Drawings of Scandinavian Plants 45–49

Juncus L.

By Örjan Nilsson and Sven Snogerup[1]

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

Subgen. **Alpini** Buchenau 1877

Rhizomateous *perennials,* small to moderately tall. *Leaves* of variable shape, flat or convolute to quite terete, pluri- or rarely uni-tubulose, usually with ± well developed internal septa at least in part of the leaf, in some species perfectly and manifestly septate. *Flowers* in dense headlike clusters, enclosing bracteols lacking. Tepals in most species non-herbaceous, chestnut, white, yellow or purplish. Anthers in most species ± exserted on long filaments. *Seeds* with a persistent seedcoat. Cytology imperfectly understood, chromosomes usually very small and numerous.

Subgen. *Alpini* occurs in arctic, alpine and cool temperate parts of the Northern Hemisphere, with most species in C Asia. In Scandinavia it is only represented by 4 species, here illustrated as Nos. 45—48.

45. **Juncus triglumis** L. 1753

Perennial, usually laxly caespitose, the shortnoded rhizome also producing nonflowering leafy shoots and prolonged subterranean runners. *Steam* 3—20 cm, thin, erect, with several basal leaves and sometimes one upper cauline leaf. *Leaves* 1—10 cm, much shorter than the stem, slightly flattened and basally canaliculate, in their middle part bitubulose, basally often up to 5-tubulose, some internal septa usually present but not externally visible, leaf tip blunt, auricles broad, obtuse. *Inflorescence* single-headed, head (2—) 3 (—5)-flowered, the flowers in a horizontal row, Basal *bracts* broad, erecto-patent, usually shorter than the flowers. *Tepals* c. 4 mm, narrowly ovate to elliptical, obtuse or rarely acutish, equal or outer ones slightly longer, usually yellowish white to straw-coloured with darker apical parts. *Stamens* 6, about equalling the tepals, *anthers* 0.7—0.9 mm, exserted, 1/4—1/3 as long as filaments. *Style* c. 0.5 mm, *stigmata* 1 mm. *Capsule* 5—6 mm, about 1.5 times as high as tepals, trigono-ellipsoidal, obtuse, mucronate, shining reddish brown to light chestnut. *Seeds* 0.8—1 mm, including the seedcoat 2—2.5 mm, ellipsoidal to slightly ovoidal, finely striate with darker tips, seedcoat forming two approximately equal appendages.

J. triglumis grows on open soil, usually with moving water and preferably on limestone. It is widely distributed throughout the Arctic and the mountains of Europe, Asia and N. America. It shows a great and hitherto insufficiently known geographic variation, its American and C. Asiatic forms being described as separate subspecies. The above description refers to Scandinavian material only.

46. **Juncus biglumis** L. 1753

Vegetatively similar to *J. triglumis. Leaves* short or occasionally up to 8 cm, uni-

---

[1] Nilsson is responsible for the drawings and Snogerup for the text.

tubulose in middle part, basally often up to 3-tubulose, internal septa usually present but rarely externally visible, leaf tip blunt, auricles small, blunt, or in some leaves quite lacking. *Inflorescence* single-headed, head (1—) 2 (—4)-flowered, flowers in a vertical row, the first basal *bract* ± erect, exceeding the flowers and often with a small lamina, second bract erecto-patent to patent. *Tepals* 2.5—3 mm, equal, elliptical to ovate or inner ones slightly obovate, broadly obtuse, variable in colour but always darker than in *J. triglumis,* often almost black, apically lighter. *Stamens* 6, equalling the tepals or usually longer, exserted, *anthers* 0.3—0.4 mm, 1/8—1/6 as long as filaments. *Style* 0.5—1 mm, *stigmata* 1—1.5 mm. *Capsule* 4—5 mm, 1.5—2 times as high as the tepals, rounded prismatic, retuse, mucronate, variable in colour but usually light, pale, with dark corners in the apical part. *Seeds* 0.7—0.9 mm, including the seedcoat 1—1.5 mm, ellipsoidal to slightly ovoidal, finely striate with darker tips, the thin, white seedcoat forming two equal or slightly unequal appendages.

