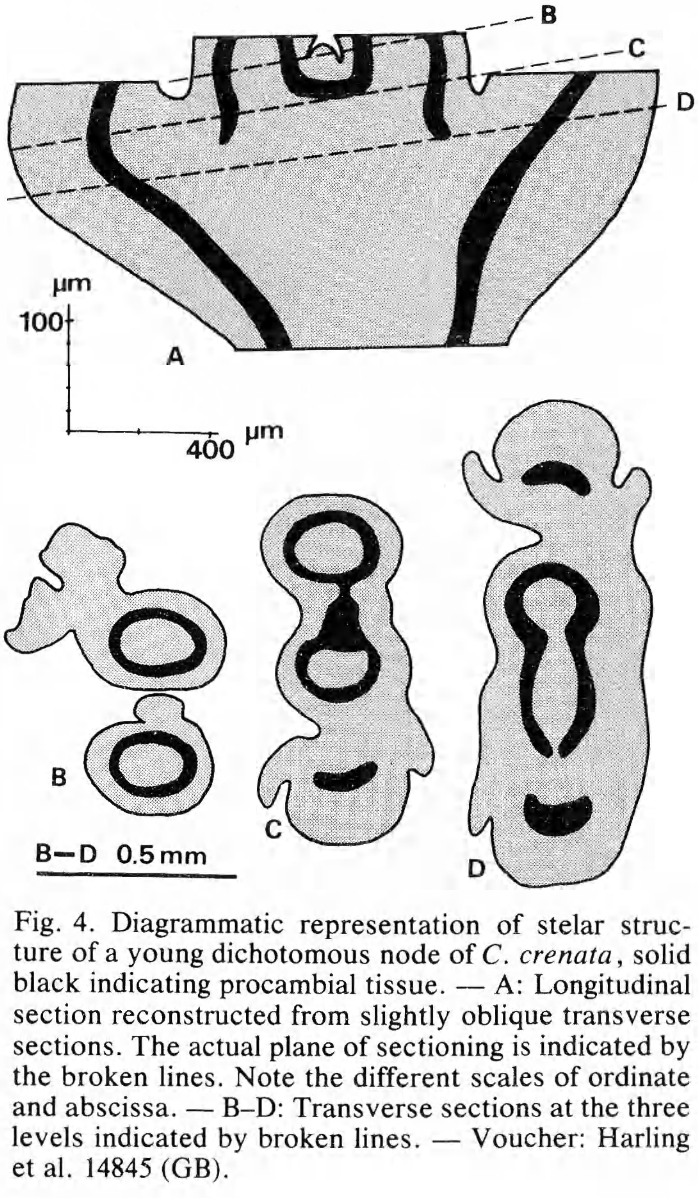

Fig. 4. Diagrammatic representation of stelar structure of a young dichotomous node of *C. crenata*, solid black indicating procambial tissue. — A: Longitudinal section reconstructed from slightly oblique transverse sections. The actual plane of sectioning is indicated by the broken lines. Note the different scales of ordinate and abscissa. — B–D: Transverse sections at the three levels indicated by broken lines. — Voucher: Harling et al. 14845 (GB).

ing the third plastochron, while they become large and conspicuous during the first plastochron in the flowering phase (cf. Fig. 5 G). This combined with the very early cessation of growth in the terminal apex is obviously the explanation for the unusual type of branching. Further evidence is offered by the intercalary inflorescence of *C. trilobata* Hemsl. and other species of sect. *Zygophylla* (cf. below).

The dichotomous branching in the *Calceolaria* inflorescence emphasizes that the difference between a pseudo-dichotomy and a secondary dichotomy is sometimes a difference of degree rather than of kind. In cases similar to the present one, the interpretation depends on how early apical growth ceases and how well we can study the process. Due to the premature formation of axillary buds, these are virtually initiated within the very apex, rather than in maturing tissues.

Front flowers. Front flowers (Vorblüten) may be defined as flowers that arise in an outer median position at a di- or monochasial branching in addition to the normally positioned flowers. Front flowers occur in the Gesneriaceae and in some genera of the Scrophulariaceae. By definition, a strict distinction is made between front flowers and accessory flowers (Vorderblüten, Beiblüten; for further discussion see Irmscher 1959, Weber 1973, 1978). The terminal flower of a dichasium and its front flower have the same orientation (Figs. 1 C, 2, 3 B, 6 B, 7 B, 11 B) and in *Calceolaria* they form a pair that is developmentally in advance of the two lateral flowers (Figs. 1 C, D, 2, 5 E, F, I–K). In *Calceolaria* the front flower always lacks a subtending bract. Front flowers have been interpreted as accessory branches (Goebel 1931, Troll 1964, 1969), as axillary branches from the "axil" of a suppressed bracteole (Irmscher 1959, Weber 1973, Ritterbusch 1976), or as one of two lateral flowers of a reduced dichasium (Molau 1978 a).

Ontogeny clearly shows that of the four flowers arising at the node of the cyme bracts, one is terminal, while the three others are lateral (Fig. 5 E, F, H, I). Of these three flowers, two arise in the axils of the cyme bracts, while one, the front flower, arises in an extra-axillary position (Fig. 5 E, I). In *C. helianthemoides* (numerous observations) the front flower is initiated before the lateral flowers (Fig. 5 E, F). In *C. trilobata* the lateral buds arise first (Fig. 5 H, I, a single observation) but are soon surpassed by the more rapidly developing front flower. The front flower and the terminal flower often reach anthesis almost simultaneously and even when there is a pronounced difference, they usually flower much before the lateral flowers.

Apparently, the position of the front flower is more favourable than that of the lateral flowers, which are squeezed in between the terminal flower and a cyme bract. It is a general phenomenon in *Calceolaria*, as in many other genera of the Scrophulariaceae and allied families, that the outer face of an inflorescence is more vigorously developed, which leads to markedly dorsiventral shoot systems (e.g. Fig. 1 C). The phenomenon is commonly termed exotrophy.

As shown by Irmscher (1959) and Weber (1973), front flowers may in some species have subtending bracts and one of the reasons for

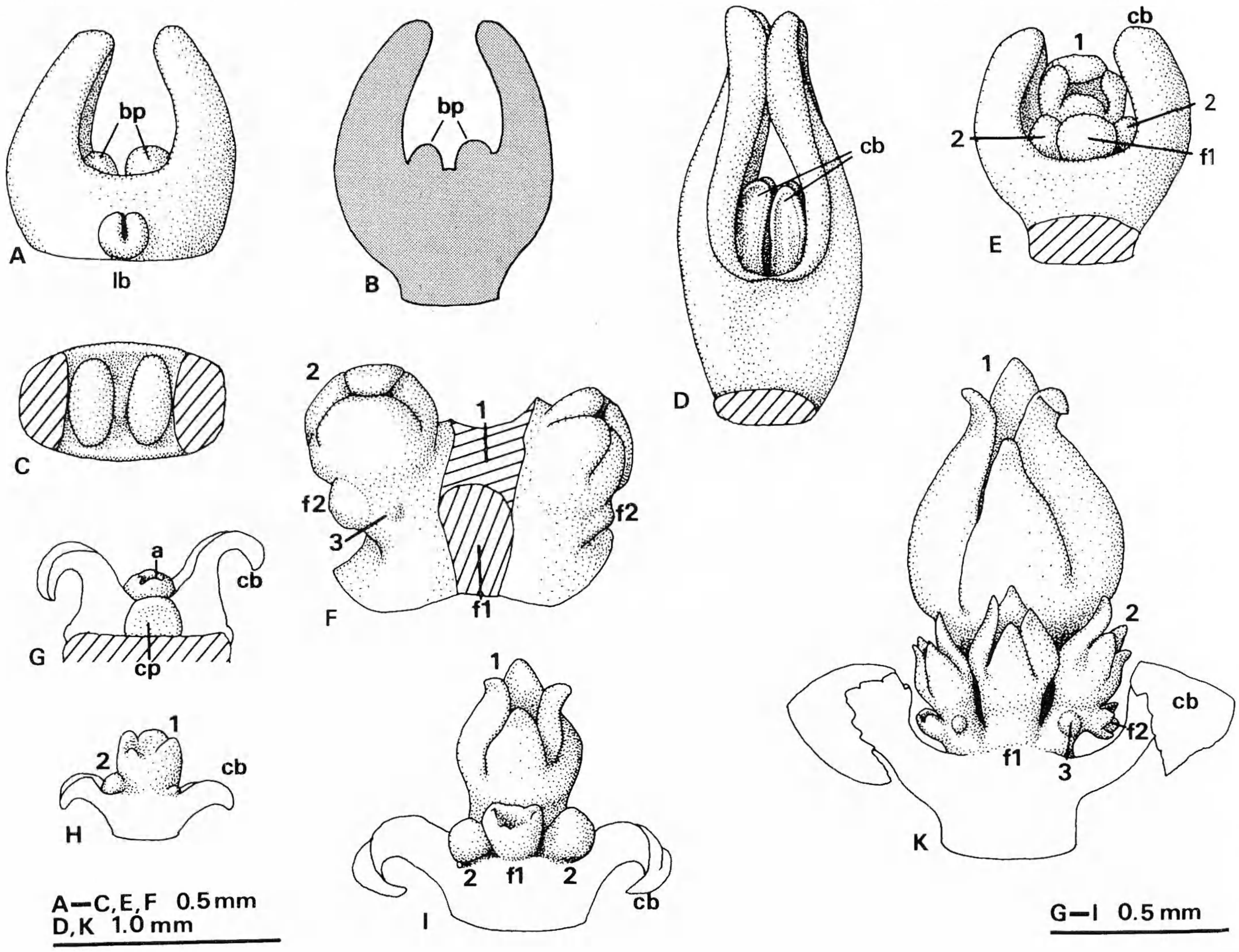

Fig. 5. Ontogenetic sequences of *C. helianthemoides* (A–F) and *C. trilobata*. — A–C. A dichotomizing shoot tip with two branch primordia. A: Lateral view. — B: Median longitudinal section. — C: Seen from above, the two leaf primordia cut off. — D: Entire inflorescence at a somewhat later stage. — E: A detached cyme, same stage as D. — F: A detached cyme at a later stage, 1 and f1 cut off. — G–K: Cymes from four successive nodes of a developing branch. G: Shoot tip with an undifferentiated cyme primordium in the axil of the second pair of leaves, H: Detached cyme with primordia of a terminal and two lateral flowers. I: Detached cyme after the formation of f1. K: Detached cyme with the second order lateral flowers differentiating. — All drawings made from live, cultivated material. — Vouchers: A–F Harling et al. 15073 (GB), G–K Harling et al. 14889 (GB). — Abbreviations: a (main shoot) apex; bp branch primordium; cp cyme primordium, lb lateral bud; the others as in Fig. 1.

regarding them as accessory (cf. Goebel 1931) is thereby removed. Their orientation coincides with what is to be expected from a flower in the bracteolar axil and ontogeny conclusively proves their lateral nature. Their peculiar development is in agreement with more general phenomena operating in the flowering phase of shoot ontogenesis, viz. premature development of axillary buds and exotrophy.

In our opinion, all facts support Weber's (1973) interpretation according to which front flowers represent "truly" axillary flowers, which have attained their present position through the suppression of the pre-prophyllar internode and of the prophyll (bracteole) itself. Through the action of extreme exotrophy, inhibition is complete at the inner median position. Some intermediate stages were discussed by Irmscher (1959) and Weber (1973).

Variations on the theme

With starting point in the description of *C. helianthemoides* and the concepts there introduced, a number of inflorescence types can be discerned. It is convenient to regard the cyme as a fundamental module and to describe the variation as differences in elaborateness, number and position of the cymes. In many species, the cymes are arranged into synflorescences, this being a higher level of organization. The limit between simple inflorescences and synflorescences is rather conditional and it is important that the entire plant be taken into consideration when the higher levels of organization are analyzed. No sharp limit can be drawn between vegetative and flowering shoot systems.

Calceolaria crenata Lam.

C. crenata belongs to the same section as *C. helianthemoides* (*Thamnobia* Pennell, cf. Molau 1978 b) and has essentially the same organization, but the inflorescence is always simple, i. e. never a synflorescence. It consists of two or three pairs of cymes and the main axis ends with a dichotomy. *C. crenata* is a somewhat stouter plant, however, and the cymes are considerably much more elaborate (Figs. 1 C, 6). In addition to the terminal flower of the cyme and its front flower there are up to ten orders of lateral flowers, each of them with a front flower. Due to the large number of flowers there is not space enough for the realization of the "ideal" angles of branching. Later-formed flowers are therefore to be found in a ventral rather than in a median position and young monochasia are curved in a boragoid-like fashion. As anthesis proceeds the monochasial chains unfold and become spreading. In spite of the large number of flowers there is still only one dichasial branching, all others being monochasial.

Calceolaria trilobata Hemsl.

The flowering shoot of *C. trilobata* is remarkable in that the main shoot does not dichotomize but produces a number of vegetative nodes distal to the uppermost pair of cymes (Fig. 7 A, B). Nevertheless, the main shoot is still determinate and the apex is apparently inactivated long before anthesis. (The term determinate is used here to designate an axis with limited capacity of growth, irrespective of whether it is terminated by the formation of a flower or not. It is thus applicable to both vegetative and flowering shoots). Although it appears quite viable even at late anthesis, it has never been observed to be reactivated. When the fruits are mature, the entire shoot dies off and growth is continued from dormant buds near the base of the stem. This kind of inflorescence has been termed subterminal (Pennell 1951, Molau 1978 b), but in order to avoid confusion caused by other usage of the term we propose the word intercalary to replace it. The contrary is called distal.

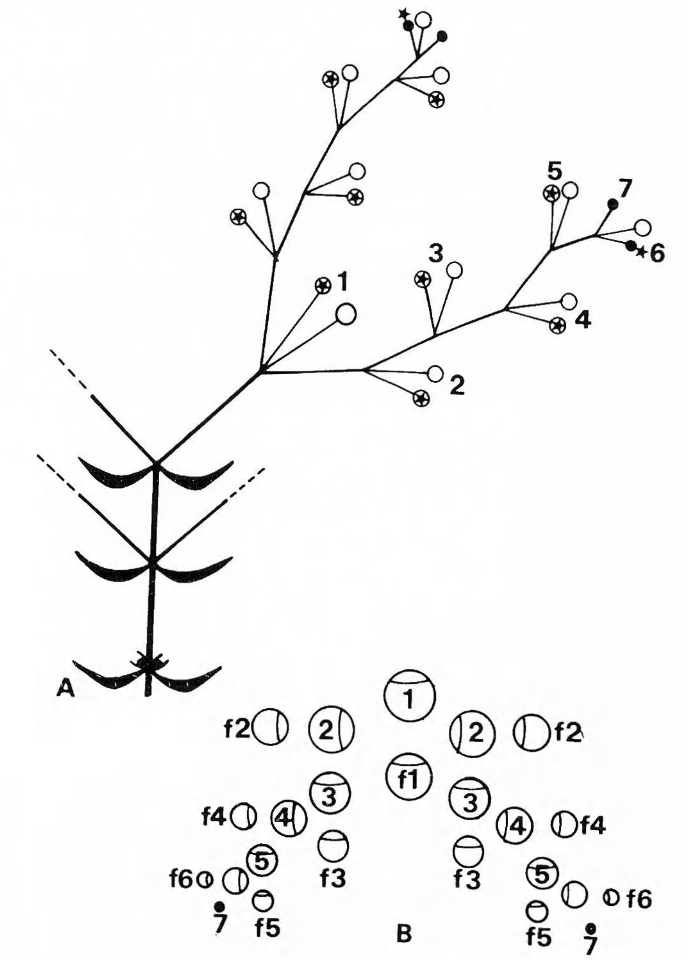

Fig. 6. Diagrammatic representation of an inflorescence of *C. crenata*. — A: Diagram illustrating connections. One cyme of four is represented in the diagram, the three others are suggested by the broken lines. — B: Projection diagram illustrating the orientation of the flowers of the same cyme. — Symbols and abbreviations: ● small flower buds; * front flower; the others as in Fig. 1. — Voucher: Harling et al. 14845 (GB).

Asymmetric development of entire inflorescences as well as of the individual cymes is very common in *C. trilobata*, resulting from one-sided inhibition of lateral branches (Fig. 7 B). Asymmetric development is obviously a response to the growth habit. *C. trilobata* has a tufted growth habit and it is always the side of the shoot that is turned towards the centre of the plant that is inhibited. In this way only those flowers develop which are turned towards the pollinators.

Phylloscopic accessory buds are regularly found at the base of the cyme peduncles (Fig. 7

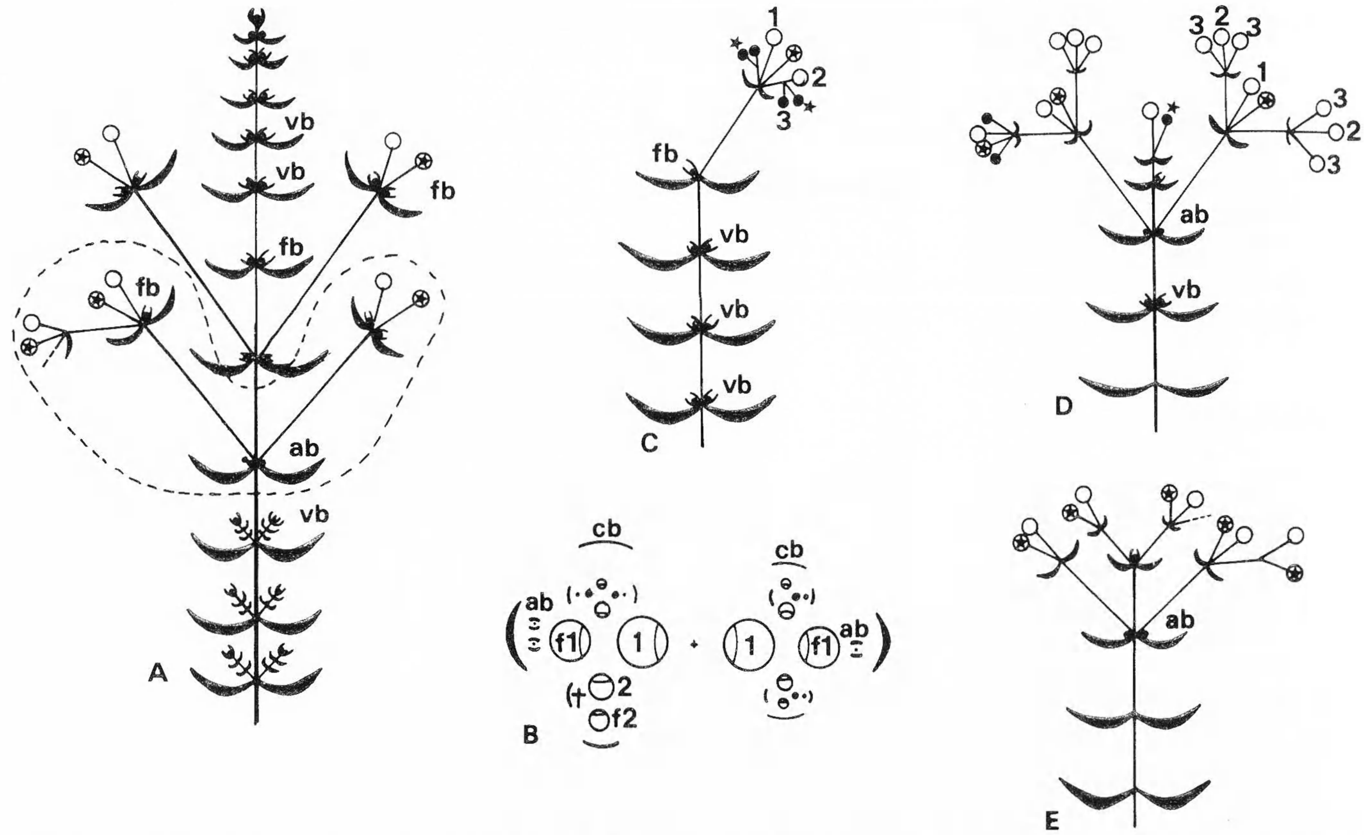

Fig. 7. Diagrammatic representation of the distal part of flowering branches of *C. trilobata* (A–B) and *C. lojensis* (C–E). — Symbols and abbreviations: ab accessory bud; cb cyme bract; fb floral bud; vb vegetative bud; † necrotic bud; * front flower; ● small bud of a flower; the others as in Fig. 1. — A–C drawn from cultivated material; C–E from herbarium specimens. — Vouchers: A–B Harling et al. 14889 (GB), C Harling et al. 15122 (GB), D Espinosa 561 (PH), E Harling 5758 (S).

B). They have not been observed to affect the architecture of the inflorescence, however, except when the plant is damaged.

Other species of sect. Zygophylla

Intercalary inflorescences are characteristic for most species of sect. *Zygophylla*. The size of the distal vegetative shoot segment is quite variable, even within a species, and varies from a mere rudiment with a few pairs of primordial leaves up to the conspicuous structure of *C. trilobata*, *C. calycina* Benth. and *C. perfoliata* L. fil. Even within *C. trilobata* it is observed, however, that the main shoot occasionally dichotomizes and in some species this is the predominant condition, viz. in *C. lojensis* Pennell and *C. lanata* H. B. K. A distal inflorescence of *C. lojensis* is represented in Fig. 7 C together with two transitional shoots encountered in the same species (Fig. 7 D, E).

Considering that the sect. *Zygophylla* is characterized by a number of advanced features (Molau, unpublished material), there can be little doubt that the intercalary inflorescence is a secondary phenomenon caused by "failing cessation" of the terminal apex. The occurrence of a terminal vegetative shoot segment in a species which usually has a dichotomous ultimate branching indicates, however, that although all traces of the terminal apex are soon lost, it maintains its individuality during the process of branch initiation and is not used up. This lends strong support to the interpretation of the dichotomy as a pseudo-dichotomy rather than as a secondary dichotomy.

The rosulate species of southern South America

In Chile and Argentina most species of *Calceolaria* are rosulate, perennial herbs. The inflorescences agree with the basic pattern described for *C. helianthemoides*, but the cymes are more or less reduced. The most striking example is offered by *C. uniflora* Lam. (Patagonia), in which there is only a single pair of cymes, each cyme being represented by a solitary terminal flower (as in Fig. 8, upper left).

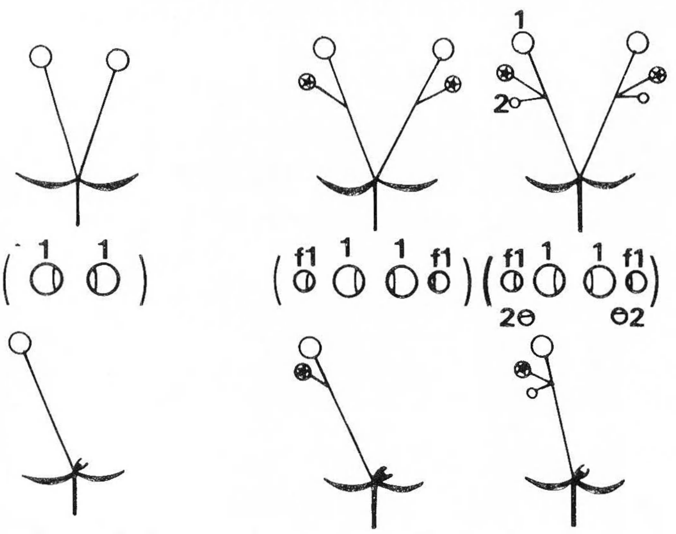

Fig. 8. Diagrammatic representation of six inflorescence types found in *C. lanceolata.* — Upper row: Symmetric inflorescences with two cymes. — Middle row: Projection diagrams corresponding to the upper row. — Lower row: Inflorescences with one of the cymes inhibited. — Symbols and abbreviations as in Fig. 6.

Furthermore, one of the cymes is usually stunted, which yields a one-flowered inflorescence.

Slightly less reduced inflorescences are found in *C. biflora* Lam. and *C. lanceolata* Cav. (both Patagonia). Here too, there is usually only a single pair of cymes, one of which is often stunted. The cymes are one- to four-flowered (Fig. 8). The majority of rosulate species have an elongate inflorescence peduncle branching dichotomously into two cymes and each cyme has a small number of flowers. Such an arrangement is typical for *C. corymbosa* R. & P., *C. crenatiflora* Cav. (both Chile) and a number of other species.

Calceolaria ericoides Vahl

C. ericoides is a small shrub native to the high Andes of Ecuador and N Peru, where it grows in grass páramo and secondary grasslands. The plant body is made up of erect, tufted primary branches (Fig. 9 A) and the major part of the main stem is more or less woody. The leaves of the main stem are alternate and subtend more or less brachyblastic secondary branches with decussate phyllotaxy. Proximally the secondary branches are vegetative and bear tertiary branches, which are extremely brachyblastic and appear to be mere fascicles of leaves. Further up on the primary branch the secondary branches are flowering, at least towards the apex. The size of these partial inflorescences decreases gradually in acropetal direction. At the base they are organized as co-florescences with a dichotomy and two cymes (Fig. 9 D), near the apex as few-flowered cymes (Fig. 9 B). The primary branches remain indefinite over a long period and new partial inflorescences are gradually produced as long as the branch is growing. Accordingly, there is always a small portion near the apex where the partial inflorescences are in bud and concealed by their subtending leaves. This lends an appearance of an intercalary inflorescence to the primary branch, but that impression is false since the terminal apex never reverts to a vegetative phase.

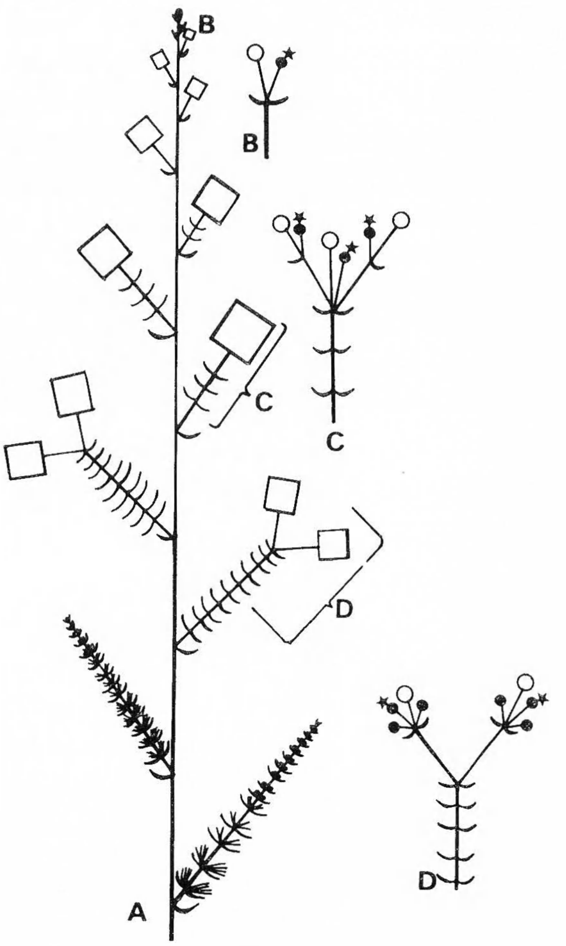

Fig. 9. *C. ericoides*, diagrammatic representation of the organization of a primary branch (A) and three partial inflorescences from different levels (B–D). — Symbols and abbreviations: □ cymes; otherwise as in Fig. 6. — Vouchers: Compiled from Barclay & Juajibioy 8194 (WIS), Harling et al. 6738 and 6833 (GB) and Sandeman 61 (BM).

Typologically, the terminal, flower-producing parts of the primary branches are best regarded as synflorescences consisting of a large main florescence with the capacity of much prolonged growth, and a varying number of small, strictly determinate co-florescences. However, the usual typological concepts are not very fruitful in this case.

The above pattern is much disturbed when the plants are grazed. The secondary and tertiary branches then begin to develop more vigorously and imitate the primary branches with varying degrees of perfection. A large proportion of the herbarium material consists of such specimens.

Calceolaria dichotoma Lam.

C. dichotoma Lam. is a typical representative of the small section *Micranthera* Pennell. It is a small annual (or rather short-lived) herb ranging from Colombia to S Peru. It is commonly found in disturbed habitats such as roadsides and pastures and often shows weedy tendencies. As in most annuals the major part of the aerial plant body is flower-producing (Fig. 10). The main stem terminates in a dichotomy at the first or second epicotylar node and each branch of the dichotomy yields a rather elaborate cyme. If there is more than one node on the main stem, small lateral cymes are usually present (Fig. 10 B). Asymmetric development due to one-sided inhibition is common but it does not follow a strict pattern. Accessory buds are occasionally encountered but rarely affect plant architecture.

Floral characters and in all probability the annual habit and the reduced plant body indicate that *C. dichotoma* is an advanced member of the genus. Architectural modification is, however, rather modest.

Calceolaria tripartita R. & P.

C. tripartita is a short-lived herb occurring spontaneously in a large part of tropical and subtropical South America and introduced in many other parts of the world. It grows in moist sites and is a common weed in disturbed habitats. In pronouncedly seasonal climates it is strictly annual. As in *C. dichotoma* the major part of the aerial plant body is flower-producing, but architectural modification is often more far-reaching (Fig. 11).

The proximal part of the stem is often prostrate and the internodes bear numerous adventitious roots. The distal flowering part is ascending, one or a few nodes remaining vegetative. The inflorescence of *C. tripartita* is very variable in elaborateness. When growing under favourable conditions the main stem is terminated by a dichotomy and two axillary cymes (Figs. 1 E, 11 C). In these cymes one of the lateral branches is more or less inhibited, yielding an inflorescence resembling that of *C. dichotoma*.

In small specimens growing under less favourable conditions, however, no dichotomy occurs and instead a single, seemingly terminal cyme is found (Fig. 11 A). In such plants the main stem is terminated by a flower pair, i.e. one terminal and one front flower. Growth is continued from one of the axillary buds, the other one being much stunted. The favoured shoot repeats the pattern at the next node, where a terminal flower, a front flower, one stunted and one favoured lateral shoot are produced. In this way several flowering nodes result, which make up the major part of the shoot system. In extremely small-sized specimens only a single terminal flower develops.

The pattern is complicated by the regular production of phylloscopic accessory buds, which,

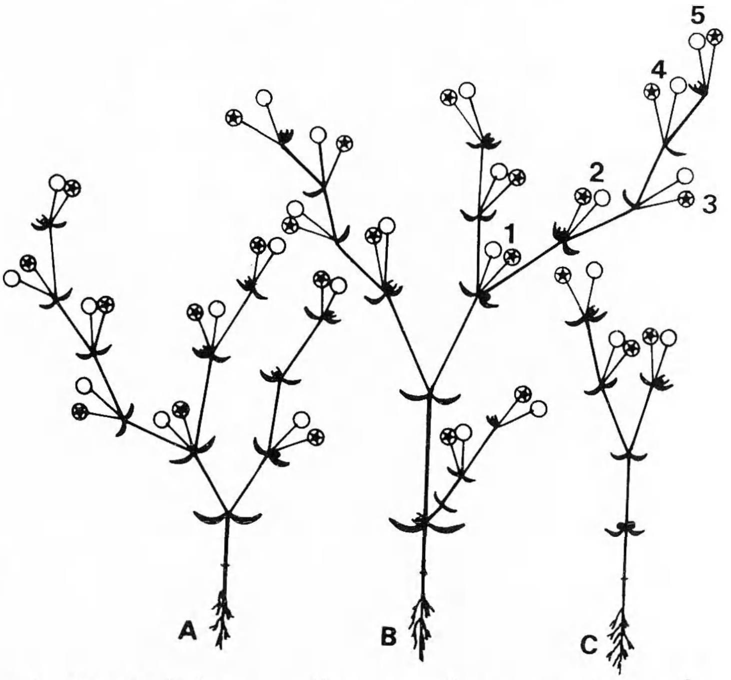

Fig. 10. *C. dichotoma*, diagrammatic representation of the organization of the plant body, most of it consisting of two more or less indefinite cymes. — Symbols as in Fig. 6. — Vouchers: A Holm-Nielsen et al. 3046 (AAU), B Harling & Andersson 14233 (GB), C Asplund 7763 (S).

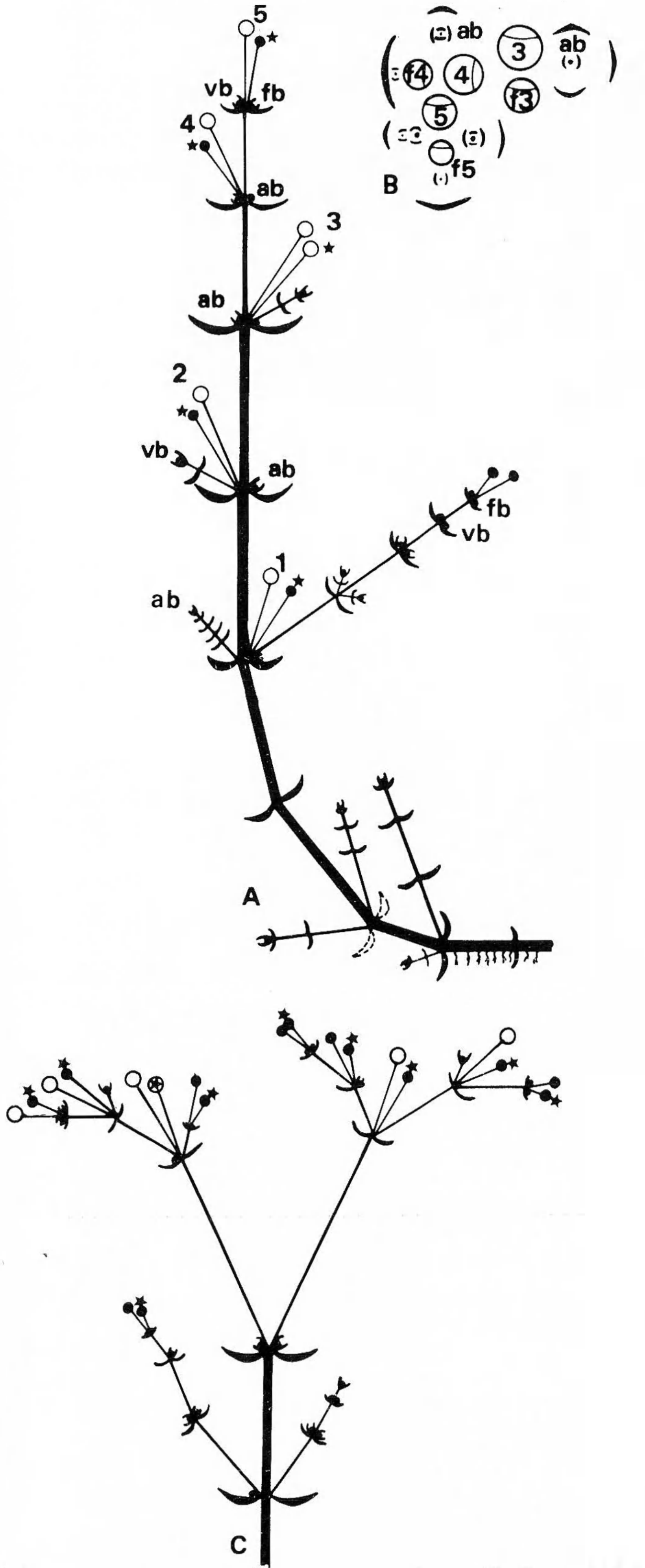

Fig. 11. Diagrammatic representation of inflorescence organization in *C. tripartita*. — A: A rather poorly developed plant (cultivated) with a terminal cyme, one branch of which is more or less indeterminate, the other one stunted. — B: Projection diagram illustrating the orientation of some of the flowers, same specimen as A. — C: Well developed specimen (herbarium material) with two lateral cymes representing branches of a dichotomy. — Symbols and abbreviations as in Fig. 7. — Vouchers: A–B Harling et al. 14904 (GB), C Harling & Andersson 13188 (GB).

however, have a limited potential of development, as long as the plant remains undamaged.

The deviating organization in small-sized specimens of *C. tripartita* seems to arise through increased activity of the terminal apex combined with regular inhibition of one of the lateral shoots. Instead of ceasing the terminal apex gives rise to a flower pair, and of the lateral buds usually producing one determinate cyme each one is inhibited, while the other one shows increased vigour and replaces the main shoot. It may conveniently be regarded as an abbreviated life cycle.

A similar pattern of variation in inflorescence organization is seen also in other wide-spread herbaceous species of this section (*Aposecos* Kränzlin), e. g. *C. pinnata* L. and *C. mexicana* Benth.

Discussion

With starting point in the comparatively large and many-flowered inflorescences of *C. rosmarinifolia* Lam. and *C. crenata*, two major trends of specializations can be discerned: (1) reduction of the number of cymes and (2) reduction of the number of flowers per cyme. The two phenomena are usually, though not always, correlated. In *C. helianthemoides* there is only one pair of cymes present (in the main florescence), while most other species of sect. *Thamnobia* have three to four pairs. Furthermore, the cymes of *C. helianthemoides* are few-flowered and there is a relatively long time lapse between the flowering of two successive flowers. In denser inflorescences with more numerous flowers (e.g. *C. rosmarinifolia*, Fig. 1 A, B) anthesis proceeds more rapidly. The same trends are found in the Ecuadorean species of sect. *Dermatophylla* Pennell (cf. Molau 1979), where *C. stricta* H. B. K. and *C. oxyphylla* Molau have several pairs of many-flowered cymes, while in *C. pedunculata* Molau there is only one pair of few-flowered cymes. In the rosulate species of southern South America these trends are carried to the extreme, ultimately leading to the one-flowered inflorescence of *C. uniflora*. In these latter species, reduction of the inflorescence is accompanied with an alteration of growth habit.

In general, species with few-flowered cymes also have very long cyme peduncles. The only exceptions to this rule are *C. uniflora* and some related species, where no cyme peduncle is differentiated, the only axial element being a long stout pedicel (as in Fig. 1 F).

When comparing species with few- and many-flowered cymes, it is found that species with few-flowered cymes all possess a relatively high number of advanced characters, vegetative as well as floral. Although all species of *Calceolaria* have basically the same highly specialized corolla structure, the species with many-flowered inflorescences generally do not show extreme specializations. We thus assume that the type of inflorescence represented by *C. crenata* and *C. rosmarinifolia* is an original one, from which all other types can be theoretically derived. Furthermore, that pattern is the normal one in the two most closely related genera, *Jovellana* R. & P. (Chile and New Zeeland) and *Porodittia* G. Don. (Peru). In these genera too, the main shoot is terminated by a dichotomy. In one species of *Jovellana, J. sinclairii* Kränzl. (New Zeeland), a very small bud is found between the branches of the dichotomy. In all other species of *Jovellana* and in *Porodittia*, this bud seems to be constantly missing. The intercalary inflorescence of sect. *Zygophylla* and the peculiar synflorescence of *C. ericoides* thus in all probability represent derived patterns of organization.

A third trend of specialization in inflorescence organization is found in small annual or short-lived species like *C. dichotoma* and *C. tripartita*. Here, the major part of the aerial plant body is engaged in flower production and the cymes show tendencies towards a prolonged period of flower production. In *C. dichotoma*, where organizational modification is comparatively slight, this prolongation is carried out by indefinite branching of the cymes, which remain essentially true to the original pattern, however. In *C. tripartita* the same aim is attained through indefinite sympodial growth of the cymes over a long period. As expected, these species are among the most highly specialized in the genus with regard to floral structure.

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References

Edwin, G. 1971: Calceolaria L. *In* J. F. Macbride (ed.), Flora of Peru. *Publ. Field Mus. Bot. Ser. 13, 5 B:* 515–654.

Goebel, K. 1931: *Blütenbildung und Sprossgestaltung. Zweiter Ergänzungsband zur Organographie der Pflanzen.* Jena.

Irmscher, E. 1959: Über Blüten- und Blütenstandsvarianten bei Saintpaulia ionantha Wendl. (Gesneriac.) und die morphologische Valenz der Vorblüten. *Flora 148:* 179–202 + Pl. 1–4.

Molau, U. 1978 a: The genus Calceolaria in NW South America. I. Taxonomic characters and generic subdivision. Fasciculata, a new section. *Bot. Notiser 131:* 219–227.

Molau, U. 1978 b: The genus Calceolaria in NW South America. II. The sections Chasmatochila, Thamnobia, Ericoides and Lehmannina. *Bot. Notiser 131:* 293–316.

Molau, U. 1979: The genus Calceolaria in NW South America. III. The sections Symplocophylla and Dermatophylla. *Bot. Notiser 132:* 31–48.

Pennell, F. W. 1951: The genus Calceolaria in Ecuador, Colombia and Venezuela. *Proc. Acad. Nat. Sci. Philadelphia 103:* 85–196.

Ritterbusch, A. 1976: Die Organopoiëse der Blüte von Calceolaria tripartita R. et P. (Scrophulariaceae). Phänomene der Morphogenese komplexer biologischer Systeme. I. *Bot. Jahrbücher 95:* 267–320.

Troll, W. 1964: *Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers I.* Stuttgart.

Troll, W. 1969: *Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers II.* Stuttgart und Portland.

Weber, A. 1973: Die Struktur der paarblütigen Partialflorescenzen der Gesneriaceen und bestimmter Scrophulariaceen. *Beiträge Biol. Pflanzen 49:* 429–460.

Weber, A. 1978: Transitions from pair-flowered to normal cymes in Gesneriaceae. *Notes Royal Bot. Gard. Edinburgh 36:* 355–368.

Weberling, F. 1965: Typology of inflorescences. *Journ. Linn. Soc. (Bot.) 59:* 215–221.

The genus Calceolaria in NW South America

IV. The sections Anacyrta, Polyclada and Phaeanthera

ULF MOLAU

Molau, U. 1980 03 17: The genus Calceolaria in NW South America. IV. The sections Anacyrta, Polyclada and Phaeanthera. *Bot. Notiser 133:* 33–45. Stockholm. ISSN 0006-8195.

Three sections of *Calceolaria* (Scrophulariaceae) in NW South America are revised, viz. *Anacyrta* (6 species in the area), *Polyclada* (1) and *Phaeanthera* (1). Sect. *Anacyrta* comprises species with ovate to elliptic, herbaceous leaves, and with the lower corolla lip strongly upcurved and internally marked with reddish spots in the throat. Sect. *Polyclada* is characterized by unequal sepals, of which the dorsal one is cordiform. Sect. *Phaeanthera*, which is closely related to sect. *Dermatophylla*, comprises species with ± coriaceous, petiolate leaves and brownish to purplish pubescence. *C. ternata* in sect. *Anacyrta* is described as new.

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Sect. 8. **Anacyrta** Pennell

Pennell 1951 p. 124. — Type species: *Calceolaria virgata* R. & P.

Shrubs, subshrubs or perennial herbs. Foliage, inflorescence and distal parts of stems pubescent with white or buffish gland-less hairs. Leaves decussate or ternate, petiolate or sessile; blades ovate to elliptic, herbaceous, on both sides beset with yellowish sessile glands (in some species concealed by hairs). Inflorescence distal. Corolla yellow to greenish yellow, with red or purplish spots or bands in the throat of the lower lip; upper lip very small; lower lip strongly upcurved and covering the orifice (the upcurved portion occupies about 2/3 of its entire length), saccate in 1/3 of its length. Anthers opening throughout; thecae divaricate or very slightly deflexed, equal. Ovary densely beset with sessile brownish glands. Capsule glandular-pubescent.

Sect. *Anacyrta* ranges from Ecuador to Bolivia, and reaches its highest species diversity in S Ecuador and N Peru. Flower morphology is very uniform throughout the section, and the species are distinguished mainly on vegetative characters. The taxonomically most important characters in this group are pubescence type, decussate vs. ternate phyllotaxy (cf. below *C. virgata*) and petiolate vs. sessile leaves.

Since the floral structure is very uniform and sympatric species often flower simultaneously, hybrids might be expected to occur regularly. No such cases have been observed, however, and species identity is thus probably maintained by internal barriers.

Key to the species of sect. Anacyrta

1. Leaves sessile .... 3. *C. serrata*
– Leaves petiolate 2
2. Leaves sparsely short-pilose above; the petiole less than 1/10 the length of the leaf-blade .... 4. *C. variefolia*
– Leaves short-hirsute to velutinous above; the petiole more than 1/10 the length of the leaf-blade 3
3. Lower leaf surface villous, lanate or velutinous (also between the veins), with the sessile glands ± covered by the pubescence 4
– Lower leaf surface pubescent mainly on the major veins; sessile glands conspicuous beneath 5
4. Leaves hirsute or strigose above; leaves and cyme peduncles usually ternate (i. e. in threes) . ... 6. *C. ternata*
– Leaves velutinous above; leaves and cyme peduncles usually decussate .... 5. *C. comosa*
5. Veins of lower leaf surface tomentose or sericeous with fine hairs; petioles white arachnoid-

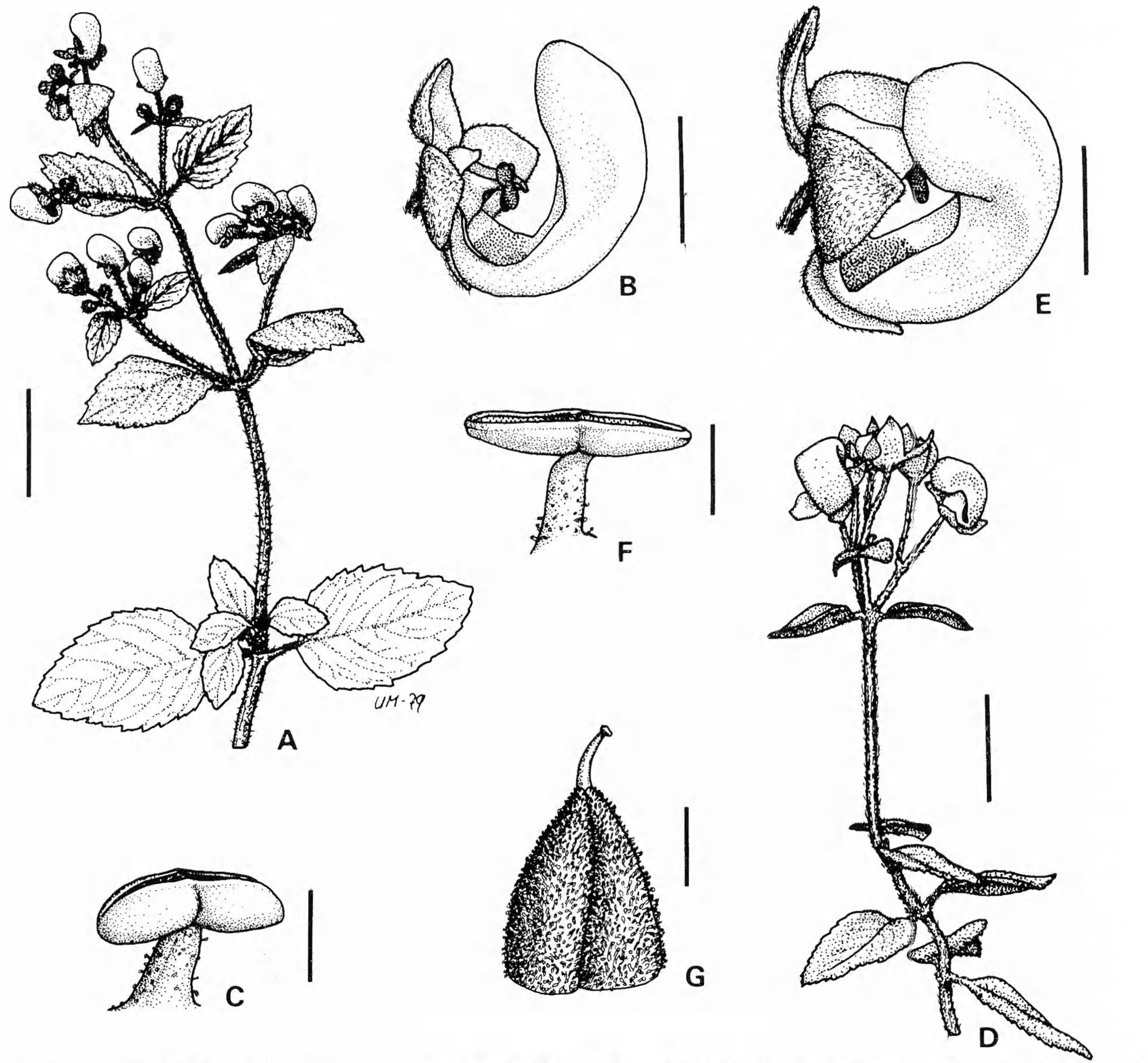

Fig. 1. A–C: *Calceolaria virgata*. — A: Flowering branch. — B: Flower. — C: Stamen. — A: Harling & Andersson 14088; B, C: Harling et al. (leg. Molau) 15241. — D–G: *C. sericea*. — D: Flowering branch. — E: Flower. — F: Stamen. — G: Capsule. — D: Løjtnant & Molau 11317; E, F: Harling et al. (leg. Molau) 14924; G: Asplund 6326. — A, G drawn from herbarium material; B, C, E, F drawn from fixed material; D drawn from photograph. — Scales: A, D 2 cm, B, E 5 mm, C, F 1 mm, G 2 mm.

lanate .... 2. *C. sericea*

- Veins of lower leaf surface strigose with short coarse hairs; petioles puberulous or short-villous with buffish hairs .... 1. *C. virgata*

1. Calceolaria virgata R. & P.

Ruiz & Pavón 1798 p. 20 — *Fagelia virgata* (R. & P.) Kuntze 1891 p. 460 — Orig. coll.: Pavón s. n. (MA lectotype).

Calceolaria uniflora R. & P. 1798 p. 16, non Lamarck — *Fagelia uniflora* (R. & P.) Kuntze 1891 p. 460 — *Calceolaria triphylla* Kränzlin 1907 p. 114, nom. nov. — Orig. coll.: Pavón s. n. (MA lectotype).

Calceolaria elliptica Weddell 1857 p. 137 — Orig. coll.: Weddell 3982 (P lectotype).

Calceolaria ramosissima Kränzlin 1905 p. 107 — Orig. coll.: Weberbauer 3825 (G lectotype).

Calceolaria forgetii Skan 1912 Tab. 8436 — Orig. coll.: Forget s. n. (K lectotype; a cultivated specimen, propagated in England by Sander & Sons, St. Albans, from seeds collected in Peru by Mr. Forget).

Calceolaria cuzcoensis Kränzlin 1929 p. 11 — Orig. coll.: Günther 13 (HBG lectotype).

Calceolaria trivialis Kränzlin 1929 p. 19 — Orig. coll.: Herrera 549 (B holotype, destroyed. Lectotype: photograph at F, copy at PH).

Calceolaria humilis Edwin 1970 p. 382—Orig. coll.: Pennell & Ferreyra 14953 (PH holotype).

Illustrations. Fig. 1 A–C; Ruiz & Pavón 1798 Pl. 31 Fig. a (*C. virgata*), Pl. 20 Fig. c (*C. uniflora*); Skan 1912 Tab. 8436 (*C. forgetii*).

Subshrub, (0.1–)0.3–1 m high, much branched. Inflorescence and distal parts of stems puberulous or tomentose with whithish hairs. *Leaves* decussate (rarely ternate), petiolate; blades ovate to almost circular, rarely elliptic, 1.2–5.0 × 0.7–3.4 cm, acute to almost obtuse, rounded or cuneate at base; green, greyish green or olivaceous above, ± densely hirsute with very short hairs, slightly rugose; pale green beneath, strigose on the raised primary and secondary veins, interspaces glabrous or sparsely villous, conspicuously gland-dotted; margins serrate. Petioles 2–21 mm, puberulous or villous. *Inflorescence* comprising 1–4 pairs of (1–)4–12-flowered cymes on primary peduncles 0.8–5.0 cm long. Cyme bracts present, though sometimes rudimentary or absent in the uppermost cymes. Pedicels 0.5–2.2 cm. *Sepals* ovate or elliptic, 3.0–5.0 × 2.3–4.3 mm at anthesis, light green, subacute, externally villous or puberulous, internally glabrous except for a puberulous border along the margin. *Corolla* pale to bright yellow, with a broad reddish band or series of spots in the throat; upper lip 1–2 × 3–4 mm; upcurved portion of lower lip 8–15 × 5–11 mm. *Anthers* light brown, 1.6–2.4 mm; thecae divaricate. *Filaments* 0.8–1.5 mm. *Style* 1.5–2.1 mm, curved. *Capsule* conic, 4–5 mm long.

Habitat. Dry mountain scrub and rocky slopes as well as in thickets and stream-banks in mountain forest, at altitudes between 1800 and 4130 m, only occasionally lower.

Distribution. Fig. 2. One of the most common species of the genus in the Andes of Peru, ranging from S Ecuador to NE Bolivia. North of the Piura Divide it is known from only three collections from southernmost Ecuador (prov. Loja). In all, 179 specimens from 112 collections have been studied. *C. virgata* has not previously been reported from Ecuador.