In its ecology *J. biglumis* closely resembles *J. triglumis,* and they often occur together. *J. biglumis* has an arctic-circumpolar distribution, and is also represented in mountains of Europe, Asia and N. America, though in Asia more northern than *J. triglumis.*

47. **Juncus stygius** L. 1750

Perennial, with stems single or a few together from a shortnoded rhizome also producing short subterranean runners. *Stem* 10—25 cm, thin, with a few basal and 1—3 upper cauline leaves. *Leaves* short or occasionally up to 15 cm, thin, terete to slightly canaliculate, pluritubulose, some internal septa usually present but not externally visible, leaf tip blunt, auricles short, broad, obtuse, stems and leaves often reddish. *Inflorescence* of 1—2 (—4) heads, heads 2—3 (—5)-flowered, flowers usually in a markedly horizontal row. At the base of the inflorescence or close to a single head one or rarely two erect *bracts* with short laminas, at the base of each head short, almost entirely scarious bracts. *Tepals* 3.5—4.5 mm, equal or outer ones slightly longer, all ovate or inner ones elliptic, obtuse to acutish, light and usually pale, green to light brown or reddish, with a broad scarious margin. *Stamens* 6, equalling tepals or slightly shorter, *anthers* 0.4—0.7 mm, 1/6—1/4 as long as filaments. *Style* 0.5 mm or less, *stigmata* c. 0.5 mm, contorted. *Capsule* 5—6.5 mm, c. 1.5 times as high as tepals, trigono-ovoidal to trigono-ellipsoidal, obtuse with a very short mucro, light and pale, brown to straw-coloured. *Seeds* 1.2—1.4 mm, including the seedcoat 2—2.5 mm, ovoidal, finely striate, with darker tips, seedcoat wide, straw-coloured, difficult to remove from seed.

J. stygius is a plant of oligotrophic fens and shores. It has a circumpolar-boreal distribution. In Scandinavia it is mainly a plant of the northern lowlands, but is found on scattered localities as far south as northern Skåne. It is not known from Denmark, but from a few localities in Switzerland and S. Germany.

48. **Juncus castaneus** SMITH 1800

Perennial with a creeping rhizome forming long subterranean runners between the usually single stems. *Stem* 10—35 cm, 2—3 mm thick, erect, with a few basal sheaths and 3—5 leaves, all subbasal or one in a higher cauline position. *Leaves* flat and ± convolute, up to 10 cm, up to 4 mm broad, pluritubulose, septa sometimes externally visible in apical part, leaf tip blunt, auricles lacking. *Inflorescence* of 1—3 heads, bracts of its branches leaflike, basal bracts of the heads usually non-herbaceous and shorter than the flowers, rarely the first one with a developed lamina, heads 3—10-flowered, in fruit ± semiglobose. *Tepals* 4.5—5.5 mm, equal or outer ones slightly longer, narrowly ovate, outer ones acute, inner ones obtuse,