Remarks. Calceolaria virgata is one of the most widespread species of subgenus *Cheiloncos*. It is very variable in leaf size and pubescence density, probably corresponding to differences in altitude, exposure, local climate etc. *Calceolaria humilis* was based upon a dwarf specimen, and is better regarded as one of the extremes of this variation. The type specimens of the other synonyms are closely similar to the type of *C. virgata*.

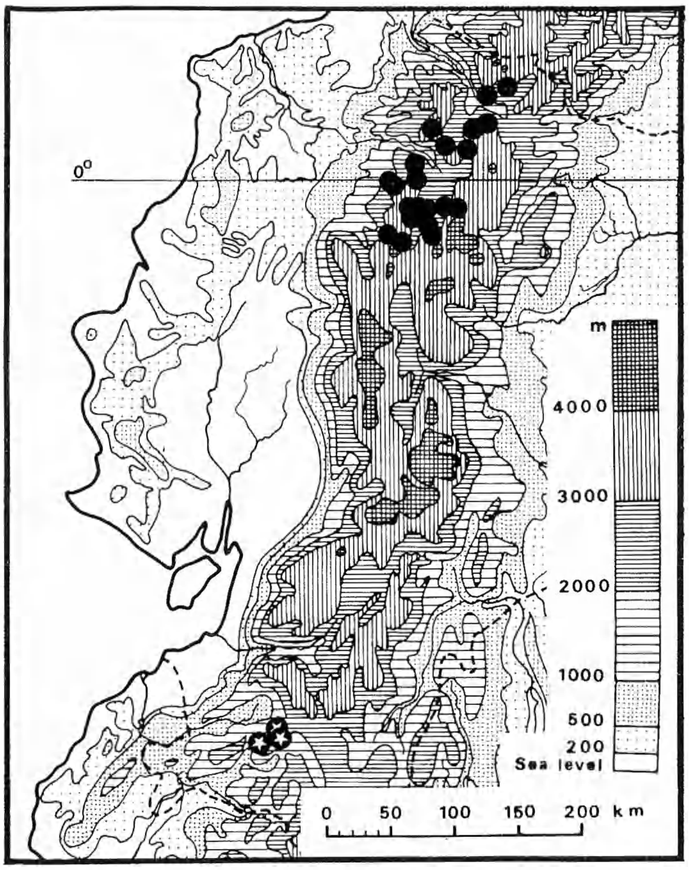

Fig. 2. Known distribution of *Calceolaria virgata* (✪) N of the Piura Divide, and *C. sericea* (●).

Calceolaria virgata normally has a decussate phyllotaxy, but a small fraction of the specimens studied (3 out of 179) possess ternate leaves (sometimes also ternate peduncles), at least on some branches. In fact, both *C. virgata* and the conspecific *C. uniflora* R. & P. were originally described and illustrated by Ruiz & Pavón (1798) as to possess ternate leaves. The type specimens of the two (unicates, preserved in the Madrid Herbarium), however, have a strictly decussate phyllotaxy, but it is likely that the authors had observed ternate-leaved specimens in the field. Of the other species of sect. *Anacyrta* with decussate phyllotaxy treated in this paper no ternate-leaved specimens are known so far.

The opposite tendency is shown by some of the ternate-leaved Peruvian species. Thus, in *C. glauca* R. & P. and *C. rugulosa* Edwin (though normally with a strictly ternate phyllotaxy throughout the shoots) a few per cent of the specimens have decussate leaves and paired cyme peduncles.

Conclusively, the decussate vs. ternate phyllotaxy is not an absolute species character, at least not in sect. *Anacyrta*. The species are either predominantly ternate or decussate in their nodal arrangement, but the opposite phyllotaxy may occur in a low percentage of the specimens.

Representative specimens. Ecuador. Loja: Loja–Zaruma road, near Las Chinches, c. 2400 m, 30.IV.1974, Harling & Andersson 14088 (GB); between Las Chinches and Sambi, 2200–2400 m, 3.V.1974, Harling & Andersson 14275 (GB) — Loja–Catacocha road, c. 25 km S of Las Chinches, c. 2200 m, 9.II.1977, Harling et al. (leg. Molau) 15241 (GB). — "Loxa", Lobb s. n. (BM). — *Peru. Cajamarca:* E of Celendín, 29.V.1966, Edwin & Schunke 3592 (G, GH, W), 3599 (G, GH, W); 2630 m, 13.V.1964, Hutchison & Wright 5056 (F, UC). — Sunchubamba, upper Chicama valley, prov. Cajatambo, 3150 m, 31.V.1957, Ellenberg 1714 (GOET, U). — Hacienda Taulis, Río La Quinua above La Playa, prov. Hualgayoc, 2950 m, 4.IX.1964, Hutchison & von Bismarck 6512 (K, MO, UC). — San Pablo, prov. Cajamarca, 2600 m, 21.V.1975, Sagástegui et al. 7964 (MO); 2200 m, 17.V.1976, Sagástegui et al. 8357 (MO); 2400–2700 m, 1906, Weberbauer 3825 (G). — *Amazonas:* W side of Cerros Calla-Calla, midway on Balsas–Leimebamba road, 3100 m, 19.VI.1964, Hutchison & Wright 5740 (G, GH, K, LE, M, MO, P, UC). — *La Libertad:* Road to Huamachuco, 8 km E of Agallapampa, 2870 m, 5.VIII.1964, Hutchison et al. 6133 (G, GH, K, LE, M, MO, P, UC). — E of Río Chusgón, 58 km from Pullac on road to Parcay, 3820 m, 7.VIII.1964, Hutchison et al. 6181 (K, M, MO, P, UC). — *Ancash:* Río Fortaleza valley, c. 12.5 km W of Comococha, 3700–3900 m, 28.VI.1966, Edwin & Schunke 3848 (G, W). — W slope of Cordillera Negra, below Paso de Collán, 3650 m, 1.VI.1948, Pennell 15474 (GH). — *Huánuco:* La Molina near Panao, 2400 m, 12.IX.1940, Asplund 13682 (S). — Pillao, 2700 m, 20.II.1946, Woytkowski 34116 (G, MO). — *Junín:* Tambo, prov. Tarma, 3800 m, 11.IV.1953, Hjerting & Petersen 1356 (C). — Huancayo, 3300–3800 m, III.1945, Soukup 2771 (GH). — *Lima:* Río Blanco, 3600 m, 4.VI.1940, Asplund 11389 (S); 3500–3700 m, 25.VII.1948, Pennell & Maldonado 15933 (GH). — San Mateo, 21.VI.1966, Edwin & Schunke 3794 (G, W); 1853, Mathews 856 (CGE, E, K, OXF); 3200 m, V.1938, Sandeman 289 (OXF). — S of Surco, 2700–3000 m, 1.V.1948, Pennell & Ferreyra 15256 (BM, GH, LE). — *Huancavelica:* Near Córdova, 3050–3300 m, 27–28.III.1942, Metcalf 30253 (G, GH, MO). — *Cuzco:* Paucartambo, c. 3500 m, 6.V.1939, Balls 6825 (BM), 6826 (BM). — *Apurimac:* Quihuala, c. 3600 m, 16.V.1939, Balls 6902 (BM, E, K, S fragment). — Between Chincheros and Andahuaylas, 3700 m, 19.IV.1953, Hjerting & Petersen 1431 (C). — Moyabamba, prov. Andahuaylas, 3650 m, 4.I.1950, Vargas 8683 (PH), 8695 (PH).

For the area N of the Piura Divide, the list includes all specimens studied.

2. **Calceolaria sericea** Pennell

Pennell 1951 p. 124 — Orig. coll.: Penland 832 (PH holotype, F, GH).

Illustrations. Fig. 1 D — G; Pennell 1951 p. 119 Fig. 6.

Herb or *subshrub*, 0.5–1 m high; main stems erect to decumbent. Inflorescence and distal parts of stems sericeous with thin whitish hairs. *Leaves* decussate, petiolate; blades ovate to elliptic, 2.0–5.2 × 1.2–3.2 cm, acute, rounded at base (rarely cuneate); olivaceous above, matt, densely hirsute with very short hairs, tomentose beneath, or sericeous on the midrib and pinnately spreading veins, tissue pale green, glabrous or pilose, conspicuously gland-dotted; margins serrate. Petioles 3–12 mm long, white arachnoid-lanate. *Inflorescence* comprising 1–2(–3) pairs of 4–14(–20)-flowered cymes on primary peduncles 1.0–8.3 cm long. Cyme bracts usually lacking, but sometimes present in the lower cymes of well-developed specimens. Pedicels 0.6–1.9 cm. *Sepals* ovate, 4.7–6.5(–8.8) × 3.3–5.0(–6.0) mm at anthesis, acute or slightly acuminate, pale green, externally minutely sericeous or villous, internally glabrous or puberulous. *Corolla* pale yellow or greenish yellow; upper lip sometimes almost white, 2–3 × 4–6 mm; lower lip with a large purplish spot in the throat (rarely absent), upcurved portion 8–13 × 6–11 mm. *Anthers* dark brown, 2.2–2.7 mm; thecae divaricate. *Filaments* 1.0–1.6 mm. *Style* slightly curved, 1.8–2.2(–2.8) mm. *Capsule* narrowly conic, 4–7 mm long.

Habitat. Relatively dry sites in mountain scrub and cloud forest, but also found in pastures, on roadsides etc. The altitudinal records range from 2000 to 3500 m.

Distribution. Fig. 2. Endemic to the Andes of N Ecuador, known only from the provinces of Pichincha, Imbabura and Carchi. However, in the mountains around Quito it is locally one of the most abundant *Calceolaria* species. In all, 122 specimens from 66 collections have been studied.

Remarks. The thin silky pubescence of stems and petioles, and the densely short-hirsute upper leaf surfaces make *Calceolaria sericea* an easily recognized species. It was collected for the first time by Bonpland in 1802, but was reported as *C. serrata* Lam., a species of central Ecuador with which it was confused until Pennell's revision (1951).

Representative specimens. Ecuador. Carchi: Quebrada del Río Angel, 3 km NE San Isidro on road to El Angel, 28.I.1967, Sparre 14323 (S). — *Imbabura:* Chota, André 3517 bis (K). — Between Shanshipamba and

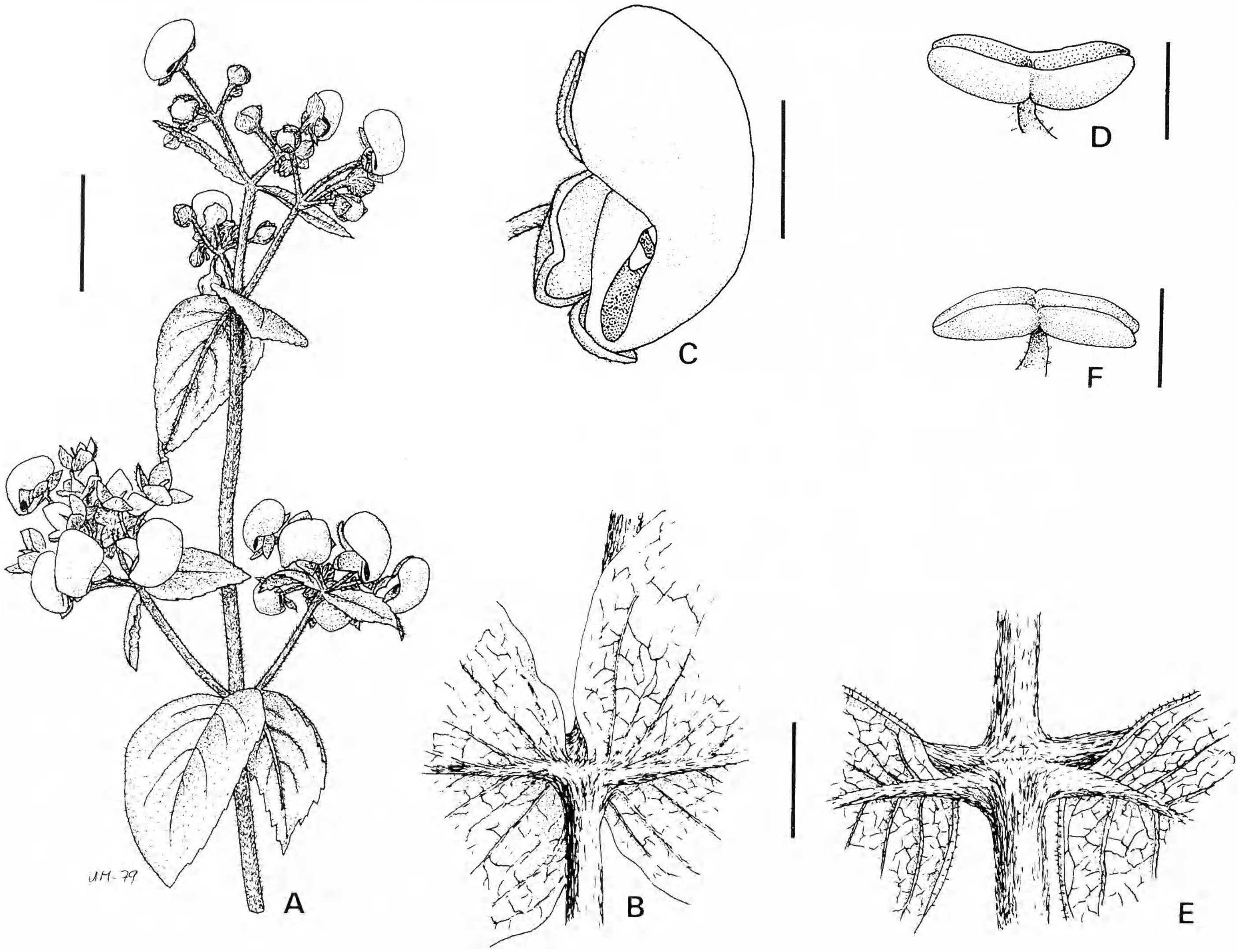

Fig. 3. A–D: *Calceolaria serrata*. — A: Flowering branch. — B: Vegetative node of the main stem. — C: Flower. — D: Stamen. — A, C: Løjtnant & Molau 14133; B: Camp E-3520; D: Camp E-4014. — E–F: *C. variefolia* (Pennell & Ferreyra 14916). — E: Vegetative node of the main stem. — F: Stamen. — A, C drawn from photograph; B, D–F drawn from herbarium material. — Scales: A 2 cm, B, C, E 5 mm, D, F 1 mm.

La Esperanza, c. 25 km ESE of Ibarra, 2950 m, 16.XI.1949, Acosta-Solís 14400 (F). — Near Morocho above Apuela, c. 2900 m, 24.VII.1974, Plowman et al. 3849 (COL, GH). — Between Otavalo and San Pablo, 9.IV.1876, André 3517 (F, K, NY). — Laguna Cuicocha, c. 3100 m, 24.V.1973, Holm-Nielsen et al. 6326 (AAU, GB, MO); 3200 m, 2.VI.1939, Penland 832 (F, GH, PH); 3400–3500 m, 23.VII.1974, Plowman et al. 3783 (GH); 3000 m, 10.XII.1966, Sparre 13383 (S). — *Pichincha:* W of Calacalí, Cordillera Occidental, 2700 m, 25.III.1979, Løjtnant & Molau 11346 (AAU, GB). — Crater of Pululahua, 16.VI.1876, André K.620 (NY); c. 2800 m, 12.VII.1959, Barclay et al. 7924 (WIS); 2600–3100 m, 12.V.1973, Holm-Nielsen et al. 5175 (AAU, GB, MO); 2800 m, 3.VI.1979, Løjtnant & Molau 14108 (AAU, GB). — Quito, 2900 m, 15.V.1939, Asplund 6031 (G, LD, S); 5.IV.1930, Benoist 2329 (P); 24.I.1935, Fosberg 22542 (NY, US); 2850 m, 16.IV.1920, Holmgren 524 (G, MO, S, US); c. 2750 m, 1856, Jameson 62 (BM, E, FI, G, K, P); 2700 m, 3.VII.1979, Løjtnant & Molau 15461 (GB); 2900 m, 14.VII.1979, Løjtnant & Molau 15899 (AAU, GB). — W of Nono, c. 2700 m, 12.VI.1968, Harling et al. 10259 (GB); 2200–2400 m, 27.I.1977, Harling et al. (leg. Molau) 14886 (GB); 2400 m, 24.III.1979, Løjtnant & Molau 11317 (AAU, GB); c. 3050 m, 15.IX.1935, Mexía 7696 (BM, GB, GH, K, MO, NY, PH, S, U, UC). — Paloquillo above Pifo, 3400 m, 18.III.1979, Løjtnant & Molau 11214 (GB). — 3 km W of Aloag, 3100–3150 m, 13.V.1979, Løjtnant & Molau 13182 (AAU, GB). — Quito–Santo Domingo road, between Aloag and Tandapi, 2850 m, 29.V.1979, Løjtnant & Molau 13988 (AAU, GB); Tandapi (Cornejo Astorga), c. 2500 m, 7–10.V.1968, Harling et al. 9373 (GB). — Rumipamba, c. 35 km SE of Quito, c. 3000 m, 29.I.1977, Harling et al. (leg. Molau) 14924 (GB); 2850 m, V.1952, Acosta-Solís/Univ. Central nr 1580 A (M).

3. **Calceolaria serrata** Lam.

Lamarck 1785 p. 555 — *Fagelia serrata* (Lam.) Kuntze 1891 p. 460—Orig. coll.: Jussieu s. n. (P holotype, C).

Calceolaria campii Pennell 1951 p. 126 — Orig. coll.: Camp E-4014 (PH holotype, F, G, GH, K, MO, NY, P, S, UC, US).

Illustrations. Fig. 3 A–D; Pennell 1951 p. 127 Fig. 7 (as *C. campii*).

Erect or scandent *subshrub*, 1–4 m high. Inflorescence and distal parts of stems tomentose with ascending pale purplish hairs. *Leaves* decussate, sessile, acute, dull green above, short-pilose, pale green beneath, villous or tomentose with ascending hairs on the midrib and pinnately spreading veins, interspaces pilose or almost glabrous, margins serrate; leaves of the main stems broadly ovate, (2.8–)4.0–8.0×(1.5–)2.7–6.0 cm, clasping and ± cordate at base; leaves of lateral branches smaller, ovate, and with rounded, non-clasping bases. *Inflorescence* comprising 2–3 pairs of 8–22-flowered cymes on primary peduncles 0.8–4.5 cm long. Cyme bracts present. Pedicels 0.6–1.8 cm. *Sepals* elliptic to ovate, subacute, light green (often turning red in exposure), 4.8–6.5×3.0–5.2 mm at anthesis, externally villous, internally puberulous. Upper *corolla* lip white, arched, c. 2 × 4 mm; lower lip pale yellow with a broad purple band and/or series of spots in the throat, upcurved portion 8–15×6–10 mm. *Anthers* brown, 2.0–2.6 mm; thecae divaricate. *Filaments* 0.8–1.1 mm. *Style* slightly curved, 1.7–2.3 mm. Capsule ovoid, 4–6 mm long.

Habitat. Mountain forest and scrub at altitudes between 1500 and 2800 m.

Distribution. Fig. 4. Restricted to the W slopes of Cordillera Occidental, Andes of central Ecuador, known from the provinces of Bolívar, Chimborazo and Caña.

Remarks. Pennell (1951) identified the type of *C. serrata* with the S Ecuadorean and Peruvian taxon later described as *C. variefolia* (Edwin 1970, cf. below). In consequence, the central Ecuadorean taxon was recognized as a new species, *C. campii*. Jussieu's original collection of *C. serrata* is labelled "Perou", but the plant conforms in all details with the central Ecuadorean species. Besides of Peru, Joseph de Jussieu did also collect in S and central Ecuador; all these collections are (according to Diels 1937) labelled in the same way. Thus, the actual collection is most likely originating from central Ecuador. Similar cases of misleading labelling are the types of *C. crenata* Lam. and *C. rosmarinifolia* Lam., also collected by Jussieu.

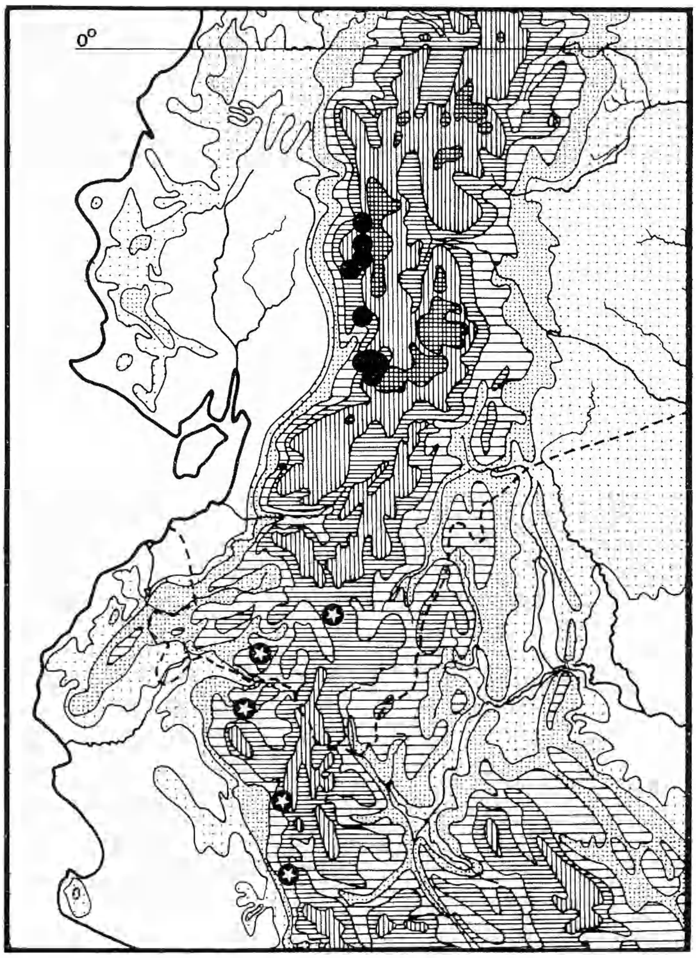

Fig. 4. Known distribution of *Calceolaria variefolia* (✪) N of the Piura Divide, and *C. serrata* (●).

Specimens studied. Ecuador. Chimborazo: Canyon of Río Chanchán, c. 5 km N of Huigra, 1500–2000 m, 19–28.V.1945, Camp E-3429 (BM, NY, PH, VEN); directly above the village of Huigra, 1500–2100 m, 28–31.V.1945, Camp E-3520 (F, G, GH, K, MO, NY, P, PH, U, UC, US). — Above Pallatanga on road to Riobamba, 2700 m, 6.VI.1979, Løjtnant & Molau 14133 (AAU, GB). — Vicinity of Huigra, 3.IX.1918, Rose 22520 (NY, US). — Above Mocha (near the border with prov. Tungurahua), IX.1881, Sodiro "63" (Sodiro Herbarium, Bibliotheca Aurelio Espinosa, Cotocollao, Quito). — Guataxi (near Chunchi), Spruce s. n. (K). — *Bolívar:* Vinchoa, "Reg. Interandina", 2800 m, 29.IX.1943, Acosta-Solís 5957 (F). — Hacienda Talahua, 2000 m, 5.V.1939, Penland 662 (F, GH, PH). — Above Balsapamba, 2500 m, VII–VIII.1934, Rimbach 215 (B, F, GH). — Guaranda valley, 2300–2700 m, IX.1858, Wagner "III" (M). — *Cañar:* Between Santa Rosa and Joyagshi (small railroad stations near the border with prov. Chimborazo), 2500–2750 m, 6–9.VII.1945, Camp E-4014 (F, G, GH, K, MO, NY, P, PH, S, UC, US). — *Sine loco:* Jussieu s. n. (C, P).

4. **Calceolaria variefolia** Edwin

Edwin 1970 p. 400 — Orig. coll.: Pennell & Ferreyra 14916 (US holotype, BM, G, GH, M, PH, S).

Illustration. Fig. 3 E–F.

Lax *shrub*, 1–2 m high. Inflorescence and distal parts of stems tomentose with ascending buffish white hairs. *Leaves* decussate, short-petiolate, blades acute or slightly acuminate, at base cuneate or rounded, green above, sparsely short-pilose, light green beneath, short-tomentose or pilose with ascending haris on the midrib and pinnately spreading veins, interspaces glabrous. Leaves of the main stems ovate, 3.7–8.0×1.8–4.3 cm. Petioles 2–8 mm, tomentose. *Inflorescence* comprising 2–4 pairs of 4–8-flowered cymes on primary peduncles 1.5–4.0 cm long. Cyme bracts present. Pedicels 0.5–1.5 cm. *Sepals* ovate, acute, light green to yellowish green, 4.0–6.0×3.0–4.2 mm at anthesis, short-tomentose on both sides. *Corolla* pale yellow; upper lip arched, c. 2×4 mm; lower lip with a maroon-red patch in the throat, upcurved portion 7–13×6–9 mm. *Anthers* brown, 1.9–2.3 mm; thecae divaricate. *Filaments* 0.9–1.5 mm. *Style* 2.0–2.3 mm. *Capsule* ovoid, 4–6 mm long.

Habitat. Mountain scrub at altitudes between 1700 and 2500 m.

Distribution. Fig. 4. Southernmost Ecuador in the province of Loja, and N Peru in the departments of Piura, Lambayeque and Cajamarca, only once collected S of the Piura Divide (Hutchison & von Bismarck 6339).

Remarks. Calceolaria variefolia is probably closely related to *C. serrata*, from which it differs most markedly in pubescence colour and the presence of short petioles. It grows at lower altitudes than most other *Calceolaria* species in NW South America, and is consequently one of the few species known to overbridge the Piura Divide.

A somewhat aberrant specimen (Hutchison & Wright 6696) is collected at an unusually low altitude in the northern part of the Piura department in N Peru. It differs from the typical specimens of *C. variefolia* in some vegetative characters, viz. the petioles are longer and the glands of the leaves are stalked. As such a variation correlated to the altitude is seen in many other taxa of the genus, this specimen is with the present material most conveniently retained within *C. variefolia*.

Specimens studies. Ecuador. Loja: Loja, 2220 m, IV.1905, Rivet 930 (P). — Zozoranga, 1.VIII.1847, Seemann 728 (K, S fragment). — *Peru. Piura:* Porculla, on Olmos–Jaén road, 21.V.1933, Carricker s. n. (PH); 12.VI.1966, Edwin & Schunke 3748 (G, GH, W); 2000–2100 m, 22.IV.1964, Ferreyra 15661 (UC). — Above Canchaque, 1700–1900 m, 21–23.III.1948, Pennell & Ferreyra 14916 (BM, G, GH, M, PH, S, US). — On the road to Ayabaca, 8 km above Puente Tandopa (Río Quiroz), 960–1180 m, 24.IX.1964, Hutchison & Wright 6696 (UC). — *Lambayeque:* La Capilla, on Olmos–Jaén road, 2000–2500 m, 8.III.1946, Olsson 3 (GH). — *Cajamarca:* Hacienda Taulis, prov. Hualgayoc, 1900 m, 29.VIII.1964, Hutchison & von Bismarck 6339 (MO, UC).

5. **Calceolaria comosa** Pennell

Pennell 1951 p. 129 — Orig. coll.: Camp (leg. Giler) E-2782 (PH holotype, NY, US).

Calceolaria cinerea Pennell 1951 p. 128 — Orig. coll.: Rose 23034 (US holotype, GH, PH).

Calceolaria mollis Pennell 1951 p. 128 — Orig. coll.: Seemann 727 (K holotype).

Illustrations. Fig. 5 A–C; Pennell 1951 p. 127 Fig. 8 (as *C. cinerea*), p. 130 Fig. 9.

Subshrub, 0.5–1 m high; inflorescence and distal part of stems densely sericeous or lanate with long ascending, whitish to brownish (often purplish tinged) hairs (colour depending on staining of the septa). *Leaves* decussate, petiolate; blades ovate, 2.5–6.5×1.6–4.2 cm, obtuse to acute, rounded to cuneate at base, greyish green or olivaceous above, ± densely velutinous, with impressed primary and secondary veins (pinnately rugose), villous to lanate beneath with buffish hairs, margins slightly serrate, ± revolute and (usually) appearing entire. Petioles densely sericeous or lanate, 3–15 mm. *Inflorescence* comprising 2–3 pairs of 4–16-flowered cymes on primary peduncles 0.5–9.3 cm long. Cyme bracts absent or present in the lower cymes. Pedicels 0.7–2.0 cm. *Sepals* ovate or elliptic, 4.0–7.0×2.8–5.5 mm at anthesis, obtuse to acute, sometimes slightly acuminate; externally sericeous to lanate; internally pale green, glabrous except for a puberulous border along the margin. *Corolla* pale sulphur-yellow, with a purplish spot in the throat; upper lip arched, 2–3×3–5 mm; upcurved portion of lower lip 8–13×6–10 mm. *Anthers* brown, 1.9–2.9 mm; thecae divaricate or slightly deflexed. *Filaments* 0.6–1.2 mm. *Style* curved, 1.5–2.5 mm. *Capsule* ovoid, 4–6 mm long.

Habitat. Mountain scrub and open slopes in the lower páramo zone, at altitudes between 1900 and 3300 m.

Distribution. Fig. 6. Disjunct. North of the Piura

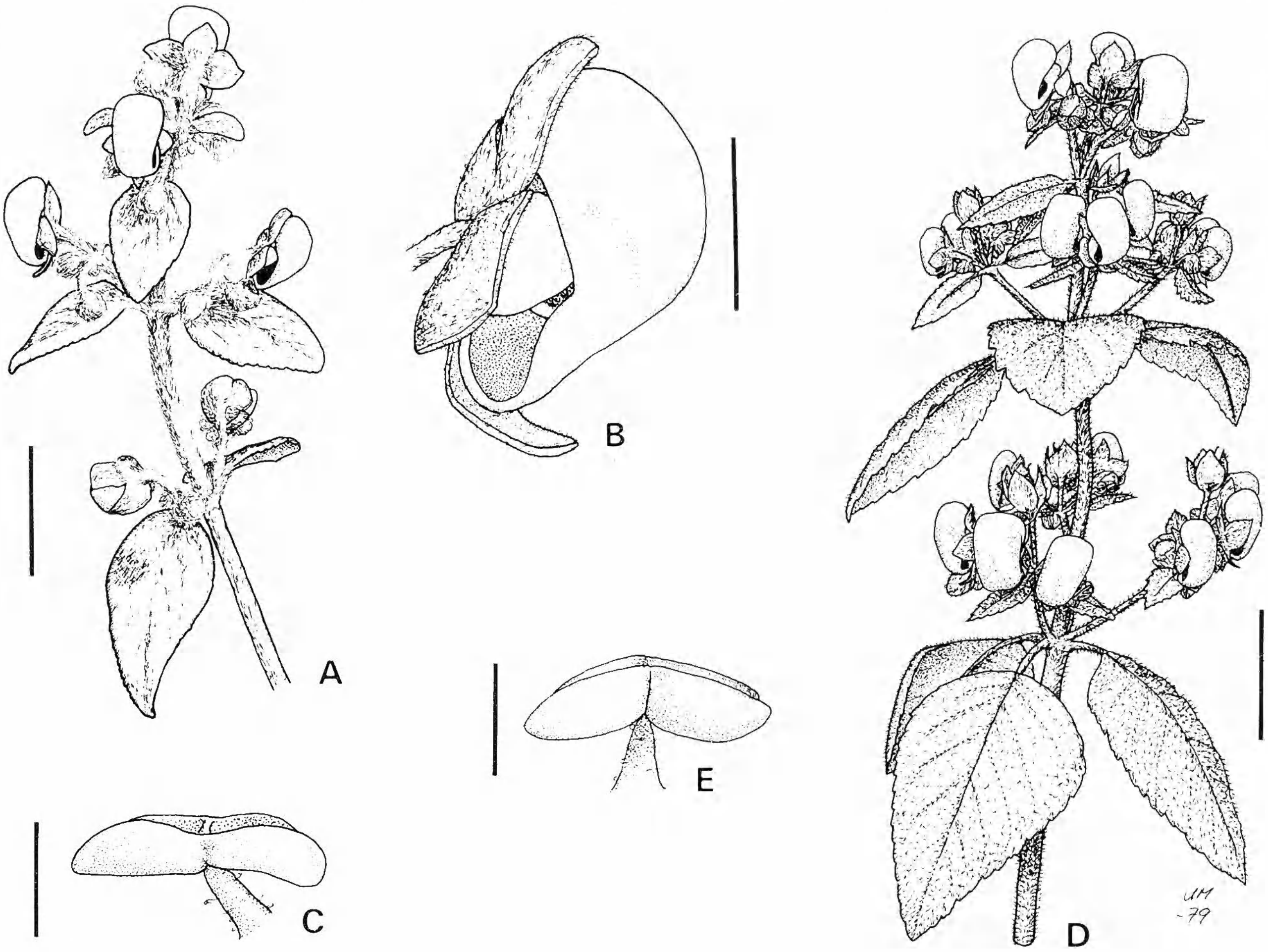

Fig. 5. A–C: *Calceolaria comosa*. — A: Flowering branch. — B: Flower. — C: Stamen. — A, B: Løjtnant & Molau 14161; C: Harling & Andersson 14538. — D, E: *C. ternata* (Harling & Andersson 14100). — D: Flowering branch. — E: Stamen. — A, B drawn from photograph; C–E drawn from herbarium material. — Scales: A, D 2 cm, B 5 mm, C, E 1 mm.

Divide it occurs in the Andes of central and southern Ecuador, where it is known from the provinces of Chimborazo, Cañar, Azuay and Loja. South of the Piura Divide there are scattered collections from the departments of Cajamarca and Amazonas in N Peru. In all, 57 specimens from 23 collections have been studied.

Remarks. Specimens from the Peruvian populations usually possess denser pubescence on stems and leaves than do specimens from Ecuador. However, these differences are not constant enough to warrant taxonomic segregation. Even within the continuously distributed Ecuadorean population variations in some vegetative characters can be observed, especially concerning pubescence density, length/width ratio of the leaf-blade, and petiole length. Relying upon five collections only, Pennell (1951) recognized three species in southern Ecuador. *Calceolaria cinerea* and *C. mollis* were separated from *C. comosa* by virtue of shorter petioles and less revolute leaf margins, and distinguished from each other by broad/narrow leaves and appressed/spreading pubescence. Furthermore, *C. cinerea* was described to have larger sepals (8–9 mm long) and more sparse pubescence. However, the only specimens of the latter cited by Pennell are in fruit and late anthesis, and the deviations concerned are quite normal to a fruiting plant of *C. comosa*.

Representative specimens. Ecuador. Chimborazo: Above Pallatanga on road to Riobamba, 3000–3100 m, 6.VI.1979, Løjtnant & Molau 14116 (AAU, GB). — *Cañar:* N rim of the valley of Río Cañar, 2000–3000 m, 23–25.IV.1945, Camp (leg. Giler) E-2782 (NY, PH, US). — About 10 km NW of El Tambo on road to El Triunfo, 3100 m, 20.VI.1979, Løjtnant & Molau 15165 (AAU, GB). — *Azuay:* W of Patul, 3 km between Huahualcay and Río Patul below Pasas de Pinglión, 2670–3275 m, 19.V.1943, Steyermark 52619 (F, PH). — Portete de Tarqui, 2800 m, 7.VI.1979, Løjtnant & Mo-

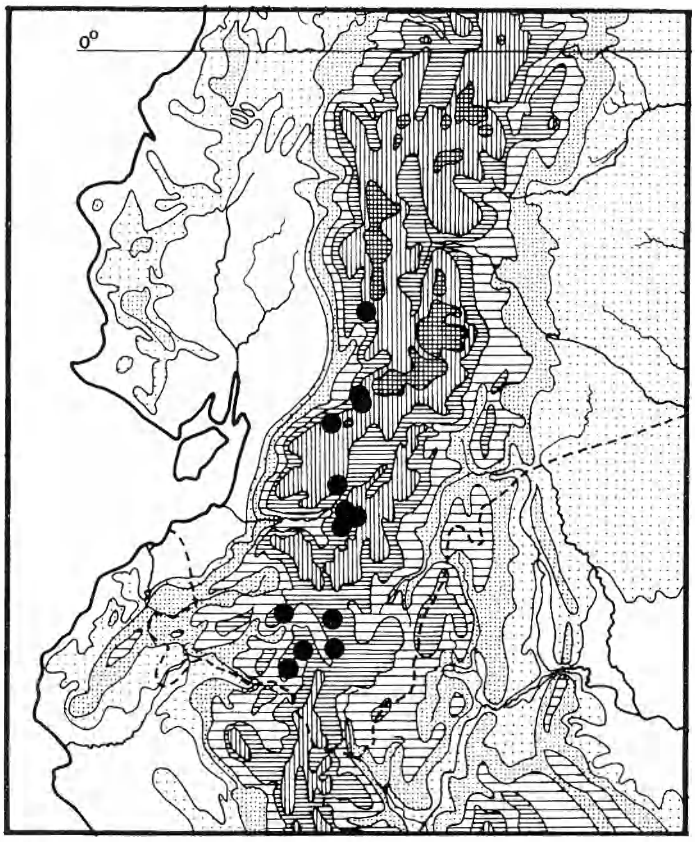

Fig. 6. Known distribution of *Calceolaria comosa* N of the Piura Divide.

lau 14161 (AAU, GB). — Vicinity of Nabón, 26.IX.1918, Rose 23034 (GH, PH, US). — Cuenca–Loja road, upper N slopes of Valle del Río León and S parts of Páramo de Tinajillas, 2800–3200 m, 9.V.1974, Harling & Andersson 14538 (GB); 2700 m, 18.VI.1979, Løjtnant & Molau 15118 (AAU, GB). — *Loja:* Forest near Loja, IX.1864, Jameson s. n. (K, PH, S, US, W). — Km 15 on road from Cariamanga to Amaluza, 21–23.VII.1959, Harling 6046 (S), 6059 (S). — Cerro Campana, between Vilcabamba and Yangana, 1900 m, 17.VI.1979, Løjtnant & Molau 15000 (GB). — *Peru. Cajamarca:* E of Celendín, 2500–3000 m, 29.V.1966, Edwin & Schunke 3616 (F, G, GH, W). — Canyon of the Río Marañón above Balsas, 3–4 km below summit of the road to Celendín, 2950 m, 21.V.1964, Hutchison & Wright 5235 (F, K, MO, NY, UC). — *Amazonas:* W side of Cerros Calla-Calla, 45 km above Balsas, midway on the road to Leimebamba, 3100 m, 19.VI.1964, Hutchison & Wright 5732 (F, MO, NY, UC, US); 5736 (F, K, M, MO, NY, P, UC).

6. **Calceolaria ternata** Molau sp. nov.

Orig. coll.: Harling & Anderson 14100 (GB holotype).

Illustration. Fig. 5 D–E.

Frutex 0.5–1 m altus. Folia herbacea, ternata, petiolata, ovata, 3.3–7.9×2.6–5.0 cm, acuta vel subacuta, ad basin truncata vel cordata, supra hirsuta vel strigosa, infra in nervis sericea vel velutina, interstitiis villosis; margines serrati. Petioli 5–14 mm. Inflorescentia terminalis, 3–4 paria cymarum 8–20 florum complectens, pedunculis primariis 0.7–4.5 cm longis. Bracteae cymarum adsunt. Pedicelli 0.5–1.8 cm. Sepala ovata vel elliptica, acuta, viridula, 4.8–7.0×3.3–5.0 mm, extra villosa, intus glabra vel puberula. Corolla sulphurea collo macula rubenti praedito; labio superiore arcuato, c. 2×4 mm; labio inferiore ascendente, tertia fere parte longitudinis saccato, parte ascendente 8–15×6–10 mm. Antherae fuscae, 1.8–2.3 mm, totae dehiscentes, thecae divaricatae vel leviter deflexae, aequales. Filamenta 0.7–1.2 mm. Stylus 1.5–1.9 mm, curvatus. Capsulam maturam non vidi.

Subshrub, 0.5–1 m high. Inflorescence and distal parts of stems villous or sericeous with buffish hairs. *Leaves* ternate, petiolate; blades ovate, 3.3–7.9×2.6–5.0 cm, acute or subacute, truncate to cordate at base; green above, hirsute or strigose with buffish hairs (most densely so on primary and secondary veins), pale green beneath, sericeous to velutinous on primary and secondary veins, interspaces villous; margins grossly serrate (sometimes doubly serrate). Petioles 5–14 mm, villous or sericeous. *Inflorescence* comprising 3–4 triplets of 8–20-flowered cymes on primary peduncles 0.7–4.5 cm long. Cyme bracts present. Pedicels 0.5–1.8 cm. *Sepals* ovate or elliptic, light green, 4.8–7.0×3.3–5.0 mm at anthesis, acute, externally villous, internally glabrous or puberulous. *Corolla* sulphur yellow with a large purplish spot in the throat; upper lip arched, c. 2×4 mm; upcurved portion of lower lip 8–15×6–10 mm. *Anthers* dark brown, 1.8–2.3 mm; thecae divaricate or slightly deflexed. *Filaments* 0.7–1.2 mm. *Style* 1.5–1.9 mm, curved. Mature *capsule* not seen.

Habitat. Dry mountain scrub at altitudes between 1600 and 2200 m.

Distribution. Fig. 7. Restricted to the low Andes of southernmost Ecuador (prov. Loja) and adjacent areas in Peru (dep. Piura).

Remarks. In NW South America *C. ternata* is unique in having a ternate phyllotaxy as what appears to be the normal condition. In the Peruvian mountains S of the Piura Divide, however, three more species of sect. *Anacyrta* with this kind of organization occur, viz. *C. glauca* R. & P., *C. angustiflora* R. & P. (synonym: *C. multiflora* Cav.), and *C. rugulosa* Edwin. *C. glauca* and *C. angustiflora* are restricted to the departments of Ancash and Lima in central Peru, and are distinct from *C. ternata* in a number of characters (*C. glauca* has lanceate, short-hirsute leaves, and *C. angustiflora* is essentially glabrous with nitidous leaves). *C. rugulosa*, ranging

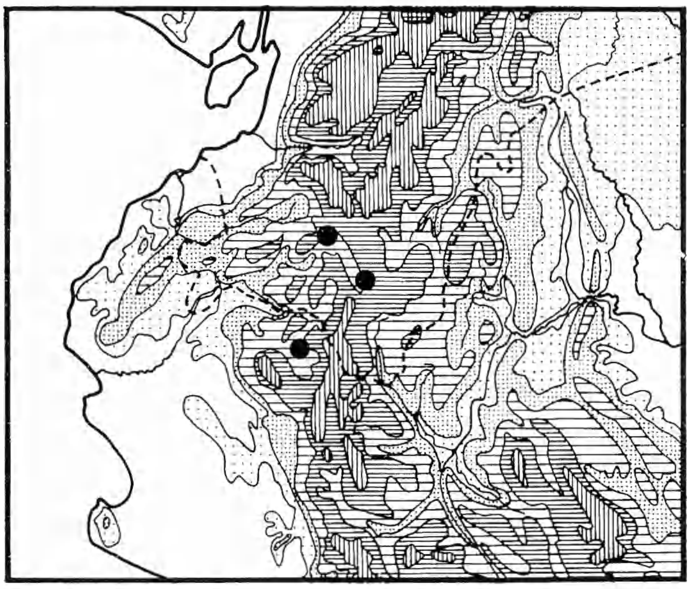

Fig. 7. Known distribution of *Calceolaria ternata*.

just S of the Piura Divide in the departments of Piura, Cajamarca and La Libertad, however, appears to be more closely related to *C. ternata*. They differ mainly in pubescence and leaf characters, and are probably best regarded as vicarious taxa. The ternate-leaved species of sect. *Anacyrta* are inadequately treated by Edwin (1971) in Macbride's "Flora of Peru", and require a taxonomic revision.

Specimens studied. Ecuador. Loja: Loja–Zaruma road, between San Pedro and Las Chinches, 1900–2200 m, 30.IV.1974, Harling & Andersson 14100 (GB). — Río Comunidades between Vilcabamba and Yangana, 1600 m, 15.V.1967, Sparre 16180 (S). — *Peru. Piura:* Olleros (c. 15 km ESE of Ayabaca), Bonpland 3509 (P).

Sect. 9. **Polyclada** Pennell

Pennell 1951 p. 134 — Type species: *Calceolaria brachiata* Kränzlin.

Scandent shrubs, much branched; branches divaricately spreading. Inflorescence and distal parts of stems minutely puberulous with purplish, ferrugineous or buffish hairs. Leaves decussate, petiolate; blades herbaceous, elliptic or lanceate. Sepals thin, glabrescent, unequal; the dorsal sepal cordiform (broadly ovate and with cordate base), the lateral ones ovate, and the ventral one lanceate. Corolla yellow, unspotted. Anthers brown, opening throughout; thecae equal, divaricate.

Sect. *Polyclada* is a well-defined natural group, by the sepals easily distinguished from all other sections of the genus. It ranges from N Ecuador to N Peru, and is at present known to comprise only two species, one of which, *C. brachiata*, occurs in the investigated area. The other one, *C. discotheca* Molau, is known only from the department of Amazonas, N Peru, just S of the Piura Divide (Molau 1979 b).

1. **Calceolaria brachiata** Sodiro ex Kränzlin

Sodiro ex Kränzlin 1905 p. 106 — Orig. coll.: Sodiro "115/10" (probably W, destroyed) — Neotype: Sodiro "115/16" (P), here designated.

Illustration. Fig. 8 A–D, here designated.

Scandent *shrub*; stems 0.5–3 m long, distally puberulous with buffish to purplish hairs. *Leaf blades* elliptic, 2.2–5.0×1.2–1.6 cm, acute, attenuate at base; dark green above, minutely pilose; pale green beneath, reticulate-venose, glabrous except for the puberulous midrib; margins serrate. Petioles 3–7 mm, puberulous. *Inflorescence* distal, diffuse, comprising 1–2 pairs of 1–4-flowered cymes on primary peduncles 0.7–3.0 cm long. Cyme bracts present. Pedicels 0.7–1.8 cm. *Sepals* light green, often suffused with purple, acute, 5.0–7.7 mm long at anthesis, glabrous or minutely puberulous on both surfaces; dorsal sepal 5.9–7.7 mm wide. *Corolla* light yellow, externally puberulous; upper lip sometimes almost white, hooded, 3–5×5–6 mm; lower lip 8–15×6–8 mm, inflated, projecting or slightly upcurved, closing the orifice, saccate in 1/3–1/4 of its length. *Anthers* brown to buffish, 2.1–2.9 mm. *Filaments* c. 1.2 mm. *Style* 3.3–4.5 mm, slightly curved near apex. *Capsule* ovoid, puberulous, c. 6 mm long.

Habitat. Cloud forest and dense mountain scrub at altitudes between 2800 and 3500 m.

Distribution. Fig. 9. Restricted to the Andes of N Ecuador, where it is scattered but uncommon in the provinces of Pichincha and Cotopaxi.

Remarks. The original material was sent to Kränzlin in Vienna and must be regarded as destroyed; no duplicates are present in the Sodiro collections in Quito, Ecuador. The number cited by Kränzlin (115/10) is not a collection number, but rather a species number. In the Sodiro herbarium in Bibliotheca Aurelio Espinosa, Cotocollao, Quito, the same species number often appears on several collections from differ-

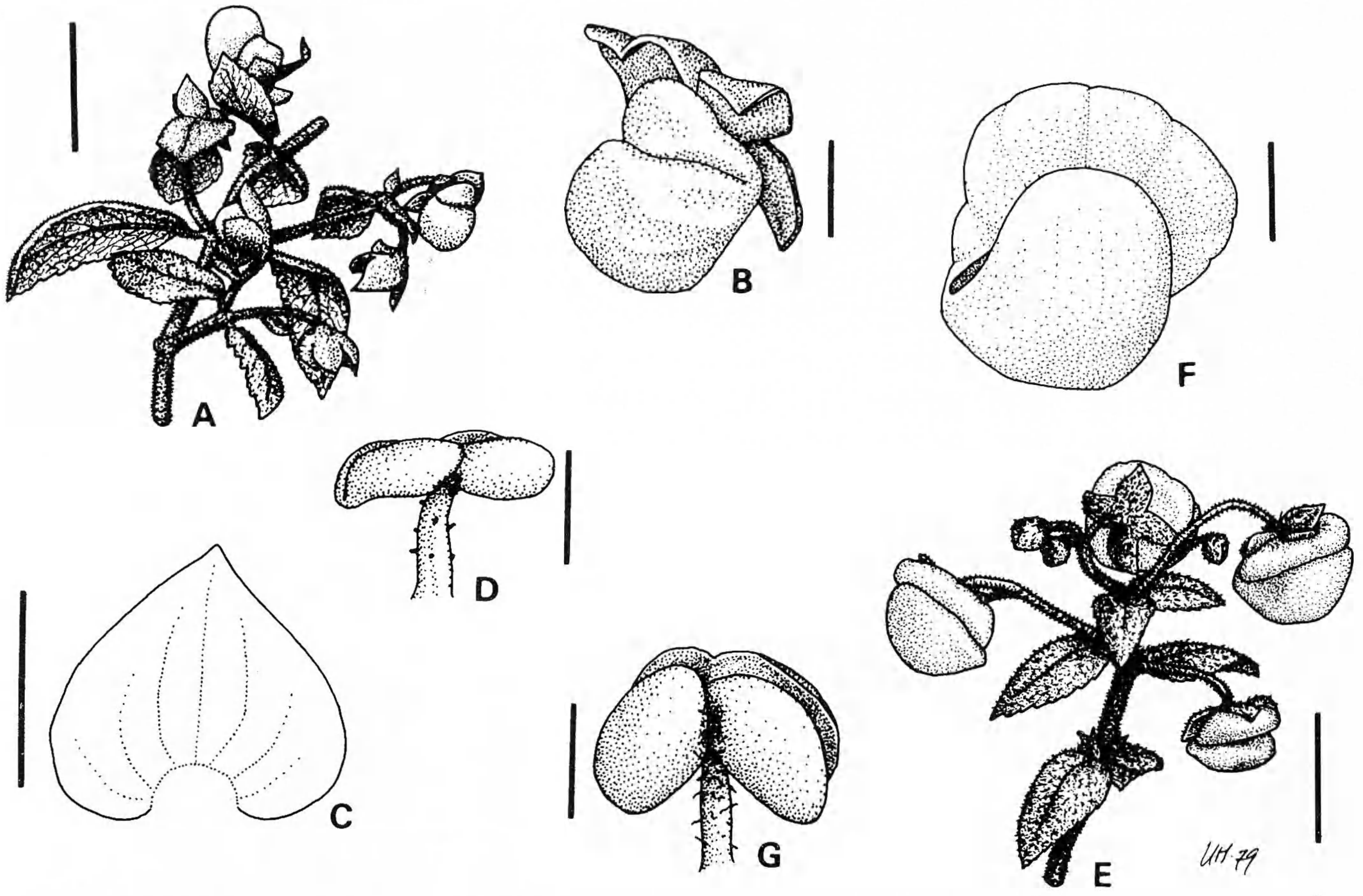

Fig. 8. A–D: *Calceolaria brachiata*. — A: Flowering branch. — B: Flower. — C: Dorsal sepal. — D: Stamen. — A, B: Løjtnant & Molau 13744; C, D: Sodiro "115/16". — E–G: *C. fusca*. — E: Flowering branch. — F: Corolla. — G: Stamen. — E, F: Løjtnant & Molau 14497; G: André K.607. — A, B, E, F drawn from photographs; C, D, G drawn from herbarium material. — Scales: A, E 2 cm, B, C, F 5 mm, D, G 1 mm.

ent occasions and localities. On the other hand, Sodiro's specimens are usually labelled with month and year of collection. The original type of *C. brachiata* is said to have been collected in May (year unknown), and no such specimen can be found in the present material. Thus, when using the Sodiro material, only date and locality are important; species number is of no value. Another well-preserved Sodiro collection from the type locality is here chosen as neotype.

Specimens studied. Ecuador. Pichincha: Between Oyacachi and Comenia, Cordillera Oriental, 3000 m, 27.X.1945, Acosta-Solís 11192 (F). — Corazón, 2900–3100 m, 22.VI.1876, André 3720 (K, NY). — N slopes of Cerro Corazón along Aloag—Santo Domingo road, 3150 m, 29.V.1979, Løjtnant & Molau 13981 (AAU, GB). — "In silvis montis Corazón", VII.1882, Sodiro "115/16" (P). — Lloa valley above Palmira, 3.VI.1873, Sodiro s. n. (BP). — Cerro Atacazo, VIII.1918, Sodiro s. n. (Bibliotheca Aurelio Espinosa); 2800 m, VII–VIII.1919, Sodiro s. n. (Bibliotheca Aurelio Espinosa). — *Cotopaxi:* E of and above Pilaló, 3500 m, 26.V.1979, Løjtnant & Molau 13744 (AAU, GB).