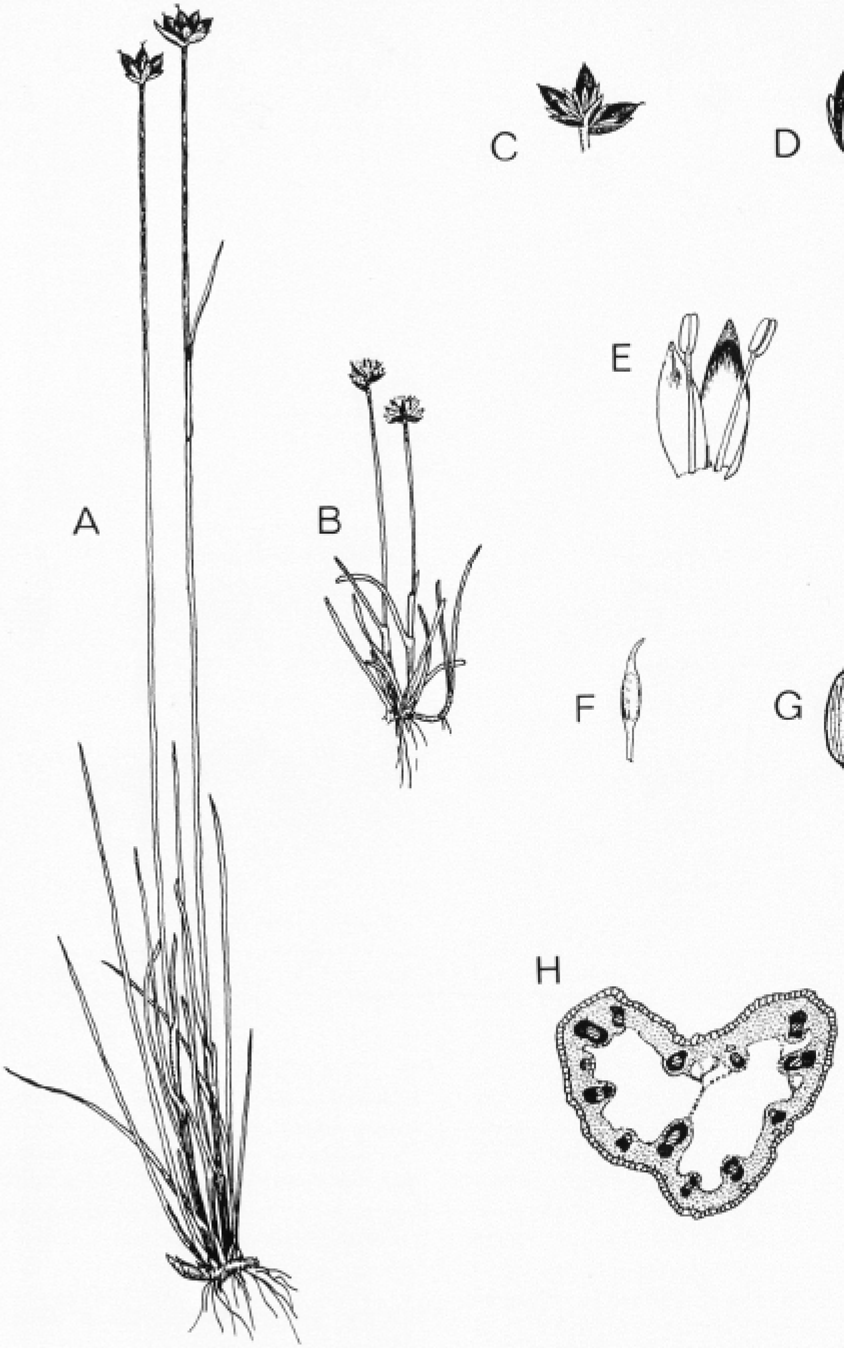


Fig. 45 *Juncus triglumis* L. — A—B: Habit, ×1. — C: Head, ×2. — D: Capsule, ×4. — E: Tepals and stamens, ×8. — F: Seed with seedcoat, ×12.5. — G: Seed, ×25. — H: Cross-section of leaf, ×50.