Sect. 10. **Phaeanthera** Pennell

Pennell 1951 p. 131. — Type species: *Calceolaria fusca* Pennell.

Shrubs or subshrubs, much branched. Foliage, inflorescence and distal parts of stems pubescent with coarse, brown to dark purplish septate hairs. Leaves decussate, petiolate, ± coriaceous. Inflorescence distal. Sepals internally with a short-tomentose border along the margin. Corolla yellow, unspotted. Anthers brown, opening throughout; thecae equal.

In NW South America sect. *Phaeanthera* comprises only a single species, viz. *C. fusca*. In the Peruvian Andes S of the Piura Divide the section is represented by *C. gaultherioides* Molau, and possibly another few species.

In some important sectional characters (viz. foliage and pubescence of inner sepal surfaces), sect. *Phaeanthera* shows certain affinities to sect. *Dermatophylla*. *C. fusca* is in many aspects

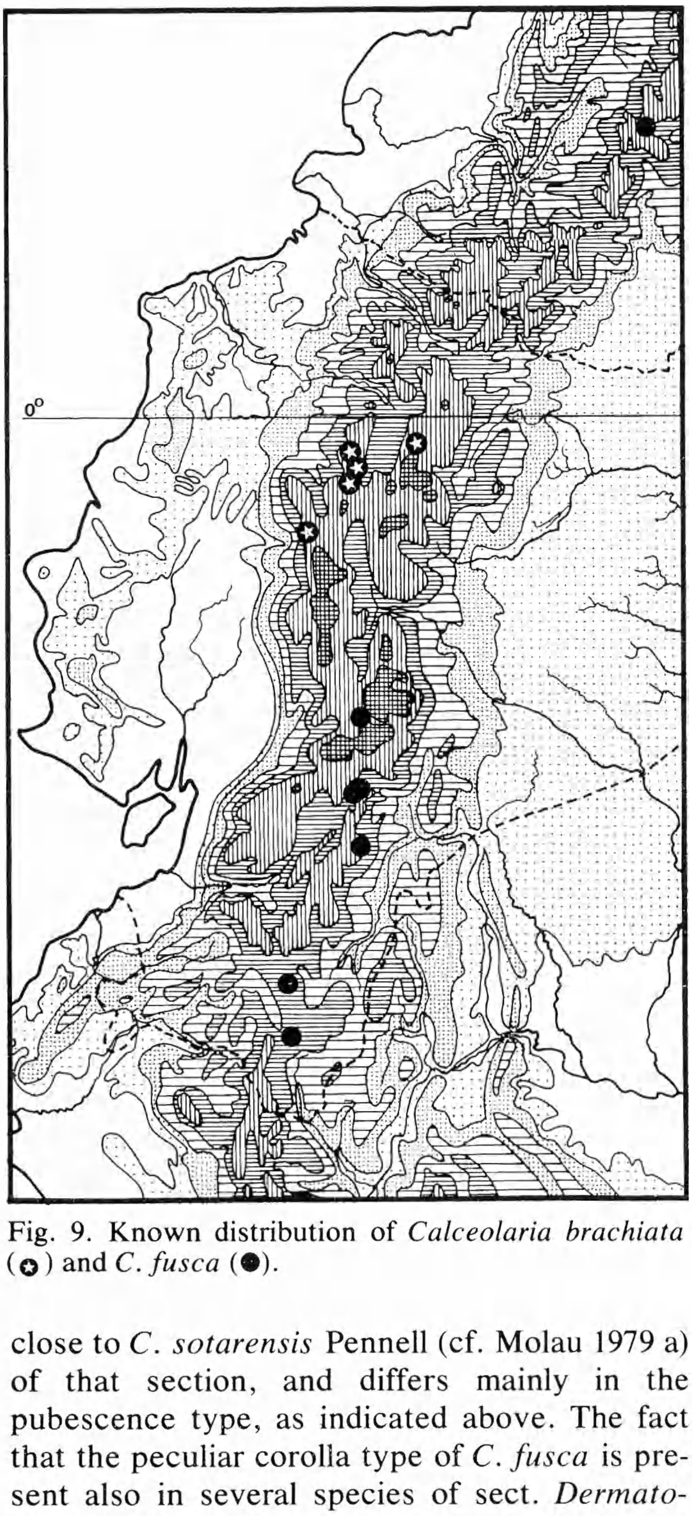

Fig. 9. Known distribution of *Calceolaria brachiata* (✪) and *C. fusca* (●).

close to *C. sotarensis* Pennell (cf. Molau 1979 a) of that section, and differs mainly in the pubescence type, as indicated above. The fact that the peculiar corolla type of *C. fusca* is present also in several species of sect. *Dermatophylla* is, however, of less importance. There are several other cases in *Calceolaria*, where highly specialized corolla shapes have evolved independently in remote species (e.g. the narrow corolla with strongly upcurved lower lip, which is present in *C. ericoides* Vahl as well as in the species of sect. *Anacyrta*). Considering the similarities in foliage and sepal pubescence it seems likely that the sections *Dermatophylla, Symplocophylla* and *Phaeanthera* are very closely allied. A satisfactory delimitation requires a complete revision of the Peruvian species. With the present knowledge I prefer to retain Pennell's (1951) system, treating the complex as three sections.

1. **Calceolaria fusca** Pennell

Pennell 1951 p. 132 — Orig. coll.: André K-607 (F holotype, K, NY).

Calceolaria acuminata Pennell 1951 p. 134 — Orig. coll.: Olsson 4 (PH holotype, US).

Calceolaria parotricha Pennell 1951 p. 133 — Orig. coll.: Camp E-4735 (PH holotype, F, G, GH, K, MO, NY, P, S, U, UC, US).

Calceolaria steyermarkii Pennell 1951 p. 132 — Orig. coll.: Steyermark 54475 (PH holotype, F, NY).

Illustrations. Fig. 8 E–G; Pennell 1951 p. 130 Fig. 10 (as *C. steyermarkii*), p. 135 Fig. 11 (as *C. parotricha*) and Fig. 12 (as *C. acuminata*).

Erect or semi-scandent *shrub*, 0.4–1.5 m high. All hairs brown to dark purplish. Inflorescence and distal parts of stems ± densely hirsute or tomentose. *Leaf blades* ovate, 1.5–4.2×0.8–2.8 cm, acute or slightly acuminate, cuneate to rounded at base; dark green above, ± rugose, sparsely pilose to densely hirsute; light green beneath with conspicuous pinnate venation (reticulate veins ± obscure), veins hirsute, interspaces pilose to glabrous; margins sharply dentate, deflexed or slightly revolute. Petioles densely hirsute, 3–12 mm. *Inflorescence* comprising 1–3 pairs of 4–10-flowered cymes on primary peduncles 0.5–5.0 cm long. Cyme bracts sometimes present, but usually rudimentary or absent. Pedicels 0.7–2.0 cm. *Sepals* ovate, 5.5–9.0×4.0–6.0 mm at anthesis, acute or slightly acuminate, light yellowish green, externally shortly hirsute or strigose, internally glabrous to puberulous on the surface. *Corolla* bright yellow; upper lip circular, hooded, frontally flattened and almost saucer-like, 6–15×10–17 mm; lower lip inflated, strongly upcurved and appressed against the upper lip, saccate in 1/4–1/5 of its length, upcurved portion 10–20×8–14 mm. *Anthers* 1.8–2.5 mm, dark brown; thecae slightly deflexed, 1.5–2.0 mm. *Filaments* 1.2–2.2 mm. *Style* almost straight, 3.2–4.2 mm. *Capsule* ovoid, 5–6 mm long, hirsute when young, later becoming glabrous.

Habitat. Mountain scrub and low cloud forest, at altitudes between 2500 and 3500 m.

Distribution. Fig. 9. A disjunct species with its main distribution in the Cordillera Oriental in S

Ecuador and an isolated population in Cordillera Central in the department of Cauca, S Colombia. In Ecuador it occurs as scattered populations in the provinces of Chimborazo, Azuay, Morona-Santiago and Loja. It is uncommon, but it is not unlikely that future collections from remote parts of the Andes of NW South America will reveal a more continuous distribution.

Remarks. Calceolaria fusca is an unusually variable species, especially in density of indumentum. The variation is not geographically ordered, however. To the contrary, a large part of the morphological spectrum may be found within a single population, as revealed by the collections from the pass on the Gualaceo-Limón road. Even specimens from the remote Colombian population are almost identical to some specimens from that population.

With the present circumscription, *C. fusca* comprises not less than four species in the sense of Pennell (1951). Three of these were based upon a single collection respectively. However, with the present knowledge of the variation pattern (largely owing to later collections), it is obvious that the complex is better treated as a single, variable species. It thus forms a parallel to *C. gossypina* Bentham (Molau 1978).

Specimens studied. Colombia. Cauca: S side of El Boquerón, Páramo de Las Papas, at the border with dept. Huila, 3350–3450 m, 6.IX.1958, Idrobo et al. 2981 (COL, P). — Valle de Las Papas, 2970 m, 5.IV.1944, Olsson 4 (PH, US). — *Ecuador. Chimborazo:* Palmira, 14.X.1876, André K.608 (K). — *Azuay:* Sevilla de Oro, 4–6 km N of the village, 2750–3050 m, 16.VIII.1945, Camp E-4735 (F, G, GH, K, MO, NY, P, PH, S, U, UC, US); c. 10 km NNE of the village, 3000–3300 m, 13.IX.1976, Øllgaard & Balslev 9438 (AAU). — *Morona-Santiago:* Gualaceo. — Limón road, E of the pass, 3300–3400 m, 2.IV.1974, Harling & Andersson 13104 (GB); 3400–3450 m, 10.VI.1979, Løjtnant & Molau 14497 (AAU, GB); 3000–3100 m, 20.IX.1967, Sparre 18789 (S). — *Loja:* Between Loja and Zamora, 3500 m (near the pass, at the border with prov. Zamora-Chinchipe), 1.XII.1876, André K.607 (F, K, NY). — Andes E of Loja, 3000–3300 m, Lehmann K.248 (K). — Between Tambo Cachiyacu, La Entrada, and Nudo de Sabanillas, 2500–3500 m, 7.X.1943, Steyermark 54475 (F, NY, PH).

References

Diels, L. 1937: Beiträge zur Kenntnis der Vegetation und Flora von Ecuador. *Bibl. Bot. 116.*

Edwin, G. 1970: New taxa and notes on the Scrophulariaceae of Peru. *Phytologia 19:* 369–406.

Edwin, G. 1971: Calceolaria L. *In* J. F. Macbride (ed.), Flora of Peru, *Publ. Field. Mus. Bot. Ser. 13, 5 B:* 515–654.

Kränzlin, F. 1905: Calceolariae generis species novae etc. *Feddes Repert. 1:* 82–85, 97–107.

Kränzlin, F. 1907: Scrophulariaceae-Antirrhinoideae-Calceolarieae. *In* A. Engler (ed.), *Das Pflanzenreich IV, 257 C.* Leipzig.

Kränzlin, F. 1929: Neue Arten von Calceolaria L. *Feddes Repert. 27:* 1–26.

Kuntze, O. 1891: *Revisio generum plantarum 2.* Würzburg.

Lamarck, J. P. de 1785: *Encyclopédie Méthodique. Botanique 1.* Paris and Liège.

Molau, U. 1978: The genus Calceolaria in NW South America. II. The sections Chasmatochila, Thamnobia, Ericoides and Lehmannina. *Bot. Notiser 131:* 293–316.

Molau, U. 1979 a: The genus Calceolaria in NW South America. III. The sections Symplocophylla and Dermatophylla. *Bot. Notiser 132:* 31–48.

Molau, U. 1979 b: New species of Calceolaria (Scrophulariaceae) from northern Peru. *Bot. Notiser 132:* 107–112.

Pennell, F. W. 1951: The genus Calceolaria in Ecuador, Colombia and Venezuela. *Proc. Acad. Nat. Sci. Philadelphia 103:* 85–196 + Pl. 6–7.

Ruiz, H. & Pavón, J. 1798: *Flora peruviana et chilensis 1.* Madrid.

Skan, S. A. 1912: Calceolaria Forgetii. *Curtis's Bot. Mag. 138:* Tab. 8436.

Weddell, H. A. 1857: *Chloris Andina 2.* Paris.

Chromosome numbers in Rubus species from Sri Lanka

HILDE NYBOM

Nybom, H. E. 1980 03 17: Chromosome numbers in Rubus species from Sri Lanka. *Bot. Notiser 133:* 47–48. Stockholm. ISSN 0006-8195.

Chromosome numbers are given for *R. indicus* (2n = 56), *R. rugosus* var. *thwaitesii* (2 n ≈ 98) and *R.* sp. (2n ≈ 70) on material collected in Sri Lanka.

Hilde Nybom, Department of Plant Taxonomy, University of Lund, Ö. Vallgatan 20, S-223 61 Lund, Sweden.

Five species of *Rubus* subgenus *Malachobatus* are reported from Sri Lanka (Alston 1931, Abeywickrama 1959): *R. indicus* Thunb., *R. rugosus* Smith var. *thwaitesii* Focke, *R. micropetalus* Gardner, *R. fairholmianus* Gardner and *R. gardnerianus* O. Kuntze. All of these, more or less intergrading species, belong to section *Moluccani*, series *Rugosi* (Focke 1910–1914). However, they are quite often treated as varieties of *R. moluccanus* L. instead (e. g. Hooker 1879, Backer & Bakhuizen van den Brink Jr 1963).

Methods

In February 1979 stem crowns together with some roots were collected from 11 populations of *Malachobatus* on Sri Lanka, Central Province. After growing the material in Sweden, root tips from the 7 surviving collections were fixed in Navashin-Karpechenko, embedded in paraffin, sectioned and dyed in crystal violet. Chromosomes in c. 5–10 cells were counted on each plant.

Results

R. indicus. Two populations comprising one plant each were counted, 2n = 56.

R. rugosus var. *thwaitesii*. Four populations comprising one, two, two and three plants, respectively, were counted, 2n ≈ 98.

R. sp. One population comprising two plants was counted, 2n ≈ 70. In the same population three plants closely resembling pure *R. fairholmianus* were collected. Unfortunately none of these survived in Sweden. *R. rugosus* var. *thwaitesii* is very common in the vicinity. As the two investigated plants look rather intermediary between *R. fairholmianus* and the latter, a hybrid origin seems possible.

Remarks

All species of *Malachobatus* (×=7) hitherto examined are polyploid (Vaarama 1954 one species, Jinno 1958 four species, Nybom two(–three) species). In the subgenus *Rubus* all diploid species seem to be sexual, and most polyploid species facultatively apomictic. Maybe the polyploid species in *Malachobatus* are also apomictic? Establishing the mode of reproduction must be essential when working with species delimitation problems. The present author intends to collect more material in India and Sri Lanka to use in morphological and experimental investigations.

Acknowledgements. Ving-Resor subsidized the journey to Sri Lanka, technical assistance was given by Lotte Herrosé and Ingrid Larsson, reference material was loaned from S, K and BM.

References

Abeywickrama, B. A. 1959: A provisional check list of the flowering plants of Ceylon. *Ceylon J. Sci. (Bot. Sc.) 2:* 119–240.

Alston, A. H. G. 1931: *Supplement to handbook to the flora of Ceylon*. London.

Backer, C. A. & Bakhuizen van den Brink Jr, R. C. 1963: *Flora of Java*. Groningen.

Focke, W. O. 1910–1914: *Species ruborum*. Stuttgart.

Hooker, J. D. 1879: *Flora of British India*. London.

Jinno, T. 1958: Cytogenetic and cytoecological studies on some Japanese species of Rubus. I. Chromosomes. *Bot. Mag. Tokyo 71:* 15–22.

Vaarama, A. 1953: Chromosome numbers of some species and hybrids of the genus Rubus. *Archiv. Soc. Zool. Bot. Fin. 8:* 192–195.

Collections

If., *R. indicus*, Norton Bridge on the road Kitulgala–Dickoya, Hatton Region. — IIf., *R. indicus*, on the road as above, c. 5 km apart from If. — IVf., *R. rugosus*, pilgrim's path Loinorn Estate–Nagrak Estate, Horton Plains, Haputale Region. — Vf., *R.* sp., c. 5 km outside Nuwara Eliya, on the road Nanu Oya–Ambewela, Nuwara Eliya Region. — VIf., *R. rugosus*, Blackpool Bridge on the road as above, Nuwara Eliya Region. — VIIf., *R. rugosus*, on the road Blackpool Bridge–Ambewela c. 2 km apart from VIf., Nuwara Eliya Region. — Xf., *R. rugosus*, Farr Inn, Horton Plains, Nuwara Eliya Region.

Voucher specimens are preserved at LD.

Pollen eating Thricops flies (Diptera, Muscidae) on Arrhenatherum pubescens and some other grasses

IVAR ELVERS

Elvers, I. 1980 03 17: Pollen eating Thricops flies (Diptera, Muscidae) on Arrhenatherum pubescens and some other grasses. *Bot. Notiser 133:* 49–52. Stockholm. ISSN 0006-8195.

Photographic evidence shows that the muscid *Thricops semicinerea* visits anthers of *Arrhenatherum pubescens, A. elatius, Dactylis glomerata*, and *Alopecurus pratensis*, to feed on pollen. In *Arrhenatherum pubescens* these fly visits may effect pollination.

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Grasses are generally considered purely anemogamous. A few cases of probable entomogamy have been reported among some tropical species (Bogdan 1962, Soderstrom & Calderon 1971, Pant & Chaturvedi 1979; see also Arber 1934 and Faegri & van der Pijl 1979), but the dominating opinion among botanists has evidently been that insect visits to grass flowers in temperate regions are ineffective for pollination.

However, the presence of pollen-consuming insects on extra-tropical grasses has also attracted some interest (Porsch 1956, Leereveld, Meeuse, & Stelleman 1976, Stelleman 1979). Leereveld et al. write (1976 p. 208–209): "There can be very little doubt that *Thricops semicinerea* is an effective pollinator of *Plantago media* and a number of grasses. Further observations are clearly indcated."

The present communication reports some observations of this kind. They were carried out with the aid of stereoscopic photographs obtained with an "Ica Polyscop" camera with accessories for close-range photography. Agfacolor film CT 18 was used, and the scale of the pictures was ×0.7. Fig. 1 A–O are black and white single-frame versions of these photographs, scale ×3.

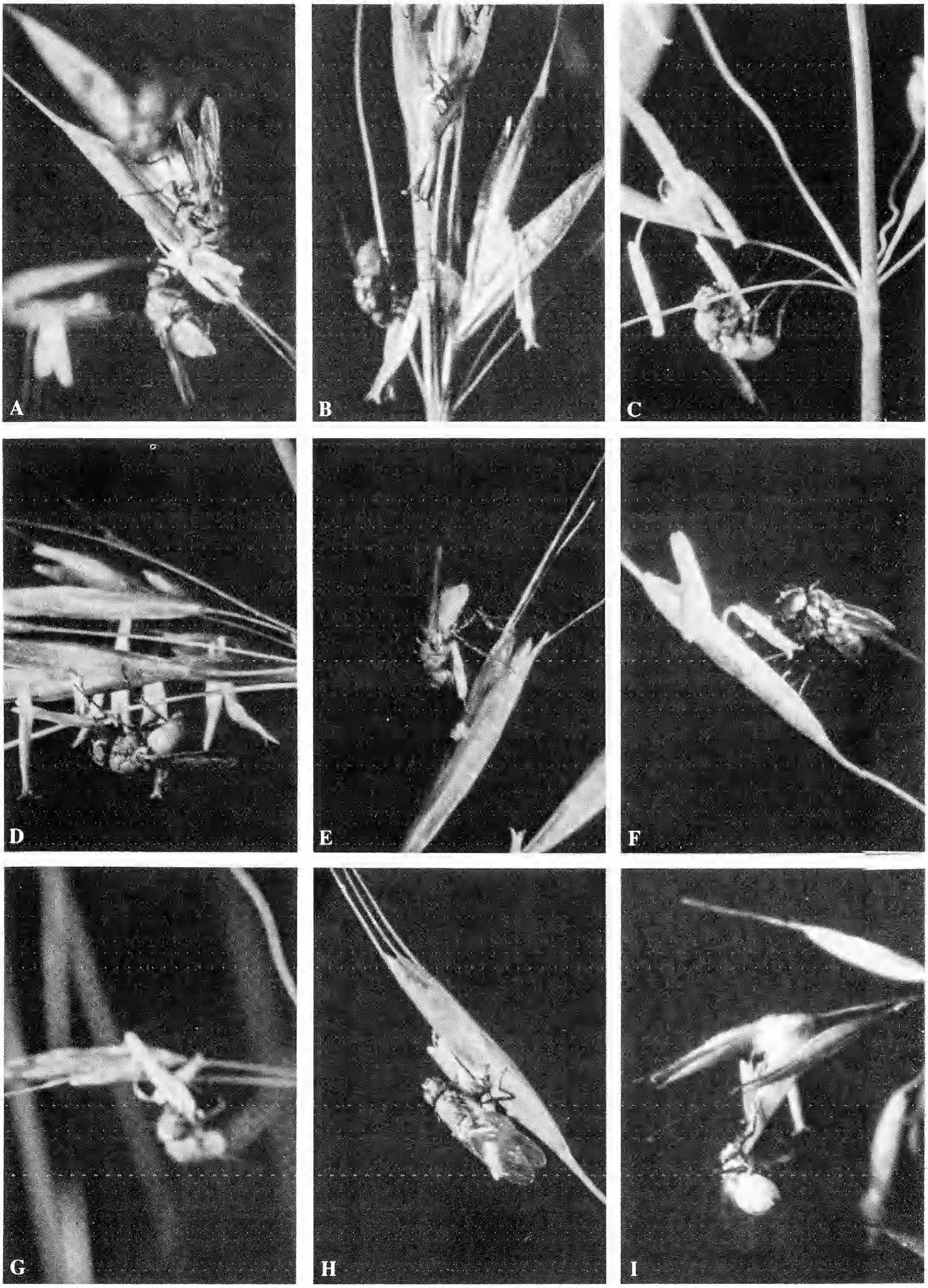
Observations

The first observations were made in 1978, when (without knowledge of the work by Leereveld et al.) I was struck by the behaviour of *Thricops* flies. In a meadow in the parish of Bettna (S Sweden) I observed great numbers of them visiting the flowers of *Arrhenatherum pubescens.* They were working with an intensity and in such numbers as to be compared to the activity of honey bees in flowering *Tilia* or to the crowd of insects on the umbels of a road-side *Pastinaca.*

In 1979 the observations were continued in the same area. The efflorescence lasted for about 10 days in the middle of June.

The observations were extended also to other grasses in the same region. In one locality (a railway bank) the related species *Arrhenatherum elatius* was growing quite extensively, but (with one exception) only very few *Thricops* or other pollen eaters were found on it. The exception was a small, isolated stand of just 2 culms, where there was quite a stir of visiting *Thricops* flies (Fig. 1 I, J).

A comparison between pictures of the two *Arrhenatherum* species indicates, to my eyes, a small, but possibly significant difference: in *A. pubescens* the anther filaments retain a considerable stiffness for some time after the opening of the flowers (e.g. note the elastically curved filaments visible in Fig. 1 F, G). In *A. elatius* the filaments have all lost their turgescence and hang down flaccidly from the flowers. This limpidness is a part of the typical wind pollination syndrome, and *A. elatius* is, in fact, one of the classical examples of an anemogamous grass-flower (Kerner v. Marilaun 1891). The difference between the filaments of *A. elatius* and *A. pubescens* may be somewhat analogous to that between the anemogamous catkins of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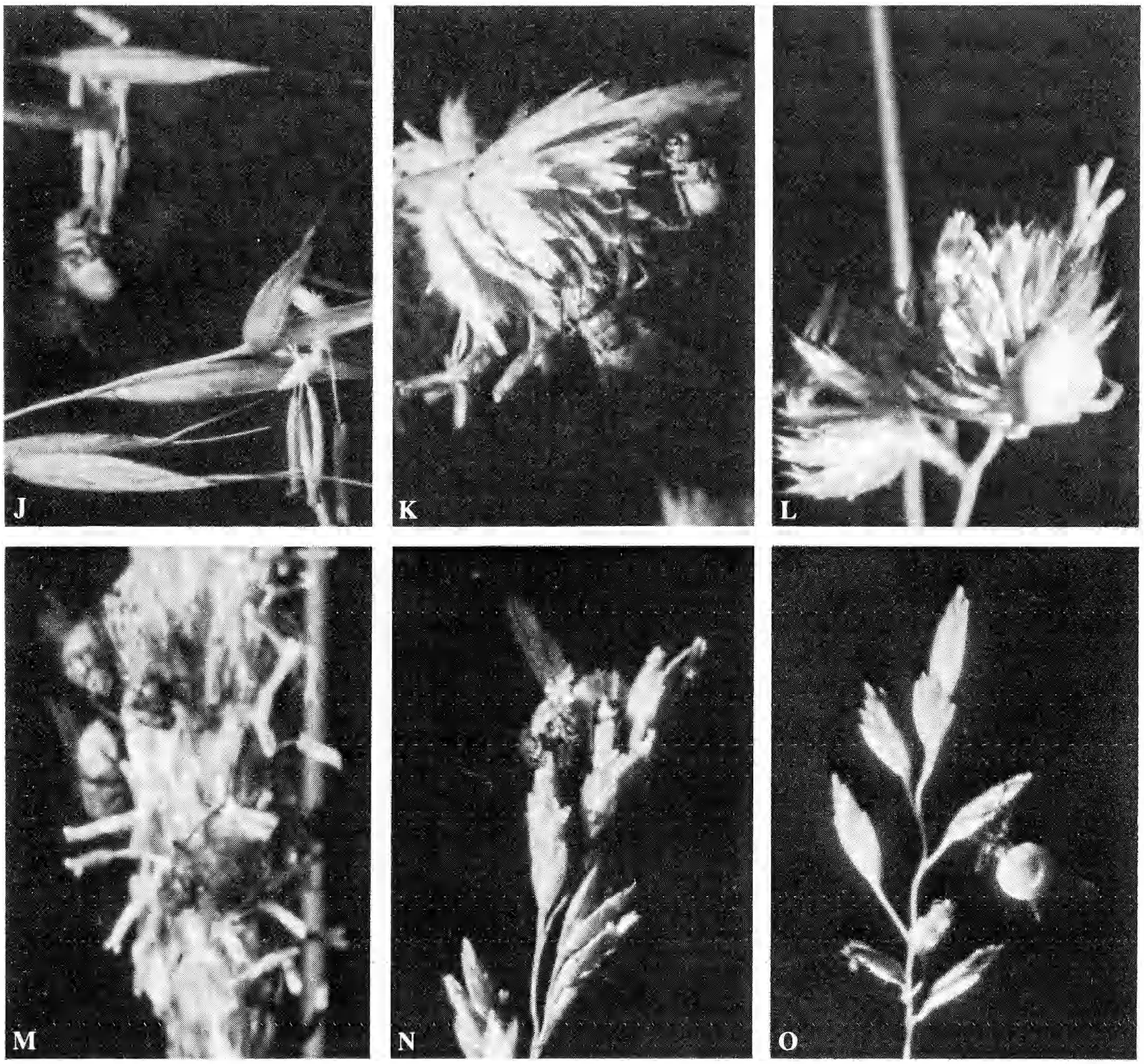

Fig. 1. — A–G. *Thricops semicinerea* on *Arrhenatherum pubescens*, photographed during the ordinary time of anthesis in this species: 4.30–6.00 p.m. — A: Several flies in action. — B–E: Flies eating pollen. — F, G: Stamen filaments elastically curved. — H: Flowers of this species can be attractive to the flies also in the mornings. Photo 8.30 a.m. — I, J: *Thricops* on *A. elatius*. Anthers drooping. (5.00 a.m. = ordinary time of anthesis in this species). — K, L: *Dactylis glomerata* with *Thricops* (7.00 a.m.), and with *Misumena* (6.00 p.m.). — M: *Thricops* on *Alopecurus pratensis* (4.30 a.m.). — N, O: *Poa pratensis* with *Thricops* specimens killed by *Entomophtora*. — Magnification in all pictures ca 3×; further information in text.

Populus and the predominantly entomogamous ones of *Salix*.

Another difference between the two *Arrhenatherum* species is that the stigmas of *A. elatius* are more protruding (cf., e.g., Fig. 1 C, I).

Pollen eating *Thricops* flies were seen also on *Dactylis glomerata* (Fig. 1 K) and *Alopecurus pratensis* (Fig. 1 M). As in *Arrhenatherum* the distribution of the visits appeared to be capricious. Some plants attracted a lively attendance from many flies, while others were ignored. In the pictures of *Dactylis* and *Alopecurus*, however, stigmas were invisible or very inconspicuous. Fly visits here could hardly be of importance for pollination.

The presence of insects in grass panicles is sometimes a pathologic phenomenon: when infested by the fungus *Entomophtora* some species have a tendency to await their death in the top regions of grass culms, sometimes in great numbers. In the literature on pollination biology the early descriptions of this by Ludwig (1881, 1884) are often cited. *Thricops* is susceptible to the fungus, but during my studies I saw only a few, solitary, infected specimens (on *Dactylis* and on *Poa pratensis*, Fig. 1 N, O).

Other visitors

A few other pollen collecting insects, mostly syrphids, were also seen, but the muscid *Thricops semicinerea* was by far the most common visitor.

An indirect indication of insect attractiveness of *Arrhenatherum pubescens* flowers is provided by a find in them of the predator *Misumena vatia*. This is a crab spider *(Thomisidae)* which normally finds its prey by sitting motionless in some suitable entomogamous flower. When an insect arrives, it is caught by the spider in a swift assault, and then slowly devoured.

The *Misumena* in the *Arrhenatherum* panicle must have reached the typical stage of complete standstill and ensuing camouflage: I did not see it myself on the plant, but found it later together with the panicle, which had been collected because of a more conspicuous hemipter sitting on it.

Another find of the *Misumena* was made on a *Dactylis* panicle (Fig. 1 L). This specimen did not display its typical hunting behaviour, however, it kept moving over the flowers. It is uncertain whether it would gradually have found its correct motionless hunting position, if I had not had to interfere with it by flashlight exposure.

Conclusions

The observations on the Bettna population of *Arrhenatherum pubescens* indicate a slight tendency towards entomogamy. The panicles of this grass are fairly conspicuous, at least as seen by human eyes. It is one of the relatively few grasses included by Arnell (1903) in his lists of Swedish plants with "dominating flowering", e.g. plants which in flower show up prominently and give colour to the landscape. Pollen eating specimens of *Thricops semicinerea* were seen on many of the plants observed, sometimes in great profusion. The structure and development of the stamens and the pistil during anthesis point to the possibility that the flies transfer pollen between them. The circumstances around the find of the crab spider *Misumena vatia* are in good agreement with its behaviour in truly entomogamic species.

The pollination in *A. pubescens* thus exemplifies and illustrates a border region between anemogamy and entomogamy, but on the whole, insects probably have only marginal value as pollen vectors for this species compared with wind. The pollen grain is of the ordinary grass type, and only few grains were found in the fur of flies collected on this species. Anthesis in grasses is of short duration, and it is not likely that sufficient armadas of insects should just then be available everywhere to serve as the main pollination agents, although the Bettna observations indicate that locally, this might be the case.

For *Arrhenatherum elatius, Dactylis glomerata*, and *Alopecurus pratensis* it is less probable that the observed *Thricops* visits have any appreciable significance for pollination.

Acknowledgements. I thank Dr Lars Hedström of the entomological department of the University of Uppsala for the determination of the insects and for other valuable information. I also thank Professor K. Faegri, Bergen, Norway, for helpful comments on the manuscript.

References

Arber, A. 1934: *The Gramineae*. Cambridge.

Arnell, H. 1903: Dominerande blomningsföreteelser i södra Sverige. *Ark. bot. 1:* 287–376.

Bogdan, A. V. 1962: Grass pollination by bees in Kenya. *Proc. Linn. Soc. London 173:* 57–60.

Faegri, K & van der Pijl, L. 1979: *The principles of pollination ecology 3rd ed.* Oxford.

Kerner von Marilaun, A. 1891: *Pflanzenleben 2.* Leipzig und Wien.

Leereveld, H., Meeuse, A. D. J., & Stelleman, P. 1976: Anthecological relations between reputedly anemophilous flowers and syrphid flies. II. Plantago media L. *Acta Bot. Neerl. 25:* 205–211.

Ludwig, F. 1881: Molinia coerulea als Fliegenfängerin. *Bot. Centralbl. VIII:* 87.

Ludwig, F. 1884: Ueber den Fliegenbesuch von Molinia coerulea. *Bot. Centralbl. XVIII:* 122–123.

Pant, D. D. & Chaturvedi, S. K. 1979: Insect pollination in some Indian Glumifloreae. *In* National Symposium on Pollination Ecology and Applied Palynology. Abstracts. *Indian Council of Agricultural Research:* 8.

Porsch, O. 1956: Windpollen und Blumeninsekten. *Österr. bot. Zeitschr. 103:* 1–19.

Soderstrom, T. R. & Calderon, C. E. 1971: Insect pollination in tropical rain forest grasses. *Biotropica 3:* 1–16.

Stelleman, P. 1979: Insecten en windbloeiers. *Vakblad voor biologen 59:* 264–269.

Notes on Annonaceae from Tanzania

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Four new species of Annonaceae are described and depicted: *Asteranthe lutea, Polyalthia tanganyikensis, P. verdcourtii, Uvaria lungonyana.* The identity of *Asteranthe trollii* and the infraspecific taxonomy of *Ophrypetalum odoratum* are discussed.

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This paper is intended as a supplement to the volume on Annonaceae in Flora of Tropical East Africa (Verdcourt 1971 b). Some species only partially known when the flora was published, and some completely new species are formally described, and the delimitation of other taxa is discussed.

A comparison of Annonaceae with most other families of similar size in East Africa, shows that it has a relatively high proportion of partially known species. There are several reasons for this. Some species are no doubt genuinely rare. Others are seldom seen in flower or have small and/or inconspicuous flowers or very few flowers at any time. The fruits often seem to be very slow in maturing which gives rise to problems when trying to relate flowering and fruiting material.

The material on which this paper is based was collected during three years of field-work in Tanzania.

Asteranthe Engl. & Diels

The genus *Asteranthe* was published by Engler & Diels (1901) to include *Uvaria asterias* S. Moore. Since then only one additional species has been published (Diels 1936), viz. *A. trollii* Diels.

Asteranthe asterias (S. Moore) Engl. & Diels is now a well known plant from the coastal forests in Kenya and Tanzania. *A. trollii* has never been re-collected and its identity has puzzled all subsequent workers on East African Annonaceae. Verdcourt (1971 a & b) discusses the possible identity of *A. trollii* pointing out that there are several discrepancies between the original description and the type-sheet at the Berlin Herbarium. He refrains from uniting it with *A. asterias*, but concludes that it will probably prove to be a form of this species.

An examination of the type-sheet from the Berlin Herbarium shows a label with the word "2. Bogen" (meaning second sheet) added in pencil. According to the Berlin Herbarium, the first sheet cannot be found and it may have been destroyed during the war. It seems clear that the description of *A. trollii* was based on the missing sheet, and the extant sheet is consequently considered to be an isotype.

The reason for re-examining the type of *A. trollii* was the discovery of a species of *Asteranthe* in S E Tanzania. This is so different from *A. asterias*, that at first it was not even recognized as an *Asteranthe*. The detailed structure of the flower, especially the sympetalous corolla and the very specialized structure of the gynoecium, is however closer to *Astherante* than to any other genus. After realising that the plant was an *Asteranthe* it was considered that it might possibly be the missing *A. trollii*, but it proved to be very different, and a new species is therefore described.

Asteranthe lutea Vollesen, sp. nov., Fig. 1

Type: Tanzania, Kilwa Distr., Selous Game Reserve, Kingupira, c. 8°25′S 38°30′E, c. 125 m a.s.l. — January

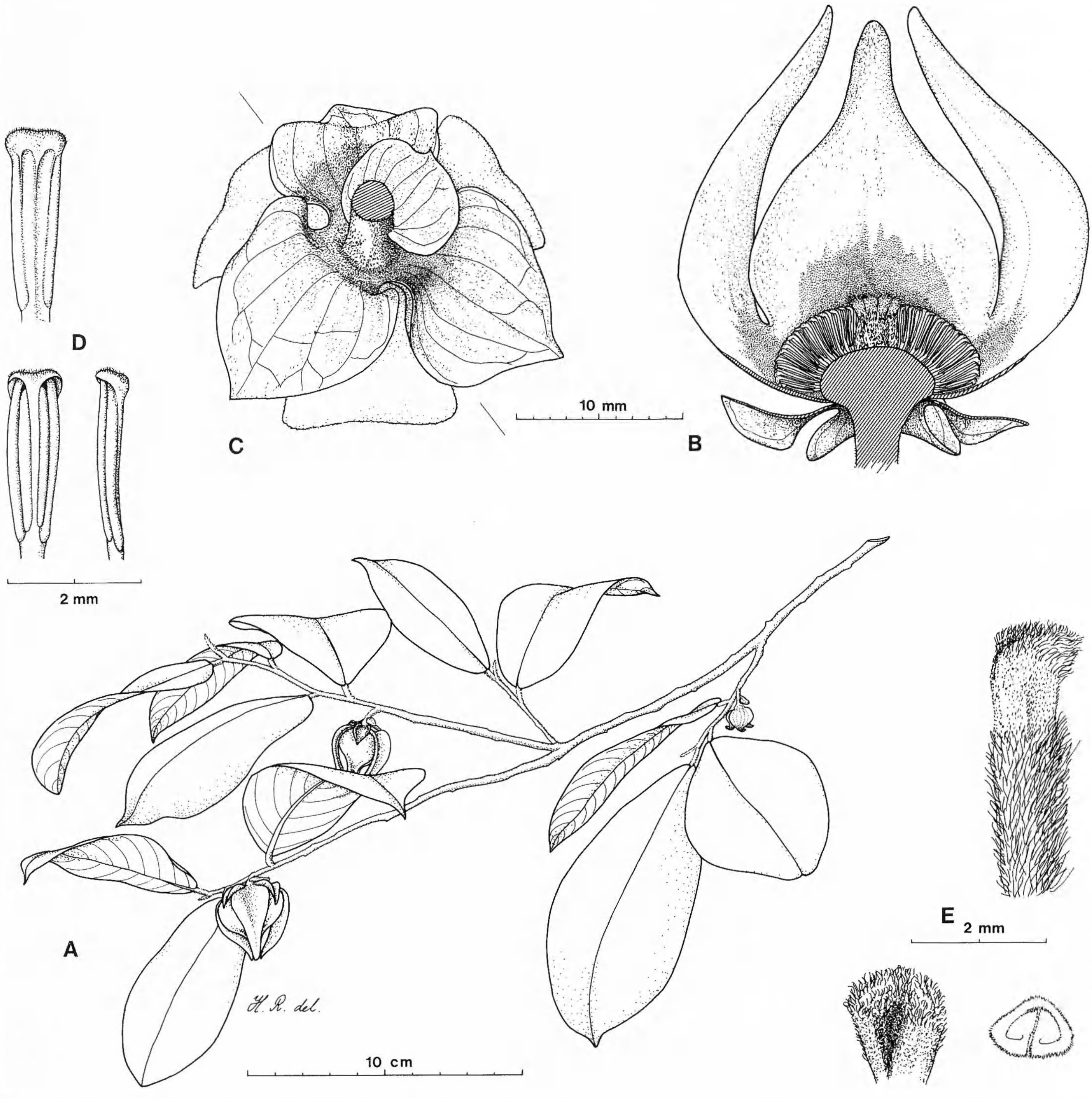

Fig. 1. *Asteranthe lutea*. — A: Habit. — B: longitudinal section of flower (as indicated in C). — C: Calyx and bracteole. — D: Stamen, back, front and side view respectively. — E: Carpel and style, transection of style. — A–E: Vollesen in MRC 4838 (C).

1, 1978, K. Vollesen in MRC 4838 (C holotype; EA, K, WAG isotypes).

A. asterias auct. non Engl. & Diels: Verdcourt (1971 b) quoad specim. Vaughan 1826.

A. asteriae (S. Moore) Engl. & Diels affinis, bracteolis late ovatis basi cordatis, 6–8 mm longis 5–7 mm latis, sepalis subglabris vel sparse sericeis, floribus luteis, petalis carnosis, basi non incrassatis, in flore maturo verticalibus ab ea diversa.

Shrub to c. 4 m tall. Young *branches* velutinous–tomentose becoming sericeous, hairs white. Indumentum and bark gradually peeling, leaving a brown indistinctly ribbed underbark. *Leaves* elliptic–obovate, on flowering branches 70–120(–134) mm long and 27–55(–65) mm wide, on sterile branches up to 185 mm long and 90 mm wide, length/width-ratio 1.8–2.8. Base rounded–cordate, apex abruptly contracted to an acuminate–actue tip, rarely broadly rounded or slightly emarginate. Midrib and lateral nerves raised beneath, reticulation impressed, lateral nerves in 10–15 pairs. Midrib and lateral nerves sparsely sericeous and lamina beneath with scattered adpressed hairs basally, otherwise glabrous. Petiole 3–5 mm long, densely tomentose. *Flowers* extra-axillary or terminal on short branches, solitary, nodding, fragrant. Pedicels (2–)5–8 mm long, densely whitish tomentose, with one green, persistent, broadly ovate–transversely ovate bracteole, 6–8 mm long and 5–7 mm wide, with cordate base and acute apex, with distinct reticulate nervation, sparsely sericeous. *Sepals* green, slightly connate at base, broadly ovate, 10–15 mm long and 8–12 mm wide, with rounded–cordate base and acute–acuminate apex, whitish sericeous at base otherwise sparsely sericeous–subglabrous, with distinct reticulate nervation. Young *petals* green soon turning yellow with dark red slightly longitudinally striate basal part, fleshy, joined into a basal tube c. 10 mm long, free parts narrowly triangular, (17–)20–24 mm long and (9–)12–15 mm wide at base, with acuminate apex and often slightly narrowed basally, dorsally densely whitish sericeous, ventrally tomentose and with scattered long crisped hairs in the apical part, subglabrous towards the base. *Stamens* c. 250–300, yellow, c. 3 mm long, with a deep longitudinal groove on each side separating the pollen-sacs. Connective prolongation convex at apex, pubescent. *Carpels* 3–10, c. 2.5 mm long, densely tomentose. Style c. 1 mm long, rectangular–cylindric, widened apically, folded in from both sides and consequently appearing with a longitudinal groove adaxially (Fig. 1 E), sericeous. *Fruit* and seed not seen.

Distribution. Tanzania, Kilwa Distr. and Zanzibar.

Habitats. A rare shrub from dense riverine forest and thicket along the Lungonya River on the eastern boundary of the Selous Game Reserve. Dominant trees are: *Pterocarpus tinctorius, Baphia kirkii, Mimusops fruticosa, Sterculia appendiculata, Xylopia parviflora, Sorindeia madagascariensis, Hymenaea verrucosa, Lettowianthus stellatus.*

There is no information regarding the habitats of the species on Zanzibar.

Collections studied. Vollesen in MRC 4838 (C, EA, K, WAG), Vaughan 1826 (K).

Key to the species of Asteranthe

1. Bracteoles 2.5–4.0×1–1.5 mm. Sepals 6–10 (–12?)×4–6(–10?) mm, densely ferrugineously tomentose. Petals thin, white-cream, spreading, with a thickened yellow basal area. Stamens 1.5–2.5 mm long .... *A. asterias*
– Bracteoles 6–8×5–7 mm. Sepals 10–15×8–12 mm, sparsely whitish sericeous-subglabrous. Petals fleshy, yellow, erect, with a dark red unthickened basal area. Stamens c. 3 mm long ...... *A. lutea*

Comments

Verdcourt (1971 b) gives the dimensions of the calyx in *A. asterias* as 6–12×4–7 mm. I have seen no specimen with a calyx longer than 10 mm or wider than 6 mm. Verdcourt's maximum dimensions possibly come from the Vaughan-collection which I refer to *A. lutea*. This collection also shows a bracteole of c. 7×5 mm, which is much larger than anything seen in *A. asterias*, the calyx is subglabrous and very distinctly veined.

The identity of Asteranthe trollii

If we consider once more the ghost-species *A. trollii*, the extant isotype comes completely within the range of *A. asterias* if the above key is used. However, some of the dimensions given in the diagnosis (leaf-size, calyx-size) do not agree with the normal variation of *A. asterias*. The description of calyx-indumentum fits *A. asterias*. The description of flower-colour is rather odd and does not fit in with any of the species. Unfortunately the flowers on the isotype are in rather bad condition, and a dissection has not been made. It seems, however, that the petals has the same basal thickened area, which is present in *A. asterias*.

Consequently the exact identity of *A. trollii* remains uncertain, although where general evidence is concerned I agree with Verdcourt (1971 b) that it is probably an extreme form of *A. asterias* from a marginal part of the distribution-area.

Polyalthia Blume in East Africa

Verdcourt (1969) transfers the African species hitherto placed in the genus *Polyalthia* to a new genus *Greenwayodendron* Verdc. Several distinguishing characters are given and the transfer seems reasonable.

On the other hand, Verdcourt (1969) shows that the species known as *Unona stuhlmannii* Engl. actually belongs to *Polyalthia* s. str. This species is distributed in the coastal regions of Kenya and Tanzania.

Verdcourt (1971 b) maintains the two genera, and in addition to *Polyalthia stuhlmannii* (Engl.) Verdc. a further species is described but left unnamed due to incomplete material. Finally another partially known species is mentioned in a footnote.

Complete material of these two species is now available and they are formally described below. Finally a key is presented to the species now known from East Africa.

The two new species are both endemic in SE Tanzania. *Polyalthia* thus becomes an example of a genus with a wide distribution in tropical Asia, and just reaching East Africa with a few species. There are about 100 species of *Polyalthia* in Asia, about 15 in Madagascar and now 3 in East Africa. (There is a further partially known species from Mozambique represented at Kew by a single fruiting collection, Torre & Correia 14564.) The genus is neither represented in the rest of Africa nor in America. Other examples of genera with this pattern of distribution are: *Wrightia* (Apocynaceae), *Alangium* shows the same general pattern but one species has a wider distribution in Africa, *Nepenthes* only reaches Madagascar in the west.

Polyalthia verdcourtii Vollesen, sp. nov., Fig. 2

Type: Tanzania, Ulanga Distr., Magombera Forest Reserve, c. 7°50′S 37°00′E, c. 250 m a.s.l. — November 22, 1976. K. Vollesen in MRC 4150 (C holotype; EA, K, WAG isotypes).

Polyalthia sp. sensu Verdcourt (1971 b).

P. stuhlmannii (Engl.) Verdc. affinis, ramis juvenibus dense ferrugineo-pilosis, foliis majoribus, subtus in nervis mediis pilosis, domatia in axillis nervorum lateralium gerentibus, floribus majoribus, petalis 23–35 mm longis, stipitibus monocarpiorum brevioribus, 5–7 mm longis ab ea diversa.

Named in honour of Dr B. Verdcourt, whose exellent account of Annonaceae in Flora of Tropical East Africa has enabled the author to recognize the species published in this paper as new.

Tree up to c. 10 m tall. Young *branches* dark brown, ferrugineously pilose, gradually becoming subglabrous and longitudinally ribbed. *Leaves* elliptic–oblong, rarely ovate or obovate, (95–)105–185 mm long and 32–61 mm wide, length/width-ratio (2.2–)2.6–3.5, those distally on the branches being the largest. Base cuneate, apex acute–acuminate, the actual tip rounded. Leaves glandular dotted with distinctly raised reticulation beneath, midrib sparsely–densely pilose in the basal part and with domatia at the lateral nerves, otherwise glabrous except sometimes for a few scattered hairs basally on the lateral nerves. Petiole dark brown, transversally wrinkled, 2–5 mm long, ferrugineously pilose. *Flowers* axillary, solitary, nodding. (Probably a reduced cyme as there are always several "bracteoles" on the basal part of the pedicel. There is also normally a dormant flowerbud ab-axially to the developed one, see Fig. 2 B.) Pedicels 13–19 mm long, not articulated, densely sericeous and with scattered erect hairs. Bracteoles c. 1 mm long, sericeous. *Sepals* free, brown, 3–4 mm long and c. 2 mm wide, apex acute, pilose dorsally and ciliate, deciduous in fruit. Petals free, yellowish green, elliptic–oblong or obovate, apex rounded, narrowed at the base, 23–35 mm long and 7–9 mm wide, sparsely sericeous dorsally, most densely in the basal part, ciliate. *Stamens* c. 100–150, 1–1.5 mm long. Connective prolongation flat-topped or slightly concave, smooth. *Carpels* c. 50, c. 1 mm long, densely sericeous, stigma rectangular, c. 0.5 mm long. *Monocarps* c. 20, red when ripe, slightly fleshy, ellipsoid, gradually tapering to apex and base, 9–11 mm long and 5–6.5 mm in diameter, one-seeded, sparsely sericeous–glabrous, ventral suture almost imperceptible. Stipes 5–7 mm long, sparsely sericeous. *Seeds* ellipsoid 8–10 mm long and c. 5 mm in diameter.

Distribution. Only known in the Magombera Forest Reserve, Ulanga Distr., Tanzania.

Habitats. A rare under-storey tree in dry evergreen lowland forest. Dominant trees are: *Erythrophleum suaveolens, Isoberlinia scheffleri, Anthocleista grandiflora, Xylopia parviflora, Dialium holtzii, Treculia africana, Parkia filicoidea, Tetrapleura tetraptera.*

Collections studied. Semsei 3381 (EA, K), Vollesen in MRC 4150 (C, EA, K, WAG), 4439 (C).

Polyalthia tanganyikensis Vollesen, sp. nov., Fig. 3

Type: Tanzania, Kilwa Distr., Selous Game Reserve,

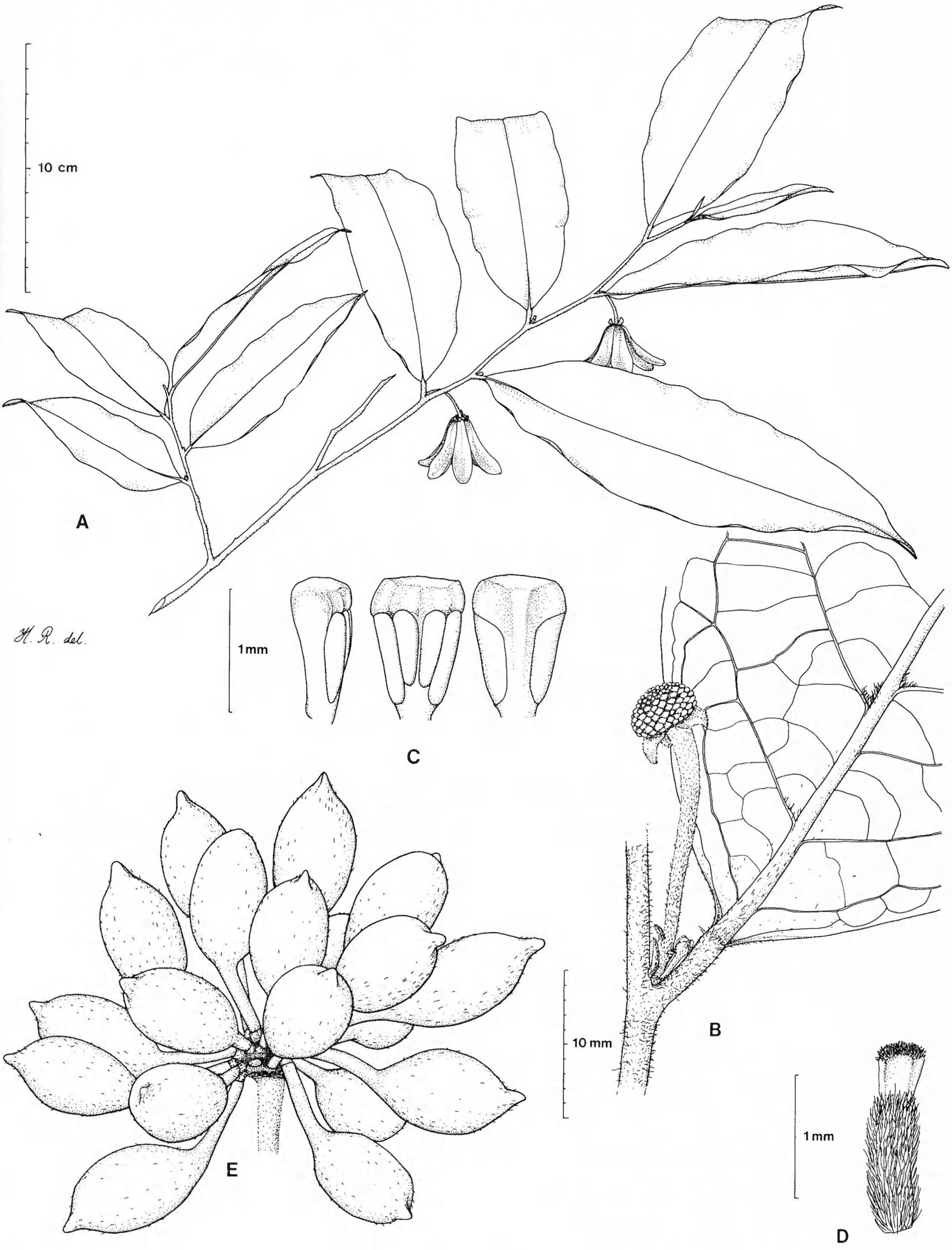

Fig. 2. *Polyalthia verdcourtii*. — A: Habit. — B: Leaf, young branch and flower with petals removed. — C: Stamen, side, front and back view respectively. — D: Carpel and stigma. — E: Fruit. — A–D: Vollesen in MRC 4150 (C); E: Vollesen in MRC 4439 (C).

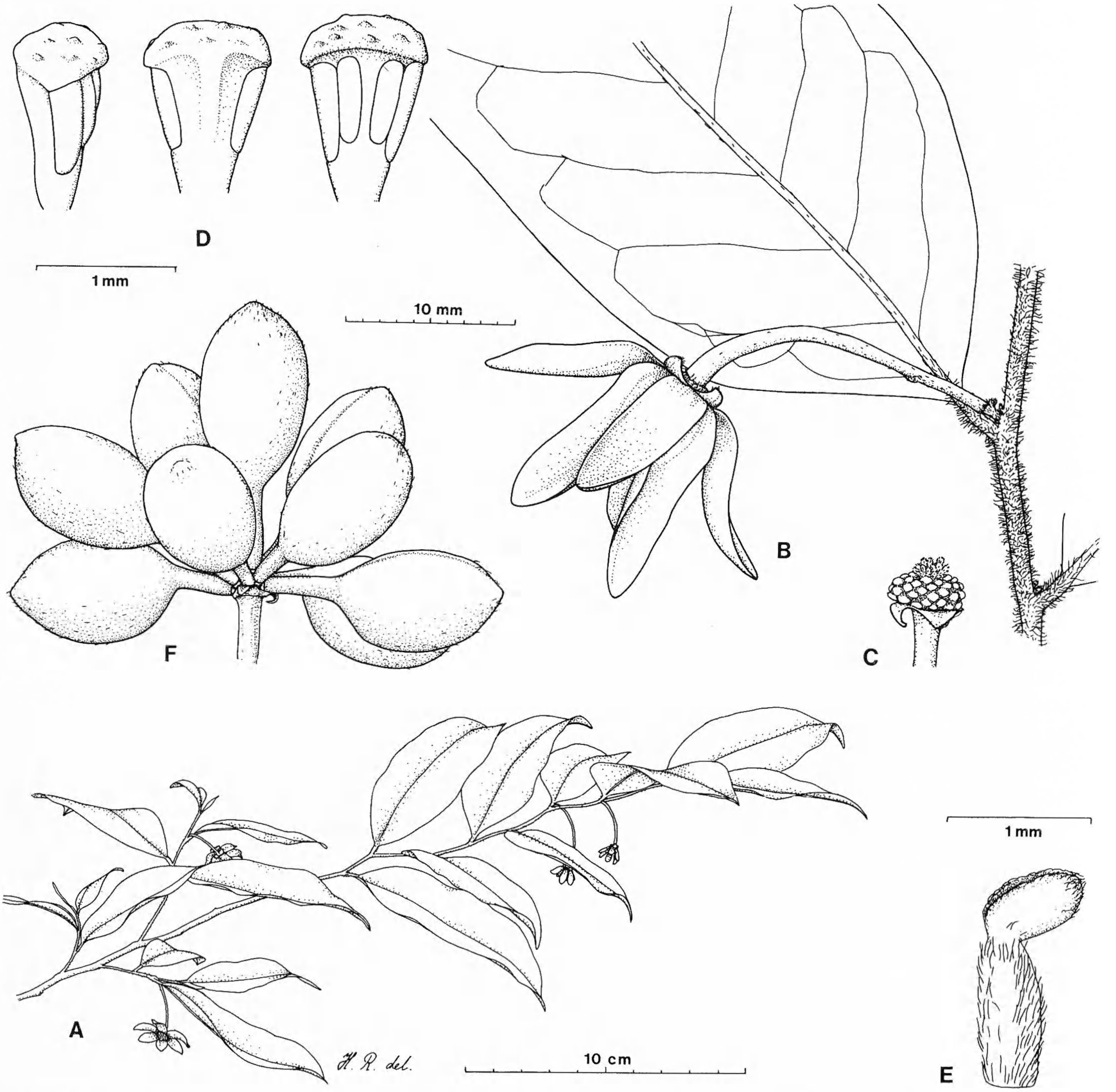

Fig. 3. *Polyalthia tanganyikensis*. — A: Habit. — B: Leaf, young branch and flower. — C: Flower with petals removed. — D: Stamens, side, back and front view respectively. — E: Carpel and stigma. — F: Fruit. — A–F: Vollesen in MRC 2466 (C).

Malemba, c. 8°40′S 38°25′E, c. 400 m a.s.l. — June 21. 1975, K. Vollesen in MRC 2466 (C holotype; EA, K, LISC, WAG isotypes).

P. stuhlmannii (Engl.) Verdc. et *P. verdcourtii* Vollesen affinis, ramis juvenibus sparse vel dense pilosis, floribus minoribus, petalis 7–12 mm longis 3–4 mm latis, stipitibus monocarpiorum brevioribus, 3–5 mm longis a priore, foliis minoribus, subglabris, floribus minoribus a posteriore diversa.

Shrub up to c. 5 m tall. Young *branches* greenish soon becoming dark brown, pilose–densely pilose, hairs white; gradually becoming glabrous and longitudinally ribbed. *Leaves* glossy, narrowly elliptic–elliptic or obovate, well-developed ones 55–100(–110) mm long and 15–34(–50) mm wide, length/width-ratio 2.6–3.7, those distally on the branches being the largest. Base cuneate, apex acute–acuminate, the actual tip mostly acute. Leaves glandular dotted with slightly raised reticulation beneath, midrib sparsely sericeous in the basal part, otherwise glabrous except sometimes for a few hairs basally on the lateral nerves, no domatia. Petiole green, transversally wrinkled, 1.5–3 mm long, pilose-sericeous. *Flowers* axillary, solitary, nodding. (Probably a reduced cyme as the lower "bracteole" sometimes supports a rudimentary bud. A supplementary bud is often found above the developed one.) Pedicels green, 15–23 mm long, articulated 1–2 mm above the base, sparsely sericeous–subglabrous. Bracteoles soon deciduous, c. 0.5 mm long, sericeous. *Sepals* basally connate, green, c. 2.5 mm long and c. 2 mm wide, with broadly acute apex, sericeous dorsally and ciliate, persistent in fruit. Petals free, yellowish green, narrowly elliptic–oblong or slightly obovate with broadly acute apex, 7–12 mm long and 3–4 mm wide, sparsely sericeous dorsally and indistinctly ciliate. *Stamens* c. 75, 1–1.5 mm long. Connective prolongation slightly convex and distinctly warted (Fig. 3 D). *Carpels* c. 20, c. 1 mm long, sericeous, stigma subglobose–ellipsoid, c. 0.5 mm long, those on central carpels erect, those on marginal carpels bent outwards (as in Fig. 3 E). *Monocarps* c. 10, red when ripe, slightly fleshy, ellipsoid, abruptly contracted at apex and base, 9–11 mm long and 5–6 mm in diameter, glabrous or with a few scattered adpressed hairs, ventral suture distinct. Stipes 3–5 mm long, sparsely sericeous–subglabrous. *Seeds* dark brown–blackish, ellipsoid, 8–10 mm long and c. 5 mm in diameter.

Distribution. Only known in the Kilwa Distr., Tanzania. It is rather strange that this species, always common or dominant where it occurs, has only been recorded in such a restricted area. The thicket and forest-types where it occurs are widely distributed both to the north and south of this area.

Habitats. A common and often dominant species in the shrub-layer of dry deciduous coastal forest and thicket on grey sandy soil at c. 300–600 m a.s.l. Dominant trees are: *Pteleopsis myrtifolia, Terminalia sambesiaca, Manilkara sulcata, Nesogordonia parvifolia, Albizia adianthifolia, A. petersiana, Cleistanthus schlechteri, Rhodognaphalon schumannianum, Lannea antiscorbutica.*

Collections studied. W. A. Rodgers in MRC 288 (EA), 608 (EA, K), 650 (EA), 870 (EA), 1059 (EA, K), 1179 (EA, K), K. Vollesen in MRC 1885 (C, EA), 2466 (C, EA, K, LISC, WAG). All these collections are from the Selous Game Reserve inside the area 8°30′S–8°50′S 38°00′E–38°30′E. The plant has also been observed on the Kichi Hills just east of the Selous (c. 8°10′S 38°40′E).

Key to the species of Polyalthia in East Africa

1. Stipes of monocarps 10–12 mm long. Petals 10–17(–20) mm long and 5–9 mm wide. Leaves with domatia. Pedicels articulated. Sepals united at base .... *P. stuhlmannii*
– Stipes of monocarps 3–7 mm long 2
2. Petals 7–12 mm long and 3–4 mm wide. Leaves without domatia. Pedicels articulated. Sepals united at base .... *P. tanganyikensis*
– Petals 23–35 mm long and 7–9 mm wide. Leaves with domatia. Pedicels not articulated. Sepals free .... *P. verdcourtii*

P. tanganyikensis is also closely related to *P. korinti* (Dunal) Hook. f. & Thoms. from S India and Sri Lanka. It differs however in a number of characters summarized here:

1. Petals 7–12 mm long. Pedicel articulated 1–2 mm above base. Monocarps 9–11 mm long. Connective appendage convex, warted .... *P. tanganyikensis*
– Petals 3–6(–9) mm long. Pedicel articulated (3–) 5–10 mm above base. Monocarps 5–8 mm long. Connective appendage slightly concave, smooth .... *P. korinti*

Note on the genus Uvaria L.

Out of a total of 14 species of *Uvaria* recorded from East Africa by Verdcourt (1971 b), 4 are partially known only from flowering or fruiting material. The knowledge of the genus is similarly lacking in other parts of Africa; from Madagascar e.g., 15 species are recorded of which 10 are partially known (Cavaco & Keraudren 1958). It was therefore difficult to decide whether this species represented a new species, a new record for East Africa or one of the partially known species. It has, however, been impossible to match it with any other taxon and it is consequently described here as a new species.

Uvaria lungonyana Vollesen, sp. nov., Fig. 4

Type: Tanzania, Kilwa Distr., Selous Game Reserve, Kingupira, c. 8°25′S 38°30′E, c. 125 m a.s.l. — January 27. 1977, K. Vollesen in MRC 4386 (C holotype; EA, K isotypes).

Differt a *U. acuminata* Oliv. et *U. leptoclado* Oliv. carpellis laevibus, globosis stipitibus 8–10 mm longis insidentibus, ramis et foliis subglabris, sepalis et petalis sparse pubescentibus.

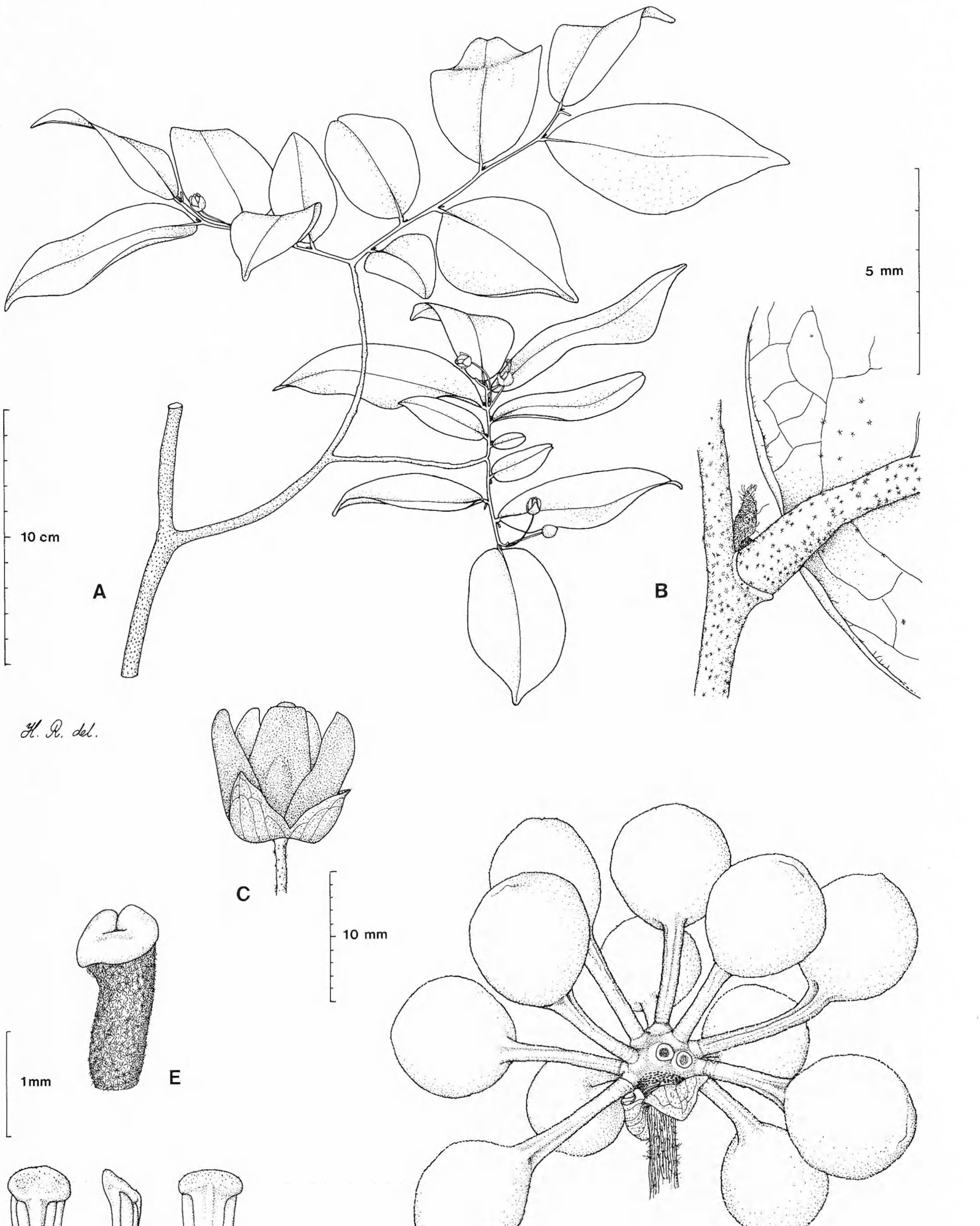

Fig. 4. *Uvaria lungonyana*. — A: Habit. — B: Basal part of leaf and young branch. — C: Flower. — D: Stamens, front, side and back view respectively. — E: Carpel and style. — F: Fruit. — A–E: Vollesen in MRC 4386 (C); F: Vollesen in MRC 4479 (C).

Named after the Lungonya River on the eastern boundary of the Selous Game Reserve, a locality rich in rare Annonaceae.

Scandent *shrub* up to c. 5 m tall. Young *branches* greenish brown with scattered white stellate hairs, later becoming brown and more densely haired. Older branches dark brown, subglabrous with numerous conspicuous white elliptic lenticels and reticulate longitudinally ribbed. *Leaves* elliptic–obovate, on flowering branches 57–114 mm long and 25–46 mm wide, on fruiting branches up to 144 mm long and 55 mm wide, length/width-ratio 1.8–3.4. Base cuneate–subcordate, apex acute–broadly rounded, the actual tip blunt–retuse often apiculate. Young leaves beneath with a few scattered stellate hairs basally and on midrib, otherwise glabrous, older leaves glabrous. Petiole 2–3 mm long, sparsely stellate pubescent, with a distinct joint, leaving a protruding scar when dropping. *Flowers* in seemingly leaf-opposed or terminal two-flowered cymes, not fully opening. (The inflorescence is probably always terminal and is then displaced by the branch developing from the uppermost leaf-axil.) Peduncle 2–3 mm long, sparsely stellate pubescent, bracts scarious, 5–6 mm long, deciduous or persistent, stellate pubescent. Pedicels 12–15 mm long in flowering state, densely stellate pubescent of white short-rayed hairs and with scattered brownish long-rayed hairs, bracteoles c. 1 mm long, scarious, soon deciduous, stellate tomentose. *Sepals* completely covering the petals in bud, later splitting into three (rarely two) parts only united at the base, often persisting as a collar around the fruiting pedicel, c. 6 mm long and wide, sparsely stellate pubescent and with a distinct apical tuft of longer hairs. *Petals* yellow, held erect in mature flowers, elliptic, 11–14 mm long and 4.5–6.5 mm wide, subacute–rounded at apex, sparsely stellate pubescent dorsally, subglabrous ventrally. *Stamens* c. 100, c. 1 mm long. Connective prolongation truncate, puberulous. *Carpels* 15–25, c. 1 mm long, stellate tomentose, style c. 0.5 mm long, rectangular, widened apically, folded in from both sides and consequently appearing with a longitudinal groove adaxially, glabrous. *Monocarps* 10–15, globose, c. 10 mm in diameter, yellowish brown, smooth, densely stellate tomentose, on 20–28 mm long longitudinally ribbed pedicels. Stipes 8–10 mm long, densely stellate tomentose. Seeds not fully developed.

Distribution. Only known in the Kilwa Distr., Tanzania.

Habitats. A rare species from dense riverine forest and thicket along the Lungonya River on the eastern boundary of the Selous Game Reserve. (See note on habitats under *Asteranthe lutea*, which occurs in the same locality.)

Collections studied. K. Vollesen in MRC 4386 (C, EA, K), 4479 (C, EA, K, WAG).

The infraspecific taxonomy of Ophrypetalum odoratum Diels

Verdcourt (1960) divides *Ophrypetalum odoratum* Diels in two subspecies using the length of the pedicel as the main criterion. The pedicels are stated to be 3–7 mm long in ssp. *odoratum*, and 15–22 mm long in ssp. *longipedicellatum* Verdc. Examination at Kew of the collections assigned to ssp. *longipedicellatum* shows that the lengths given above refer to the longest pedicels only. Measuring pedicels of all open flowers results in the variation 10–22 mm instead. Verdcourt (1960) also mentions a certain difference in leaf size and shape. Leaves in ssp. *odoratum* being 28–98 mm long and elliptic, obovate or narrowly elliptic–obovate, while leaves in ssp. *longipedicellatum* are 40–120 mm long and obovate or lanceolate–obovate.

Since the original description of ssp. *longipedicellatum* and the account in Verdcourt (1971 b) several collections have been made in the Ruaha–Kilombero–Rufiji basin in Tanzania. These collections are all intermediate in pedicel-length between the two subspecies having pedicels 6–13 mm long.

The total distribution of the species is made up of three rather widely separated areas: One in the coastal regions of Kenya, one in the central part of coastal Tanzania from east of Morogoro south to the Rufiji River and one in SE Tanzania around Lindi (the type-collection, no other collections have been seen from this area). All collections from Kenya have short pedicels and this also applies to the collection from the Lindi area. The collections from the Morogoro–Rufiji area have a great variation in pedicel-length, from very short as in the Kenya material to the very long pedicels characteristic of ssp. *longipedicellatum*.

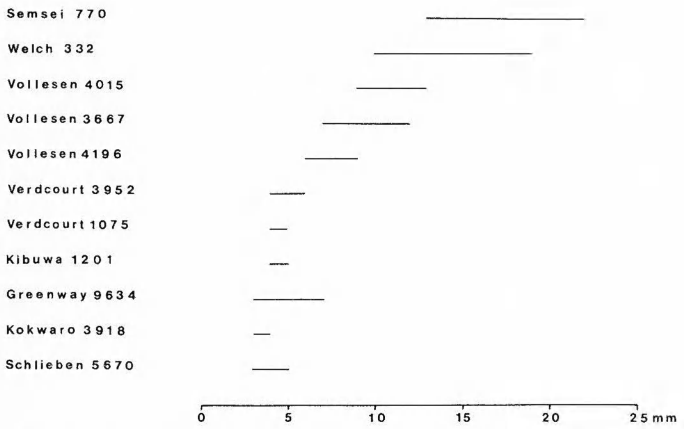

Fig. 5. Variation in pedicel length in *Ophrypetalum odoratum*. — *Kenya*. Kwale and Kilifi Distr.: Greenway 9634 (K), Kibuwa 1201 (K), Kokwaro 3918 (K), Verdcourt 1075 (K), 3952 (K). — *Tanzania*. Lindi Distr.: Schlieben 5670 (BM, type collection). Morogoro Distr.: Semsei 770 (K, type collection of ssp. *longipedicellatum*), Vollesen in MRC 3667 (C), Welch 332 (K). Rufiji Distr.: Vollesen in MRC 4015 (C). Kilwa Distr.: Vollesen in MRC 4196 (C).

Fig. 5 shows the variation in pedicel length for all collections studied. It can be seen, that there is a complete continuity from the short pedicels (3–7 mm) of the Kenya material to the very long pedicels of some of the material from the Morogoro area. I therefore suggest this character should not be used for dividing the species into infraspecific taxa.

The differences in leaf size and shape are so slight and overlapping, that with the disappearance of the pedicel character they cannot be used for any subdivision either. Moreover some of the new collections from the Rufiji area fall into one group and some into the other. Nor is there, in my opinion, any patterns in ecology and altitudinal distribution which suggest that more than one taxon is involved.

I therefore propose that the infraspecific division of *Ophrypetalum odoratum* is abandoned and propose the following synonym:

Ophrypetalum odoratum Diels 1936 p. 270 & Fig. 9/1. Syn. *O. odoratum* ssp. *longipedicellatum* Verdcourt 1960 p. 346.

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Thanks are also due to Tyge Christensen, who translated the diagnoses into latin, to Hanne Rasmussen for her skilful drawings and to Ib Friis for his critical reading of the manuscript.

References

Cavaco, A. & Keraudren, M. 1958: Annonaceae. *In* H. Humbert (ed.), *Flore de Madagascar et des Comores*. Paris.

Diels, L. 1936: Annonaceae. *In* J. Mildbraed (ed.), *Neue und seltene arten aus Ostafrika (Tanganyika-Territ. Mandat) leg. H. J. Schlieben, 9.* Notitzbl. Bot. Gart. Berlin 13: 265–272.

Engler, A. & Diels, L. 1901: *Monographien Afrikanischer Pflanzen-familien und -Gattungen 6. Annonaceae*. Leipzig.

Verdcourt, B. 1960: Notes from the East African Herbarium 11. *Kew Bull. 14:* 345–352.

Verdcourt, B. 1969: The status of the genus Polyalthia Blume (Annonaceae) in Africa. *Adansonia, ser. 2, 9:* 87–94.

Verdcourt, B. 1971 a: Notes on East African Annonaceae. *Kew Bull. 25:* 1–34.

Verdcourt, B. 1971 b: Annonaceae. *In* E. Milne-Redhead & R. Polhill (eds.): *Flora of Tropical East Africa*. London.

Valantia deltoidea Brullo, sp. nov. from Sicily

SALVATORE BRULLO

Brullo, S. 1980 03 17: Valantia deltoidea Brullo, sp. nov. from Sicily. *Bot. Notiser 133:* 63–66. Stockholm. ISSN 0006-8195.

Valantia deltoidea Brullo, sp. nov. (Rubiaceae) is described. It is a therophyte collected from the calcareous mountain meadows on Rocca Busambra (Sicily). The difference between this species and its closest relatives are given.

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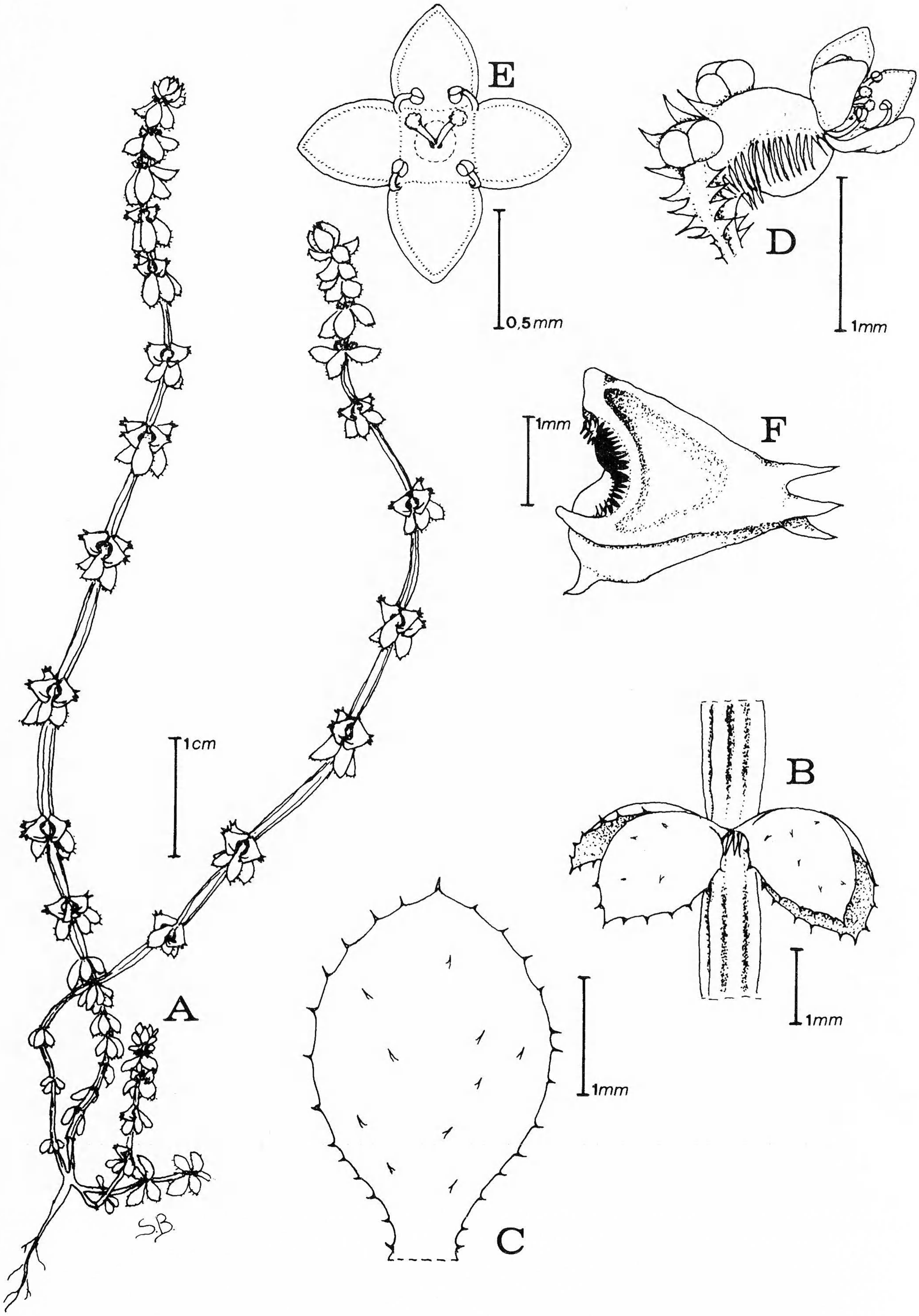
Valantia deltoidea Brullo, sp. nov.—Fig. 1

Holotypus: Italy, Sicily, Rocca Busambra, 2.6.1976, Brullo (CAT).

Planta annua, 3–10 cm longa, valida, basi ramosa, ramis simplicibus, erectis vel prostrato-ascendentibus, rigidis, quadrangulato-costatis, nitidis, inferioribus glabris, terminalibus pilosis. Internodia basalia brevia, sterilia; intermedia elongata, fertilia, usque ad 13 mm longa; superiora approximata, fertilia. Folia verticillato-quaterna, subrotunda vel leviter ovata, 2,5–4×2–2,5(3) mm, subsessilia vel breviter petiolata, ad marginem laxe pectinata, dentibus inconspicuis pilo brevi, recurvo, rigido praeditis, pagina superiore paucis pilis adspersa. Cymae axillares triflorae in verticillos quaternos dispositae. Flos medius hermaphroditus, 4-merus, corolla diametro 1,2–1,5 mm. Flores laterales masculini, 3-meri, corolla diametro <1 mm. Corollae lobi obtusiusculi, staminibus alternantes. Corpus fructiferum a latere leviter compressum, laeve, luteolum, deltoideum, 2–2,5×2,5–3 mm, dorsaliter coronula (2–)3(–4) cristata praeditum, apice tricorni, cornu medio longiore, ad annulum seminiferum versus curvo, cornibus lateralibus brevioribus rectis vel leviter incurvatis; carina cornuum 0–3 cristis praedita; annulus seminifer ciliis longis marginatus. Mericarpium unicum, 1–1,2 mm longum, nigrum, laeve, setulis albidis, brevibus, adhaerentibus, ad hilum adpressis.

Annual herb, 3–10 cm long, branched from the base. *Stems* unbranched, glabrous below and hairy in terminal part, erect or prostate-ascending, rigid, 4-ribbed, nitid. Lower internodes short, sterile; intermediate ones fertile, elongated up to 13 mm long; upper ones fertile, shorter. *Leaves* in whorls of 4, almost round to slightly ovate, 2.5–4×2–2.5(–3) mm, subsessile to shortly petiolate, laxly pectinate along the margin with very short teeth terminating in small, rigid and curved hairs; adaxial surface with scattered hairs. In the lower part of the foliar whorl in the middle of each side of the stem four groups of 3–4 hairs are present. *Cymes* axillary in whorls of 4, 3-flowered. Central flower hermaphrodite, 4-merous; lateral flowers male, 3-merous. *Corolla* yellowish–green, 1.2–1.5 mm in diam. in hermaphrodite flowers, less in male ones; corolla lobes obtuse. *Stamens* epipetalous alternating with corolla lobes; anthers yellow, 2-locular. *Style* 2-fid; stigmas capitate. *Fructiferous corpus* compressed laterally, deltoid, 2–2.5×2.5–3 mm, smooth, yellowish, glabrous (except for ventral cilia), with a coronule formed by (2–)3(–4) bristles dorsally, apically 3-horned; central horn longer, distinctly curved towards the seed-bearing annulus; lateral ones horizontal or slightly curved; horns provided with 0–3 bristles on the keel; seed-bearing annulus bordered by long cilia. *Mericarp* solitary, 1–1.2 mm long, smooth, reniform, black, with short, whitish, adhering hairs near hilum.

Distribution and habitat. Valantia deltoidea is only to be found on the top of Rocca Busambra, a calcareous mountain c. 1600 m high, to the south of Palermo (N. Sicily). According to herbarium research it seems that it has not been collected until now. *V. deltoidea* is very frequent in the ephemeral meadows of this locality, where it is associated with *Xeranthemum inapertum* (L.) Miller, *Sedum album* L., *Bivonea lutea* (Biv.) DC., *Gagea busambarensis* (Tin. in Guss.) Parl., *G. nebrodensis* (Tod.) Nyman, *Helianthemum ledifolium* (L.) Miller, *Saxifraga tri-*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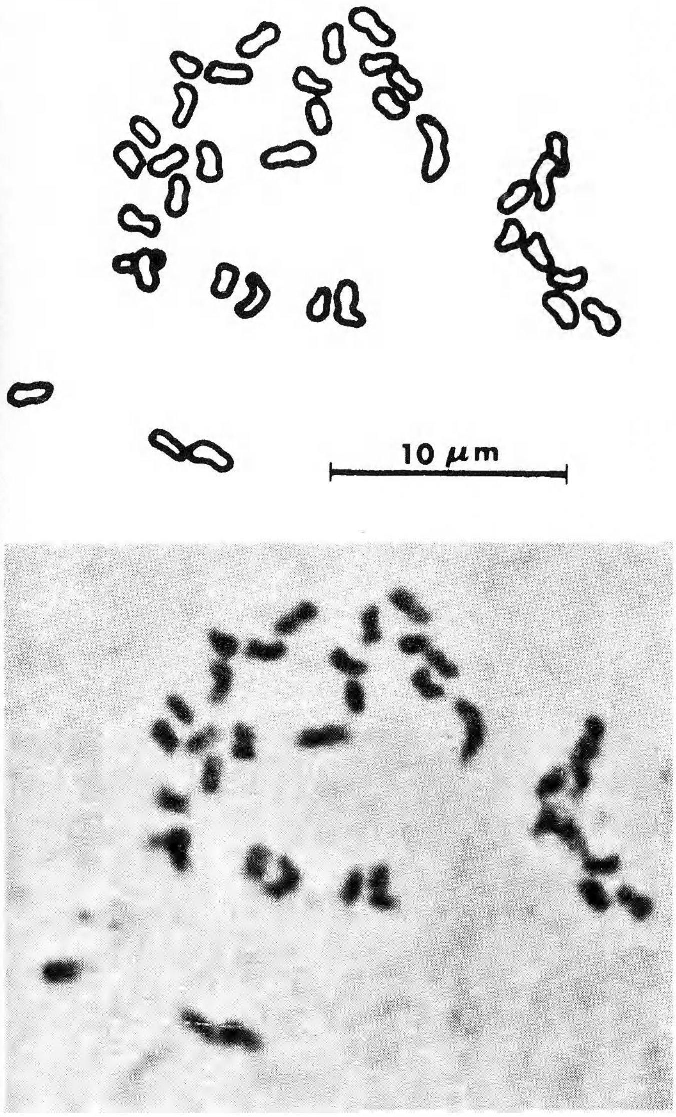

Fig. 2. *Valantia deltoidea*, root-tip mitosis, metaphase plate.

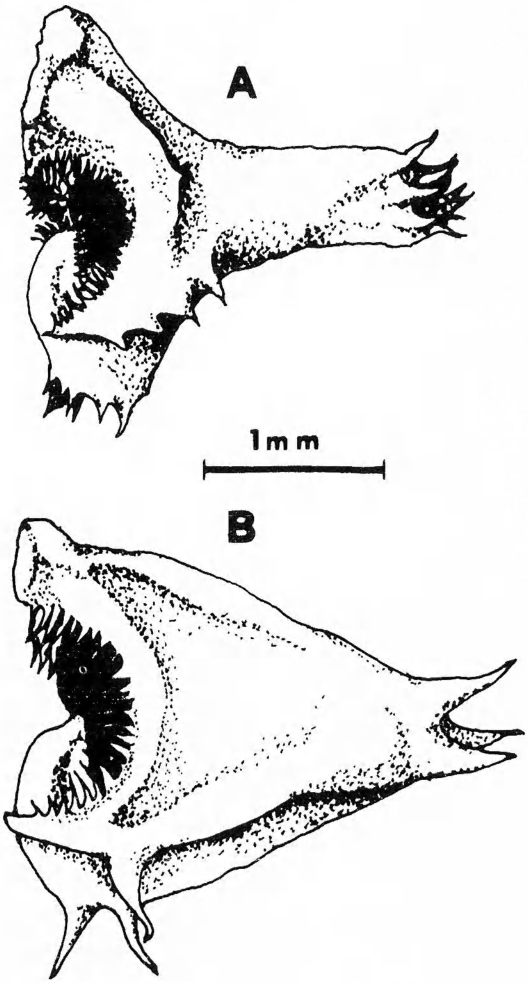

Fig. 3. Fructiferous corpus of *Valantia muralis* (A) and of *V. deltoidea* (B).

dactylites L., *Phleum echinatum* Host., *Alyssum siculum* Jord., *Poa bulbosa* L., *Arenaria leptoclados* (Reichenb.) Guss., etc.

Chromosome number. The counts were made from root tips of cultivated progeny from the type collection; the root tips were pretreated with 0.2 % colchicine, fixed in Carnoy, stained in Feulgen after hydrolysis in HCl, and squashed in 45 % HAc. The chromosome number of *V. deltoidea* is 2n=36 (Fig. 2). Consequently this species is tetraploid unlike *V. muralis* L., *V. hispida* L. and *V. calva* Brullo (Fagerlind 1937, Brullo 1979), which have a chromosome number of 2n=18.

Taxonomic relationships. *V. deltoidea* is a taxon which differs greatly from other species of the genus *Valantia*. Among these, *V. muralis* is a species with a pan-mediterranean distribution and the most closely related to *V. deltoidea*. *V. muralis* differs from *V. deltoidea* in several important characters such as the leaves obovate to oblanceolate, glabrous, with margin obsolutely entire; fructiferous corpus (Fig. 3) whitish, with dorsal subcylindric rostrum 1–1.5 mm long at apex with a coronule formed by 5–15 shorter bristles, where the three apical horns each are provided with 3–10 shorter bristles, the lateral borders of the seed-bearing annulus are thickened and frequently have 1–3 bristles, with a

Fig. 1. *Valantia deltoidea*, type collection. — A: Habit. — B: Whorl or leaves. — C: Leaf. — D: Inflorescence. — E: Hermaphrodite flower. — F: Fructiferous corpus.

central horn and a seed-bearing annulus with finer and denser cilia; hairs of the mericarp are golden-yellow.

V. deltoidea in having leaves pectinate at the margin and whitish mericarp hairs is similar to *V. hispida*, but otherwise differs considerably.

The presence of the new taxon on Rocca Busambra is not exceptional, but it is probably endemic to this mountain. It is rich in endemic species and, two are exclusive to this mountain namely *Gagea busambarensis* (Tin. in Guss.) Parl. and *Armeria gussonei* Boiss.

References

Brullo, S. 1979: Valantia calva, a new species from Linosa, Sicily. *Bot. Notiser 132:* 61–64.

Fagerlind, F. 1937: Embryologische, zytologische unde bestäubungsexperimentelle Studien in der Familie Rubiaceae nebst Bemerkungen über einige Polyploiditätsprobleme. *Acta Horti Bergiani 11(9).*

The genus Benthamiella (Solanaceae)

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Arroyo, S. 1980 03 17: The genus Benthamiella (Solanaceae). *Bot. Notiser 133:* 67–76. Stockholm. ISSN 0006-8195.

Diagnostic descriptions and a key are provided for the 12 species of the S Patagonian genus *Benthamiella* (Solanaceae), including the new species, *B. sorianoi*, described here. Recent collections have permitted the reinterpretation of several taxa, principally *B. patagonica*, B. *nordenskjoldii* and *B. longifolia*, and show that the genus has a wider distribution in Patagonia than was hitherto known, including the first records from Chile. The distributions of all species are mapped.

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The Patagonian endemic genus *Benthamiella* Speg. is placed in the tribe Nicotianeae of the Solanaceae. It is most closely related to *Pantacantha* Speg., which differs in its very spiny calyx and aristate seeds. Following its description by Spegazzini (1883), *Benthamiella* was subsequently studied by Skottsberg (1916), and was last revised by Soriano (1948). The excellent treatment by Soriano was necessarily limited in certain aspects by the difficulty of assessing the status of some of Skottsberg's taxa on the basis of the scanty material held in South American herbaria and because of the non-availability of some of the type specimens.

During the past 30 years the botanical exploration of Patagonia has made substantial advances. For example, the extensive studies south of 40°S lat. by collaborators associated with *Flora Patagonica* (Correa 1969, 1971, 1978) and the field programmes of the Transecta botánica de Patagonia Austral (T.B.P.A, a collaborative programme between CONICET, Argentina, the Royal Society of London, U. K. and the Instituto de la Patagonia, Punta Arenas, Chile) between 51° and 52°S lat. have significantly increased the material of *Benthamiella* available for study. In consequence, it has proved possible to understand rather more clearly the variation shown by the genus and, since virtually all type specimens have been located and examined, to define more precisely some taxa of hitherto uncertain status.

In order to accommodate these new data some modifications to the treatment of Soriano (1948) have been found to be necessary. In consequence, it was felt useful to provide an updated key to the taxa that can now be recognized and brief comparative descriptions of them. It is thus hoped that this account, supplementing the valuable work of Soriano, will provide a firm basis for future studies of this typically Patagonian genus of cushion-forming Solanaceae.

Benthamiella Speg.

Pulvinate *chamaephytes*; cushions hemispherical, dense or lax. *Stems* woody, much branched, densely leafy. Lower *leaves* dead and blackened, the upper green, imbricate, adpressed, sessile; sheath generally hyaline or membranous, linear to oblanceolate or obovate, glabrous or pubescent; lamina rather thick or membranous, linear to lanceolate, acute to obtuse or truncate, glabrous or with simple, branched, lanuginose or glandular hairs. *Flowers* hermaphrodite, axillary, borne singly, sessile or shortly pedunculate, subtended by 2 free leaf-like bracts, rarely with 2 pairs of decussate, connate basal bracts. *Calyx* tubular or campanulate, 5-dentate, green, glabrous or pubescent on one or both surfaces; teeth linear to lanceolate, acute to obtuse or truncate, equal or subequal, longer to shorter than tube, glabrous or pubescent with simple or glandular hairs. *Corolla* actinomorphic, tubular to slightly infundibuliform, rarely somewhat ventricose, whitish, glabrous or pubescent; tube 0.5–3 times as long as calyx; lobes 5, obtuse or acute, glabrous or pubescent. *Stamens* (1), 2 or 5, included or exserted; filaments filiform, equal, subequal or didynamous, inserted at 1 or 2 well defined levels, glabrous or pubescent, rarely *(B. chubutensis)* with small, lanuginose basal appendages; anthers dorsifixed, broadly elliptical; rarely 2 staminodes present. *Disc* present or absent. *Ovary* globose, 2-locular; ovules numerous; style erect, exserted or included and about as long as, or half as long as, the corolla-tube; stigma capitate or indistinctly 2-lobed. *Fruit* a dehiscent capsule, ovoid, with 2-fid valves; seeds 1–3(–4), fusiform, with reticulate testa; embryo curved.

Distribution (Fig. 1). The genus is endemic to Patagonia between latitudes 37°S and 54°S. The species are concentrated in the southern Argentinian provinces of Santa Cruz (9/12 species) and Chubut (7/12 species), with 1 each in Neuquén, Río Negro and Tierra del Fuego. Two species, *B. patagonica* and *B. azorella*, also occur in the eastern central part of the Chilean province of Magallanes near the Argentinian frontier.

Following the phytogeographical classification of Cabrera (1971) the genus *Benthamiella* is confined to the Andean–Patagonian and Subantarctic Dominion. The species predominantly occur in open steppe communities on rocky-sandy soil between 300 and 1700 metres altitude.

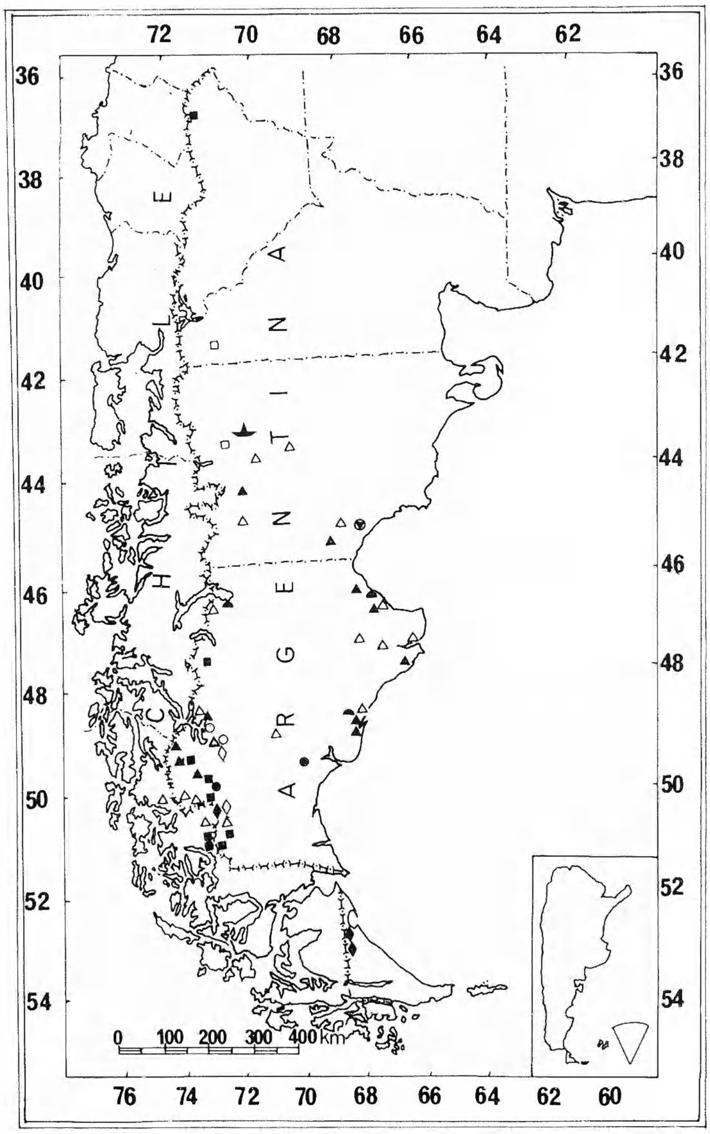

Fig. 1. Distribution of species of *Benthamiella* in Argentina and Chile. *B. skottsbergii* ●; *B. azorella* ■; *B. spegazziniana* ○ ; *B. azorelloides* ⏏; *B. sorianoi* ⟠; *B. graminifolia* □; *B. pycnophylloides* ▲ ; *B. lanata* ⊗; *B. patagonica* △ ; *B. nordenskjoldii* ♦ ; *B. longifolia* ◓ .

Key to the species

1\. Stamens (1) 2 2
– Stamens 5 4
2\. Corolla at least twice as long as calyx; stamens included .... 1. *B. skottsbergii*
– Corolla c. 1.5× as long as calyx; stamens exserted 3
3\. Filaments pubescent; style exserted .... 2. *B. azorella*
– Filaments glabrous; style included .... 3. *B. spegazziniana*
4\. Corolla c. 1.5× as long as calyx 5
– Corolla at least twice as long as calyx 6
5\. Flowers 2-bracteate; corolla pubescent on adaxial surface; stamens exserted; filaments pubescent .... 4. *B. azorelloides*
– Flowers 4-bracteate; corolla glabrous on adaxial surface; stamens included; filaments glabrous .... 5. *B. sorianoi*
6\. Corolla with glandular hairs on abaxial surface 7
– Corolla glabrous 8
7\. Bracts connate at base; filaments glabrous, not widened at base .... 6. *B. graminifolia*
– Bracts not connate at base; filaments pubescent, widened at base .... 7. *B. chubutensis*
8\. Leaves and calyx-teeth lanate on margin 9
– Leaves and calyx-teeth ciliate on margin 10
9\. Style reaching mouth of corolla-tube; stigma at same level as uppermost anthers; disc generally present .... 8. *B. pycnophylloides*
– Style reaching middle of corolla-tube; stigma not exceeding level of insertion of filaments; disc absent .... 9. *B. lanata*
10\. Leaves and calyx-teeth truncate and glandular at apex; filaments didynamous. .... 10. *B. patagonica*
– Leaves and calyx-teeth acute and glabrous or with sparse simple hairs at apex; filaments equal or subequal 11

11. Leaf-sheath often somewhat widened at base; calyx pubescent on adaxial surface and tooth-margins .... 11. *B. nordenskjoldii*
 – Leaf-sheath distinctly widened at base; calyx glabrous on adaxial surface and tooth-margins .... 12. *B. longifolia*

1. **B. skottsbergii** Soriano, Fig. 2 A–C

Soriano, Darwiniana 8: 256 (1948).

Cushions dense. *Leaves* 2.0–2.5×0.5–1.0 mm, pubescent; sheat obovate, widened at base, hyaline; lamina linear, acute, rather thick. *Flowers* sessile, emerging above leaves. *Calyx* 2.0–2.5 mm, tubular, pubescent; teeth c. 0.75 mm, subequal, acute, pubescent on margin. *Corolla* 5.0–6.5 mm, tubular or somewhat infundibuliform, glabrous. *Stamens* (1) 2, included; filaments equal, inserted at same level, glabrous; staminodes 0–2. *Disc* absent. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: C Santa Cruz.

Material examined. Argentina: Santa Cruz; depto Corpen Aike, "in campo prope praedium Yvovich ad marginem vallis flum. Río Santa Cruz", Dusén 5530 (SI holotype); depto Lago Argentino, 25 km de El Cerrito hacia Calafate, Boelcke 12498 (BAB).

2. **B. azorella** (Skottsb.) Soriano, Fig. 2 D–F

Soriano, Darwiniana 8: 259 (1948).
Saccardophyton azorella Skottsberg, *K. Svenska Vet. akad. Handl. 56(5):* 297 (1916).

Cushions dense. *Leaves* 1.5–2.5×0.5 mm, pubescent; sheath linear, hyaline; lamina linear, acute, rather thick. *Flowers* sessile, hidden between the leaves. *Calyx* 2–3 mm, subcampanulate, pubescent on adaxial surface; teeth c. 1.25 mm, equal, acute, pubescent on margin. *Corolla* c. 4 mm, subtubular, glandular hairy on adaxial surface. *Stamens* 2, long exserted, emerging above leaves; filaments equal, inserted at same level, pubescent. *Disc* present. *Style* exserted.

Distribution. Argentina: C Santa Cruz, NW Neuquén. *Chile*: SE Magallanes.

Material examined. Argentina: Santa Cruz; depto Rio Chico, Patagonia Andina, parada de Lago Belgrano, Skottsberg 695 (S holotype); depto Deseado, R. P. 502, 10 km N Dos Manantiales, Boelcke et al. 16240 (BAB); depto Lago Argentino, Cerro El Calafate, cumbre 968 m.s.m., Sleumer 1179 (K, S); depto Güer Aike, Ea. La Verdadera Argentina, Cerro de La Virgen, al N. casco Ea, 1000 m.s.m. T.B.P.A. 2265, 2269 (BAB, RNG); Ea Las Vizcachas, lomada a 2 km de la laguna Vizcacha, T.B.P.A. 2383, 2577 (BAB, RNG); entre Lago Viedma y Arroyo Chadia, Dusén 6020 (S). Neuquén; depto Minas, Cordillera del Viento, filo N., Boelcke et al. 11549 (BAB). *Chile:* Magallanes; depto Ultima Esperanza, Sierra Baguales, Ea La Cumbre, co. Sin Nombre, T.B.P.A. 736, 776 (BAB, RNG).

3. **B. spegazziniana** Soriano, Fig. 2 J–L

Soriano, Darwiniana 8: 257 (1948).
Saccardophytum pycnophylloides Spegazzini, Anales Soc. Ci. Argent. 53: 181 (1902).

Cushions dense. *Leaves* 1.5–1.6×c.0.5 mm, with lanuginose hairs; sheath linear, hyaline; lamina linear, obtuse, rather thick. *Flowers* sessile, hidden between the leaves. *Calyx* c. 1 mm, subcampanulate, glabrous; teeth c. 0.5 mm, equal, obtuse, with lanuginose hairs on margin. *Corolla* c. 1.75 mm, subcampanulate, pubescent. *Stamens* 2, exserted, emerging above leaves; filaments equal, inserted at same level, glabrous. *Disc* present. Style included, usually reaching middle of corolla-tube.

Distribution. Argentina: C Santa Cruz.

Material examined. Argentina: Santa Cruz; depto Lago Argentino, Sehuenaik (R. Sehwey), 1897–98, Ameghino, s. n. (LPS 12513, LP holotype); "Rio Fosile in montibus, c. 1100 m.s.m." 6.1897, Dusén s. n. (K, S).

4. **B. azorelloides** Speg., Fig. 2 G–I

Spegazzini, Anales Soc. Ci. Argent. 53: 173 (1902).

Cushions dense. *Leaves* 1.5–5×c.0.5 mm, pubescent on margin; sheath linear, hyaline; lamina linear, obtuse, membranous. *Flowers* sessile, hidden between the leaves. *Calyx* 3.0–4.5 mm, subtubular, glabrous; teeth 1–2 mm, subequal, obtuse, pubescent on margin. *Corolla* 4–5 mm, tubular, pubescent on adaxial surface. *Stamens* 5, exserted, emerging above leaves; filaments subequal, inserted at same level, glabrous. *Disc* present. *Style* included, usually reaching top of corolla-tube, or exserted.

Distribution. Argentina: C Chubut.

Material examined. Argentina: Chubut; 1899, Illin s. n. (LPS, 12534, LP lectotype); depto Languineo, Vervoorst 5836 (BAB).

5. **B. sorianoi** S. Arroyo sp. nov., Fig. 3.