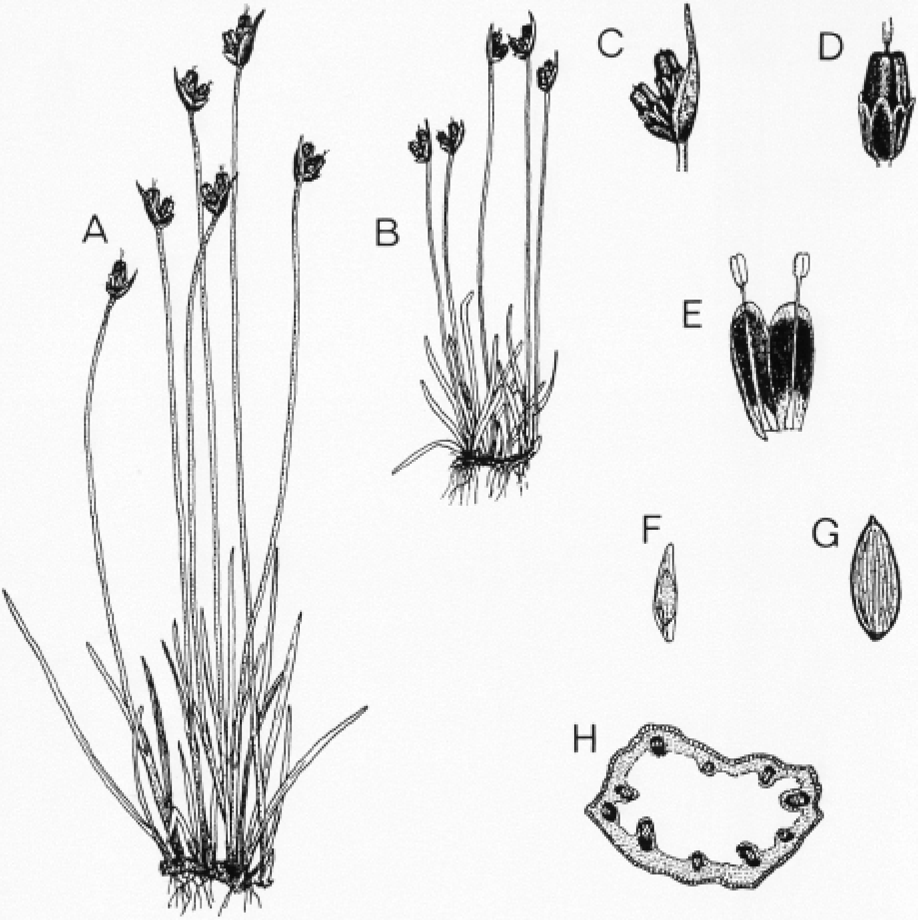


Fig. 46. *Juncus biglumis* L. — A—B: Habit, ×1. — C: Head, ×2. — D: Capsule, ×4. — E: Tepals and stamens, ×8. — F: Seed with seedcoat, ×12.5. — G: Seed, ×25. — H: Cross-section of leaf, ×50.

chestnut-coloured with lighter tips. *Stamens* 6, equalling the tepals or usually slightly shorter, *anthers* 1—1.5 mm, 1/4—1/3 as long as filaments, with a short, acute connective prolongation. *Style* 0.5—1.5 mm, *stigmata* 1.5—2.5 mm. *Capsule* 6—7.5 mm, c. 1.5 times as high as tepals, ovoidal to ellipsoidal, obtuse, mucronate, shining, apically chestnut-coloured, basally lighter. *Seeds* 0.8—0.9 mm, including the seedcoat 2—3 mm, ovoidal to almost ellipsoidal, finely striate, with darker tips, seedcoat white, forming two approximately equal appendages.

J. castaneus grows in fens, in wet grassland and on open soil, preferably on limestone. It has a wide arctic-circumpolar-alpine distribution.

Subgen. **Juncinella** KRECZ. & GONTSCH. 1935

Annual, small usually caespitose plants. *Leaves* small with large sheath, flat to