Holotypus. Argentina: prov. Santa Cruz; depto Güer Aike, Ea. Las Vizcachas, Ensenada de Riqués, 1700

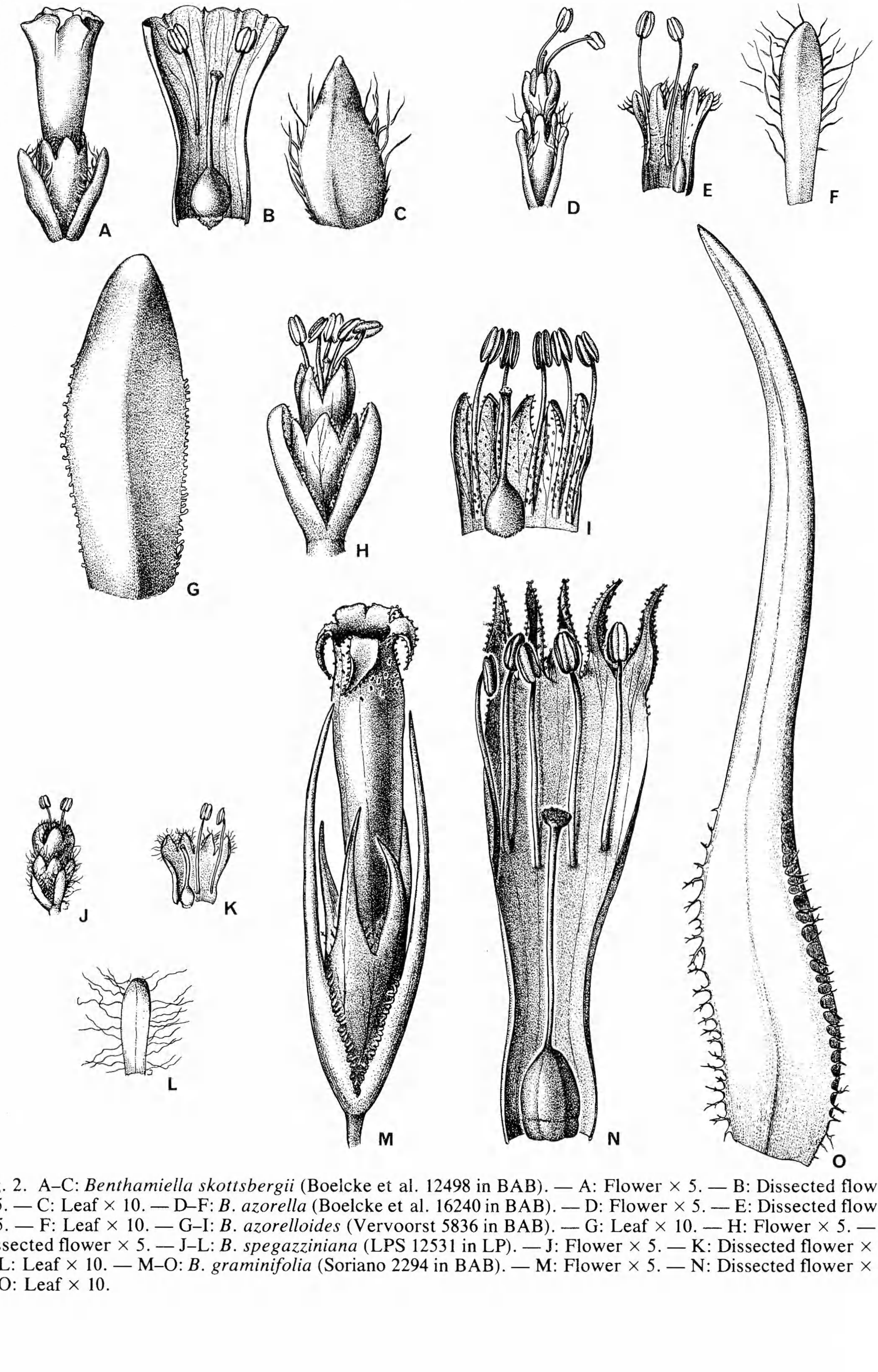

Fig. 2. A–C: *Benthamiella skottsbergii* (Boelcke et al. 12498 in BAB). — A: Flower × 5. — B: Dissected flower × 5. — C: Leaf × 10. — D–F: *B. azorella* (Boelcke et al. 16240 in BAB). — D: Flower × 5. — E: Dissected flower × 5. — F: Leaf × 10. — G–I: *B. azorelloides* (Vervoorst 5836 in BAB). — G: Leaf × 10. — H: Flower × 5. — I: Dissected flower × 5. — J–L: *B. spegazziniana* (LPS 12531 in LP). — J: Flower × 5. — K: Dissected flower × 5. — L: Leaf × 10. — M–O: *B. graminifolia* (Soriano 2294 in BAB). — M: Flower × 5. — N: Dissected flower × 5. — O: Leaf × 10.

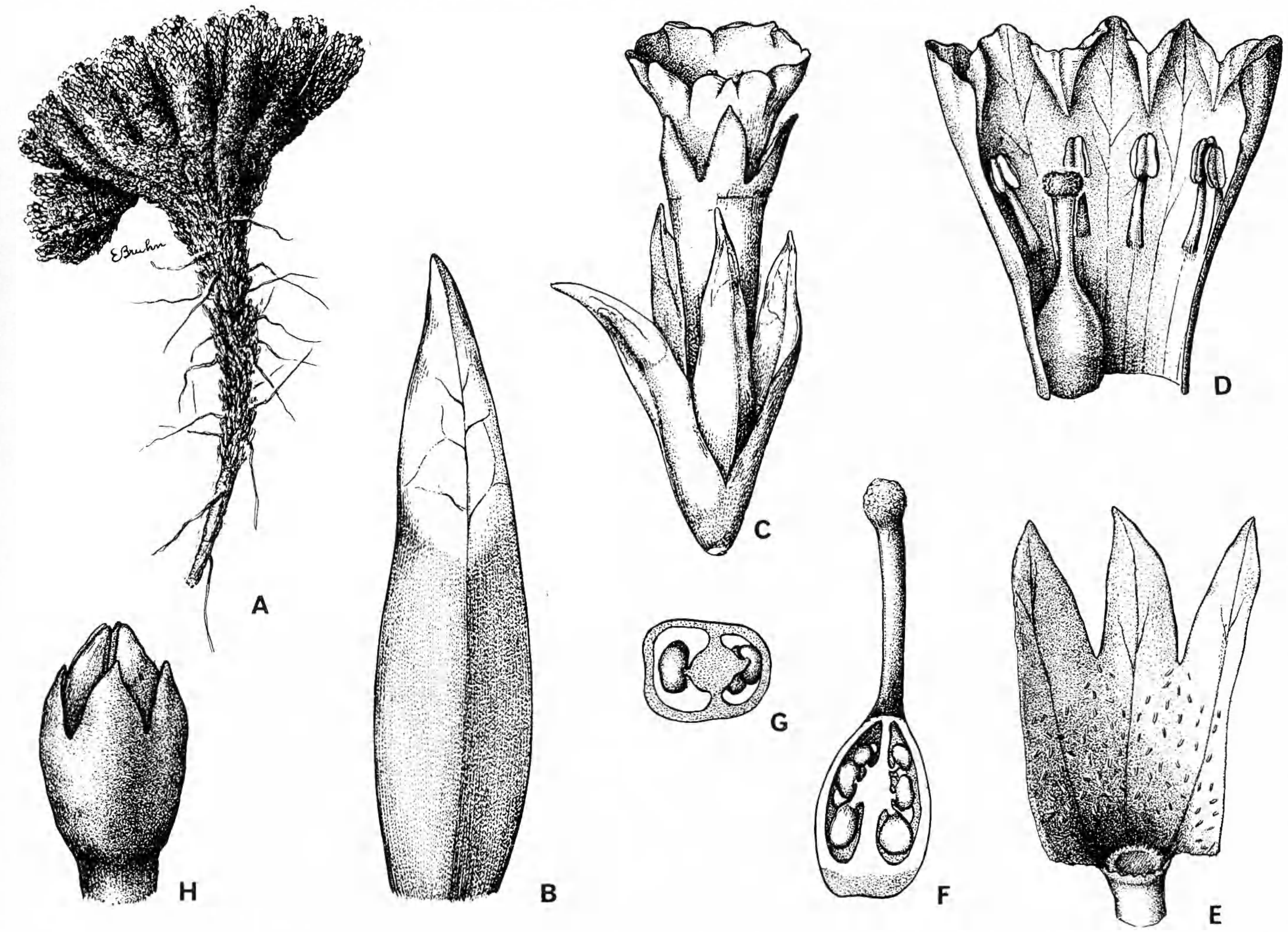

Fig. 3. A–H: *B. sorianoi* (Boelcke et al. T.B.P.A. 2711 in BAB, SI, RNG). — A: Cushion × 0.5. — B: Leaf × 10. — C: Flower × 5. — D: Dissected flower × 5. — E: Calyx; adaxial surface × 5. — F: Gynoecium with ovary in L.S. × 10. — G: Ovary in T.S. × 10. — H: Capsule × 10.

m.s.m. 50°45′ S, 72°12′ W, 30.1.1977, Boelcke et al., T.B.P.A. 711 (BAB).

Chamaephytum pulvinatum, ramosissimum, dense foliosum, hemisphaericum, 9 cm diam. 1,5–3,0 cm altum. Folia dense imbricata, crassiuscula adpressa, linearia vel anguste ovata, acuta, integerrima glabra vel margine pilosa. Flores in axillis foliorum superiorum solitarii et inter folia oculti sessiles vel brevissime pedunculati, bracteis plerumque 4 decussatis per paribus basi connatis, raro 3 basi connatis, 1 liberi. Calyx 3,5–4,5 mm. longus, campanulatus, externo glaber, interne glanduloso-pubescens. Corolla albescens 5–6 mm longa subinfundibuliformis, glabra, 5-lobata; lobulis ca. 0,5 mm longis. Stamina 5, inclusa, in dimian parte tubum inserta; filamentis aequilongis, ca. 1 cm. longis, glabris, ad insertionem leviter dilatatis; antheris dorsifixis, lato ellipticis, ca. 0,5 mm longis et latis. Discus brevis, inconspicuus. Ovarium globosum ca. 1 mm diam., 2-lobulare, pauci ovalatum; stylo 1,0–1,5 mm longo; stigmate capitato. Capsula 3,0–3.5 mm longa, 2 mm lata, ovoidea.

Pulvinate *chamaephyte*; cushions semihemispherical, c. 9.0×1.5–3.0 cm; stems woody, much branched, densely leafy. Lower *leaves* dead and blackened, the upper green, imbricate, adpressed, sessile, 6–12×1.5–2.0 mm, glabrous or pubescent on margin; sheath linear, hyaline; lamina linear to slightly ovate, acute, rather thick. *Flowers* hermaphrodite, axillary, borne singly, sessile or shortly pedunculate, obtended by 2 pairs of decussate, connate basal bracts, rarely 3 connate and 1 free. *Calyx* 3.5–4.5 mm, campanulate, glabrous on the abaxial surface and with glandular hairs on adaxial surface; teeth 1.0–2.5 mm, equal, acute. *Corolla* 5–6 mm, infundibuliform, whitish, 5-lobed, glabrous; lobes c. 0.50 mm, obtuse. *Stamens* 5, included; filaments c. 1 mm, equal, inserted at same level, glabrous, rather wide at the base; anthers c. 0.50×0.50 mm, dorsifixed, elliptical. *Disc* inconspicuous. *Ovary* c. 1 mm diameter, globose, 2-locular; ovules few; style 1.0–1.5 mm, erect, included; stigma capitate. *Capsule* 3.0–3.5×2 mm, ovoid; seeds 1–3 (4), fusiform with reticulate testa; embryo curved.

Distribution. Argentina: SW Santa Cruz.

Material examined. Argentina: Santa Cruz; depto Güer Aike, Ea. Las Vizcachas, Ensenada de Riqués, T.B.P.A. 2736 (BAB, RNG); depto Lago Argentino, Cerro Buenos Aires, Spegazzini 505, 582 (BAB).

Note (1). In the monograph of Soriano (1948) neither the material cited nor the plate given for *B. nordenskjoldii* agrees with the description, and must be referred to *B. sorianoi*. Soriano's description of *B. nordenskjoldii* agrees well with the original description (Brown 1900) and with the type specimen.

Note (2). This new species reinforces Soriano's opinion that *Saccardophytum* Speg. and *Benthamiella* are congeneric since, together with *B. skottsbergii*, *B. azorelloides* and *B. pycnophylloides*, it shows characters intermediate between those used to separate the two genera: *Benthamiella*, with 5 included stamens, the corolla 3 times as long as the calyx and erect ovules, and *Saccardophytum*, with 2 exserted stamens, the corolla 1.5 times as long as the calyx and pendent ovules.

6. **B. graminifolia** Skottsb., Fig. 2 M–O

Skottsberg, K. Svenska Vet. akad. Handl. 56(5): 297 (1916).

Cushions dense. *Leaves* 15–18×0.5–1.5 mm, pubescent; sheath 4–5×c.1.5 mm, obovate membranous, with simple or branched hairs on margin; lamina 11–13×c. 0.5 mm, linear, acute, membranous or coriaceous. *Flowers* sessile, emerging above leaves, subtended by 1 pair of decussate, connate basal bracts. *Calyx* 9–11 mm, tubular, pubescent on adaxial surface; teeth 5–7 mm, subequal, acute, with simple or branched hairs on margin. *Corolla* 14–16 mm, tubular to slightly ventricose, with glandular hairs distally on abaxial surface. *Stamens* 5, included; filaments subequal, inserted more or less at same level, glabrous. *Disc* present. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: W Chubut, Río Negro.

Material examined. Argentina: Rio Negro; depto Norquinco, Skottsberg 536 (holotype S). Chubut; depto Languiñeo, Quichaura, 40 km al E de Tecka, Soriano 2294 (BAB), Illin sn. (BAB 10474). Lago Gral. Paz, 1908, Skottsberg s. n. (S).

7. **B. chubutensis** Soriano, Fig. 4 A–C

Soriano, Darwiniana 8: 253 (1948).

Cushions lax. *Leaves* 5–13×1.0–1.5 mm, pubescent; sheath 3–4×c.1.5 mm, broadly linear or subovate, membranous, with short and branched hairs on margin; lamina 3–9×c.1 mm, linear, acute. *Flowers* sessile, hidden between the leaves. *Calyx* 5.0–7.5 mm, tubular, pubescent on adaxial surface; teeth c. 3.5 mm, equal, acute, with hairs similar to those of the leaves. *Corolla* 11.0–12.5 mm, tubular, with glandular hairs on abaxial surface, especially distally. *Stamens* 5, included; filaments equal or subequal, inserted at same level, wider at base, with small, lanuginose basal appendages. *Disc* inconspicuous. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: Chubut.

Material examined. Argentina: Chubut; Travesía de Rawson à la cordillera, 30.1.1903, Illin 29 (SI holotype).

8. **B. pycnophylloides** Speg., Fig. 4 D–F

Spegazzini, Revista Fac. Agron. Veterin. La Plata 30–31: 556 (1897).

Cushions dense. *Leaves* 2.5–4×c.1.5 mm, pubescent; sheath 1.5–2.5×c. 1 mm, obovate to narrowly obovate, hyaline; lamina 1.0–1.5×c. 1 mm, linear, acute, membranous, with lanuginose hairs on margin. *Flowers* sessile, emerging above leaves. *Calyx* 3–5 mm, subcampanulate, pubescent; teeth c.1.5 mm, equal, acute, with hairs similar to those of leaves. *Corolla* 6–8 mm, tubular, glabrous. *Stamens* 5, included; filaments subequal to didynamous, inserted at same level, glabrous. *Disc* inconspicuous. *Style* included, as long as the corolla-tube.

Distribution. Argentina: CW Chubut, W and E Santa Cruz.

Material examined. Argentina: Santa Cruz; depto Deseado, Golfo San Jorge, II.1896, Ameghino s. n. (LPS), 12601 (LP holotypus); depto Tehuelches, Donat 191 (K, MO, S, SI); camino Tellier á Paso Gobernador Gregores, R.P. 282 km 57, Correa et al. 2645 (BAB); 8 km Cabo Blanco hacia Tellier, Correa et al. 3349 (BAB); depto Lago Argentino, Fitz Roy, Vervoorst 5654, 5646 (BAB); entre Lago Viedma y Laguna Tar, c. 1000 m.s.m., Dusén 6020 (K); depto Magallanes, camino á San Julián, Correa et al. 3501 (BAB); Puerto San Julián, Blake 260 (K); depto Corpen Aike, Dusén 5530 (K); depto Tehuelches, Jaramillo, Crespo & Troncoso 1684 (BAB).

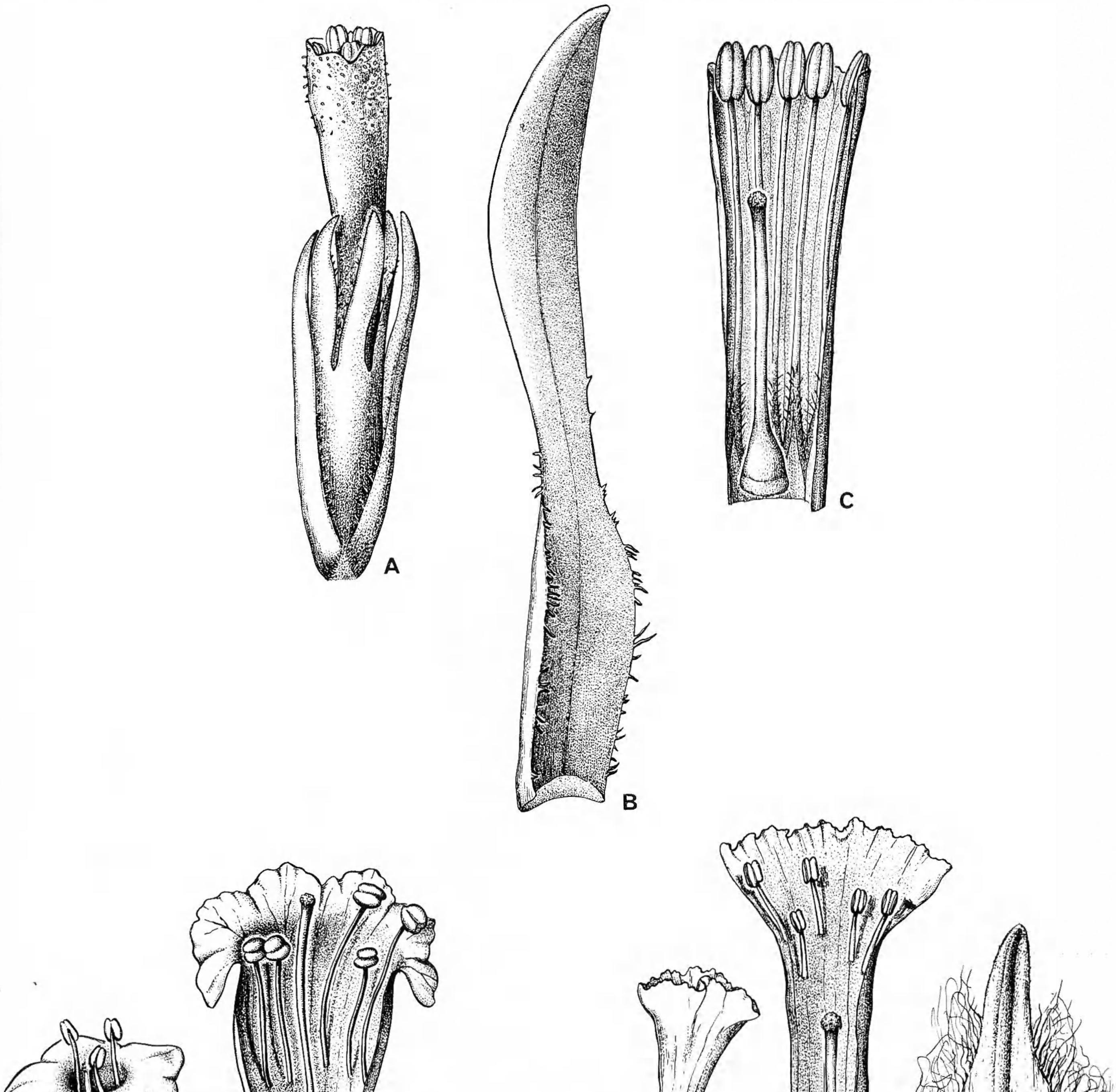

Fig. 4. A–C: *B. chubutensis* (Illin 29 in BAB). — A: Flower × 5. — B: Leaf × 10. — C: Dissected flower × 5. — D–F: *B. pycnophylloides* (Correa et al. 3349 in BAB). — D: Flower × 5. — E: Dissected flower × 5. — F: Leaf × 10. — G–I: *B. lanata* (Soriano 2066 in SI). — G: Flower × 5. — H: Dissected flower × 5. — I: Leaf × 10.

9. **B. lanata** Soriano, Fig. 4 G–I

Soriano, Darwiniana 8: 249 (1948).

Cushions dense. *Leaves* 6.0–8.5×0.5 mm, pubescent; sheath 3.5–4.5 mm, narrowly obovate, hyaline; lamina 2.5–3.5×0.5 mm, linear, obtuse, membranous, with lanuginose hairs on margin. *Flowers* sessile, emerging above leaves. *Calyx* 4.0–4.5 mm, tubular to subcampanulate, glabrous; teeth 2 mm, equal, acute, with hairs similar to those of the leaves. *Corolla* 7.0–8.5 mm, tubular to subcampanulate, glabrous. *Stamens* 5, included; filaments didynamous or subequal, often inserted at 2 well-defined levels, glabrous. *Disc* present. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: SE Chubut.

Material examined. Argentina: Chubut; depto Escalante, camino de Comodoro Rivadavia à las Heras, en la pampa, Soriano 2066 (SI holotype).

10. **B. patagonica** Speg., Fig. 5 D–F

Spegazzini, Anales Soc. Argent. 35: 110 (1883).
B. montana Dusén, Ark. Bot. 7(2): 35 (1908).
B. abietina Skottsberg, K. Svenska Vet. akad. Handl. 56(5): 295 (1916).
B. intermedia Skottsberg, loc. cit.: 296.
B. aurea Skottsberg, loc. cit.: 296.

Cushions lax. *Leaves* 6–12×0.75–1.50 mm, pubescent; sheath 3.5–6.5×1.0–2.5 mm, obovate, hyaline, with short hairs on margin; lamina 2.5–6.0 mm, linear to narrowly lanceolate, truncate, glandular, with short hairs on margin and on abaxial surface. *Flowers* sessile or shortly pedunculate, emerging above the leaves. *Calyx* 4–7 mm, tubular to subcampanulate, pubescent on adaxial surface; teeth 1–2 mm, subequal, truncate, with short hairs on margin. *Corolla* 9–13 mm, tubular, with glandular hairs on adaxial surface. *Stamens* 5, included; filaments didynamous or sebequal, often inserted at 2 well-defined levels or all at different levels, glabrous. *Disc* present. *Style* included, usually reaching middle of corolla-tube, sometimes shorter.

Distribution. Argentina: S and C Chubut to S Santa Cruz. *Chile:* SE Magallanes.

Material examined. Argentina: Santa Cruz; depto Lago Buenos Aires, "Lago San Martín, río Fosiles in montanus ad benan nudan, c. 1000 m.s.m. April 1905", Dusén 6318 (K, holotype of *B. montana*; S, isotype); Río Zeballos, c. 1500 m.s.m., Skottsberg 686 (S, holotype of *B. abietina*), Patagonia Andina, Valle Frias y Arroyo Apelej, Skottsberg 589, (S, holotype of *B. aurea*), Río Fenix, Skottsberg 763 (S, holotype of *B. intermedia*), s. c., s. n. (LPS); 12620 (LP, holotype of *B. patagonica*); depto Corpen Aike, Piedra Buena, 11 km al S., Boelcke et al. 12295 (BAB); depto Río Chico, entre Cañadón León y Casa Riera, Vervoorst 5747 (BAB); depto Magallanes, Puerto San Julián, Blake 259 (K); depto Deseado, Puerto Nazareno, Dusén 5261 (BM, K, S), Puerto Deseado, O'Donell 3562 (K), 3935 (BM, S); depto Güer Aike, Ea. Los Posos, T.B.P.A. 133 (BAB, RNG), Laguna La Leona, T.B.P.A. 241 (BAB, RNG), Ea. Las Vizcachas, T.B.P.A. 2578, 2580 (BAB, RNG), lomada á 2 km de laguna Las Vizcachas, T.B.P.A. 2370, (BAB, RNG); Prov. Chubut, depto Río Senguerr, 6.5 km al N de alto de Río Senger, Boelcke et al. 12987 (BAB); depto Escalante, Ea. la Begonia, Krapovickas 4559 (BAB); depto Tehuelches R. 19 a 21 km NE Gdor. Costa, Arroyo et al. 416 (BAB), Donat 41 (BM, K, MO,S); depto Paso de Indios, a 51 km SO, R. 24 Ea. La Marfil, Arroyo et al. 209 (BAB). *Chile*: Prov. Magallanes; depto Ultima Esperanza, Sierra Baguales, cerro Cono, T.B.P.A. 774 (BAB, RNG).

In his revision Soriano (1948) demonstrated the affinities between *B. patagonica, B. montana, B. abietina, B. aurea* and *B. intermedia*, and suggested that they might better be treated as one species with 4 varieties. A study of the type specimens and the wider range of material now available supports the suggestion of Soriano and leads me to consider all these taxa as being conspecific and the name given by Spegazzini, *B. patagonica*, has priority.

11. **B. nordenskjoldii** Dusén ex N. E. Brown, Fig. 5 G–J

Brown, Hooker's Icon. Plant. ser. 4.7(2): 2636 (1900).

Cushions lax. *Leaves* 6–10×0.75–2.00 mm, glabrous; sheath 3–5×c. 1.75 mm, oblanceolate, hyaline, glabrous; lamina 3–5×0.75–1.0 mm, linear, acute, rather thick, glabrous or subglabrous on margin. *Flowers* sessile or shortly pedunculate, emerging above leaves. *Calyx* 4–5 mm, slightly campanulate to tubular, pubescent on adaxial surface; teeth 1.0–1.5 mm, equal, acute, the margin with pubescence similar to that of leaves. *Corolla* 9–11 mm, tubular, glabrous. *Stamens* 5, included; filaments equal or subequal, inserted at the same level, glabrous. *Disc* present. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: Santa Cruz, NE Tierra del Fuego. *Chile*: C Magallanes.

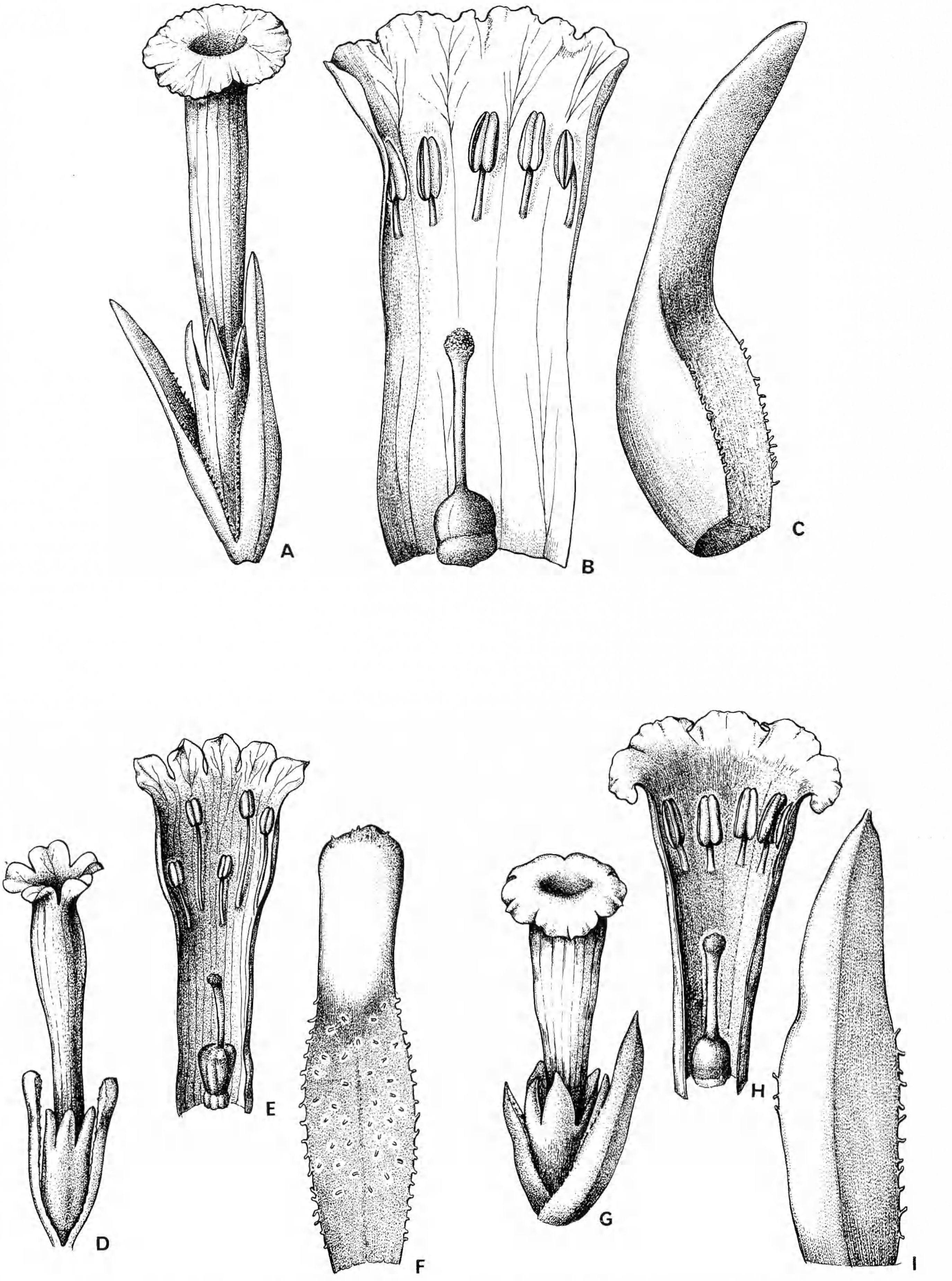

Fig. 5. A–C: *B. longifolia* (Donat 288 in S, K, MO). — A: Flower × 5. — B: Dissected flower × 5. — C: Leaf × 10. — D–F: *B. patagonica* (Correa et al. 6539 in BAB). — D: Flower × 5. — E: Dissected flower × 5. — F: Leaf × 10. — G–I: *B. nordenskjoldii* (Boelcke et al. T.B.P.A. 2706 in BAB, RNG). — G: Flower × 5. — H: Dissected flower × 5. — I: Leaf × 10.

Material examined. Argentina: Patagonia Austral, XII.1896; Santa Cruz; Nordenskjöld (K, holotypus), depto Güer Aike, Ea Las Vizcachas, Ensenada de Riqués, al fondo, T.B.P.A. 2706. (BAB, RNG); Ea Las Vizcachas, lomada a 2 km de laguna Las Vizcachas, T.B.P.A. 2371 (BAB, RNG), Sierra Los Baguales, Skottsberg 722 (SANT, S, BAB); Tierra del Fuego; depto Río Grande, Ea El Salvador, Boelcke et al. 15092 (BAB), Ea San Julio, Cerro Hongo, Goodall 4281 (RNG), 3 km NE, El Salvador, Moore 2563 (RNG), sin localidad, Castellanos s.n. (BA 45737).

Note (1). The most southerly occurrence of *Benthamiella*, in Tierra del Fuego, was referred to *B. patagonica* by Moore and Goodall (1974). The clarification of the features of *B. nordenskjoldii* in the present study shows that the Fuegian material correctly belongs to this species.

Note (2). From the remarks on the route followed by Skottsberg in his journey of 1909 (Skottsberg 1911), his material cited above from Sierra Baguales almost certainly was collected in the valley of the Rio Centinela. The locality probably was on the Argentinian side of the frontier, where other collections are known, but it may have been in the Chilean part of the valley.

12. **B. longifolia** Speg., Fig. 5 A–C

Spegazzini, Revista Fac. Agron. Veterin. La Plata 30–31: 555 (1897).
B. acutifolia Spegazzini, loc. cit.

Cushions lax. *Leaves* 10–16×0.75–2.50 mm, glabrous; sheath 3–5×1.5–2.5 mm, obovate, hyaline; lamina 5–8×0.75–1.50 mm, linear, acute, rather thick, glabrous to subglabrous on margin. *Flowers* sessile or shortly pedunculate, emerging above leaves. *Calyx* 4–7 mm, tubular to subcampanulate, glabrous; teeth 3.0–4.5 mm, equal, acute, glabrous. *Corolla* 9–15 mm, tubular, glabrous. *Stamens* 5, included; filaments unequal, inserted at different levels, glabrous. *Disc* present. *Style* included, usually reaching middle of corolla-tube.

Distribution. Argentina: W and E Santa Cruz.

Material examined. Argentina: Santa Cruz; depto Deseado, Golfo San Jorge, II.1896, Ameghino s. n. (LPS 12619, LP holotype, LPS 12622, LP holotype of *B. acutifolia*); depto Magallanes, San Julián, Blake 90, 119, 134, 139, 319, 320 (K); depto Lago Buenos Aires, El Calafate, Sleumer 1180 (K, S), Donat 288 (K, MO, S).

In his original descriptions Spegazzini (1897) noted the affinity between *B. longifolia* and *B. acutifolia* but considered them as specifically distinct on the basis of leaf-width, shape of the leaf-apex and pubescence. These have not proved to be constant or reliable characters in the present study and *B. acutifolia* is consequently reduced to synonymy.

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References

Brown, N. E. 1900: Benthamiella nordenskjoldii Dusén, Sp. nov. *Hooker's Icones Plant. ser. 4, 7 (2):* pl. 2636.

Cabrera, A. L. 1971: Fitogeografía de la República Argentina. *Bol. Soc. Argent. Bot. 14(2):* 1–42.

Correa, M. N. (ed.) 1969: *Flora Patagonica* II. Buenos Aires.

Correa, M N. (ed.) 1971: *Flora Patagonica* VII. Buenos Aires.

Correa, M. N. (ed.) 1978: *Flora Patagonica* III. Buenos Aires.

Moore, D. M. & Goodall, R. N. 1974: Further additions to the native vascular flora of Tierra del Fuego. *Bot. Notiser 127:* 38–43.

Skottsberg, C. J. F. 1911: *The Wilds of Patagonia.* London.

Skottsberg, C. J. F. 1916: Benthamiella Speg. and Saccardophytum Speg. *Bot. Jahrb. Syst. 54 (1):* 44–50.

Soriano, A. 1948: El género Benthamiella (Solanaceae). *Darwiniana 8:* 233–262.

Spegazzini, C. 1883: Plantae novae nonnullae america australis. *Anales Soc. Ci. Argent. 15:* 97.

Spegazzini, C. 1897: Plantae Patagoniae australis. *Revista Fac. Agron. Veterin. La Plata 30–31:* 485–589.

Notes on the lichen genus Baeomyces in New Zealand

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Galloway, D. J. 1980 03 17: Notes on the lichen genus Baeomyces in New Zealand. *Bot. Notiser 133:* 77–83. Stockholm. ISSN 0006-8195.

Three species of *Baeomyces* Pers., occur in New Zealand viz. *B. absolutus* Tuck., *B. fungoides* (Sw.) Ach., and *B. heteromorphus* Nyl. ex Bab. & Mitt. in Hook. f. A key to species is given together with details of their morphology, chemistry, distribution, habitat and taxonomy. The following taxa are rejected as synonyms: *B. arcuatus* Stirt., *B. subgranosus* Stirt. *(B. fungoides), B. cupreus* Müll. Arg., *B. cinnabarinus* Zahlbr., *B. fuscocarneus* F. Wils., *B. granosus* Stirt., *B. haemotropus* Leighton, *Cladoniopsis caespitosa* Zahlbr. *(B. heteromorphus), B. novaezelandiae* Knight *(B. absolutus).*

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Baeomyces is a cosmopolitan genus of some 44 species which is, together with the genus *Icmadophila* Trevis., included in the family Baeomycetaceae Fée (Frey 1933, Thomson 1967, Jahns 1970, Imshaug 1972, Henssen & Jahns 1973, Poelt 1974). The genus was founded by Persoon (1794) and its typification discussed by Imshaug (1972). *Baeomyces* is defined by the following characters: *Primary thallus* crustose, squamulose or marginally foliose, attached by medullary hyphae or rhizines. *Podetia* supporting apothecia, simple or 1–4 branched towards apices in some species, scarcely developed in other species. *Algal layer* in primary thallus continuous, algae green, *Cystococcus. Apothecia* round, swollen, or expanded, on tips of podetia, often clustered on ± distinct stalks. *Spores* fusiform or ellipsoid, colourless, simple or 1–4-septate, 8 per ascus.

Discovery of Baeomyces in New Zealand

Hooker & Taylor (1844) first recorded *Baeomyces* from New Zealand, using the Northern Hemisphere name *B. rupestris* Pers., for the undescribed Southern Hemisphere species *B. heteromorphus*. Although Nylander (in Babington & Mitten 1859) described *B. heteromorphus* from Tasmania, he named the New Zealand material of this species *B. rufus* (Nylander 1860).

Nineteenth century botanists in New Zealand made frequent collections of *B. fungoides*, naming it *B. roseus* (Babington 1855, Nylander 1860, Hooker 1867). Babington recognised the affinity of the Northern Hemisphere *B. roseus* with the Jamaican lichen *B. fungoides* (Fig. 1) collected by Swartz in 1782, noting in his account of the New Zealand lichens "... Swartz's lichen from Jamaica does not seem to be more than a variety of the European; an authentic specimen is to be seen in the BM. Found also in North America. Mr Colenso's plant has much longer podetia than the European forms and would probably be called *B. fungoides* by those who distinguish two species ..."

Taylor (1972) on the basis of comparing the variation in width of apothecia and length of stipe in collections of *B. roseus* and *B. fungoides*, concludes that the two taxa are conspecific with the earlier epithet *fungoides* taking priority. This is an erroneous view since the thallus of each species is distinctive and separable even when sterile. *B. roseus* has a coarsely granular thallus ± covered with flattened verrucose or ± spherical isidiate projections and is never truly sorediate, whereas *B. fungoides* has a thallus that is scurfy, leprose and ± consistently white-sorediate.

B. haemotropus was described from New Zealand by William Leighton (1869) but is merely a form of *B. heteromorphus*. The Scottish lichenologist James Stirton added several species of *Baeomyces* to the New Zealand flora

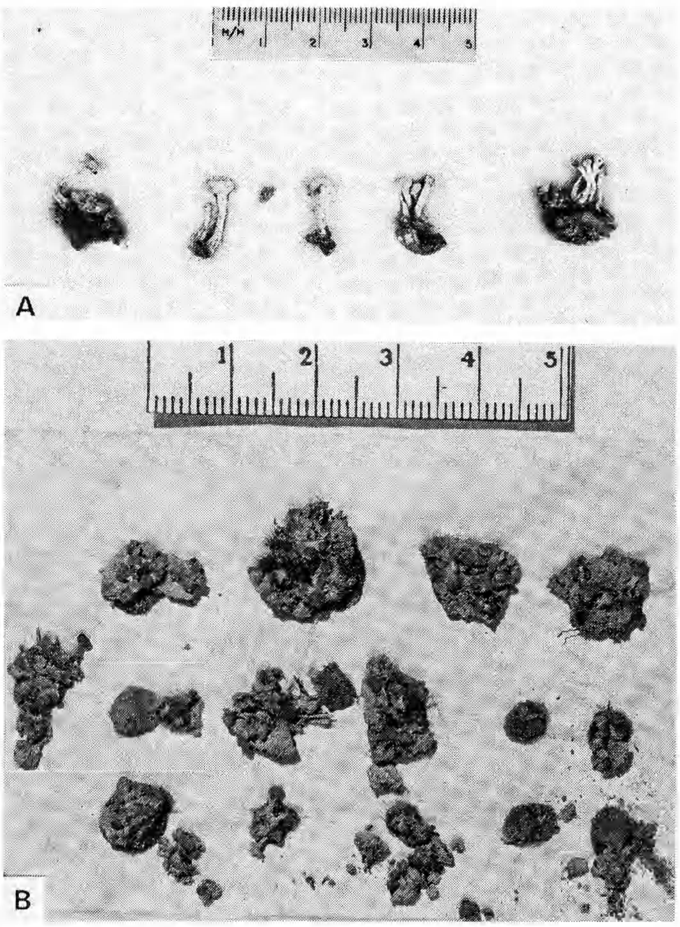

Fig. 1. A: *Baeomyces fungoides*, Jamaica, Swartz (UPS-THUNBERG, isotype). — B: *B. heteromorphus*, Tasmania, Gunn (BM, lectotype). Scale in mm.

but in my opinion not one of them can be upheld today. *B. pertenuis* Stirt., (Stirton 1873, 1874) is not a *Baeomyces* at all but *Dimerella lutea*, an error recognized by Charles Knight (1875) who however renamed it *Lecidea planella*. *B. arcuatus* Stirt., and *B. subgranosus* Stirt. (Stirton 1875) are now referable to *B. fungoides*, and *B. granosus* Stirt., to *B. heteromorphus*. Charles Knight (1883) described *B. novaezelandiae* for New Zealand material referable to *B. absolutus*.

Although the 19th century catalogues of New Zealand lichens (Nylander 1888, Müller Argoviensis 1894, Hellbom 1896) contain a profusion of names in *Baeomyces*, in my opinion they define only three species. Zahlbruckner (1941) described both *B. cinnabarinus* and *Cladoniopsis caespitosa* (see also Lamb 1953) for differing forms of *B. heteromorphus*. The most recent account of *Baeomyces* in New Zealand (Martin & Child 1972) lists five species, two of which however I consider to be synonyms of *B. heteromorphus*.

Baeomyces is divided into two subgenera based on the ontogeny of the apothecium (Müller Argoviensis 1862, Frey 1933, Lamb 1963, Thomson 1967, Jahns 1971, Jahns & Smittenberg 1970, Jahns & Horst-Iwema 1972). These are defined by Thomson (1967) as subgen. *Baeomyces* (Müll. Arg.) J. W. Thoms., "... Apothecia originating in the medulla, the podetia containing no algae, almost hollow or with a very loose arachnoid medulla, very soon emarginate and spherical; hypothecium not distinct from stalk of the podetium ...", and subgen. *Sphyridium* (Flotow) Müll. Arg. "... Apothecia originating exogenously from the algal and cortical layers of the thallus, the podetia containing algae; the stipe horny, solid, the only cavities formed by fissures; apothecia remaining flat with a distinct margin, the thecium visibly distinct".

Habitat

The three species of *Baeomyces* discussed below are, in New Zealand, successional plants characteristic of disturbed habitats such as landslides, mountain tracks, river gravels, roadside verges and coastal cliffs. *B. heteromorphus* shows considerable variation in morphology throughout its range of distribution in New Zealand and this diversity in form is reflected in a confused nomenclature.

Materials

In the present account, all published taxa relating to *Baeomyces* in New Zealand have been re-examined. All relevant 19th century collections from New Zealand were checked, and numerous collections made from 1925 to the present were investigated. These later collections range from Northland (Lat. 36°30′ S) to Stewart Island (Lat 47° S). Type and other material was obtained from the following herbaria: BM, CANU, CHR, FH, GLAM, H-ACH, H-NYL, OTA, S, UPS, UPS-ACH, UPS-THUNBERG, UPSV, W, and WELT.

Chemistry

Hot acetone extracts of most species examined were analysed by thin-layer chromatography using the method of Culberson (1972).

Key to Baeomyces in New Zealand

1. Primary thallus greyish-white ± granulose, leprose, ecorticate, sorediate, apothecia capitate, immarginate .... 1. *B. fungoides*

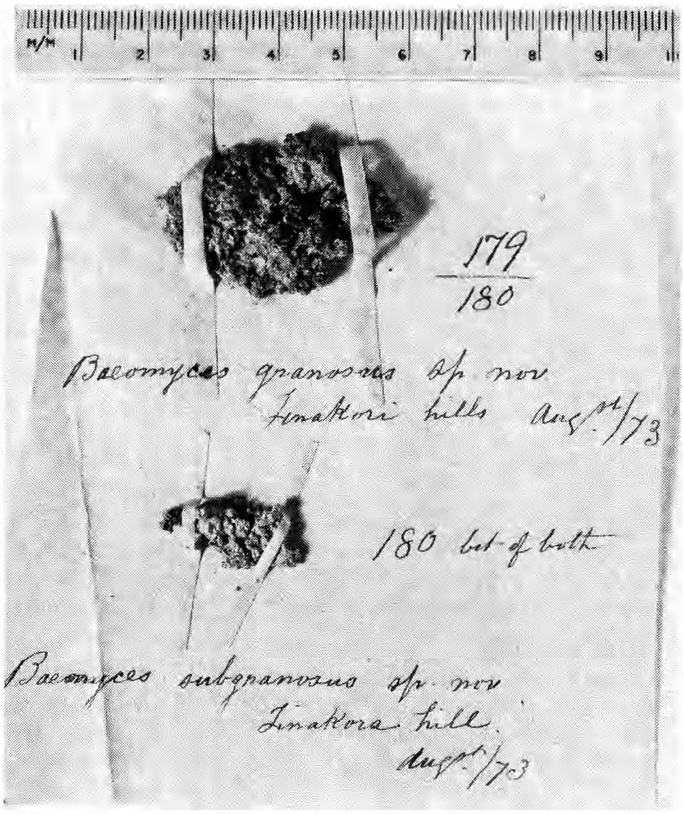

Fig. 2. *Baeomyces granosus* (isolectotype) and *B. subgranosus* (lectotype), New Zealand, John Buchanan (WELT). Scale in mm.

- Primary thallus green or greenish-yellow, corticate, not sorediate, apothecia marginate 2
2. Apothecia sessile, solitary, disc pale rose-pink, white-pruinose .... 2. *B. absolutus*
- Apothecia on well developed stalks, clustered, disc red-brown to orange-red, not pruinose .... 3. *B. heteromorphus*

1. **Baeomyces fungoides** (Sw.) Acharius 1803 p. 320.

Basionym: *Lichen fungoides* Swartz, 1788 p. 146 — Orig. coll.: Jamaica, O. P. Swartz (UPS-THUNBERG! Fig. 1 A: BM-ACH! H-ACH! isotypes). Taylor (1972) discusses a type collection from Swartz's herbarium (S) which must be presumed to contain a lectotype selected by him, but I have not seen the material and no authentic *B. fungoides* from Jamaica labelled by Swartz (as *Lichen fungoides*) was seen in visits made to Stockholm in 1974, 1978 and 1979.

Baeomyces arcuatus Stirton 1875 p. 460 — Orig. coll.: New Zealand, near Wellington, J. Buchanan 28/74 (BM! lectotype, here designated).

Baeomyces subgranosus Stirton 1875 p. 460 — Orig. coll.: New Zealand, Tinakori Hills, VIII.1873, J. Buchanan 180 (WELT! lectotype, here designated. Fig. 2).

Primary thallus whitish or greyish-white, crustose, scurfy, ecorticate, in parts densely white-sorediate. *Podetia* simple, to 2 cm tall, terete or compressed, surface rather scabrid, vertically grooved, pale whitish-pink. *Apothecia* terminal, globose, capitate, often convoluted, pale flesh-pink to orange-pink, convex, without a defined margin, surface rather finely warted. *Spores* fusiform, 1-septate, 12–30×2–4μm.

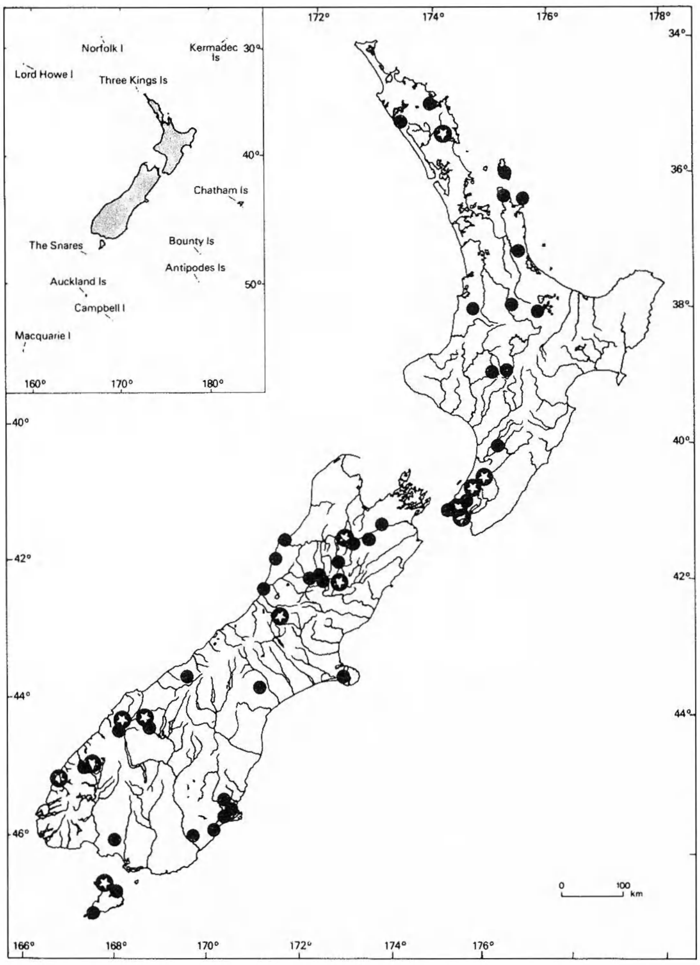

Fig. 3. Known New Zealand distribution of *Baeomyces absolutus* (✪) and *B. fungoides* (●).

Chemistry. Thallus and podetia K+ yellow, C–, KC–, Pd+ yellow turning orange. Baeomycesic and squamatic acids (UV + white).

Habitat and distribution. B. fungoides is a tropical species occurring in the West Indies, Central and South America, Hawaii, Australia and New Zealand. A characteristic substrate is clay or clay soils. It is frequently seen along roadside cuttings where it is often a component in the succession involved in revegetation. It is rarely found on rock, bark or litter. Distribution in New Zealand is wide (Fig. 3) and it occurs from sea level to 1000 m. Ontogenetic studies place *B. fungoides* in subgen. *Baeomyces* (Jahns & Smittenberg 1970, Jahns & Horst-Iwema 1972).

Specimens examined. Northland: Kawerua, 1973, B. W. & G. C. Hayward (CHR) see Hayward & Hayward (1974 b) — Bay of Islands, Paton (BM) — *Central Auckland*: Great Barrier Island, 1972, B. W. & G. C. Hayward (CHR) see Hayward & Hayward (1973 a, 1973 b) — Rangitoto Island, 1936, H. H. Allan (CHR) — *South Auckland Bay of Plenty*: Mt Moehau, Coromandel Peninsula, 1974, B. W. & G. C. Hayward (CHR) see Hayward et al. (1975) — Great Mercury Island, 1975, B. W. & G. C. Hayward (CHR) see Hayward et al. (1976) — Mt Te Aroha, 1936, H. H. Allan (CHR) — Mangaotaki Valley, 1972, D. J. Galloway (CHR) — Maraetai, 1966, A. E. Wade (BM) — Kaingaroa Plains, 1937, K. W. Allison (CHR) — *Wellington*: Ohakune, 1938, J. E. Attwood (CHR) — Ruahine Range, Wharite Peak, 1972, D. J. Galloway (CHR) — Tararua Range, Field Hut, 1971, D. J Galloway (CHR) — Wellington Botanic Gardens, 1956, W. Martin (CHR) — Tinakori Hills, Wellington, 1873, 1874, J. Buchanan (BM, WELT) — *Nelson*: St Arnaud Range, 1977, J. Singleton (CANU) see Galloway & Simpson (1978) — Hopeless Creek, 1972, L. F. Molloy (CHR) — Maruia Valley, 1978, D. J. Galloway (CHR) — Mt Haast, 1978, D. J. Galloway (CHR) — *Marlborough*: Wairau Valley, 1956, W. Martin (CHR) — Leatham River, 1956, W. Martin (CHR) — *Canterbury*: Lewis Pass, 1978, D. J. Galloway (CHR) — Okuti Valley, Banks Peninsula, 1977, D. J. Galloway (CHR) — Mt Peel, 1972, D. J. Galloway (CHR) — *Westland*: Aorangi Scenic Reserve, Greymouth, 1958, W. Martin (CHR) — Punakaiki, 1961, W. Martin (CHR) — *Otago*: Humboldt Mountains, 1965, D. J. Galloway (CHR) see Galloway (1966) — Matukituki Valley, 1957, R. Smith (OTA) — Swampy Hill, Dunedin, 1971, W. Martin (CHR) — Mt Maungatua, 1954, J. Murray (OTA) — Balclutha, 1955, J. Murray (OTA) — *Southland*: Lake Thomson, Fiordland, 1962, P. W. James (BM) see Mark et al. (1964) — Makarewa, 1961, D. J. Galloway (CHR) — Oban, Stewart Island 1964, D. J. Galloway (CHR) — Frazer Peaks and Port Pegasus, Stewart Island, 1967, D. J. Galloway (CHR).