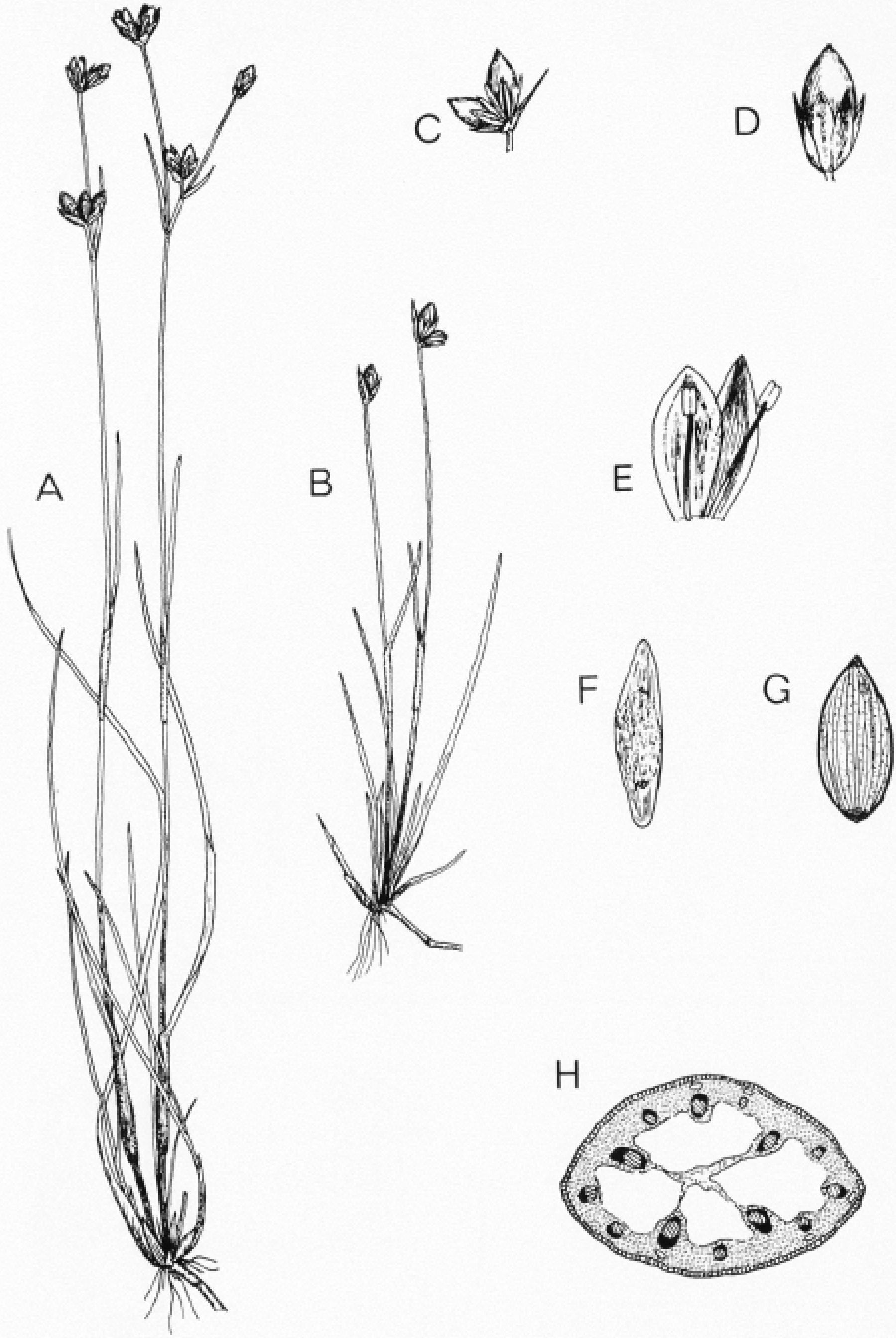