2. **Baeomyces absolutus** Tuckerman 1859 p. 201

Orig. coll.: Moulton, Alabama, 139 Mr Peters (FH! holotype) — *Tubercularia absolutus* (Tuck.) O. Kuntze 1891 p. 877.

Baeomyces novaezelandiae Knight 1883 p. 348 — Orig. coll.: New Zealand, sine loco, Charles Knight (WELT! lectotype, here designated) — *Baeomyces absolutus* var. *subsessilis* Müller Argoviensis 1894 p. 25 — *Baeomyces* var. *novaezelandiae* (Knight) Zahlbruckner 1926 p. 408.

Primary thallus thin, varnish-like, bright emerald-green when fresh, pale olive or yellowish when dry. *Podetia* absent or very poorly developed. *Apothecia* sessile, or very shortly stalked, whitish-pink, disc minutely wrinkled-scabrid, matt, ± white-pruinose, 1–3 mm in diam., flat or slightly convex, thinly marginate or immarginate. *Spores* oblong or fusiform-ellipsoid, uniseriate or biseriate, colourless, simple, 7–15×4–5 μm, 8 per ascus.

Chemistry. Thallus and apothecia K+ yellow, C–, Pd–. Baeomycesic acid.

Habitat and distribution. *B. absolutus* grows on rocks and rarely on sandy soil, in shaded moist habitats and in New Zealand is found from sea level to 1000 m (Fig. 3). It is a tropical species known from the West Indies, Central America, the United States, Brazil, Ecuador, Japan, the Philippines (Thomson 1967), south-eastern Australia and New Zealand. It is placed in subgen. *Baeomyces* (Jahns & Horst-Iwema 1972).

Specimens examined. *Northland*: Whangarei, W. A. Given (CHR) — *Wellington*:Tararua Range, 1932, E. M. Heine (CHR) — *Nelson*: Lake Rotoiti, 1977, D. J. Galloway (CHR) see Galloway & Simpson (1978) — Lake Daniells track, 1978, D. J. Galloway (CHR) — *Canterbury*: Arthurs's Pass, 1962, P. W. James (BM) — Boyle River, 1979, D. J. Galloway (CHR) — *Otago*: Matukituki Valley, Mt French, 1967, D. J. Galloway (CHR) — Humboldt Mountains, 1965, D. J. Galloway (CHR) see Galloway (1966) — *Southland*: Secretary Island, 1959, J. Murray (OTA) see Murray (1963) — Lake Thomson, Fiordland, 1962, P. W. James (BM) see Mark et al. (1964) — Mt Anglem, Stewart Island, 1966, D. J. Galloway (CHR) see Galloway (1968 a).

3. **Baeomyces heteromorphus** Nyl. ex Bab. & Mitt. in Hook. f., 1859 p. 351

Orig. coll.: Tasmania, supra terram argillaceam Gunn (BM! lectotype here designated. Fig. 1 B, H-NYL 40290! isolectotype) — *Tubercularia heteromorpha* (Nyl. ex Bab. & Mitt. in Hook. f.) O. Kuntze, 1891 p. 877.

Baeomyces cupreus Müller Argoviensis, 1892 p. 25 — Orig. coll.: New Zealand, sine loco, W. Colenso 8/83 on clay (BM! lectotype, here designated).

Baeomyces haemotropus Leighton, 1869 p. 31 — Orig. coll.: New Zealand, Northern Island, W. Colenso (BM! lectotype, here designated).

Baeomyces fuscocarneus F. Wilson, 1889 p. 67 — Orig. coll.: Australia. Victoria. "Supra terram argillaceam" in Lilydale, F. R. M. Wilson 66 (BM! lectotype, designated here).

Baeomyces granosus Stirton 1875 p. 46 — Orig. coll.: New Zealand. Near Wellington, J. Buchanan 179 (BM! lectotype, here designated: GLAM! WELT! isolectotypes: Fig. 2).

Baeomyces heteromorphus f. *rubens* Hellbom 1896 p. 95 — Orig. coll.: New Zealand, Otira Gorge, 2–300 p. s. m. II.1874, S. Berggren 135 (S! lectotype, here designated).

Baeomyces cinnabarinus Zahlbruckner 1941 p. 325 — Orig. coll.: New Zealand. Mt Te Aroha, on moss in *Dracophyllum* shrubland, 900 m H. H. Allan (W! holotype: CHR 338063! isotype).

Cladoniopsis caespitosa Zahlbruckner 1941 p. 325 — Orig. coll.: New Zealand. Mt Ruapehu, on soil, 600 m E. Chamberlain ZA 487 (CHR 338065! isotype, W! holotype).

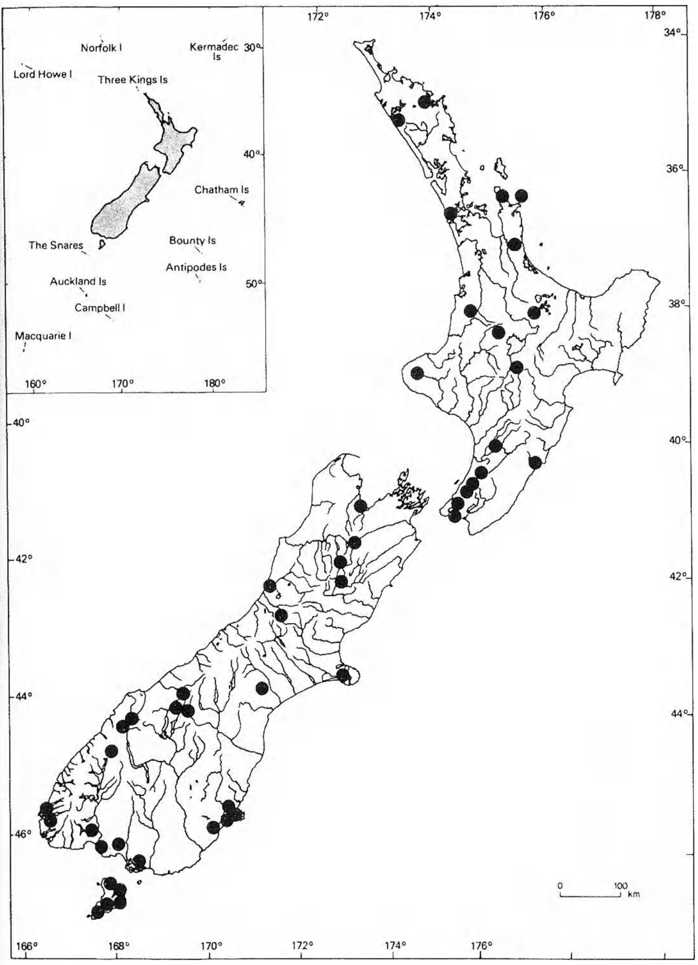

Fig. 4. Known New Zealand distribution of *Baeomyces heteromorphus*.

Primary thallus greenish when fresh, greenish-yellow to greyish-green or dirty white when dry, minutely squamulose, corticate, irregularly cracked and warted, not sorediate. *Podetia* 10–15 mm tall, simple or 1–4-branched near apices, stalks pale flesh-coloured, yellowish-white or suffused reddish, often superficially invested with green algae, surface smooth, often waxy, corrugated and coarsely vertically grooved. *Apothecia* terminal or subterminal, often clustered, disc pale pink to dark readdish-brown, plane or convex with a distinct, pale, flexuous margin, thalline exciple pale. *Spores* oblong, simple, colourless, $7–10\times3–5\,\mu$m, 8 per ascus.

Chemistry. Thallus and apothecia K+ yellow turning red, C–, Pd+ orange. Norstictic, connorstictic and hypoprotocetraric (trace) acids.

Habitat and distribution. *B. heteromorphus* is a common and widely distributed lichen in New Zealand (Fig. 4) and is the most frequently collected species of *Baeomyces* in New Zealand. Although most commonly found on soil and rock, it will colonise old wood and decumbent vegetation. It is a very polymorphic species with differences in microclimate and microhabitat influencing its morphology which varies from much branched, elongated structures (plants growing on scoria are of this kind and Zahlbruckner's taxon *Cladoniopsis caespitosa* refers to such forms) to short, ± sessile, simple tufts (Wilson's *B. fuscocarneus* is of this type). The variation in form while not supported by any variation in chemical constituents, is reflected in a confused nomenclature. *B. heteromorphus* is an Australasian species, and in New Zealand, where it ranges from sea level to 1200 m, it is an early and active coloniser of exposed soils and gravels and may be of importance in soil consolidation. It seems best to place *B. heteromorphus* in subgen. *Sphyridium* (Jahns 1971).

Specimens examined. Northland: Bay of Islands, Paton (CHR) — Kawerua, 1973, B. W. & G. C. Hayward (CHR) see Hayward & Hayward (1974 b) — *Central Auckland*: Waitakere Range, 1958, J. Murray (OTA) — *South Auckland Bay of Plenty*: Great Mercury Island, B. W. & G. C. Hayward (CHR) see Hayward et al. (1976) — Mt Moehau, Coromandel Peninsula, 1974, B. W. & G. C. Hayward (CHR) see Hayward et al. (1975) — Mt Pirongia, 1925 H. H. Allan (CHR) — Waiotapu Valley, 1936, K. W. Allison (CHR) — Waituti Lookout, 1976, D. J. Galloway (CHR) — *Taranaki*: Mt Egmont, 1925, H. H. Allan (UPSV) see Galloway (1976) — *Wellington*: Akitio, 1972, D. J. Galloway (CHR) — Waipakahi Valley, 1972, D. J. Galloway (CHR) — Ruahine Range, Wharite Peak, 1972, D. J. Galloway (CHR) — Otaki River, Tararua Range, 1969, D. J. Galloway (CHR) — Hutt River, 1941, H. H. Allan (CHR) — York Bay, 1976, D. J. Galloway (CHR) — *Nelson*: Kaiteriteri, 1956, W. Martin (CHR) — St Arnaud Range, 1977, M. J. A. Simpson (CHR) see Galloway & Simpson (1978) — Hopeless Creek, 1972, L. F. Molloy (CHR) — Maruia Valley, 1978, D. J. Galloway (CHR) — *Canterbury*: Boyle River, 1979, D. J. Galloway (CHR) — Arthur's Pass, 1972, D. J. Galloway (CHR) — Okuti Valley, Bank's Peninsula, 1977, D. J. Galloway (CHR) — Mt Peel, 1972, D. J. Galloway (CHR) — *Westland*: Aorangi Reserve, Greymouth, 1958, W. Martin (CHR) — *Otago*: Mt Brewster, 1968, D. J. Galloway (CHR) — Makarora, 1968, D. J. Galloway (CHR) — Canyon Creek, Ahuriri Valley, 1966, D. J. Galloway (CHR) — Humboldt Mountains, 1965, D. J. Galloway (CHR) see Galloway (1966) — Mt Cargill, 1949, W. Martin (CHR) — Maungatua, 1966, D. J. Galloway (CHR) — *Southland*: Dusky Sound, Cascade Cove, 1969, D. J. Galloway (CHR) — Secretary Island, 1959, J. Murray (OTA) see Murray (1963) — Lake Thomson, Fiordland, 1962, P. W. James (BM) see Mark et al. (1964) — Longwood Range, 1957, W. Martin (CHR) — Mt Anglem, Stewart Island, 1966, D. J. Galloway (CHR) see Galloway (1968 a) — Oban, Stewart Island, 1966, D. J. Galloway (CHR) — Tin Range, Stewart Island, 1969, D. J. Galloway (CHR) — Frazer Peaks and Port Pegasus, 1967, D. J. Galloway (CHR) see Galloway (1968 b).

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References

Acharius, E. 1803: *Methodus lichenum*. Stockholmiae.

Babington, C. 1855: Lichenes. *In* Hooker, J. D. *Flora Novae Zealandiae II:* 266–311. London.

Babington, C. & Mitten, W. 1859: Lichenes. *In* Hooker, J. D. *Flora Tasmaniae II. Flowerless Plants:* 343–354. London.

Culberson, C. F. 1972: Improved conditions and new data for the identification of lichen products by a standardised thin-layer chromatographic method. *J. Chromatogr. 72:* 113–125.

Frey, E. 1933: Cladoniaceae (unter Ausschluss der Gattung Cladonia) Umbilicariaceae. *In* Zahlbruckner, A. (ed.) *Dr. L. Rabenhorst's Kryptogamen-Flora von Deutschland, Oesterreich und der Schweiz (4).*

Galloway, D. J. 1966: Vegetation studies on the Humboldt Mountains Fiordland. Part 2: The lichens. *Proc. N. Z. Ecol. Soc. 13:* 19–23.

Galloway, D. J. 1968 a: The lichens of Stewart Island. 1. The Mount Anglem highlands. *Transact. Royal Soc. New Zealand (Bot.) 3:* 231–236.

Galloway, D. J. 1968 b: The lichens of Stewart Island. 2. Port Pegasus. *New Zealand Journ. Bot. 6:* 309–314.

Galloway, D. J. 1976: H. H. Allan's early collections of New Zealand lichens. *New Zealand Journ. Bot. 14:* 225–230.

Galloway, D. J. & Simpson, M. J. A. 1978: Lichens of Nelson Lakes National Park, New Zealand. *New Zealand Journ. Bot. 16:* 507–527.

Hayward, B. W. & Hayward, G. C, 1974 a: Botany of Shoe Island and the Slipper Island group—Coromandel Peninsula Part III. Lichens. *Tane 20:* 72–85.

Hayward, B. W. & Hayward, G. C. 1974 b: Lichen flora of the Kawerua area. *Tane 20:* 124–139.

Hayward, B. W., Hayward, G. C. & Galloway, D. J. 1975: Lichens from northern Coromandel Peninsula. New Zealand. *Tane 21:* 15–28.

Hayward, G. C. & Hayward, B. W. 1973 a: Lichens from part of Great Barrier Island. *Tane 19:* 189–191.

Hayward, G. C. & Hayward, B. W. 1973 b: A summary of lichen associations in different habitats from four offshore islands, north-east New Zealand. *Tane 19:* 205–211.

Hayward, G. C., Hayward, B. W. & Galloway, D. J. 1976: Lichens of Great Mercury Island. *Tane 22:* 51–57.

Hellbom, P. J. 1896: Lichenaea neo-zelandica seu lichenes Novae Zelandiae a Sven Berggren annis 1874–1875 collecti. *Bih. Kungl. Svenska Vetensk.-Akadem. Handl. 21:* 1–150.

Henssen, A. & Jahns, H. M. 1973: *Lichenes, eine Einführung in die Flechtenkunde*. Stuttgart.

Hooker, J. D. 1867: *Handbook of the New Zealand Flora*. London.

Hooker, J. D. & Taylor, T. 1844: Lichenes Antarctici ... *Hook. Lond. J. Bot. 3:* 634–658.

Imshaug, H. A. 1972: Typification of Lichen ericetorum L., and Baeomyces Pers. *J. Hattori Bot. Lab. 35:* 299–302.

Jahns, H. M. 1970: Untersuchungen zur Entwicklungsgeschichte der Cladoniaceen unter besonderer Berücksichtigung des Podetienproblems. *Nova Hedwigia 20:* 1–177.

Jahns, H M. 1971: Untersuchungen zur Taxonomie der Gattung Baeomyces. *Herzogia 2:* 133–148.

Jahns, H. M. & Smittenberg, J. C. 1970: Baeoymces roseus Pers., Ontogenie und Regeneration der Fruchtkörper. *Herzogia 2:* 79–88.

Jahns, H. M. & Horst-Iwema, J. R. 1972: Untersuchungen zur Taxonomie der Gattung Baeomyces (II). *Herzogia 2:* 267–276.

Knight, C. 1875: Descriptions of some New Zealand lichens. *Transact. New Zealand Inst. 7:* 356–367.

Knight, C. 1883: On the lichenographia of New Zealand. *Transact. New Zealand Inst. 15:* 346–358.

Kuntze, O. 1891: *Revisio generum plantarum ... II.* Würzburg.

Lamb, I. M. 1953: New, rare or interesting lichens from the Southern Hemisphere II. *Lilloa 26:* 401–438.

Lamb, I. M. 1963: *Index nominum lichenum*. New York.

Leighton, W. A. 1869: Additions to the lichens of New Zealand. *Journ. Linn. Soc. Lond. (Bot.) 10:* 30–33.

Mark, A. F., Scott, G. A. M., Sanderson, F. R. & James, P. W. 1964: Forest succession on landslides above Lake Thomson, Fiordland. *New Zealand Journ. Bot. 2:* 60–89.

Martin, W. & Child, J. 1972: *Lichens of New Zealand*. Wellington.

Müller Argoviensis, J. 1862: Principes de classification des lichens et énumeration des lichens des environs de Genève. *Mém. Soc. Phys. Hist. Nat. Genève 16 (2):* 343–435.

Müller Argoviensis, J. 1892: Lichenes Knightiana, in Nova Zelandia lecti additis nonnulis aliis ejusdem regionis, quos exponit. *Bull. Soc. Roy. Bot. Belg. 31:* 22–42.

Müller Argoviensis, J. 1894: Conspectus systematicus lichenum Novae Zelandiae. *Bull. Herb. Boiss. 2. App. 1:* 17–114.

Murray, J. 1963: Vegetation studies on Secretary Island, Fiordland. Part 7: Bryophytes and lichens. *New Zealand Journ. Bot. 1:* 221–235.

Nylander, W. 1860: *Synopsis methodica lichenum ... I. Part II.* Paris.

Nylander, W. 1888: *Lichenes Novae Zelandiae*. Paris.

Poelt, J. 1974: Classification. *In* Ahmadjian, V. & Hale, M. E. (eds.) *The Lichens*. Academic Press: London & New York. 599–632.

Persoon, C. H. 1794: Einige Bemerkungen über die Flechten. Nebst Beschreibungen einiger neuen Arten aus dieser Familie der Aftermoose. *Usteri Ann. Bot. 7:* 1–32; 155–158.

Stirton, J. 1873: Additions to the lichen flora of New Zealand. *Rept. Transact. Glasgow Soc. Field Nat. 1:* 15–23.

Stirton, J. 1874: Descriptions of some New Zealand lichens collected by John Buchanan in the Province of Wellington. *Transact. New Zealand Inst. 6:* 235–241.

Stirton, J. 1875: Additions to the lichen flora of New Zealand. *Journ. Linn. Soc. Lond. (Bot.) 14:* 458–474.

Swartz, O. P. 1788: *Nova genera et species plantarum* ... Stockholmiae.

Taylor, R. M. 1972: The lichen genus Baeomyces in the West Indies, *J. Hattori Bot. Lab. 35:* 303–311.

Thomson, J. W. 1967: The lichen genus Baeomyces in North America north of Mexico. *Bryologist 70:* 285–298.

Tuckerman, E. 1859: Supplement to an enumeration of North American lichens. Continued. *Amer. Journ. Sci. Arts. ser. 2, 28:* 200–206.

Wilson, F. R. M. 1889: A description of forty-one Victorian lichens new to science. *Vict. Nat. 6:* 61–69.

Zahlbruckner, A. 1926: *Catalogus lichenum universalis. IV*. Leipzig.

Zahlbruckner, A. 1941: Lichenes Novae Zelandiae a cl H. H. Allan eiusque collaboratoribus lecti. *Denkschr. Akad. Wiss. Wien Math.-Naturwiss. Kl. 104:* 249–380.

Redefinition of Homeria and Moraea (Iridaceae) in the light of biosystematic data, with Rheome gen. nov.

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Homeria has a basic chromosome number of $x=6$. Two species, with derived karyotypes have $2n=8$ and $2n=10$ and 9, and two more species have $x=10$ and an apparently unrelated karyotype. The majority of species can be crossed with one another. However, the blue flowered species, *H. speciosa* and *H. lilacina*, cannot be hybridized with other *Homeria* species, but cross with section *Polyanthes* of the related genus *Moraea*. A second group, comprising only *H. maximiliani* and *H. umbellata*, have a base number of $x=10$, and cannot be crossed with a range of species of *Homeria* nor with selected species of *Moraea*. The species that cross with *Moraea* sect. *Polyanthes* resemble the latter closely in leaf and corm characters, though not in flower. *Homeria maximiliani* and *H. umbellata* have leaf, corm and habit characteristics found in *Moraea* subgenus *Moraea*. Most likely *Homeria* has, in the past included three species groups of independent origin which resemble one another in critical floral features alone, but differ in vegetative characters. Thus the *Homeria* type flower appears to have evolved independently in these species groups. The following systematic realignments are made: *Homeria speciosa, H. lilacina* and the presumably related *H. rogersii* are transferred to *Moraea*, while *H. umbellata* and *H. maximiliani* are placed in a new genus, *Rheome*. The appropriate new nomenclatural combinations are provided, together with a revised key to the genera of Iridaceae-Homeriinae.

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When I began a revision of *Homeria*, a moderate sized genus of some 28 species in southern Africa, as part of an overall systematic study of African Iridaceae-Irideae, I was impressed by the strong vegetative resemblance of some species of *Homeria* to certain species of the closely related African *Moraea* (95 species) which I had recently revised (Goldblatt 1973, 1976 b, 1977). This brought to mind the example of *Homeria simulans*, a species with a *Homeria*-type flower, but with vegetative morphology identical with that of *Moraea* subgenus *Visciramosa*, which has a characteristic and unusual appearance. Cytology of *H. simulans* proved unlike that of any other species of *Homeria* then known, but matched closely the species of subgenus *Visciramosa*. I had little doubt that *H. simulans* was correctly a member of *Moraea* subgenus *Visciramosa*, and that it had evolved independently the characteristics of the flower of *Homeria*. Consequently I felt compelled to transfer this species to *Moraea* where it required a new name, as *M. elsiae* (Goldblatt 1976 a). This decision was later supported by the discovery in *M. viscaria*, also a member of subgenus *Visciramosa* and in other species of *Moraea* of only some populations which had similar *Homeria*-like features in their flowers.

The species of *Homeria* which resemble certain species of *Moraea* are:

(1) *H. speciosa* L. Bol., which approaches *M. polystachya* (Thunb.) Ker;

(2) the species currently known as *H. lilacina* L. Bol. (*Moraea polyanthos* L. fil. is an earlier name, see Goldblatt 1979) which is strikingly like *M. bipartita* L. Bol. (better, but incorrectly, known as *M. polyanthos* L. fil. sensu auct.).

(3) *H. umbellata* (Thunb.) Lewis and the allied *H. maximiliani* Schltr. which have features reminiscent of several different groups of *Moraea* including *M. fugax* (de la Roche) Jacq., *M. margaretae* Goldbl., *M. papilionacea* (L. fil.)

Table 1. Chromosome numbers in *Homeria* and those species previously placed in this genus and now transferred to *Moraea* or to the new genus *Rheome*. See also Appendix.

Species	Diploid chromosome number 2n
Homeria	
H. bifida L. Bolus (*H. salmonea* L. Bolus)	12, 12+4B, 24
H. brachygne Schltr. (*H. papillosa* L. Bolus)	12
H. britteniae L. Bolus	12, 24
H. bulbillifera Lewis	12, 12+1B, 18, 24
H. cedarmontana Goldbl. in press	12
H. collina (Thunb.) Salisb.	24
H. comptonii L. Bolus (*H. maculata* sensu auct.)	12
H. cookii L. Bolus (*H. pillansii* L. Bolus)	12, 24, 36
H. elegans (Jacq.) Sweet	12
H. fenestrata Goldbl. in press	12
H. flaccida Sweet	24, 36
H. galpinii L. Bolus	24
H. longistyla Goldbl. in press	12
H. marlothii L. Bolus	24
H. miniata Andr. Sweet	12 (24)
H. minor (Eckl.) Goldbl. (*H. framesii* L. Bolus)	12
H. ochroleuca Salisb.	12, 24, 24+2–3B
H. odorata L. Bolus	12
H. pallida Baker	12, 8
H. pendula Goldbl. in press	12
H. ramosissima Schltr.	12
H. schlechteri L. Bolus	12
H. spiralis L. Bolus	12
H. tenuis Schltr.	10, 9
H. tricolor Lewis	12
H. vallisbelli Goldbl. in press	12
Moraea	
M. crispa Thunb. (*H. rogersii* L. Bolus)	12, 24
M. polyanthes Thunb. (*H. lilacina* L. Bolus)	12
M. speciosa (L. Bolus) Goldbl. (*H. speciosa* L. Bolus)	12
Rheome	
R. maximiliani (L. Bolus) Goldbl. (*H. maximiliani*)	20
R. umbellata (Thunb.) Goldbl. (*H. umbellata*)	30 (triploid)

Ker and to a lesser extent, species of *Moraea* subgenus *Monocephalae*.

These impressions based on vegetative morphology have now been supported by two independent lines of investigation, chromosome cytology and experimental hybridization. The results of these two studies are described in detail below, after which I will discuss their significance to the systematics of *Homeria* and *Moraea*.

Materials and Methods

Chromosomes were studied from root tips only, taken from sprouting corms or seeds, originally collected in the wild. Root tips were pretreated in 0.003 M hydroxyquinoline for 6–8 hours in the refrigerator, fixed in Carnoy's 3:1 ethanol-acetic acid and either stored in 70 % ethanol or hydrolyzed immediately in 10 % HCl at 60°C for 6 minutes. After washing, tips were squashed in lacto-propionic orcein. Chromosomes of *Homeria* are large, and easy to study, so that detailed comparisons of karyotypes can be made. A list of the species studied and their chromosome numbers is provided in Table 1. Detailed locality and voucher data for these counts are included as an appendix at the end of the paper.

Observations

Cytology

Results (Table 1) in general confirm findings in a preliminary study (Goldblatt 1971) that most

Homeria species have chromosome numbers based on x=6, a number also frequently found in *Moraea*. The karyotype for all species with x=6 is similar (Fig. 1 A–D), chromosomes being large, and acrocentric (Fig. 1 G). Exceptions to this pattern are few. However, the morphologically divergent species pair *H. umbellata* and *H. maximiliani* have x=10 (Fig. 1 J) (*H. umbellata* studied here is evidently triploid) and a karyotype identical with that found in species of *Moraea* subgenus *Moraea* that have the same base number (Goldblatt 1976 a). Two other exceptions are some populations of *H. pallida*, n=4, others n=6 and *H. tenuis*, n=5 (and 2n=9) (Fig. 1 H, I). In both examples of numbers lower than n=6, the number of major chromosome arms is the same, there being two large metacentrics in *H. pallida* with n=4, and one metacentric in *H. tenuis* with n=5, suggesting chromosomal rearrangements of the Robertsonian type (Jones 1977, 1978), involving the basic *Homeria* karyotype. The cytology of these two species is still being investigated and will be dealt with in greater detail in a later paper. The different number of n=10 in *H. umbellata* and *H. maximiliani* appears more significant, and most likely indicates that these species are not closely related to other species of *Homeria* at all. They are probably distantly related to *Moraea* subgenus *Moraea*, with which they share the same basic chromosome number, x=10, and certain similarities in vegetative morphology.

Homeria speciosa and *H. lilacina* also have x=6 and karyotypes similar to other species of *Homeria*, but with two chromosome pairs rather more submetacentric than acrocentric (Fig. 1 E, K). These karyotypes resemble those found in *Moraea bipartita* (syn. *M. polyanthos* sensu auct.) (Goldblatt 1976 a). The similarity between karyotypes of *H. lilacina* and *M. bipartita* is especially noticeable.

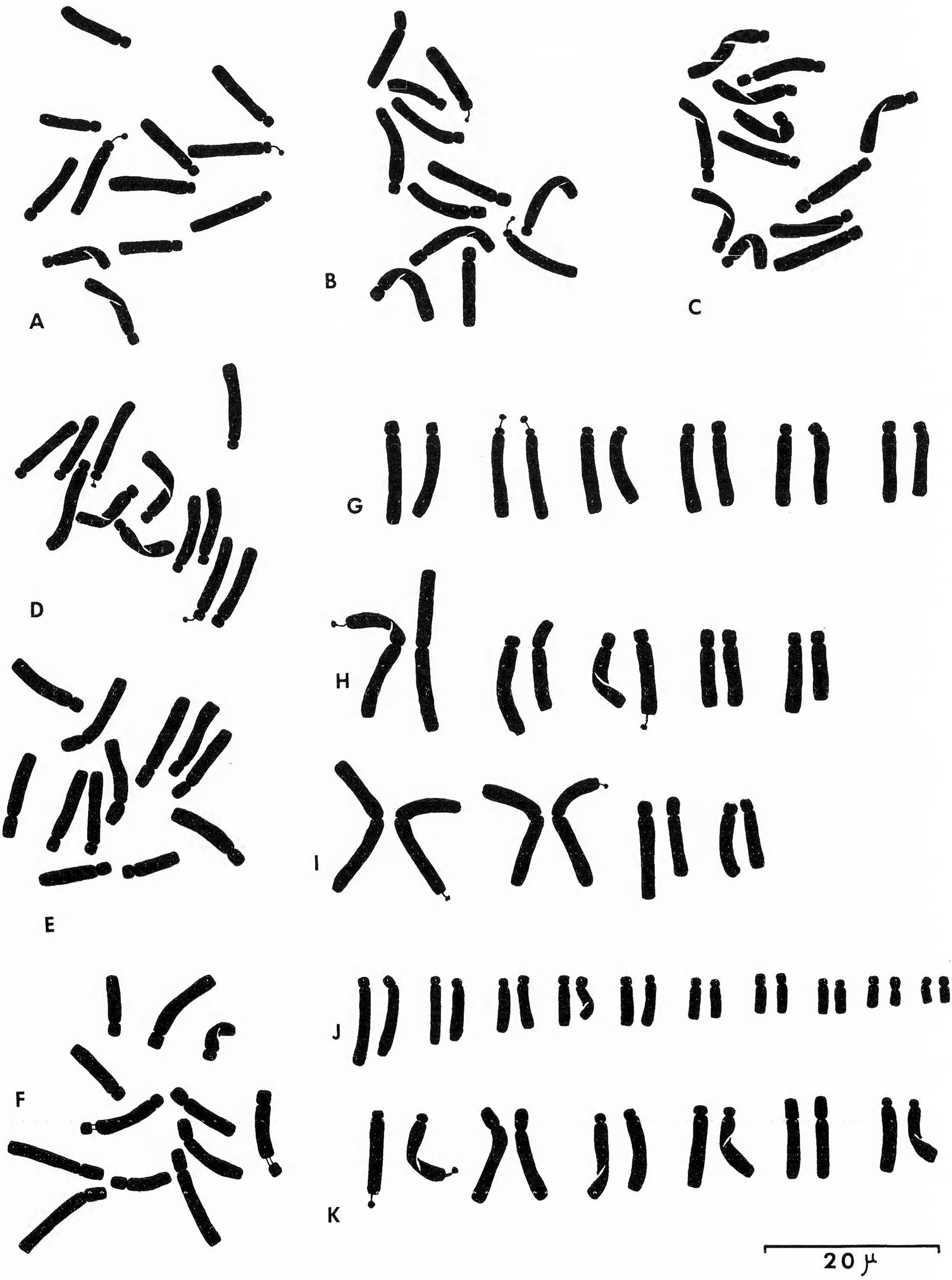
Crossing Studies

Several hundred crosses were attempted between a large number of species of *Homeria* in cultivation. Crosses were also made with a limited number of *Moraea* species. The results are striking (Fig. 2) in revealing patterns of crossing or non crossing that correlate with cytological and morphological discontinuities. Most species of *Homeria* (like those of *Moraea*) are self-incompatible but can be easily crossed with obviously related species, and sometimes even apparently distantly related species will cross successfully. Crossing patterns indicate that there is one large group of the genus in which almost all species will hybridize. However, *H. maximiliani* cannot be crossed with any of the species of *Homeria* that flowered in cultivation. Attempts to hybridize *H. speciosa* or *H. lilacina* or its variety *alba* with any other species of *Homeria* also resulted in no fruit or seed production. The latter failures were particularly striking since *H. speciosa* has been crossed to *Moraea polystachya* (J. Loubser, pers. comm.), yielding vigorous, though sterile hybrids and I have repeatedly crossed *H. lilacina* and *H. lilacina* var. *alba* with *Moraea bipartita* (*M. polyanthos* sensu auct.) with good seed set and good germination.

The results of the hybridization studies support the following hypothesis. One, *H. speciosa* and *H. lilacina* are more closely related to *Moraea* section *Polyanthes* to which both *M. polystachya* and *M. bipartita* belong, than to the remaining species of *Homeria*. Two, *H. maximiliani*, and presumably *H. umbellata*, are unrelated or very distantly related to any other species of *Homeria* (too few crosses to species of *Moraea* could be attempted to draw any further information). Three, most remaining species of *Homeria* constitute a natural, fairly closely related assemblage. (One important species, currently known as *H. rogersii* was not investigated since it is difficult to flower in cultivation. It is a blue-flowered species of *Homeria*, along with *H. lilacina* and *H. speciosa*, and its affinities probably lie with the latter. Further discussion is presented in a later chapter on systematics.)

Discussion

It is now evident that *Homeria* as presently constituted is most probably an unnatural genus comprising elements of at least three separate phylogenetic lines, each most likely having had a separate origin from different lineages of *Moraea*. In the case of *H. speciosa* and *H. lilacina*, hybridization with species of *Moraea* indicates their likely origin and relationships. In *H. maximiliani* and *H. umbellata* similarities in vegetative morphology with some groups of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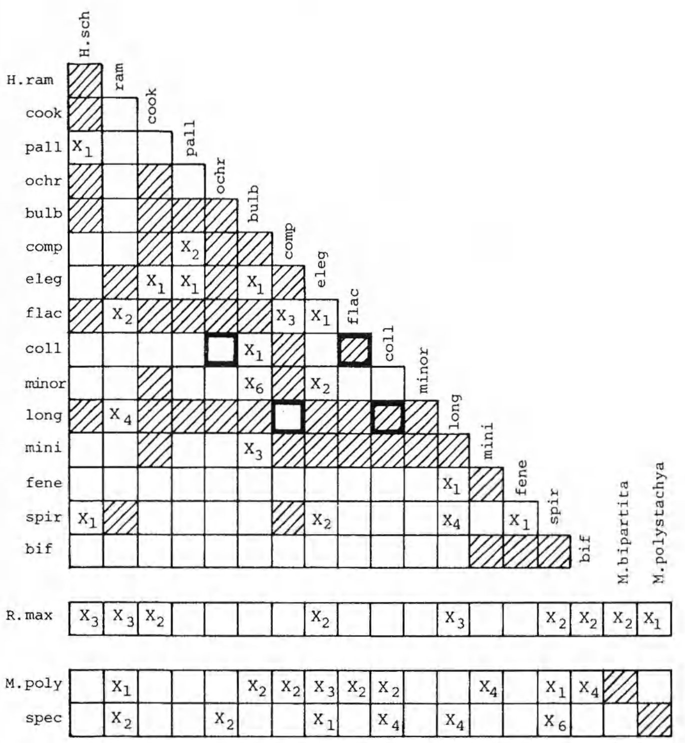

Fig. 2. Diagram of crosses made between species of *Homeria* and *Moraea*. Shading indicates a successful cross with fertile seed produced. An x indicates a failed cross and figures are the number of times the cross was attempted. Heavily outlined squares represent naturally occurring inter-specific hybrids. Species are arranged in order of their presumed relationships, and as they will appear in the revision of the genus (Goldblatt, in prep.). Abbreviations will be evident from the text and from Table 1.

Moraea, and a base number of x=10 suggests a derivation from some fairly primitive *Moraea* line, although its direct ancestors may be extinct. Inability to cross with other *Homeria* species, all x=6, as well as differences in basic chromosome number, make it seem reasonable to presume that these two species are not directly related to *Homeria*, and had a separate origin.

From this hypothesis follows logically the premise that the *Homeria* type flower has evolved independently several times. This presumably occurred by the reduction and simplification of the apparently complex and elaborate flower type characteristic of *Moraea* (Fig. 3 A–B). The following section explores this suggestion in detail after broadly outlining the systematics of Old World Irideae.

Evolution of the Homeria flower type

Moraea and *Homeria* belong to a group of almost exclusively African members of Iridaceae. They are closely related to the northern hemisphere genus *Iris*, perhaps sharing a common origin in the ancestors of the modern tropical and subtropical African genus *Dietes* (Goldblatt 1976 a and in prep.). *Iris, Dietes* and *Moraea* share many floral characters, but most importantly, the very unusual flattened petaloid style branches with paired supra-stigmatic crests (Fig. 3 A–B), and these genera and their allies are grouped in the tribe Irideae. *Moraea* itself differs substantially from *Dietes* and *Iris*, especially in vegetative features, having a characteristic single-internode corm (versus rhizomes or bulbs in *Iris* and *Dietes*) and a bifacial strap-like leaf (versus usually monofacial ensiform leaves in *Iris* and *Dietes*). *Moraea* is also distinctive in having partly united filaments.

On the basis of vegetative morphology, *Moraea* and a group of allied genera are segregated in subtribe Homeriinae (Goldblatt 1971, 1976 b), defined by the characteristic leaf and unique corm type. Genera included in this subtribe are *Moraea, Homeria, Hexaglottis, Gynandriris, Barnardiella* and *Galaxia*. Amongst these genera, *Moraea* is the only one in which there are species with numerous leaves, many branches, filaments basally united (rarely free but contiguous), and a more or less typical *Iris*-type flower with large outer tepals, small inner ones, large petaloid style branches and crests. With the exception of *Gynandriris*, clearly a *Moraea* offshoot with a tubular ovary extension, the remaining genera have subequal tepals and less elaborate style branches, either slightly flattened with or without tiny crests (*Homeria, Barnardiella*) or short, with apices broadly lobed (*Galaxia*) or deeply divided (*Hexaglottis*).

Moraea is a large genus of over 95 species which ranges widely in sub-Saharan Africa, with a center in the southwestern Cape. It appears to be a natural grouping, although composed of several old and divergent lineages, treated as subgenera (Goldblatt 1976 a). Within *Moraea*,

Fig. 1. Chromosome cytology of *Homeria, Moraea* and *Rheome*. — A: Mitotic metaphase in *H. miniata*. — B: *H. fenestrata*. — C: *H. odorata*. — D: *H. bifida*. — E: *M. speciosa*. — F: *M. crispa*. — G: Karyotype of *H. pendula*, 2n=12. — H: *H. tenuis*, 2n=10. — I: *H. pallida*, 2n=8. — J: *R. maximiliani*, 2n=20. — K: *M. polyanthos*, 2n=12. (Compare *Rheome* with published karyotypes of *Moraea* (Goldblatt 1976 Fig. 1).)

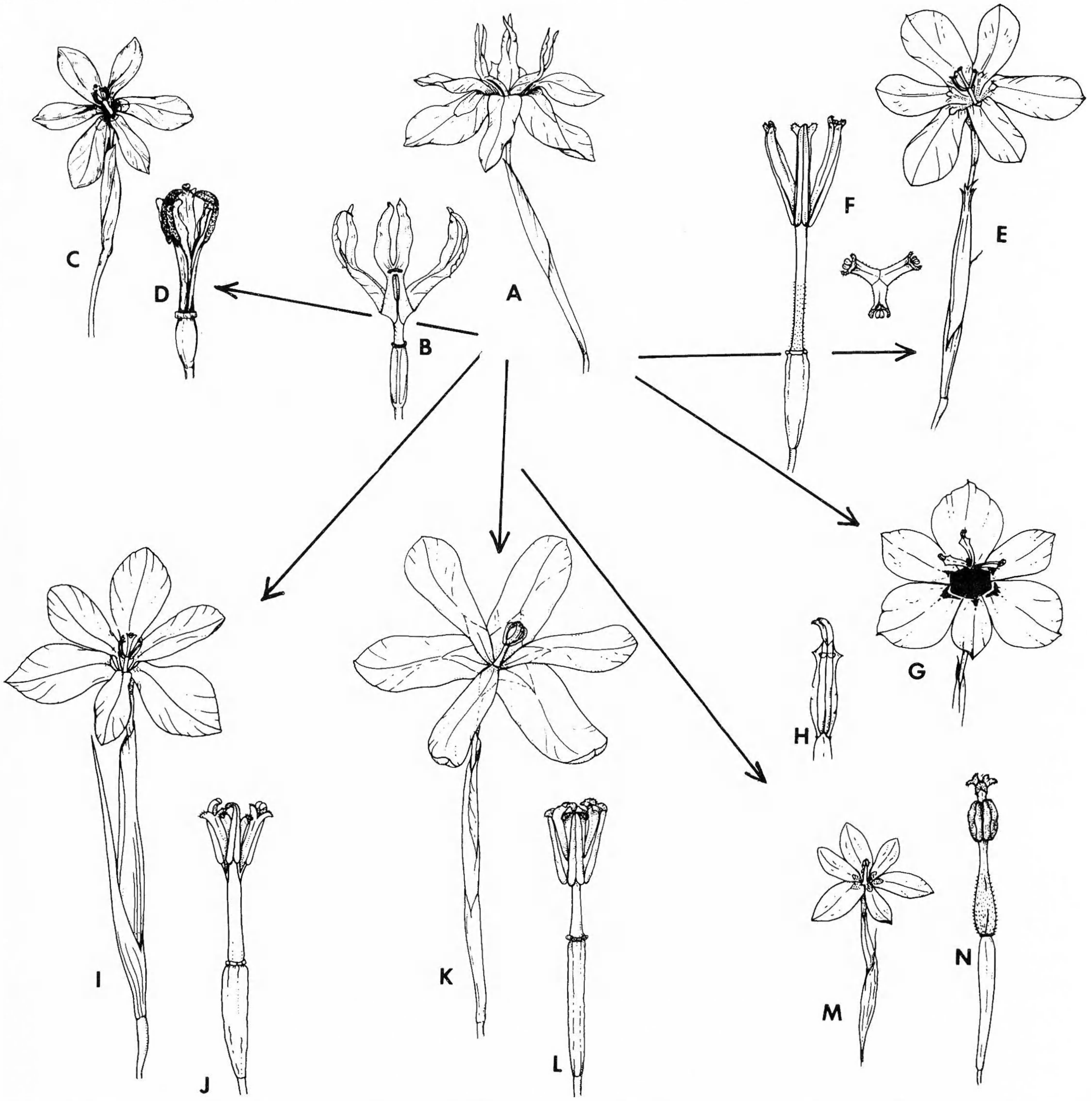

Fig. 3. Flower types in *Moraea, Homeria* and *Rheome*. — A: Basic flower type in *Moraea (M. ramosissima)*. — B: Androecium and gynoecium enlarged. — C–N: Derived flower types with united filaments, narrow style branches with or without short crests. — C–D: *M. elsiae* (subgenus *Visciramosa*). — E–F: *M. polyanthos* (section *Polyanthes*). — G–H: *M. insolens* (section *Vieusseuxia*). — I–J: *R. maximiliani*. — K–L: *H. flaccida*. — M–N: *H. miniata*. (Flowers all approximately × 2/3, details of stamens and style branches much enlarged).

there is a tendency for reduction of the style branches in several lines. This occurs particularly in subgenus *Visciramosa* where *M. viscaria* has populations with slender, crestless style branches and *M. elsiae* (Fig. 3 C–D) has a typical *Homeria* type flower, for which reason it was first placed in this genus (as *H. simulans*). In a few species of subgenus *Vieusseuxia* reduction of the crests also occurs, e. g., Central African forms of *M. thomsonii*; a few populations of *M. elliotii*; in *M. neopavonia* and *M. insolens* (Fig. 3 G–H) the crests are present but short; and in *M. gigandra* the crests are so short they are almost concealed by the stigmatic lobe. From these forms it is only a small step to a *Homeria* flower (Fig. 3 K–L) in which the filaments are fully connate (partly in most *Moraea* species) and the tepal whorls are subequal. Further evolution in this sequence has led to the suppression of the style crests entirely, which has presumably occurred in *H. miniata* (Fig. 3 M–N) for example. In *Galaxia* and *Hexaglottis* the style branches are not developed at all and are merely short stalks which bear stigma lobes in the first genus, or deeply divided filiform stigmas in the second.

When the flower types of subtribe Homeriinae are compared in this way it seems reasonable to conclude that complex characteristics have gradually become simplified and reduced. There is, in the extant members of the subtribe, an almost entire reduction series from species with large style branches, prominent crests (Fig. 3 A–B), basally connate stamens and dissimilar tepals whorls to species with narrow style branches, short (to absent crests), entirely united filaments and subequal tepals (Fig. 3 C–N). This pattern of reduction was evidently repeated in several lines, as evidenced by the vegetative morphology in each, as well as cytological and hybridization data. In some lines the trend is still evident so that species with reduced flowers are best left with obvious relatives (*M. elsiae* in *Moraea* subgenus *Visciramosa*; *M. (Homeria) speciosa* and *M. polyanthos (H. lilacina)* in *Moraea* section *Polyanthes*). In others, some links in the sequence are missing. Thus neither *Homeria* sensu stricto nor *H. umbellata-H. maximiliani* can be directly linked with any species or species groups within *Moraea*.

The opposite line of argument that the apparently simple *Homeria* type flower gave rise to the more elaborate *Moraea* type is difficult to accept. It would lead to the hypothesis that the very remarkable *Moraea* flower evolved independently several times; also that many leafed and multiple branched forms were derived from ancestors with few leaves and branches; and that fused filaments gave rise to progressively less united, and ultimately free filaments. This reasoning also makes it impossible to relate the obviously primitive, rhizomatous *Dietes*, with its *Moraea* type flower and free stamens, to the *Homeria-Moraea* alliance, and hence supposes the independent origin in *Dietes* also, of a *Moraea* type flower. A further difficulty with this hypothesis is that it would presume the small, relatively homogenous *Homeria* gave rise to the vastly more variable heterogenous, and richly developed *Moraea*. The elaboration theory creates more problems than it might seem to solve and ultimately becomes untenable.

Taxonomic conclusions

The current taxonomy of *Homeria* appears, in the light of the cytological and crossing data presented above, to be unacceptable since the genus is shown to be most likely composed of three independently derived species groups. Several solutions are possible. One would be to combine *Homeria* in *Moraea*, distributing species in their correct subgeneric positions as knowledge permits. This, I believe is undesirable because it would enlarge *Moraea* to an unmanageable size, and at the same time merge two well known, and by and large, readily recognizeable genera.

A second solution would be to recognize separate genera for the unrelated species groups within *Homeria*. I thinkt this an unnecessary step (and to be perfectly consistent any species of *Moraea* with reduced style branches might be assigned a separate genus including for example *M. elsiae*). A compromise, and probably the best treatment would be to unite with *Moraea* those species that still have demonstrably or visibly close links to *Moraea* and to recognize as generically distinct others whose immediate ancestors in *Moraea* are no longer clear.

In practical terms I suggest uniting *H. speciosa* and *H. lilacina* with *Moraea* section *Polyanthes* where crossability and vegetative morphology clearly show they belong. *Homeria maximiliani* and *H. umbellata* cannot, at least in the light of available knowledge be accommodated in any existing subgenus or section of *Moraea*. I believe it most satisfactory to place them in a separate genus, and the new genus *Rheome* (a semi-anagram of *Homeria*) is proposed to accommodate these species. If, in the future hybridization or other data demonstrate a clear relationship between *Rheome* and a group within *Moraea*, the new genus could be united with *Moraea*.

Lastly, the bulk of species of *Homeria* should remain a distinct genus. They comprise what seems a natural alliance of easily recognizeable species which have similar or related karyotypes, can readily be hybridized and seem obviously related at the morphological level.

Systematics

Rheome Goldbl. gen. nov. Type species: *R. maximiliani* (Schltr.) Goldbl.

Planta distincta, tunicis cormi brunneis, internodio basali longo, foliis (1–)2–3, supra terram insertis et ramis apicem versus, caulis congestis. Flores *Homeria* similes, fugacei; tepala subaequalia, unguibus erectis, limbis expansis. Filamenta connata, parte superiore interdum libera ad 1.5 mm. Rami styli breves, apicem versus bifurcati.

Plants of distinctive habit, with a long basal internode, leaves inserted well above ground and close together, and branches many, of equal length, clustered at apex of basal internode. *Corm* 1–2 cm in diameter, with brown tunics of initally entire, ± woody layers, later becoming split from base, tending to become fibrous; usually bearing cormlets near base. *Leaves* (1–)2(–3) linear, channeled, borne well above ground, lowermost long and trailing, others smaller, becoming bract-like. *Stem* erect, terete, with long basal internode; much branched in umbellate manner. *Spathes* herbaceous, brown tipped, obtuse-emarginate, outer sheathing, or free distally. *Flowers* stellate; fugaceous; tepals free, subequal, basal part (claw) ascending, limb outspread. *Filaments* united or free in upper 1.5 mm. *Anthers* erect, to slightly diverging,appressed to style branches. *Style branches* short, apically bifurcate. *Capsule* ovoid, seeds many, angular. *Basic chromosome number* x=10.

Distribution: southwestern Cape, from the Caledon district in the south, along the west coast to the Clanwilliam district; two species only.

R. umbellata (Thunb.) Goldbl. comb. nov.

Moraea umbellata Thunb., Diss. de Moraea: 13. 1787. Type: S. Africa, Cape, near Piketberg, Thunberg s. n. (Herb. Thunberg 1230, UPS, lectotype). — *Homeria umbellata* (Thunb.) Lewis, J. S. African Bot. 14: 86. 1948.

Homeria bobartioides L. Bolus, J. Bot. 69: 12. 1931. Type: S. Africa, Cape, Mulder's Vlei, Stellenbosch, Bolus s. n. (BOL 19085, holotype).

R. maximiliani (Schltr.) Goldbl. comb. nov.

Homeria maximiliani Schltr., Engler's Bot. Jahrb. 27: 94. 1900. Type: S. Africa, Cape, Clanwilliam district, near Hoek, Schlechter 8700 (B, lectotype, BOL, K, MO, S, isotypes).

Relationships. As already outlined, *R. maximiliani* and *R. umbellata* are segregated from *Homeria* as a result of combined cytological, morphological and negative crossing data, all of which suggest that they are not related to the species of this genus. They are morphologically distinctive in corm structure, general habit, and have a different basic chromosome number, x=10, from *Homeria*, x=6. Furthermore, attempts to cross *R. maximiliani* with several species of *Homeria* (in which most species are readily crossable) failed. *Rheome* is probably related to *Moraea* subgenus *Moraea* which also has a basic chromosome number of x=10 and very similar karyotype. (A few crosses attempted between *R. maximiliani* and *Moraea* species at hand did not succeed.) Species with which *Rheome* has some similarity are *M. margaretae* and *M. papilionacea*, especially in their characteristic brown corm tunics; and *M. gracilenta* and *M. fugax*, in which the habit is similar in having a very long basal internode and leaves and branches clustered at the stem apex. The very characteristic beak of the capsule found in the two latter species does not occur in *Rheome*, and similarity of habit here may be due to convergence. At present I am unable to make more specific comments on the possible relationships of *Rheome*.

Moraea Mill.

No change is required in the description of *Moraea*, since species or forms with subequal tepals, united filaments and reduced style branches and short or absent crests (*M. elsiae*; populations of *M. viscaria, M. thomsonii*) are already accommodated in current generic descriptions. However, the following taxonomic changes are required.

Moraea speciosa (L. Bolus) Goldbl. comb. nov.

Homeria speciosa L. Bolus, Ann. Bol. Herb. 3: 10. 1827. Type: S. Africa, Cape, near Prince Albert, Krige s. n. (BOL 13486, holotype).

Moraea polyanthos L. fil.

Linnaeus fil., Suppl. Pl.: 99. 1781. non sensu auct. pre 1979. Type: S. Africa, Cape, "in regione Kore rivier", Thunberg s. n. (Herb. Thunberg 1226, UPS, lectotype).

Homeria lilacina L. Bolus, Ann. Bol. Herb. 3: 9. 1920. syn. nov. Type: S. Africa, Cape, near Matjesfontein, Beattie & F. Bolus s. n. (BOL 15186, holotype).

As pointed out recently (Goldblatt 1979) *Moraea polyanthos* is an earlier name for *H. lilacina*. In the past I, and others (Goldblatt 1976 b, Brown 1928) had thought *M. polyanthos* was the common Little Karoo *Moraea* with large style branches and crests. Careful reexamination of the type material in the Thunberg herbarium has revealed that the original collections consist of plants with small, narrow style branches without crests. *Moraea polyanthos* sensu auct. must now become *M. bipartita* L. Bolus.

Moraea crispa Thunb.

Thunberg Diss. de Moraea 13. 1787, non *M. crispa* (L. fil.) Ker. 1804, nom. illeg. Type: S. Africa, Cape "Roggeveld", Thunberg s. n. (Herb. Thunb. 1214 UPS, holotype).

Homeria rogersii L. Bolus, Fl. Pl. Africa 8: sub tab. 306. 1928, syn. nov. Types: S. Africa, Cape, Naauwpoort, Rogers 12078 (BOL, lectotype); Vlakplaats, Richmond Div., Bolus s. n. (BOL 13835, syntype).

After careful consideration of Thunberg's description and type of *Moraea crispa* (Goldblatt 1979), I have reached the conclusion that it is very likely that this name is an earlier synonym for the plant known as *Homeria rogersii*. There is, however, some doubt whether *M. crispa* correctly belongs in *Moraea* or in *Homeria*. It seems most closely related to *Moraea polyanthos* which also has blue flowers. *Moraea crispa* typically has a solitary leaf and partially free stamens, both unusual characteristics, clearly isolating it from *M. polyanthos*. Unlike *M. polyanthos* and *M. speciosa*, removed in this paper from *Homeria*, I have no crossing information for *M. crispa* which has flowered poorly under greenhouse conditions. Karyotypic differences between *Homeria* and *Moraea* section *Polyanthes* are small as both have x=6, and large more or less acrocentric chromosomes. Section *Polyanthes* differs slightly in having two chromosome pairs that are less acrocentric than in *Homeria*, and this characteristic is found in *M. crispa* as well (Fig. 1 F). On the basis of these rather minor cytological and morphological features, *M. crispa* is assigned to *Moraea* section *Polyanthes* with *H. rogersii* as a synonym.

Homeria Vent.

A complete revision of *Homeria* will shortly be published (Goldblatt in prep.) which will deal more thoroughly with some questions and problems raised here. However, as a number of changes in *Homeria* and *Moraea* have been made at generic level in this paper, I am providing a revised key to all genera of Homeriinae (Goldblatt 1971 emend. Goldblatt 1976 b) the subtribe to which are assigned the corm-bearing and bifacial-leafed genera of Old World Irideae.

Key to Iridaceae-Irideae-Homeriinae

The subtribe is defined by a characteristic tunicate corm of the single-internode type, and a basic leaf form that is bifacial, channeled and strap-like. These features easily distinguish Homeriinae from Iridinae, and the related Ferrariinae.

1. Ovary usually pedicellate, and usually exerted from spathe, not produced above to form a long sterile tubular beak 3
– Ovary subsessile, enclosed in spathe and produced above forming a long sterile tubular beak 2
2. Style branches prominent, petaloid with large paired crests extending above stigma lobe; leaf channeled .... *Gynandriris*
– Style branches slender, not petaloid, dividing near apex with short recurved stigmatic branches; leaf terete .... *Barnardiella*
3. Stem entirely underground, leaves and spathes clustered at ground level 4
– Stem produced above ground, leaves and spathes usually separated on stem, occasionally clustered together 5
4. Perianth tube well developed, ovary subsessile; tepals subequal; style branches short, not petaloid, crests lacking or obscure .... *Galaxia*
– Perianth tube absent, ovary exerted, tepal whorls dimorphic; style branches prominent, petaloid with large paired crests .... *Moraea*
5. Style branches short, diverging at apex of filament column; each divided to base, thus forming six horizontally extended filiform branches .... *Hexaglottis*
– Style branches various, simple and filiform, or divided near apex, either forming small to large large paired crests, or diverging, stigmatic lobes or arms 6
6. Style branches filiform to tubular, or somewhat flattened, but not noticeably petaloid, no wider than twice the width of the anthers; sometimes forked or divided at apex, either with apical stigmas or with short to obscure crest-like extensions 8
– Style branches flattened and petaloid with a transverse stigma lobe, and extending apically

paired petaloid crests 7

7\. Tepal whorls usually dimorphic, outer much larger and with nectar guide, inner sometimes reduced, or lacking, often erect; style crests usually at least twice as long as width of style branch, if not stigma lobes continuous with margin of style branch .... *Moraea*

– Tepal whorls subequal, outer slightly larger, but nectar guides if present usually on both whorls, inner tepals always spreading; style crests usually less than twice the width of the style branch, and continuous with margin of style branch .... *Homeria*

8\. Stems branching repeatedly and very sticky below the nodes .... *Moraea*

– Stems simple to much branched but never sticky below the nodes 9

9\. Flowers blue, purple, or white, but if white, anthers 5–6 mm long and tepal cup well developed, enclosing anthers 10

– Flowers yellow, orange or pink, rarely white and if so anthers less than 2.5 mm long and tepal cup not developed 11

10\. Stamens partly to entirely united ...... *Moraea*

– Stamens free to base .... *Roggeveldia*

11\. Stem many branched, branches short and clustered around insertion of leaves in umbellate fashion; corm tunics brown, layers ± entire, fragmenting irregularly to become fibrous .... *Rheome*

– Stem simple to many branched, but branches seldom clustered around leaf insertion; if so corm tunics composed of heavy black reticulate fibres .... *Homeria*

Acknowledgements. Funded by grant DEB 76-19907 from the U.S. National Science Foundation. I thank Mr. J. Loubser for permission to present information on the hybrid *M. polystachya* × *H. speciosa* which he produced.

References

Brown, N. E. 1928: The Iridaceae of Thunberg's Herbarium. *J. Linn. Soc. Bot. 48:* 34–42.

Goldblatt, P. 1971: Cytological and morphological studies in the southern African Iridaceae. *J. S. African Bot. 37:* 317–460.

Goldblatt, P. 1973: Contributions to the knowledge of Moraea (Iridaceae) in the summer rainfall region of South Africa. *Ann. Missouri Bot. Gard. 60:* 204–249.

Goldblatt, P. 1976 a: Evolution, cytology and subgeneric classification in Moraea (Iridaceae). *Ann. Missouri Bot. Gard. 63:* 1–23.

Goldblatt, P. 1976 b: A revision of Moraea (Iridaceae) in the winter rainfall region of southern Africa. *Ann. Missouri Bot. Gard. 63:* 657–786.

Goldblatt, P. 1977: Systematics of Moraea (Iridaceae) in tropical Africa. *Ann. Missouri Bot. Gard. 64:* 243–295.

Goldblatt, P. 1979: The Homeria species of Thunberg's herbarium. *Ann. Missouri Bot. Gard. 66:* 588–590.

Jones, K. 1977: The role of Robertsonian change in karyotype evolution in higher plants. *Chromosomes Today 6:* 121–129.

Jones, K. 1978: Aspects of chromosome evolution in higher plants. *Adv. Bot. Res. 6:* 120–194.

Appendix

Locality and voucher data for species of *Homeria, Moraea,* and *Rheome* for which chromosome counts were obtained. Chromosome number (diploid) is given for each locality. Previously published counts are given in parenthesis. All Goldblatt collections listed are at MO, unless a different herbarium is indicated.

Homeria

H. bifida. Cape Province: 7 km S. Loeriesfontein, Goldblatt 3950 (12); Calvinia–Loeriesfontein road, Goldblatt 3942 (12); Rebunieberg, Calvinia, Goldblatt 3894 (12); Blomfontein road, S. W. Calvinia, Goldblatt 4279 (12); E. slopes of Kamiesberg, Goldblatt 4053 (12+4B); E. of Nieuwoudtville, Goldblatt s. n., no voucher (24).

H. brachygyne. Cape Province: Olifants R. valley near Trawal, Goldblatt 3930 (12); 23 km N. Clanwilliam, Goldblatt 3931 (12); (also Goldblatt, 1971 as *H. papillosa* (12)).

H. britteniae. Cape Province: Grahamstown, Bayliss s.n., no voucher (24); S. of Humansdorp, Goldblatt 4927 (12).

H. bulbillifera. Cape Province: Peninsula, Karbonkelberg slopes, Goldblatt 4418 (18); Hermanus–Onrus road, Goldblatt s. n. (12); The Poort, Breadsdorp, Goldblatt 4856 (12+1B); Cloetes Pass, Goldblatt 4157 (12); Stormsvlei Kloof, Goldblatt 4130 (12); E. of Swellendam, Goldblatt 4137 (12); Cloetes Pass—Wagenbooms, Goldblatt 4168 (12); Albertinia—Herbertsdale, Goldblatt s. n. (24).

H. cedarmontana. Cape Province: Cedarberg Pass, E. of Algeria, Goldblatt 3871 (12); Sneeuberg, near hut, Goldblatt 4289 (12).

H. collina. Cape Province: E. end du Toits Kloof, Goldblatt 4701 (24); Clifton, Goldblatt 4800 (24); Kommetje, Goldblatt 4123A (24); foot of Houw Hoek Pass, Goldblatt 4004 (24); Redhill, Simonstown, Goldblatt s. n. no voucher (24); (five other counts of 24 in Goldblatt 1971; 1972); (also Sakai, 1952: 24).

H. comptonii. Cape Province: Bot R.—Caledon, Goldblatt 3997 (12); Leeu R., N. Albertyn, Goldblatt 3990 (12); foot of Babylons Tower, Goldblatt 4022 (12); N. slopes, Eseljag Pass, Goldblatt 2663 (12); N. of Stanford, Goldblatt 4845 (12).

H. cookii. Cape Province: Roggeveld, N. Sutherland, Goldblatt s. n., no voucher (12); Op-de-Tradouw, W. Barrydale, Goldblatt 4186 (36); Cedarberg, top of Cedarberg Pass, Goldblatt 4055 (36); E. Smartts Syndicate Dam, Britstown Goldblatt 4680 (24); Victoria West, Goldblatt 4861 (24); (also 24, Goldblatt, 1971, as *H. pallida*).

H. elegans. Cape Province: near Krige, E. Caledon, Goldblatt 4879 (12); S. E. of Shaws Pass, Goldblatt 4095 (12); (also 12, Goldblatt, 1971), (count of 24 by

Brittingham, 1934 is probably due to a misidentification).

H. fenestrata. Cape Province: 60 km S. Calvinia, Goldblatt 3906 (12).

H. flaccida. Cape Province: Twenty Four Rivers, Goldblatt 3924 (24); Lynedoch, Stellenbosch, Goldblatt 4416 (24); N. of Klawer, Goldblatt 3932 (36); Hout Bay, Goldblatt 4974 (36); (four other reports of 36 in Goldblatt, 1971; 1972).

H. galpinii. Cape Province: Foot of Houw Hoek Pass, Goldblatt 3682 (24).

H. longistyla. Cape: Breede R. flats, Goldblatt 3918 (12); near Pr. Alfreds Hamlet, Goldblatt s. n., no voucher (12); Koo, Goldblatt 4181 (12); Swaarmoed Pass, Goldblatt 4413 (12); Eseljag–Queen Anne, Goldblatt 3999 (12); Zebra Kloof, Brandvlei, Goldblatt 4733 (12).

H. marlothii. Cape Province: Calvinia–Klipwerf road, Goldblatt 4284 (24).

H. miniata. Cape Province: Knersvlakte, Vars R., Goldblatt 3679 (12); Matsikamma road S. E. VanRhynsdorp, Goldblatt 3849 (12); Alpha, Goldblatt 3928 (12); VanRhynsdorp–Klawer, Goldblatt 3886 (12); Spektakel Mts., Goldblatt s. n., no voucher (12); near Lynedoch, Stellenbosch, Goldblatt 4415 (24); (also 12, Goldblatt, 1971).

H. minor. Cape Province: Peninsula, Kommetje, Goldblatt 4124 (12); Silvermine Plateau, Goldblatt 4098 (12); Donkergat Peninsula, Goldblatt 4085A (12); 35 km E. Citrusdal, Goldblatt 4203A (12); N. of Pikeniers Kloof Pass, Goldblatt 3929 (12).

H. ochroleuca. Cape Province: Constantia Nek, Goldblatt 4742 (24); Du Toits Kloof Mts., Goldblatt 5087 (24+2–3B). Dasklip Pass, Porterville, Goldblatt s. n., no voucher (12); Fonteintjiesberg, 4000′, Goldblatt 4205A (24); (see Goldblatt, 1971, 12).

H. odorata. Cape Province: Glenlyon, Nieuwoudtville, Goldblatt 4372 (12); near Nieuwoudtville, Goldblatt no voucher (12).

H. pallida. O. F. S.: Harmony, Goldblatt s. n. no voucher (8); N. Brandfort, Goldblatt 4679 (8); Virginia–Hennenman, Goldblatt s. n. no voucher (8); Dealesville, Goldblatt 4678 (8); Virginia, Goldblatt 4677 (8); *Transvaal*, E. of Machadodorp, Davidson 3223 (MO) (12); (also 12 [from Transvaal] Goldblatt, 1971, as *H. pura* and *H. glauca*).

H. pendula. Cape: Kamiesberg, Goldblatt 4306 (12).

H. ramosissima. Cape: Knersvlakte, Goldblatt 3984 (12).

H. schlechteri. Cape: N. Okiep, Goldblatt 2393 (12); 13 km E. Springbok, Goldblatt 4253 (12); 3 km N. Garies, Goldblatt 3981 (12); Platbakkies–Kliprand, Goldblatt 4054 (12).

H. spiralis. Cape: Nieuwoudtville waterfall, Goldblatt 3934 (12); Theunisdrif road, N. E. Nieuwoudtville, Goldblatt 3961 (12).

H. tenuis. Cape: Turn off to Krom River, Goldblatt 4816 (9); Dwars R. farm, Cedarberg, Goldblatt 4817 (9); Cedarberg Pass, Goldblatt 4683 (9); Cedarberg, beyond top of Cedarberg Pass, Goldblatt 4682 (10).

H. tricolor. Cape: near Matroosberg station, Goldblatt s. n., no voucher (12); Op-de-Tradouw, Kalkoenhoek road, Goldblatt 4183 (12); (also 12, Goldblatt, 1971).

H. vallisbelli. Cape: near waterfall at Nieuwoudtville, Goldblatt 3952 (12); S. of Nieuwoudtville–van Rhyns Pass road, Goldblatt 4032 (12).

Rheome

R. maximiliani. Cape: Pakhuis Pass–Brandewyn R., Goldblatt 3884 (20).

R. umbellata. Cape: Paarl, golf course, Goldblatt 4414 (30).

Moraea

M. crispa. Cape: Matjesfontein, Goldblatt 3217 (12); Pietermeintjies, Goldblatt 4157A (12); Calvinia–Middelpos, Goldblatt 4397 (12); Hantamsberg, S. slopes, Goldblatt s. n. (BOL) (12); top of Verlaten Kloof, S. Sutherland, Goldblatt s. n. no voucher (24).

M. polyanthos. Cape: Little Karoo, S. VanWyksdorp, Goldblatt 4168A (12); Stormsvlei Kloof–Bonnievale, Goldblatt 4131 (12); W. Robertson, Goldblatt 2837 (12); (also 12 in Goldblatt, 1971, as *Homeria lilacina*).

M. speciosa. Cape: Tanqua basin, Goldblatt s. n. no voucher (12); near Tulpfontein, Goldblatt 3907 (12).

A new yellow-flowered Hymenocallis (Amaryllidaceae) from North Peru

PIERFELICE RAVENNA

Ravenna, P. 1980 03 17. A new yellow-flowered Hymenocallis (Amaryllidaceae) from North Peru. *Bot. Notiser 133:* 97–98. Stockholm. ISSN 0006-8195.

Hymenocallis heliantha sp. nov., from N Peru, is described. The small size of the plant and the large yellow flowers are horticuturally valuable features, suggesting the possibility of a breeding program in the genus.

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In 1973, Prof. Isidoro Sanchez Vega, of the Universidad Técnica de Cajamarca, Peru, told the writer about a yellow-flowered Andean *Hymenocallis* and presented bulbs for further study. In the spring of 1974 a plant flowered at Santiago, Chile, proving to be a new species.

Hymenocallis heliantha Ravenna, sp. nov.

Typus: Culta in Santiago ex bulbis in regione Magdalenae inter Pacasmayo et urbi Cajamarcae Peruviae a domine I. Sánchez Vega collectis; leg. Ravenna 2059, XI.1974 (holotypus in Herb. Ravennae, isotypus in USM).

Planta usque 26–30 cm alta. *Bulbus* subglobosus ad 4 cm latus tunicis pluribus corrugatis fusco-castaneis vestitus; pseudocollus brevis. *Folia* linearia crassiuscula viridia canaliculata patentia ad anthesin circ. 4–5 ad 25–35(–40) cm longa 12–20 mm lata. *Scapus* brevis compressus 9–11 cm longus 8–9 mm latus. Inflorescentia uniflora. *Spatha* bivalvata valvis inaequalibus membranaceis delicatis albo-viridescentibus, exterior lanceolato-attenuata usque 55 mm longa, interior 30–34 mm longa, angustior. *Flos* cernuus aureo-luteus circ. 16 cm latus. *Ovarium* sessile aellypticum fusco-viride ad 10–12 mm longum circ. 6–7 mm latum. *Tepala* lineari-lanceolata recurve patentia canaliculata vel marginibus saepe convolutis 9–10 cm longa circ. 6 mm lata. *Pocula staminalis* magna lutea delicata vittis viridibus notata ad 8 cm longa 11–12,5 cm lata sex-lobata lobis 25–28 mm longis ad apicem usque 11–13 mm indentatis. *Filamenta* conniventia pallide lutea 25–28 mm longa. *Antherae* versatiles lineares luteae ad 18–22 mm longae. *Stylus* filiformis viridis declinatus usque 18–20 cm longus. *Stigma* capitatus fusco-viridis viscosus.

Habitat. Grassy slopes in the region of Magdalena, between Pacasmayo and the town of Cajamarca, Peru.

Comments. This handsome species belongs to the subgenus *Ismene.* There is only one more species with yellow flowers, viz., *H. amancaes* (Ruiz et Pav.) Nich., a much stouter plant with larger, oblanceolate leaves, and a 2–3-flowered inflorescence. The other species of *Hymenocallis* have white flowers.

Fig. 1. *Hymenocallis heliantha* Rav. — Part of plant and bulb. Drawing by P. Ravenna.

Both the small size and the one-flowered inflorescence suggests a relationship with *H. quitoensis* Herb. and *H. andreana* (Herb.) Bak., two white-flowered species. In the former, the staminal cup is distinctly adnate below to the lower part of tepals; in the latter, the leaves are thinner.

The inclusion in *Hymenocallis* Salisb, is tentative, since in the writer's opinion, *Ismene* Salisb. should be restored as a genus embracing three subgenera: *Ismene, Elisena*, and *Pseudostenomesson*. *Hymenocallis* s. str. seems to be a natural unit.

H. heliantha offers useful characters to be selected by breeders of *Hymenocallis*, such as small size and very large yellow flowers.

Acknowledgements. Thanks are due to Prof. I. Sánchez Vega, Cajamarca, Peru, for the plant material, and to Dr Ghillean T. Prance, New York, for correcting the English text.

Flowering strategies in the Helianthemum oelandicum (Cistaceae) complex on Öland, Sweden

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Widén, B. 1980 03 17: Flowering strategies in the Helianthemum oelandicum (Cistaceae) complex on Öland, Sweden. *Bot. Notiser 133:* 99–115. Stockholm. ISSN 0006-8195.

Helianthemum oelandicum is represented by two flowering strategies on Öland, Sweden. The concentrated flowering (CF) strategy has inflorescences borne on the previous year's growth. The protracted flowering (PF) strategy has inflorescences borne on the current year's growth and also a small and polymorphic proportion of inflorescences borne on the previous year's growth. The flowering of the two strategies has been checked in permanent quadrats in the field since 1974. The fruit-setting of the two strategies is differently affected by summer drought. The short and concentrated flowering period of CF in early June avoids the hazard of the common summer drought more efficiently than PF during its extended flowering period from early June until October. There was a predominantly synchronized increase in the number of inflorescences in both flowering strategies during 1974–1976 followed by a pronounced decrease in 1977. Another period of an increasing number of inflorescences started in 1977. Possible causes of this periodicity are briefly discussed. Plants with the two strategies are allopatrically distributed though scattered PF plants occur in the area of CF plants even far away from the boundary between the two distributional areas.

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This paper is the first in a series of articles dealing with patterns of differentiation and variation, reproduction, ecology and taxonomy of the *Helianthemum oelandicum* complex on Öland, SE Sweden. The present paper deals with the shoot system and the flowering strategies. A subsequent paper on seed set is being prepared.

The Öland populations belong to a taxonomically complex aggregate which has its main distribution in C and S Europe. It has geographically isolated outposts on Öland, in Britain, in Pinega in N Russia, and in N Africa. Broadly speaking it also extends to Turkey and the Caucasus. The taxa show a wide range of geographical and interpopulational variation (Proctor 1957).

In a revision of the complex Janchen (1907) accepted 5 species: *H. canum* (L.) Baum., *H. oelandicum* (L.) Willd., *H. italicum* (L.) Pers., *H. rupifragum* Kerner, and *H. alpestre* (Jacq.) DC. Within these species many subordinate taxa were recognized. Proctor in Flora Europaea (Tutin et al. 1968) divided the complex into 2 species: *H. canum* with 7 subspecies and *H. oelandicum* with 5 subspecies. These two species were separated on the presence or absence of a felt of stellate hairs on the lower surface of the leaves. In reality this character breaks down in some areas (cf. Davis 1965 p. 514).

On Öland there is a great variation in pubescence, qualitatively and quantitatively, as well as in flowering time. Janchen (1907) treated the complex on Öland as a single species with 2 formae, f. *canescens* and f. *praecox*. He also included a population from G. Britain (Teesdale) in *H. oelandicum* as well as an obviously erroneous record from Spitzbergen. Törnblom (1908) suggested that the material from Öland should be subdivided into 4 formae and referred to the C European *H. canum*. Sterner (1936 a) recognized 3 species on Öland: *H. oelandicum* (endemic), *H. canum* (C European) and a third taxon which he suggested should be referred to *H. italicum* ssp. *rupifragum* (SE European).

Extensive biosystematic studies are needed for an understanding of differentiation and variation patterns in the *H. oelandicum* complex. Öland is a suitable area for a detailed analysis of morphological variation and its ecological significance. In the very limited area of Öland the variation covers many of the characters traditionally used to separate taxa within the complex. The populations on Öland are geographically well isolated from the remainder of the distributional area of the complex. Recent outside introgression is therefore improbable.

Provisionally I use the name *H. oelandicum* in the same sense as Janchen (1907), excluding the British population. It means that *H. oelandicum* is treated as endemic to Öland and includes all forms of the complex on the island. Preliminary results of crossing experiments (Widén, unpublished) support such a treatment. No reduction in pollen fertility was found in F_1 between plants from Öland of the three species recognized by Sterner. Crossings between plants from Öland and other parts of Europe gave F_1 with a varying degree of reduced pollen fertility.

The area. The island of Öland is situated in the southern Baltic off the coast of S Sweden. The bedrock of most of Öland is Ordovician limestone. The southern part of the island is dominated by the Stora Alvaret (the Great Alvar), a more or less treeless horizontal limestone plateau consisting of a mixture of exposed bedrock, a thin cover of weathered soils and quaternary deposits (Königsson 1968). Small areas of exposed bedrock occur in other parts of Öland (Fig. 1). The Stora Alvaret, c. 300 km², is covered by a mosaic of more or less unique plant communities (Du Rietz 1923, Sterner 1925, Albertson 1950). One of the dominant plants in large areas of the Stora Alvaret is *H. oelandicum*. It is scattered outside this area and is also locally dominant on the alvar of northern Öland (Sterner 1936 a).

Climate. There is no comprehensive study of the climate of Öland. Sjögren (1961) and Königsson (1968) supplied information regarding the climate. If not otherwise stated the figures given below are based on data supplied by SMHI (Swedish Meteorological and Hydrological Institute, Norrköping).

The proximity of Öland to the mainland of S Sweden causes a low annual precipitation. The prevailing westerly cyclones deposit rain when passing the Swedish mainland, and Öland can be

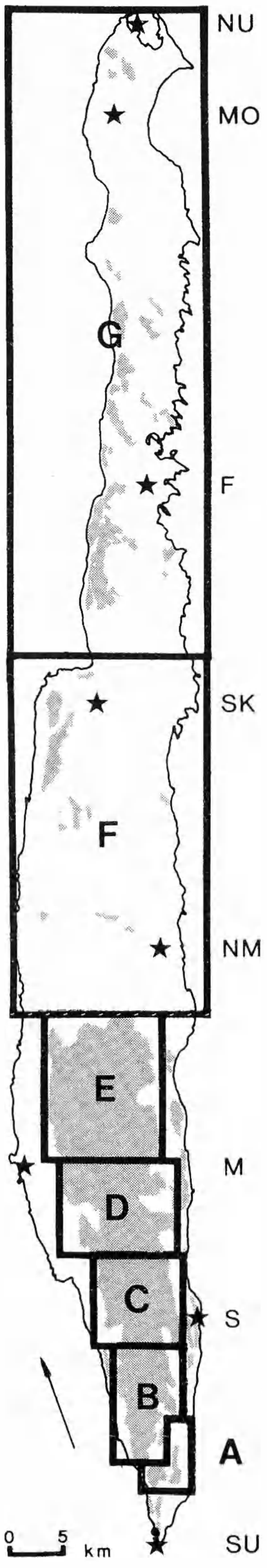

Fig. 1. Öland with the position of sections and meteorological stations. — Grey indicates areas dominated by exposed bedrock and a thin cover of weathered soils (alvars). — Meteorological stations: Ölands N. Udde (NU), Mossen (MO), Föra (F), Skedemosse (SK), N. Möckleby (NM), Mörbylånga (M), Segerstad (S), Ölands S. Udde (SU). (Redrawn from Königsson 1968 p. 13.)

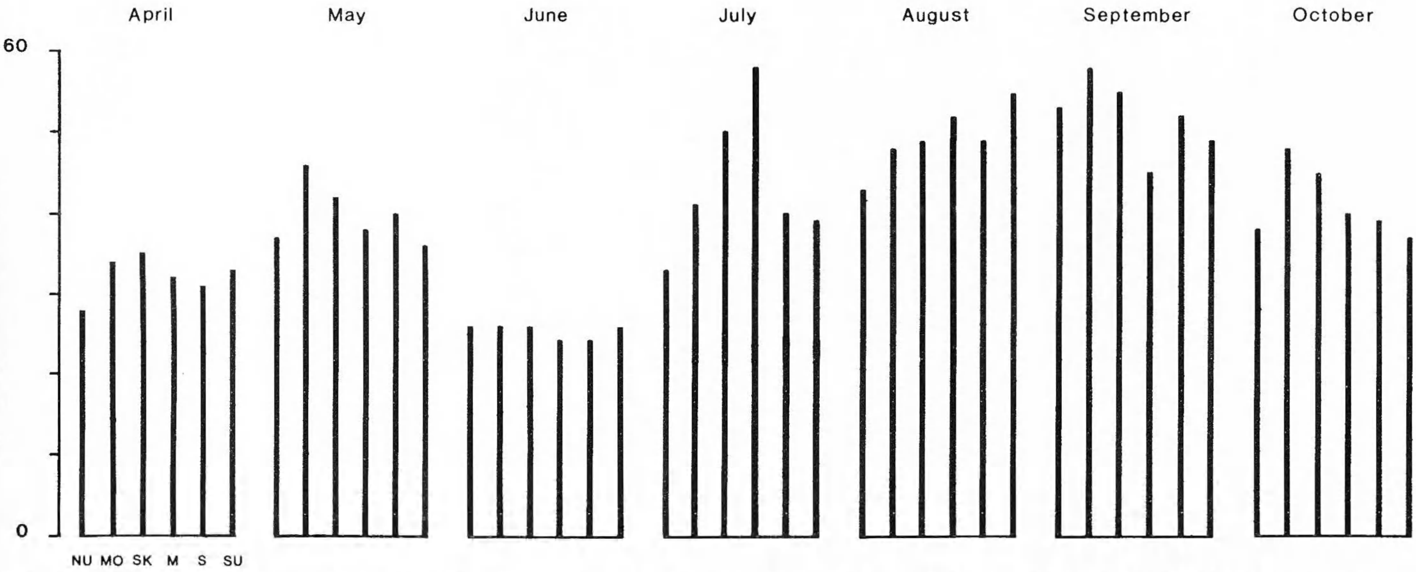

Fig. 2. Mean monthly precipitation for six meteorological stations on Öland during 1961–1977 (1964–1977 for S).

considered to be in the rain shadow (Sjögren 1961). Sjögren gave the mean annual precipitation for the period 1945–1956; 460 mm (Ölands norra udde), 517 mm (Skedemosse) and 461 mm (Mörbylånga). Corresponding values for the period 1961–1977 are 430, 501 and 466 respectively.

The distribution of precipitation during the growing season 1961–1977 is shown from six official meteorological stations on Öland (Fig. 2). Sjögren gave the mean precipitation of 235 mm for April–September at Mörbylånga (1945–1956). This is below the critical value for cultivation without irrigation on Öland. Most rainfall occurs in the second part of the growing season, but the rain falls mostly in showers with an uneven distribution. For example, in August 1976 the precipitation at Mossen was 4 mm, at Skedemosse 66 mm, at Segerstad 9 mm and at Mörbylånga 38 mm. The variation between years is pronounced (Fig. 3).

The annual hours of sunshine vary between 1640 and 2290 at Ölands södra udde (1961–1977) with a mean of 1906 hours which is considerable for Sweden. The prevailing winds are westerly or southwesterly (Östman 1926 Fig. 3 p. 15), with a submaximum of NE winds during winter and spring. The number of days with snow cover is less than 40 in the southern part of the island (Ångström 1974). The temperature climate of Öland is maritime, with late and coolish springs and warm autumns, depending on the water temperature in the Baltic. The number of foggy days is greater on Öland than on the Swedish mainland. The frequency of foggy days is somewhat greater on south and middle Öland (15–20 %) than on north Öland (10–15 %) (Sjögren 1961 Table 3).

Unfortunately, there are no climatic records from the alvar plain. The official meteorological stations are situated near to the sea or in the forest areas. We do not know if the official records are representative of the tree-less Stora Alvaret. Even if they are the effect on the vegetation by the low precipitation is greater on the alvar than in the forest areas. The thin and exposed soil cover is rapidly dried up in the summer by the intense solar radiation and by the more or less constant winds on the alvar. Severe drought occurs almost every year during any part of the growing season. The low mean precipitation during April–June (Fig. 2) is partly compensated for by the well supplied natural water reservoirs (depressions in the bedrock etc.) after the snow melting or winter precipitation. In extremely dry springs drought may affect the vegetation as early as in June, but the normal summer drought does not occur until July or August.

Material and methods

Regional sampling. The selection of material for statistical studies was made in a number of steps.

(1) The known distributional areas of *H. oelandicum* were divided into 7 sections (A–G, Fig. 1).

(2) 145 sites of 100×100 m were selected. They were

geographically dispersed to cover as much of the distributional area as possible. The exact position of the sites was indicated at random on a map. In a few sites *H. oelandicum* was lacking. A new site was then chosen to include the nearest *Helianthemum* population. A greater number of sites were chosen in section B because of the known morphological variation in this area. The number of sites in the sections were: 7 (A), 65 (B), 24 (C), 13 (D), 18 (E), 8 (F), 10 (G).

(3) Within a site a 1×1 m quadrat was drawn from a list of random digits. If the quadrat contained less than 5 mature plants it was moved so as to contain at least 5 plants. When a quadrat contained less than 20 plants, additional quadrats were selected at random within an area of 10×10 m with the NW corner of the original quadrat as the origin until 20 plants in all had been found. The quadrats were marked with stones in each corner for further studies.

(4) One twig with inflorescences and a terminal leaf rosette was chosen at random from each of the 20 plants on each site. On 36 sites the entire plants were pressed, while they were left intact on the other sites. 46 sites were sampled in 1973 and the remainder in 1974.

(5) During the following years reproductive studies were performed in the quadrats of 50 of the sites. These sites were chosen to cover the morphological variation and the geographical distribution of the species as well as for practical purposes of availability (along routes across the alvar etc.).

(6) A further 10 quadrats in section B and E were selected in order to register an interesting gradient of morphological variation detected in the course of the field work. These quadrats are indicated by means of a capital letter in addition to a number.

Transection sampling. Transections across the alvar were made in section B (Fig. 12), C and E. The distance between the transections was c. 400 m. Quadrats (1×1 m) were thrown at every 50 m along the transections if there were at least 5 mature plants of *H. oelandicum* per m^2 within a radius of 10 m. One mature plant was systematically chosen in each corner and one in the middle of each quadrat. Plants that had been effected by drought were avoided. The morphological attributes of these plants were recorded on a tape recorder. Section B and E were investigated in 1975, section C in 1976.

The sampling method in the regional studies was not carried out completely at random, but very nearly so. Therefore serious objections can hardly be raised against statistical treatment using variance analysis.

Plants used in the investigation were always taken from quadrats with at least 5 mature individuals of *H.*

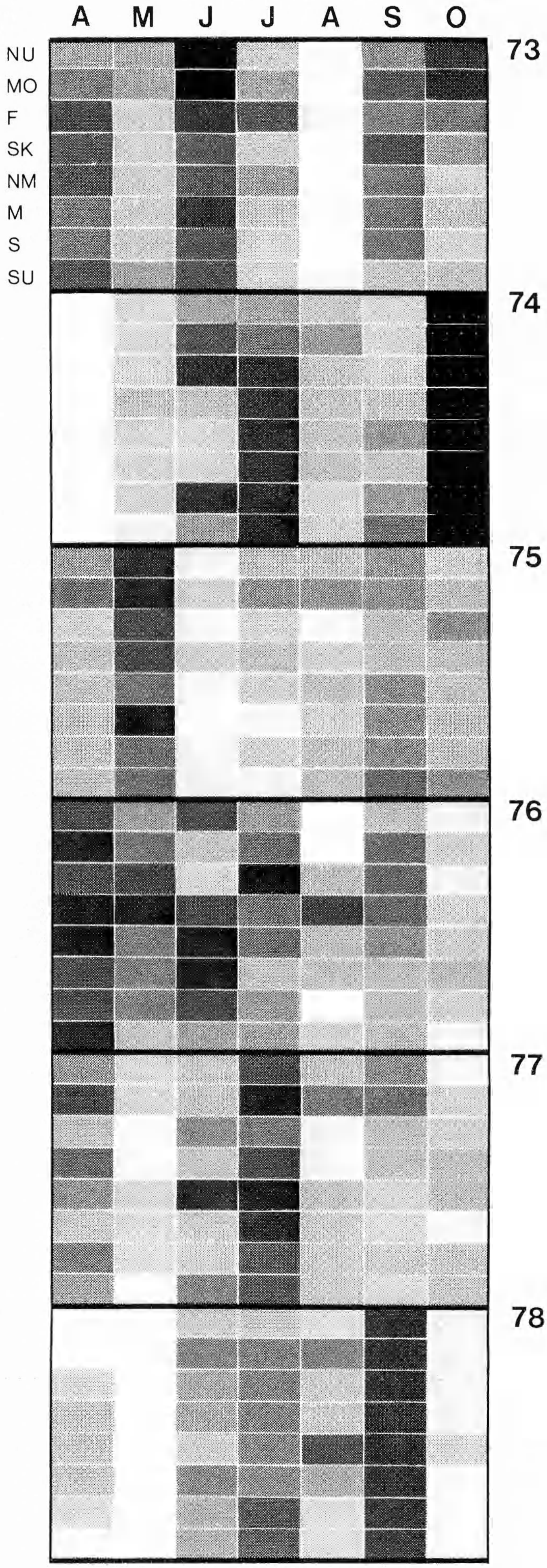

Fig. 3. The monthly precipitation for 8 meteorological stations during 1973–1978 expressed as per cent of the mean of six meteorological stations (cf. Fig. 2). — The intervals on the grey tone scale are:

0 20 40 60 90 110 130 150 180 230 - %

oelandicum. Consequently only plants in well established, rather dense populations have been investigated. Therefore a possible, wider variation in marginal habitats with scattered individuals is not covered.

Cultivation. The total seed production of the permanent quadrats on 20 sites was collected in 1973. The seeds were rubbed on sandpaper to break dormancy. Seeds were sown in April 1974, 100 per site in each pot. All the pots were placed in open frames in the Botanical Gardens, Lund. In May up to 25 seedlings from each pot were transplanted (one seedling per pot). If possible 20 of these were placed at random in uniform conditions outdoors. The remainder were kept for replacement. Seeds collected in 1974 from a further 5 quadrats in section B were sown in May 1975 (no. 111 B–D, 133 and 137 in Table 2).

Seedling establishment was not always successful. Many of the plants died during the first winter, but most plants that overwintered continued to grow vigorously.

One shoot per plant was sampled and preserved in FAA in June and in a few cases in July, when the plants were two or three years old. Some CF plants (Fig. 4) from seeds sown in 1974 were pressed in August 1976, the remainder being still under cultivation.

Mature well established plants were transplanted from selected field localities to the Botanical Gardens, Lund, during 1972–74 to be used in crossing experiments. Other plants were transplanted during the course of the field work in order to be checked for flowering strategy. These transplants were not always easy to establish.

Flowering strategy

Plants of *H. oelandicum* flower in the field after 2–3 years under favourable conditions (when cultivated they may flower in the first year but this is an exception). Under favourable conditions they can thrive for at least 20 years (Sterner 1936 b). In extreme habitats they may be killed by drought or frost-heaving within a few years.

Plants under environmental stress (drought, frost-heaving etc.) have shoots of short duration. The main axis of a shoot system is normally developed during a few growth periods. The axis may eventually be terminated by an inflorescence or more usually by a leaf rosette which is most likely killed by summer drought.

Some shoots continue to grow for several years, and thus the size of the plant increases. Under favourable and protected conditions old plants can become large, up to 50 cm in diameter (cf. Aulin 1912 p. 380). Under normal conditions the shoots die sooner or later and the plants usually become less than 20–25 cm in diameter.

The main axis develops 8–15 internodes per year. At the third node and often at some of the following nodes 1–2 lateral branches may develop. These branches have a growth period of 1–2 years and are normally terminated by an inflorescence. They may develop lateral branchlets especially in favourable years.

Some lateral branches especially those in the basal part may not give rise to inflorescences. Instead they develop into new main axes giving rise to an intricate branching system. Adventitious buds from any part of the plant may give rise to new shoots.

Two flowering strategies can be distinguished on Öland, both of which are also represented in plants from other parts of Europe.

Concentrated flowering (CF) strategy

The inflorescences which normally consist of 2–5 flowers, are only borne on branches of the previous year's growth. Consequently the shoot has no flowers during the first year. During the second year the lateral branches are terminated by inflorescences while the main axis continues to grow and develop branches. During the third year the main axis may continue to grow and develop branches or it may die (Fig. 4).

Protracted flowering (PF) strategy

Several lateral branches of the current year's growth are terminated by inflorescences which do not begin to flower until July and then continue throughout the season. A few branches (usually those of the second order or higher) do not develop inflorescences, but continue growing till the end of the season. They will bear inflorescences in June next year (Fig. 4).

Main biological consequences

(1) The CF strategy results in a very concentrated flowering period in June while the PF strategy gives an extended flowering period from June to October. In Sterner's classification *H. oelandicum* belongs to CF and *H. canum* and *H. italicum* ssp. *rupifragum* belong to PF.

(2) CF and PF have overlapping flowering periods. Sterner (1936 b) discussed the separation of flowering times on Öland and he observed that the late flowering plants had a low frequency of inflorescences borne on the previous year's

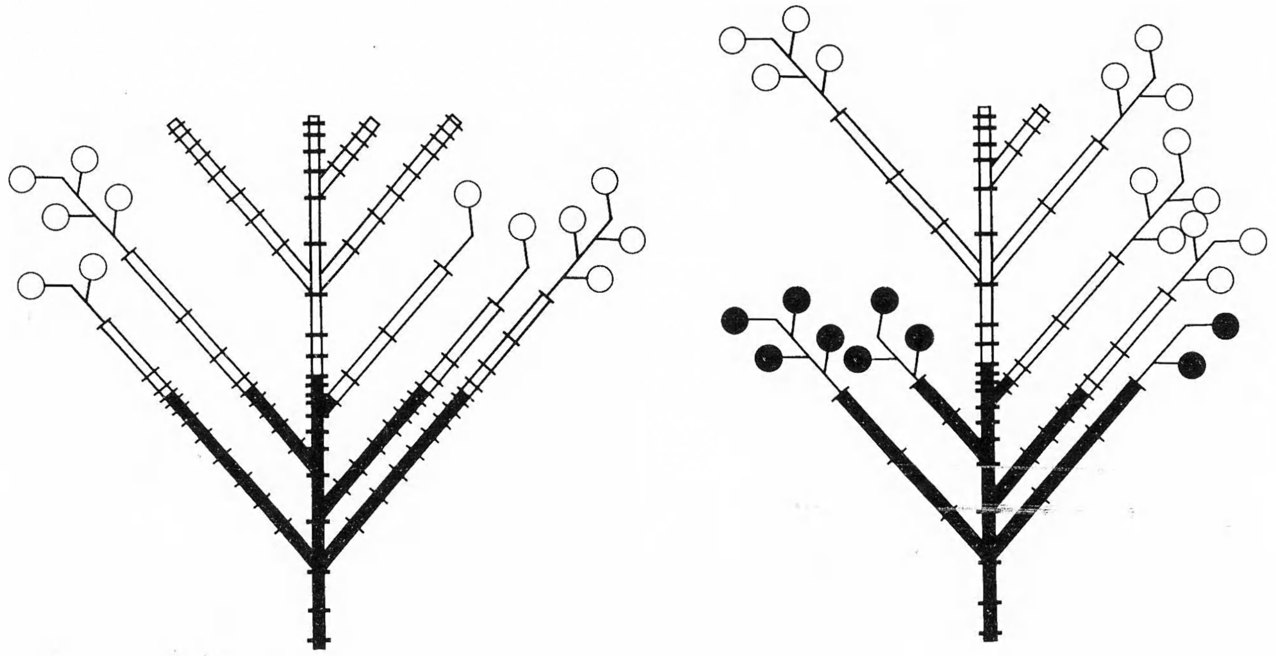

Fig. 4. Diagrammatic shoot systems of the two flowering strategies (see the text). — Black indicates growth during the first year and white during the second year in two arbitrarily chosen years.

growth. Despite this he first stressed a separation of flowering times between early and late flowering taxa. Later he suggested that the three taxa started to flower at about the same time (Sterner 1948 p. 194).

Actually, PF plants when cultivated begin to flower from the previous year's growth earlier than CF plants (Table 1). PF plants when cultivated develop a low frequency of inflorescences borne on the current year's growth throughout the autumn. Occasional inflorescences occur as late as December or January in favourable years. Flowering in PF plants is almost continuous and the development of inflorescence buds is only retarded during the winter. These inflorescences are then visible at an early time in the following spring and they give rise to an earlier start of flowering in PF than in CF. A low frequency of PF plants with fully developed inflorescences with flowers in bud can be found in the field during the winter.

Table 1. The date of the first open flower recorded on at least two inflorescences borne on the previous year's growth per plant in cultivation. The difference between the two flowering strategies is significant at $p < 0.001$.

Date	CF	PF
1976		
5–10.6	32	33
13–17.6	104	35
21–23.6	57	15
1977		
2.6	20	37
5–6.6	26	12
12.6	15	2

On the other hand, the formation of inflorescences in CF plants does not start until the early spring. The growth of the inflorescences in CF is faster and more synchronized than in PF. Five plants chosen at random were checked during cultivation in 1979. The time of development from the first visible inflorescence bud to the first open flower was 16 and 17 days for two CF plants. The corresponding time for three PF plants was 24, 31 and 32 days. The time from the first open flower to the last open flower was 11 and 13 days for the two CF plants. Corresponding figures for inflorescences borne on the previous year's growth in the three PF plants were 16, 19 and 20 days.

In the field there is more or less complete separation of flowering times only in years with a low frequency of inflorescences from the previous year's growth in PF (Fig. 6, 1974 and 1977).

(3) The reproduction of the two flowering systems is affected differently by climatic conditions. For instance, fruit-setting in CF is de-

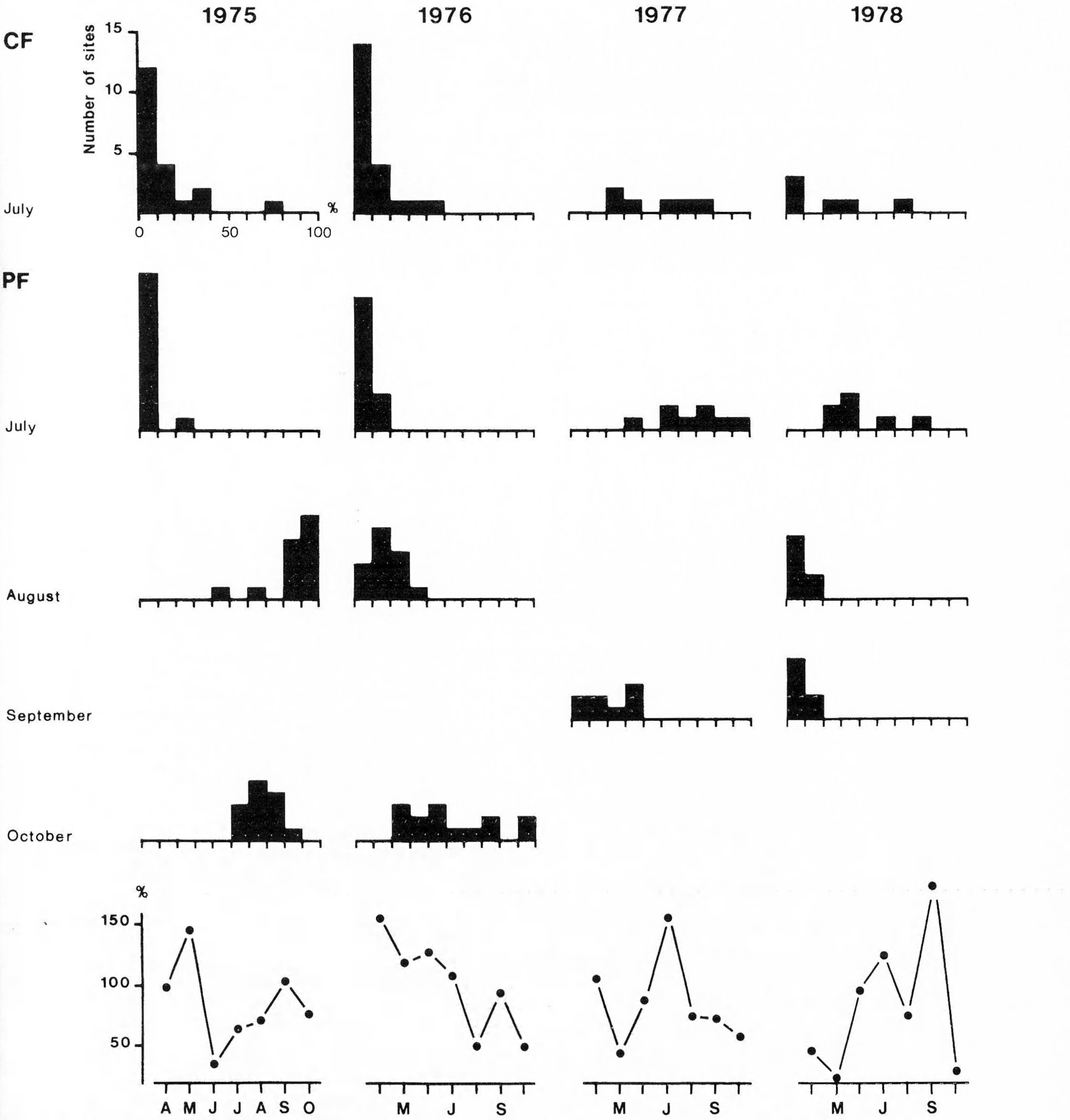

Fig. 5. Unsuccessful fruit-setting during 1975–1978. The horizontal axis show per cent of unsuccessful inflorescences of 20 plants on each permanent site. The months indicate the time of harvesting. — The two upper rows show inflorescences borne on the previous year's growth, the rest show inflorescences borne on the current year's growth. — The graphs in the bottom row show the mean precipitation for six meteorological stations on Öland as per cent of each monthly average (1961–1977).

creased by drought only in spring but not in summer, and fruit-setting in PF is affected by drought both in spring and summer (Fig. 5). The drought affects the development of the inflorescences and if it occurs during an early stage of development the inflorescences wither. The precipitation was very low in May (the crucial time of development of inflorescences borne on the previous year's growth) in 1977 and 1978 (Fig. 3). This had a great effect on fruit-setting in

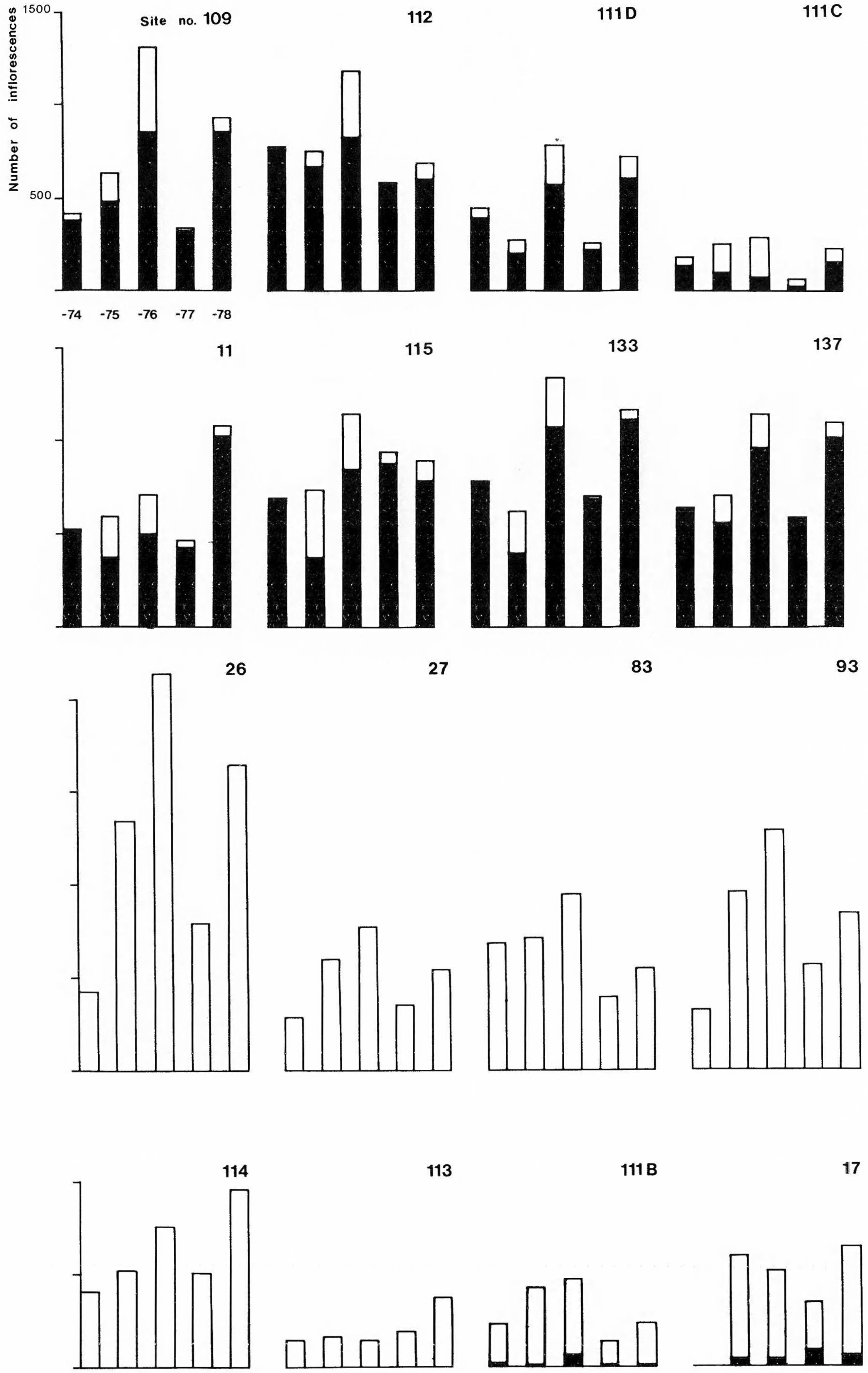

Fig. 6. The number of inflorescences of 20 plants on each permanent site during 1974–1978. — White indicates inflorescences borne on the previous year's growth and black indicates inflorescences borne on the current year's growth.