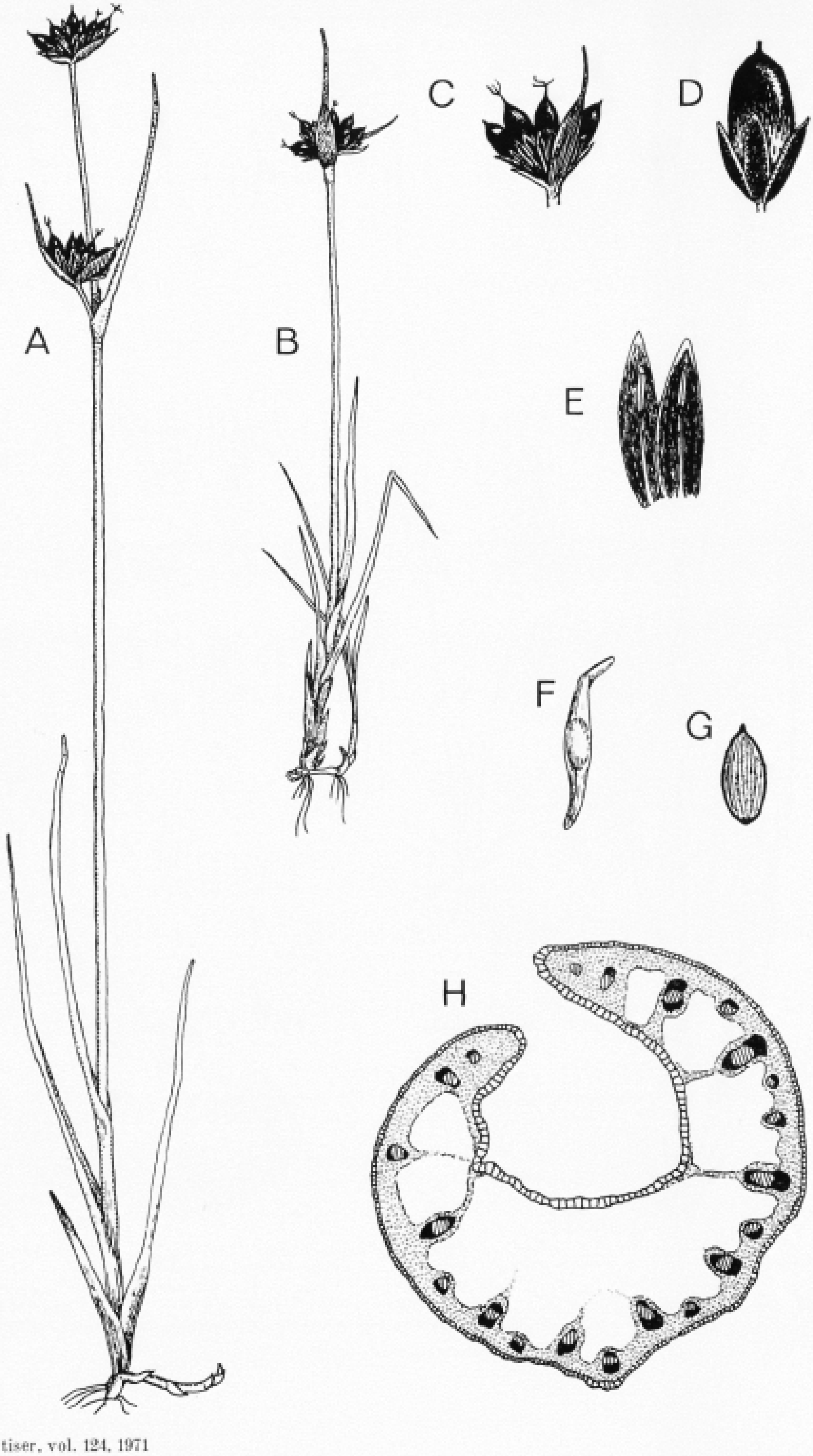