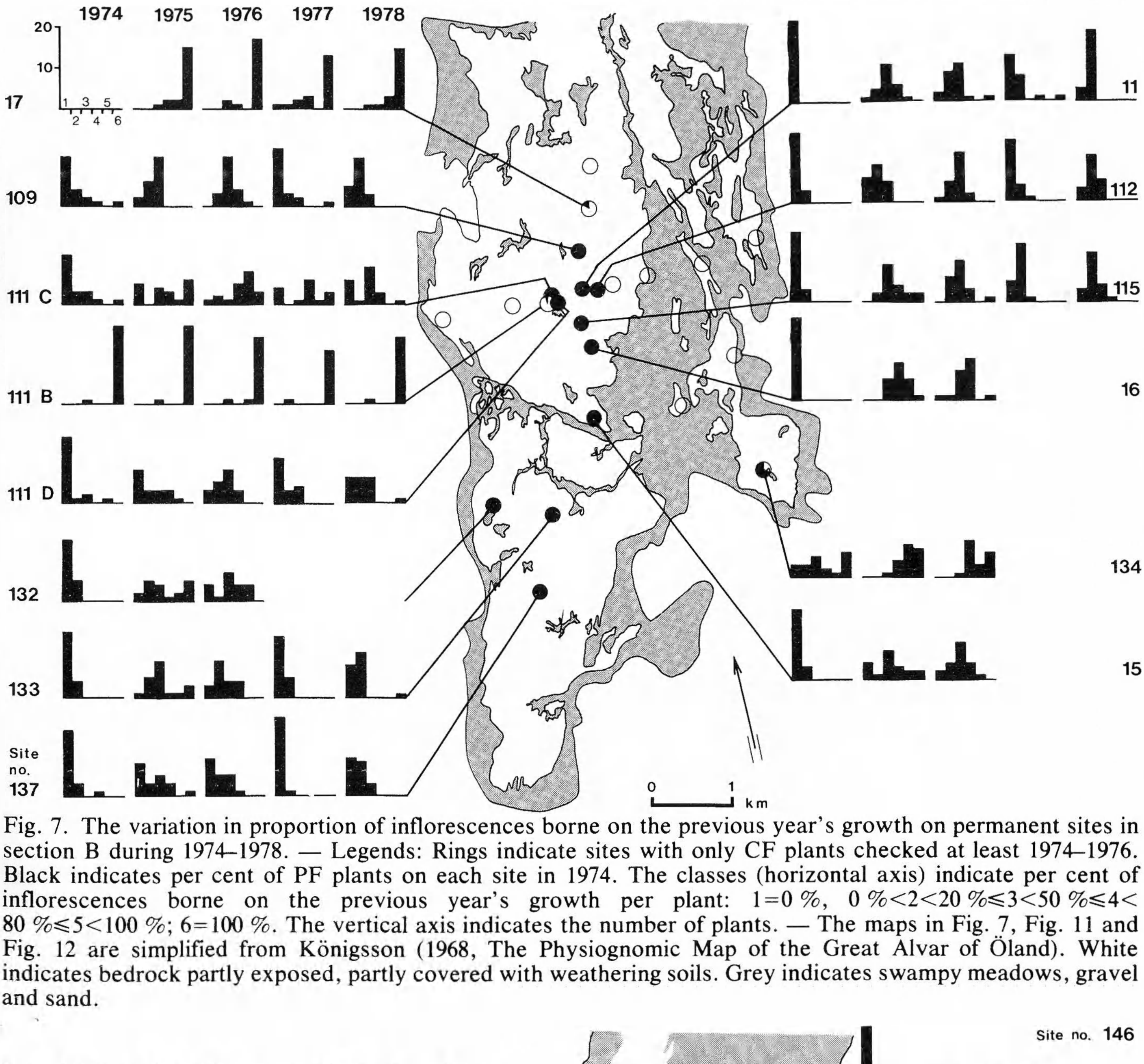

Fig. 7. The variation in proportion of inflorescences borne on the previous year's growth on permanent sites in section B during 1974–1978. — Legends: Rings indicate sites with only CF plants checked at least 1974–1976. Black indicates per cent of PF plants on each site in 1974. The classes (horizontal axis) indicate per cent of inflorescences borne on the previous year's growth per plant: 1=0 %, 0 %<2<20 %≤3<50 %≤4<80 %≤5<100 %; 6=100 %. The vertical axis indicates the number of plants. — The maps in Fig. 7, Fig. 11 and Fig. 12 are simplified from Königsson (1968, The Physiognomic Map of the Great Alvar of Öland). White indicates bedrock partly exposed, partly covered with weathering soils. Grey indicates swampy meadows, gravel and sand.

both CF and PF. However, if the drought occurs at a later stage of development of the inflorescences it does not affect the fruit-setting. The low precipitation in June (the time of development of infructescences borne on the previous year's growth) in 1975 had no effect on fruit-setting (Fig. 5). The low precipitation in the summer months of 1975 resulted in an inefficient fruit-setting on the current year's growth in PF. The drought was less extreme at the end of the summer and consequently the fruit-setting was better in October than in August 1975.

(4) There is a pronounced periodicity in the number of inflorescences between different years (Fig. 6). There is also a periodicity in the proportion of inflorescences developed on the previous year's growth in PF (Figs. 7 and 8).

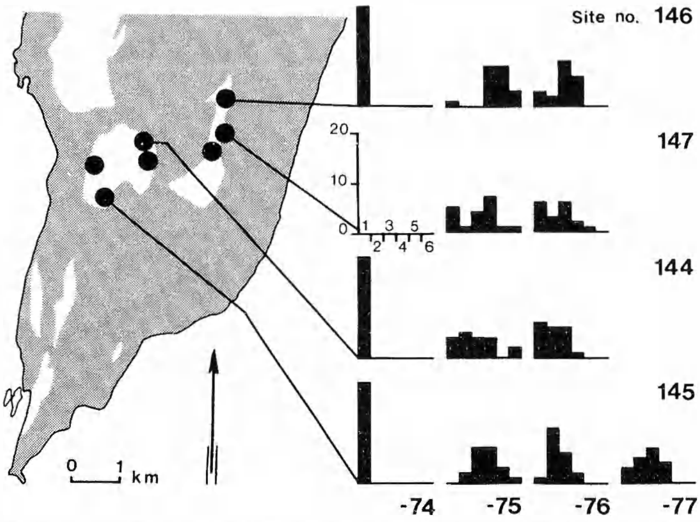

Fig. 8. The variation in proportion of inflorescences borne on the previous year's growth in section A during 1974–1977. — Legends: see Fig. 7. The dots without diagrams are sampled sites not checked for the proportion. White approximately indicates alvar areas and grey areas outside the alvars.

Flowering periodicity

The inflorescences were counted and classified from 1974 to 1978 in the permanent quadrats selected for reproductive studies. Ripe infructescences and withered inflorescences were gathered at varying intervals. In early July each year the infructescences and withered inflorescences of the previous year's growth were cut off and those of the current year's growth from the middle of August to the middle of October. When the final visit was paid in the autumn all inflorescences not yet in fruit and all inflorescence buds were counted. As the summer of 1974 was wet few inflorescences withered and were consequently ignored. This probably affected the number of inflorescences by a few per cent for 1974 in Fig. 6.

During the first three years of cultivation (1974–1976) when pots were moved each autumn the rapidly growing root system was disturbed. In 1977–1979 the pots were not moved, but this period was too short to allow a definitive comparison with field observations. Proctor (1957) cultivated the related *H. canum* in Britain. His observations show that shoots died in the third year and were replaced by new growth from the base.

Number of inflorescences

There are two alternative hypotheses for the causes of the variation in the number of inflorescences between years (Fig. 6).

(1) The variation in number of inflorescences between years may be due to wet and dry summers. Low precipitation during the summer months tends to decrease the number of inflorescences on the current year's growth in PF. When lateral branches, which would normally produce inflorescences in the subsequent year, have died, flowering is delayed in both CF and PF. In particularly dry years many distal shoots may die. I observed an exceptional number of plants suffering from drought in 1973 and 1975. Many plants appeared to have died but a number of them were found to have recovered in the autumn or the following spring when new growth appeared from the base.

During wet summers conditions for bud development are favourable. These buds give rise to new shoots which may develop few inflorescences in the first year in PF but none at all in CF. The number of inflorescences on these shoots increases in the following years in both CF and PF.

The summer of 1974 was wet (Fig. 3). Adventitious buds developed in abundance increasing the number of inflorescences present in 1975 and 1976. The effect of the good conditions in 1974 lasted till 1976, but locally the drought of 1975 killed entire plants or parts of plants, thus decreasing the number of inflorescences in 1976. The drastic decrease in the number of inflorescences in 1977 may have been due to the drought of 1975 and partly that of 1976, when few new shoots were developed and many distal shoots died. July, 1977 was wet and again the plants started to build up a new period of increasing number of inflorescences.

(2) Most cultivated plants showed synchronized increases in the number of inflorescences during 1977–1979. Plants which did not follow this trend were usually weak and suppressed by neighbours in the experimental beds. Plants of different ages showed the same synchronized trend. Seeds derived from site no. 11 were sown in 1974 and seeds derived from site no. 137 were sown in 1975 (Fig. 10).

Many plants in the field showed the same synchronized trends in the number of inflorescences during 1974–1976 and 1977–1979 (Fig. 9) as cultivated plants did during 1977–1979 (preliminary field observations are available for 1979).

The synchronized increases in the number of inflorescences during 1974–1976 and 1977–1979 may not be due to environmental influence on the behaviour of the shoot system, but on genetically fixed 3-year cycles of shoot development in *H. oelandicum*. In the dry habitats of *H. oelandicum* there is an obvious advantage with a shoot system which does not expand the size of the plant indefinitely.

The increase in the number of inflorescences between 1974 and 1975 seems to be more regular in CF than in PF (Fig. 6). This difference is only apparent. The drought of 1975 was fatal for the development of inflorescences on the current year's growth. When I counted withering inflorescences in the field I did not discover inflorescences withering at an early stage of development and I did not make a note if plants

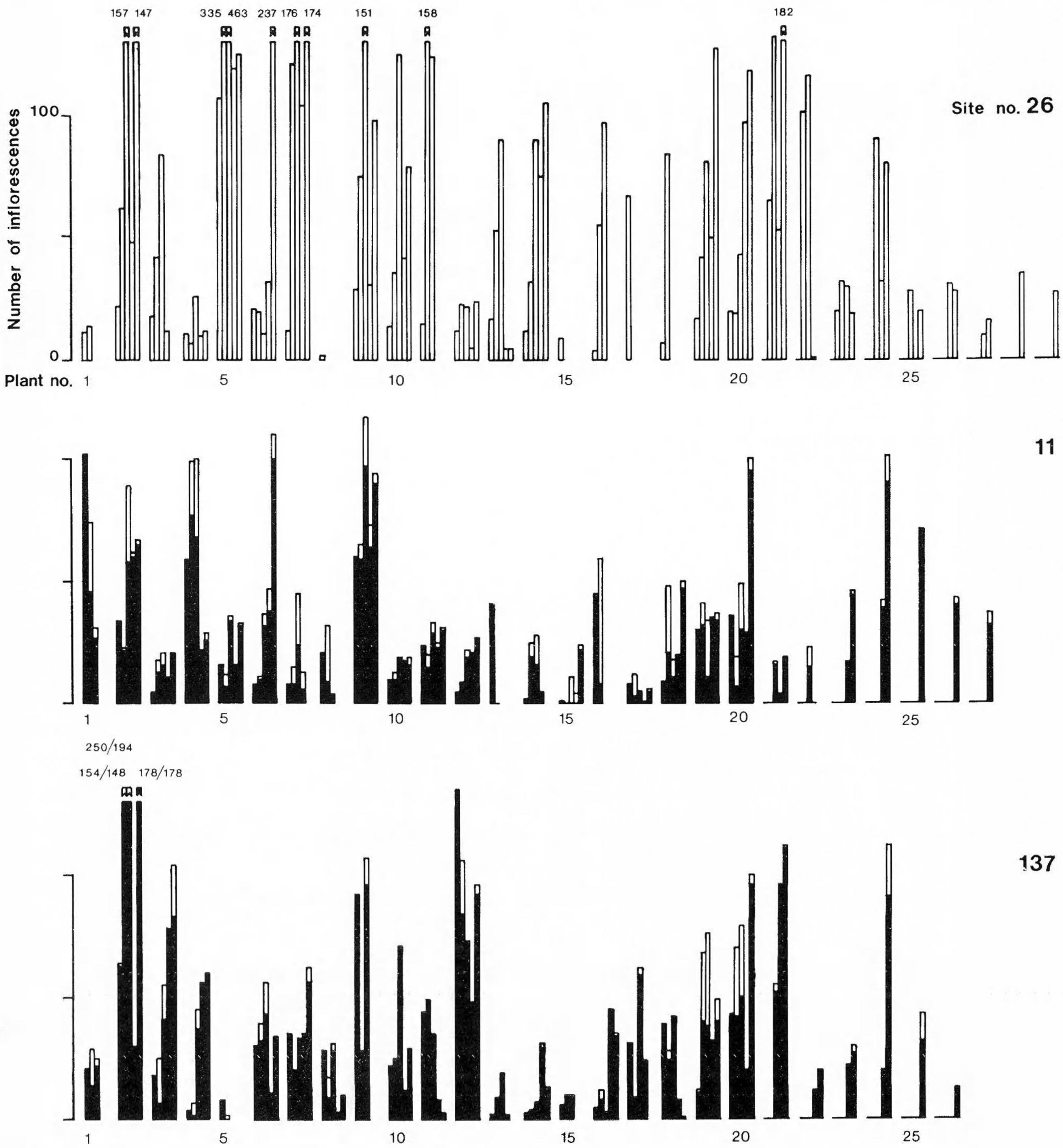

Fig. 9. The number of inflorescences per plant during 1974–1978 (horizontal axis) on three sites. Each group of histograms represents one plant alive from one to five years. 20 plants were checked each year. (Plants no. 1–20 were checked during 1974. For example, plants no. 8, 15 and 17 on site no. 26 died before fruit-setting in 1975 and plants no. 21–23 were added in order to keep the number of plants constant, etc.) — The numbers at the top of the bars indicate the number of inflorescences (on site no. 137: the total number of inflorescences/the number of inflorescences borne on the current year's growth). White indicates inflorescences borne on the previous year's growth and black indicates inflorescences borne on the current year's growth.

partially died. Consequently my estimates of the number of inflorescences on the current year's growth may be biased. This is evident from a comparison between 1974–1975 and 1977–1978. The summer of 1978 was wet and all possible inflorescences developed.

If there exists an innate periodicity in the number of inflorescences, environmental influences such as drought and competition from neighbours may have modifying effects only on the recurrent increase and decrease in the number of inflorescences of single plants.

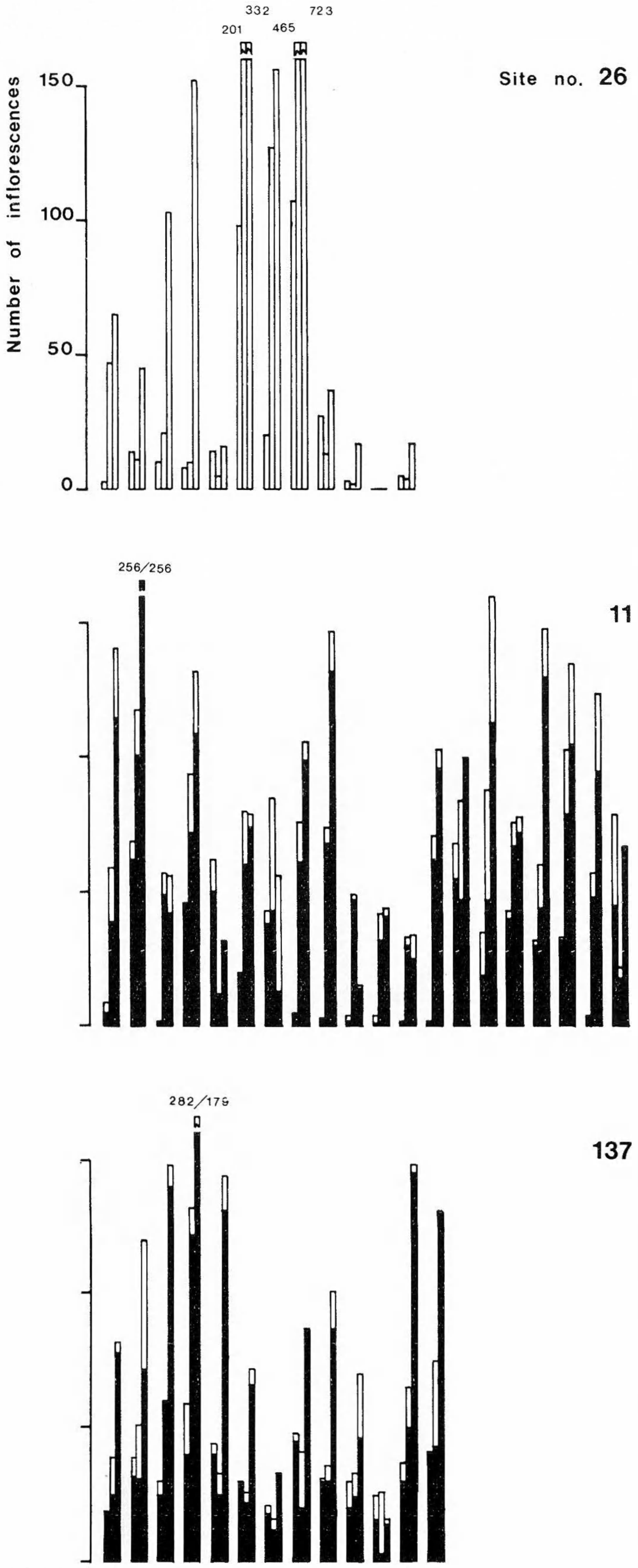

Fig. 10. The number of inflorescences per plant during 1977–1979 on cultivated plants derived from the same sites as in Fig. 9.

H. oelandicum is predominantly wind-pollinated (Törnblom 1908) and self-incompatible (Widén unpubl.). Preliminary calculations of seed set show that there is a correlation between the number of inflorescences present in the population and the number of seeds per capsule (Widén unpubl.). A plant obtains the most efficient seed set if it has the optimum number of inflorescences in the same year as the rest of the population. Natural selection may then favour genotypes which give rise to synchronized shoot development in the population.

A few years more of cultivation and field observations will probably reveal which of the two hypotheses for the causes of the variation in number of inflorescences is the most probable one.

There is no clear difference between the two flowering strategies in total production of inflorescences per year, but there are differences between sites. This may be due to different age structures of the populations or to genetical differentiation between populations. However, more studies are needed before this can be evaluated.

The short and synchronized flowering of CF early in the summer avoids the hazard of the usual summer drought. The flowering from the previous year's growth in PF also avoids the summer drought. It seems reasonable to suppose that the shoot system of CF has an advantage over that of PF under present climatic conditions (cf. Sterner 1936 b p. 190). However, during some years the drought occurs early in the season, and this affects the fruit-setting from the previous year's growth (Fig. 5, 1977 and 1978). Accordingly, a possible advantage of one or the other flowering strategy can not be completely judged before other stages of the reproductive cycle have been studied. The results of such studies will be discussed in a future paper.

The proportion of inflorescences from the previous year's growth in the PF strategy

A number of plants recorded as PF in 1974 did not flower at all in 1975 (Fig. 9, plant no. 15 on site no. 11). Others bore inflorescences on the previous year's growth but died or ceased to grow early in the season (Fig. 9, plant no. 5 on site no. 137). These would have been classified as CF in 1975 if they had not been recorded as

PF in 1974. The only reliable immediate method for classifying some weak plants during dry years, is to dissect buds of the current year's growth (Sterner 1936 a p. 426).

The variation in proportion of inflorescences borne on the previous year's growth between the years is mainly a consequence of the behaviour of the shoot system. There are slight possibilities of inflorescences being borne on the previous year's growth the year after dying back of many distal shoots (Fig. 7, 1974, 1977). Fig. 9 illustrates the variation of individual plants between the years on two sites of PF plants. There are obvious differences between individuals. For instance, plant no. 10 on site no. 137 bore no inflorescences on the previous year's growth during 1974–1978. When cultivated all PF plants (except two weak plants of 185 cultivated plants) bore inflorescences on the previous year's growth in any year. Evidently environmental influences play a part in the variation between individuals in the field. However, preliminary results of cultivation indicate a genetical polymorphism within populations (cf. Fig. 10) and even between populations. In particular PF plants derived from seeds collected on the boundary between the distributional areas of the two flowering strategies have a high proportion of inflorescences on the previous year's growth. On site no. 16, 3 plants have not yet flowered from the current year's growth in cultivation although all the seeds were collected from PF plants (Table 2). This suggests introgression between CF and PF strategies. Reproductive isolation and gene flow will be discussed in a future paper.

Distribution

Sterner (1936 a) published distributional maps. From these it is obvious that PF plants are restricted to a small area in the southernmost part of Öland. The area covers c. 10 km of the southern part of the distributional area of *H. oelandicum* (my sections A and B in Fig. 1). There are scattered records outside this area (in section C and E), but it is doubtful whether all these records belong to PF (*H. canum* and *H. italicum* ssp. *rupifragum* in Sterner's classification).

It is evident from Sterner's distributional maps that CF and PF occur sympatrically. Later he stressed that one or the other of the three taxa is dominant in different areas (Sterner 1955). Sjögren (unpubl.) stressed a mosaic distribution pattern of the three taxa recognized by Sterner.

Table 2. The number of CF and PF specimens in natural and cultivated populations.

Site no.	Section	Field		Cultivation	
		CF	PF	CF	PF
1	A		20		17
2	A		20		20
11	B		20		20
15	B		20		20
25	B		20		7
111 D	B		20		15
133	B		20		9
137	B		20		13
6	B	17	3	14	6
12	B	17	3	15	5
17	B	17	3	13	6
24	B	5	15	8	12
111 B	B	19	1	18	
111 C	B	1	19	1	19
16	B		20	3	16
9	B	20		18	
10	B	20		20	
13	B	20		19	
20	B	20		19	
21	B	20		18	
26	C	20		18	
27	C	20		18	
34	D	20		19	
36	E	20		20	
41	G	20		20	

The distribution of sites sampled in sections A and B is shown in Figs. 8 and 11 (regional sampling). Sampling was carried out either from late June to late July, 1974, or if at an earlier date the quadrats were visited several times during the summer of 1974 (except one quadrat which was not possible to find again). Plants with at least one well-developed inflorescence from the current year's growth were classified as PF. The summer of 1974 was wet and conditions thus favourable for the development of inflorescences on the current year's growth so that it was highly unlikely that PF plants would be overlooked.

In sections C–G 73 sites were sampled. No PF plants were found on these sites. CF plants rarely bore one or two rudimentary inflorescences on the current year's growth (Sterner 1936 b p. 185), but this did not occur in the permanent quadrats (n=20) visited in sections C–G during 1974 or later.

The investigation of transections across the alvar (transection sampling) was made between

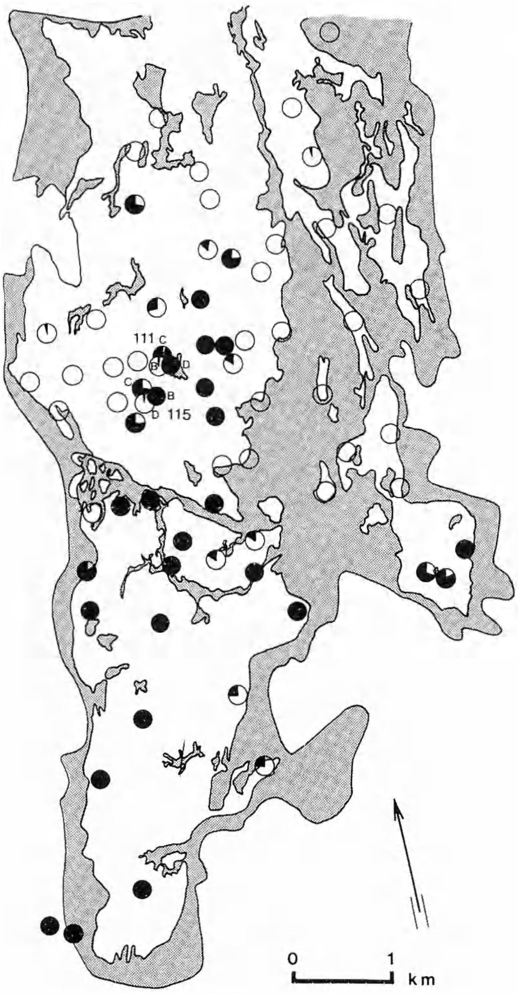

Fig. 11. The distribution of sites sampled in section B. — White sectors indicate % of CF plants and black indicates % of PF plants. Sites mentioned in the text are indicated on the map.

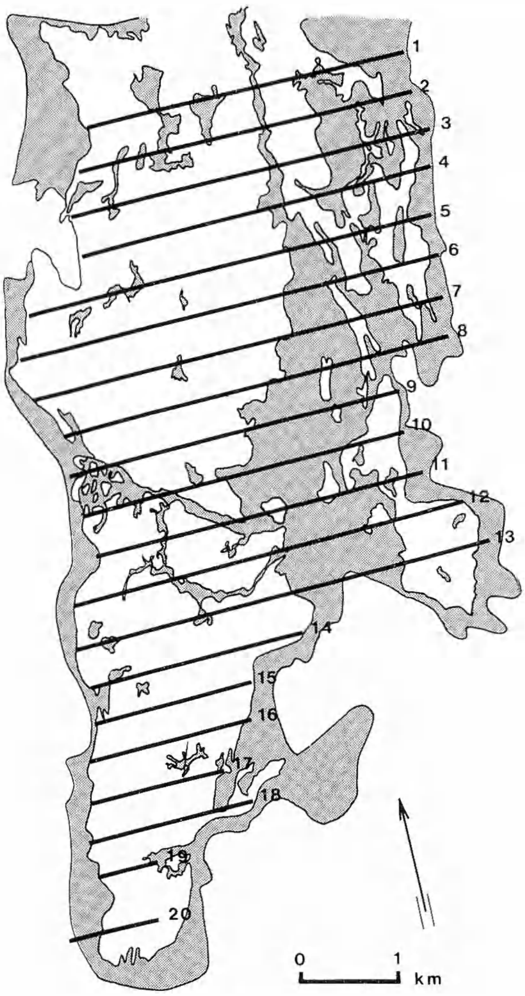

Fig. 12. The positions of the transections across the alvar in section B.

the middle of July and late October, 1975, in section B (Fig. 13), in the middle of July, 1975 in section E, and from July to August, 1976, in section C. PF plants were only found in the sampled quadrats in section B.

In section B 560 quadrats containing at least 5 *Helianthemum* plants were studied. Of the five plants investigated all were PF plants in 255 quadrats and CF plants in 248 quadrats. Mixed samples were found in only 57 quadrats (10.2 %).

It is important to stress that plants with the two flowering strategies have separate distributional areas. CF and PF plants occur mixed mainly by the boundary between the two distributional areas though scattered PF plants occur in the area of CF even far away from the boundary (cf. Fig. 13, transect no. 4). I have seen three PF plants as far as c. 5 km north of the distributional area of PF. One of them has been checked in cultivation since 1975 and it has proved to be a PF plant.

All checked plants, which were suspected of being CF in the central part of the PF area in section B have proved to be PF. Only one plant c. 100 m from the boundary at transection no. 6 has proved to be CF when checked in cultivation (1974–1978). This plant is interesting because it was first classified as *H. canum* according to Sterner's species concept. I have never seen any CF plant in section A. However, plants in this area have a higher proportion of inflorescences on the previous year's growth than PF plants in section B, and consequently, it is easy to make incorrect classifications or to overlook CF plants.

The transection sampling in section B was made during a dry year. The risk of overlooking weak PF plants was obvious. I avoided plants suffering from drought, and this may have

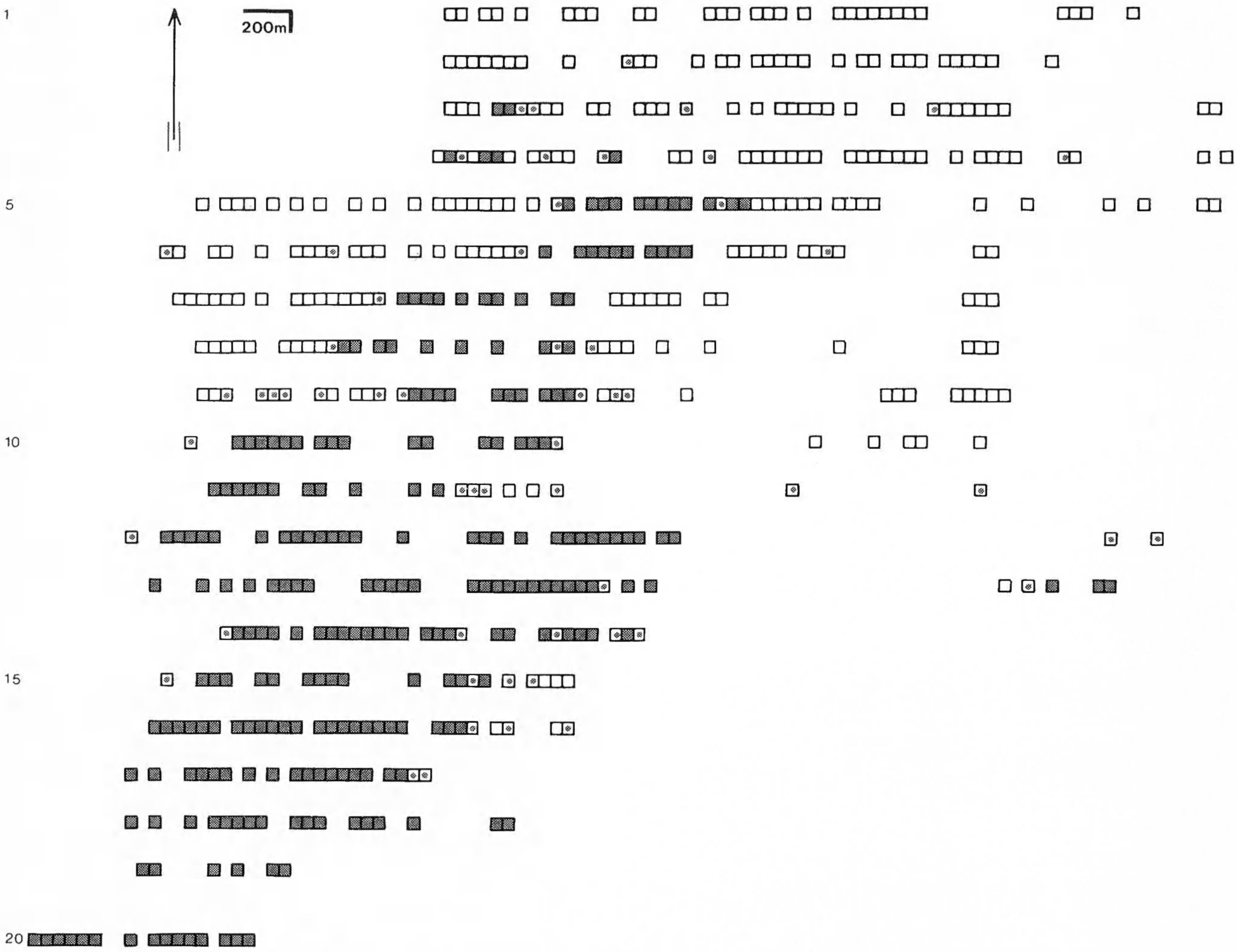

Fig. 13. Diagrammatic map of transections across the alvar in section B. — Each quadrat indicates a 50 m distance with *Helianthemum* and empty spaces 50 m distances without *Helianthemum*. White quadrats indicate 5 CF plants, filled quadrats indicate 5 PF plants and dots indicate mixed samples. For reference to the position of the transections see Fig. 12.

affected the results. However, I have no reason to believe that drought affects PF plants more than CF plants.

The boundary between the distributional areas of CF and PF is sometimes very distinct. For instance, quadrats 111 B, C and D are situated at the three corners of a triangle where the sides B–C, C–D and B–D are 65 m, 82 m and 128 m respectively. The distance between quadrats 115 B and C is c. 15 m and between C and D c. 20 m (Fig. 11).

The topography of the limestone plateau is particularly variable where the boundary is distinct. The two distributional areas are often separated by depressions running in a N–S direction. These damper depressions are occupied by communities where *H. oelandicum* is lacking.

The boundary NW of the village of Sebberneby is particularly diffuse (Fig. 13, transections 15, 16) with CF and PF plants mixed. Here the topography changes gradually, from flat poorly drained habitats occupied by CF plants to more variable and well-drained habitats with PF plants. I agree with Sterner (1936 a p. 422) that late-flowering plants grow in better drained habitats than early-flowering plants. Environmental factors and variation will be discussed in a future paper.

Discussion

The two flowering strategies described in this paper are not restricted to *H. oelandicum*. Most species of the aggregate concerned have both systems. Sterner (1936 a p. 427) compared the flowering times of S and C European taxa with those of the three taxa on Öland. He concluded that most taxa had the same shoot system as *H. canum* (PF) on Öland. I have cultivated the five species recognized by Janchen (1907) from different parts of Europe. Up to the present only *H. alpestre* has been found to have only one of the systems (CF). Most populations, both cultivated and those checked from herbarium collections, have the same basic system as CF on Öland.

The shoot system of PF has been used as a taxonomic character in some cases (cf. Tutin et al. 1968) for separation of geographically restricted taxa. However, modified systems of PF can also be found in many other cases in S and C Europe.

The occurrence of the two flowering strategies throughout the whole species group suggests that it is reasonable to regard it as a well-established adaptive system. One or the other strategy has or had a selective advantage during different environmental conditions.

There are two plausible hypotheses for the origin of the two flowering strategies on Öland.

(1) The two flowering strategies represent two migration groups, which have reached Öland separately, at different times or along different routes. They make slightly different demands upon or show different advantages in the habitats and these differences are manifested in the present predominantly allopatric distributions.

Pollen-analytical studies have shown that *H. oelandicum* s. lat. was abundant in S Scandinavia during late glacial time (cf. Berglund 1966 Figs. 59–62). The common opinion is that the pollen records from late glacial time belong to the early flowering form (*H. oelandicum* s. str. according to Sterner). However, the pollen of the two flowering strategies seems to be undistinguishable (Widén unpubl.).

(2) The shoot systems of the two flowering strategies are similar in character. It is easy to understand how they can be converted into each other. This transformation can be achieved by genetical changes step by step and each step can be selectively advantageous. A transformation from PF to CF is the most natural one. If the plant has an advantage in flowering from previous year's growth, PF can successively derive a larger proportion of inflorescences from the previous year's growth till a system with all inflorescences borne on the previous year's growth has been fixed (directional selection).

The reverse transformation from CF to PF is less probable. When a single CF plant derives occasional inflorescences from the current year's growth it will loose reproductive capacity. These inflorescences do not occur until the main flowering period has ceased. In a self-incompatible plant such as *H. oelandicum* (Widén unpubl.) it means a low or probably no fruit-setting of these inflorescences at all (stabilizing selection). However, a CF system without a rapid and synchronized development of inflorescences borne on the previous year's growth is a possible starting point in a transformation from CF to PF.

The shoot system makes a differentiation by natural selection in a heterogenous environment possible. Edaphical, microclimatical or other conditions may favour one or the other flowering strategy. Natural selection may diversify polymorphic PF populations especially if they are isolated from each other (disruptive selection).

Königsson (1968) has outlined the Holocene history of the Stora Alvaret on Öland. Today the Stora Alvaret is a barren, more or less tree-less area. Pollen records show a forest period from the late Preboreal period to the transition between the Atlantic and Subboreal periods. The forest was open and must have been restricted to areas of open joint systems in the bedrock and gravelly deposits. A possible more extensive soil cover may have widened these areas. Light demanding plants such as *Artemisia* and *Helianthemum* existed during the forest period. However, the pollen records of *Helianthemum* during this period are few (Königsson 1968 Fig. 116). This indicates that *H. oelandicum* existed in small isolated populations, restricted to areas with exposed bedrock. This isolation may have speeded up the differentiation.

After the forest period human influence has been great. This is reflected in the pollen diagrams in the increasing records of *Helianthemum* (Königsson 1968 Fig. 116). The present distribution of *H. oelandicum* is probably a result of the opening up of the landscape by man. It spread from restricted refugia and became a dominant member of the alvar communities. CF was the superior competitor and became the most widely distributed. PF is perhaps restricted to its old refuge-area today.

I cannot make a final decision based on the facts presented in this paper as to which hypothesis regarding the origin of the two flowering strategies on Öland is the most probable; they can both be considered as possible. However, even though *H. oelandicum* was probably differentiated into two flowering strategies when it reached Öland, the question remains as to when this differentiation occurred.

Irrespective of the early history of *H. oelandicum*, the present variation pattern on Öland is an interesting model of the variation pattern of the species group as a whole. For example, I have seen the same distinct microgeographical boundary between two traditional taxa (*H. canum* and *H. alpestre*) in the Balkans (on Mt Botin, Jugoslavia), as between the two flowering strategies on Öland. The differentiation on Öland may represent an early stage of speciation in a process which is common for the species group as a whole.

At present the mechanisms behind the allopatric distribution of the flowering strategies on Öland are obscure. An understanding of these mechanisms will not only give an insight into the evolution of *H. oelandicum*, but also an increased knowledge of the population biology of the plant. Field experiments have been carried out and at the moment long-term competition experiments are going on with the purpose of studying the interaction between the two flowering strategies in each others habitat.

Acknowledgements. Field work during 1973–1976 was carried out at the Ecological Station of Uppsala University, Ölands Skogsby. I would like to express my sincere thanks to the Principal and to the staff of the Station. Thanks are also due to Professor Hans Runemark who suggested the present investigation and made valuable criticism regarding the manuscript.

References

Albertson, N. 1950: Das grosse südliche Alvar der Insel Öland. Eine pflanzensoziologische Übersicht. *Svensk Bot. Tidskr. 44:* 269–331.

Ångström, A. 1974: *Sveriges klimat.* 3rd ed. Stockholm.

Aulin, F. R. 1912: Botaniska anteckningar från Öland. *Svensk Bot. Tidskr. 6:* 373–386.

Berglund, B. 1966: Late-Quaternary vegetation in eastern Blekinge, southeastern Sweden. A pollen-analytical study. I. Late-Glacial Time. *Opera Bot. 12:(1).* Lund.

Davis, P. H. 1965: *Flora of Turkey and East Aegean Islands. 1.* Edinburgh.

Du Rietz, G. E. 1923: Studien über die Helianthemum oelandicum-Assoziationen auf Öland. *Svensk Bot. Tidskr. 17:* 69–82.

Janchen, E. 1907: Helianthemum canum (L.) Baumg. und seine nächsten Verwandten. *Abhandl. Zool.-Bot. Gesellsch. Wien 4:(1).*

Königsson, L.-K. 1968: The Holocene history of the Great Alvar of Öland. *Acta Phytogeogr. Suec. 55.*

Östman, C. J. 1926: Om stormar vid Svealands och Götalands kuster. (Les grandes vents près des côtes du Svealand et du Götaland.) *Medd. fr. Stat. Meteor.-Hydr. Anst. Bd. 3. No. 6.* Stockholm.

Proctor, C. M. F. 1957: Variation in Helianthemum canum (L.) Baumg. in Britain. *Watsonia 4:* 28–40.

Sjögren, E. 1961: Epiphytische Moosvegetation in Laubwäldern der Insel Öland (Schweden). *Acta Phytogeogr. Suec. 44.*

Sterner, R. 1925: Einige Notizen über die Vegetation der Insel Öland. *Svensk Bot. Tidskr. 19:* 1–20.

Sterner, R. 1936 a: Helianthemum oelandicum (L.) Willd. och dess anförvanter på Öland. *Svensk Bot. Tidskr. 30:* 419–432.

Sterner, R. 1936 b: Ekologiska iakttagelser över Helianthemum oelandicum (L.) Willd. *Medd. Göteborgs Bot. Trädg. 11:* 183–208.

Sterner, R. 1948: Ölands flora. *In* B. Palm, L. Landin and O. Nordmark (eds.), *Öland I:* 91–235. Lund.

Sterner, R. 1955: Ölandsväxter. *In* R. Sterner and K. Curry-Lindahl (eds.), *Natur på Öland:* 88–97. Stockholm.

Tutin, T. G. et al. 1968: *Flora Europaea 2.* Cambridge.

Törnblom, G. 1908: Iakttagelser öfver Helianthemum canum (L.) Baumg. och H. oelandicum (L.) Willd. på Ölands alvar. *Svensk Bot. Tidskr. 2:* 32–37.

Botanical literature

Emoto, Y. 1977: *The Myxomycetes of Japan.* 263 pp., including 128 plates. Sangyo Tosho Publishing Co., Ltd., Tokyo. Available from Maruzen Co., Ltd., P.O. Box 5050, Tokyo International, Tokyo 100-31, Japan. Price U.S. $125.

The species of myxomycetes generally accepted today number something between 500 and 550. Attempting to give a reasonably correct figure is rather meaningless, since the range of intraspecific variation is poorly known in many cases and some forms seem to bridge the gap between previously accepted species. In several cases cultivation under controlled conditions will be necessary in order to solve taxonomic problems. Although it is generally agreed that the majority of species are more or less cosmopolitan, some species show a definite preference for tropical regions, others for cold regions. Thus myxomycete floras of certain geographical areas may be justified. Such a flora is Emoto's *The Myxomycetes of Japan.* It is a rather special book however, being mainly a collection of carefully prepared illustrations and lacking much of the information normally expected in a scientific publication.

The book comprises 123 coloured plates and 5 black-and-white plates, 3 of which are photographs. The illustrations are on the right-hand pages and brief descriptions are given on the opposite pages. 250 species are treated. The colour illustrations are of high quality and whole fructifications as well as microscopic details are carefully figured. The illustrations are based on the same original sketches as the black-and-white pictures in Emoto's (1942) myxomycete volume of Nova Flora Japonica (eds. T. Nakai & M. Honda), but about five times as many species are illustrated in this new book. The general style and standard of the illustrations are surprisingly even throughout the book, despite the fact that three different artists are involved. The book starts with an enumeration of the species illustrated and ends with an index. There is no bibliography.

The identity of the species generally appears correct, although a question mark might be put on Fig. 11, Plate 120. It is possible that this figure was based on a not very typical specimen, but it gives the impression of *Didymium verrucosporum* rather than *D. iridis* as indicated. Unfortunately the quality of the text is far below that of the illustrations. Some descriptions are very brief and the English should have been checked by an expert. Several taxa have been misspelt. The spelling is the same in the species list at the beginning of the book and in the index. As examples can be mentioned *toycogala exiguurn* (instead of *L. exiguum*), *Caromyxa metallica (Calomyxa m.), Arcyrodes incarnata (Arcyodes i.),* and *Didymium melanosporum (D. melanospermum).*

In the foreword it is said that most of the illustrations are based on material collected by the author and now available for investigation at the National Science Museum, Hyakunincho, Shinjuku, Tokyo (TNS). However, from a scientific point of view it would have been valuable if the collection on which each illustration is based had been indicated. There are some species illustrated which have not been found in Japan (*Arcyria leiocarpa, Badhamia versicolor, Physarum bitectum, P. ovisporum*), and which supposedly have not been collected by Emoto. The origin and collection would be important to know here, as well as in cases where the interpretation and intraspecific variation have been under debate. This holds for e. g. *Licea tenera* and *Physarum ovisporum*. Also, where more than one collection has been illustrated in a species (e. g. *Arcyria incarnata*), it would have been useful to know from which sample the microscopic details have been figured.

The book contains four taxa which are not found in modern myxomycete literature. They are *Ceratiomyxa descendens* Emoto, *Dictydiaethalium cinnabarium* (Berk. & Br.) Hiranuma, *Stemonitis syncarpa* (Yamashiro) Emoto, and *Physarum puniceum* Emoto. Since there are no literature references the reader is left in a vague supposition that the formal establishment of these new species and combinations are to be found in recent Japanese literature. This is, however, not necessarily the case. Thus *Physarum puniceum* is found also in Emoto's (1942) myxomycete volume of Nova Flora Japonica, where a full reference is given to its original publication (Bot. Mag. Tokyo 45: 229, 1931). The other three taxa enumerated do not exist at the species level in the volume mentioned. However, although there is unfortunately no citation of synonyms in Emoto's new book, the precursors of the three taxa are apparent at the variety level in Nova Flora Japonica. Thus *Ceratiomyxa descendens* is reasonably the same as *C. fruticulosa* var. *descendens* Emoto. *Dictydiaethalium cinnabarium* (apparently misspelling for *cinnabarinum*) is presumably what is called *D. plumbeum* var. *cinnabarinum* (Berk. & Br.) Hiranuma, and which is based on *Licea cinnabarina* Berk. & Br., a name generally degraded into synonymy with the variable *D. plumbeum*. *Stemonitis syncarpa* is apparently the same as *S. confluens* var. *syncarpa* Yamashiro. In this as well as in the two previous cases the publications in which the varieties are raised to the species level are unknown to the reviewer, and unfortunately Emoto's new book gives no help. The illustration of *Stemonitis syncarpa* shows a species of *Symphytocarpus*-type with striking characteristics.

This is a beautiful book, completely built up around its outstanding illustrations. From a scientific point of view, however, its value is limited. Collection indications on all illustrations, addition of synonyms in a few cases, and a bibliography with adequate references to at least recently established taxa, would have greatly increased the scientific value of the book. Because of these omissions it is hardly worth its high price.

Uno Eliasson

Jørgensen, P. M. 1978: *The lichen family Pannariaceae in Europe*. Opera Botanica 45. Stockholm. 123 pages, 53 figures and distribution maps in text. ISSN 0078-5237. ISBN 91-546-0241-6. Price SKr 66:–, libraries SKr 110:– (wrappers).

Pannariaceae is a family of crustose, squamulose or slightly foliose lichens mainly containing *Nostoc* or other blue-green algae as phycobionts. It is usually placed near Peltigeraceae. The present revision by P. M. Jørgensen (Bergen, Norway) deals with the European species only. He recognizes 20 species from this area in 3 genera, viz. *Pannaria* (14), *Parmeliella* (5) and *Psoroma* (1 species divided into 2 varieties). Five European species of *Pannaria* are described as new. In addition 3 new extra-European *Pannaria* species are described in an appendix. Some other genera such as *Massalongia, Placynthium* (with the segregates *Moelleropsis* and *Vestergrenopsis*) and *Erioderma,* which have often been included in Pannariaceae, are not treated.

The author's approach is somewhat unconventional. A brief Historical outline and a short chapter on Nomenclature (somewhat superfluous as there are no deviations from the Code of Nomenclature) precede the main part of the work, viz. Taxonomy. The 20 European species are described in detail. Much attention has been devoted to nomenclature and typification. Some well-known species have had their names changed. *Pannaria pityrea* has become *P. conoplea, P. microphylla* is now *P. leucophaea* and *P. lepidiota* is *P. praetermissa*. *Parmeliella corallinoides* has become *P. triptophylla*. The 5 species described as new are *Pannaria ahlneri* (known from a limited area in Central Norway and Jämtland, Sweden), *Parmeliella jamesii* (Western Scandinavia, British Isles and Portugal), *Pannaria olivacea* (Mediterranean area), *P. tavaresii* (Portugal) and *Parmeliella testacea* (oceanic: W Norway, British Isles, W France, Portugal, Spain, Italy and Macaronesia). *Pannaria maritima, P. poeltii* and *P. pulveracea* are described from outside Europe (Canada, Nepal and California, U.S.A. respectively). Differences between related species are discussed in detail; for some species distinguishing features are listed in tables.

The distribution of the species is interesting. All avoid dry lowlands, having high humidity requirements. Thirteen species are restricted to the oceanic areas of Europe or to the Mediterranean area, two (*Pannaria hookeri* and *P. praetermissa*) are arctic-alpine, the other species are more or less widespread. Maps of the European distribution are given for all species. Fairly detailed lists of localities are provided except for the commonest species. Most of the Pannariaceae are sensitive to the activities of man. They have low power of resistance to air pollution. Several of them have declined considerably in numbers during the last few decades.

The following chapters deal with Morphology, Anatomy and Chemistry. Morphological concepts such as hypothallus, isidia, soredia and apothecia, are discussed with instructive illustrations. The anatomy of the thallus and apothecia is elucidated by means of photos of cross-sections studied by light microscopy or scanning electron microscopy. Chemistry is of little interest in the Pannariaceae. The only substance recorded with certainty from some species is atranorin.

In the brief concluding chapters the author discusses certain concepts in taxonomy, habitat ecology and phytogeography. However, several important questions, such as definition and circumscription of the family, are left open. We also find hardly any taxonomy at the generic level. When defending his thesis at Bergen the author gave expectation of a fuller treatment of the supraspecific taxonomy of the Pannariaceae in a forthcoming second part dealing with the extra-European species. The thorough and skilful treatment of the taxa studied in the first part guarantees that the completed work will constitute an important monograph of an interesting lichen family.

Ove Almborn

Kärnefelt, I. 1979: *The brown fruticose species of Cetraria*. Opera Botanica 46. Stockholm. 150 pages, 74 figures (25 in colour) and distribution maps. ISSN 0078-5237. ISBN 91-546-0254-8. Price SKr 81:–, libraries SKr 135:– (wrappers).

The Iceland lichen, (or "Iceland moss") is well-known not the least for its presumed medical effects. Earlier European lichenologists did not consider that these lichens involved any great taxonomic problems. They generally recognized two species, *C. islandica* (with either one or two varieties) and *C. delisei* (syn. *C. hiascens*). Since the middle of the 19th century *C. islandica* var. *crispa* has generally been raised to specific level, during the last few decades under the newly-established name *C. ericetorum*. However, some authors, e.g. Du Rietz (1945) and Kristinson (1969), have questioned its specific rank and recognized *C. islandica* s.lat. as a single species with continuous variation between broad-lobed and narrow-lobed, ± canaliculate specimens.

In the first half of this century Russian authors described several species within this group, mainly from the Asiatic parts of the USSR. Most of these were eventually recognized as also occurring in North America. In the 1950s and 1960s two further species were described from North America.

In spite of our increased knowledge of the group it has been evident that several taxa were insuffiently known and that all brown fruticose species of *Cetraria* greatly needed a critical revision. The present study by I. Kärnefelt (Lund, Sweden) is a well-written and welcome addition to the monographic literature on lichens.

Some general introductory chapters are devoted to Morphology and anatomy, Chemistry, Delimitation and taxonomy, Environment and ecology and Phytogeography. The value of several morphological characters for classification, such as habit, branching, colour, lobes, pseudocyphellae, marginal structures, soralia and pycnidia, is discussed. Structures from the cortex, apothecia and pycnidia, as well as cross-sections of the thallus, have also been studied under the interference contrast microscope and scanning electron microscope. The results are reproduced as micrographs of high quality. However, it seems doubtful whether these refined methods provide any important new characters for distinguishing taxonomic units.

Chemistry plays an important part in the taxonomy of this group. Spot tests have earlier been used to differentiate between *C. delisei* and the related *C. fastigiata* on the one hand, both C (calcium hypochlorite)+, gyrophoric acid present, and the remainder of the species on the other hand which are C–. In the same way PD (paraphenylene-diamine) has been known to give a positive reaction in *C. islandica* (fumarprotocetraric acid present), whereas *C. ericetorum* is

PD–. All taxa in the extensive material examined by Kärnefelt have been tested by thin-layer chromatography and the results are reported in detail.

The taxonomic part deals with 19 taxa (8 of them described or remodelled by Kärnefelt), viz. *C. andrejevii* (Asiatic Russia, N. America), *C. arenaria* (N. America), *C. australiensis* (Australia), *C. delisei* (N. Hemisphere), *C. ericetorum* ssp. *ericetorum* (N. Hemisphere), ssp. *patagonica* (Tierra del Fuego), ssp. *reticulata* (N. America), *C. fastigiata* (N. Hemisphere), *C. inermis* (easternmost Siberia, northernmost N. America), *C. islandica* ssp. *islandica* (N. Hemisphere), ssp. *antarctica* (southernmost S. Hemisphere), ssp. *crispiformis* (N. Hemisphere), ssp. *orientalis* (Japan and adjacent parts of E. Asia), *C. kamczatica* (Bering Sea District), *C. laevigata* (Siberia, Japan and adjacent parts of E. Asia, India, northernmost N. Hemisphere, Nepal, New Guinea; earlier placed in another group of *Cetraria*), *C. nigricascens* (northernmost Russia and N. America) and *C. subalpina* (western N. America). All taxa are described in detail using morphological and chemical characters and distinguishing features are discussed.

Distribution maps are provided for all taxa. Many of them show interesting areas, in several cases with a marked concentration to the Bering Strait Region where they have presumably survived the Pleistocene glaciations. There are also many analogies with the distribution of other lichens and with that of several vascular plants whose ranges were presented in a classical work by Hultén (1937) and in his later plant atlases (1958–1971).

Thallus fragmentation and apomixis are important factors ruling the dispersal of the taxa treated. Interesting from an ecological point of view is the distinction between primary and secondary habitats depending on where the species reaches its optimal development.

To the merits of the book should be added the excellent colour plates illustrating all taxa; whereas many of the black-and-white photographs are less informative as is often the case with lichens.

The well-known problem of how many localities, if any, should be listed when the distribution is documented by maps has been solved in an elegant way. Exsiccata and a large choice of localities studied (in several cases all of them) are recorded in miniprint at the end of the book. With the aid of a hand-lens the reader can easily find all necessary information.

As with Jørgensen's thesis (reviewed above) Kärnefelt's is part of an extensive project. Other groups of *Cetraria* (and related genera) also need to be revised according to modern lines. It is to be hoped that Kärnefelt will extend his work to these and other groups.

Ove Almborn

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