Fig. 47. *Juncus stygius* L. — A—B: Habit, ×1. — C: Head, ×2. — D: Capsule, ×4. — E: Tepals and stamens, ×8. — F: Seed with seedcoat, ×12.5. — G: Seed, ×25. — H: Cross-section of leaf, ×50.


A
B
C
D
E
F
G
H

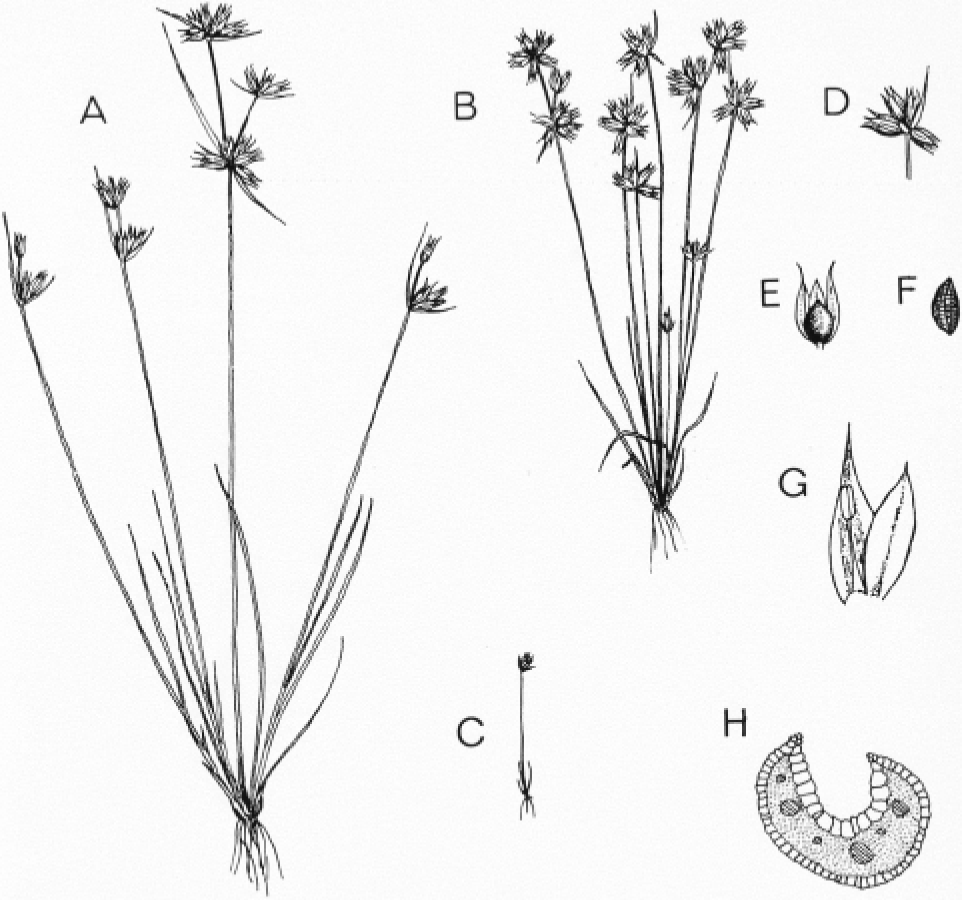


Fig. 49. *Juncus capitatus* Weig. — A—B: Habit, ×1. — C: Dwarf specimen, ×1. D: Head, ×2. — E: Capsule, ×4. — F: Seed, ×25. — G: Tepals and stamens, ×8. — H: Cross-section of leaf, ×50.

canaliculate or semiterete, without sclerenchyma in the margins, for the major part filled with uniform parenchyma, in most species with epidermis papillae, auricles lacking. *Flowers* in dense headlike clusters and then lacking enclosing bracteols, or single and then often with a full set of bracteols. *Seeds* without seedcoat, reticulate.

Subgen. *Juncinella* occurs in Africa, SW. Asia, Europe and N. America, with its centers of variation in S. Africa and W. North America. In Scandinavia represented only by *J. capitatus* Weig.

Fig. 48. *Juncus castaneus* Smith — A—B: Habit, ×1. — C: Head, ×2. — D: Capsule, ×4. — E: Tepals and stamens, ×8. — F: Seed with seedcoat, ×12.5. — G: Seed, ×25. — H: Cross-section of leaf, ×50.

49. **Juncus capitatus** Weig. 1772

Annual, single-stemmed or usually caespitose, without developed rhizome. *Stems* 1—20 cm, thin, with several basal leaves but never any cauline ones. *Leaves* 0.5—5 cm, narrow, flat to canaliculate, sheaths comparatively large, auricles lacking. *Inflorescence* of 1—4 heads, 2 basal bracts of each head with well developed laminas, heads (1—) 5—10-flowered, enclosing bracteols lacking. *Tepals* unequal, outer ones (2—) 3—4 mm, ovate, acuminate, inner ones shorter, ± entirely membranaceous, acute to acuminate. *Stamens* 3, 1/2—2/3 as long as outer tepals, *anthers* (0.2—) 0.4—0.7 mm, c. 1/2 as long as filaments. *Style* 0.2—0.5 (—1) mm, stigma 0.5—1 mm, downwards contorted. *Capsule* (1—) 1.5—2 mm, much shorter than the tepals except in extreme dwarfs, ovoidal to sphaeroidal, obtuse, not or shortly mucronate, shining light brown to dark reddish brown. *Seeds* c. 0.3 mm, without seedcoat, ovoidal, reticulate from c. 15 tuberculate longitudinal ridges and weaker but obvious transverse striae between them.

J. capitatus grows on different types of open soil, preferably in winterwet positions drying up in summer. It occurs in Europe, the Mediterranean, and in a few East African localities as far as the Drakensbergen. It has also been introduced or found as a casual in many places outside its natural distribution. In Scandinavia it is limited to the southern coastal areas.

This species shows an unusually large variation in all size characters, including those of floral parts. According to my cultivation experiments most of these differences are due to modification. In extremely starved specimens the single flower may even be changed to a dimereous state.

New South African Compositae

By Bertil Nordenstam

Museum of Natural History,
S-104 05 Stockholm, Sweden

ABSTRACT

NORDENSTAM, B. 1971. New South African Compositae. — Bot. Notiser 124: 9—15.

Pteronia elata B. NORD. and *P. anisata* B. NORD. are described, both from the Richtersveld, NW. Cape Province. A tuberous-rooted new *Othonna* from Calvinia Division is described as *O. hederifolia* B. NORD. Its chromosome number is 2n=20.

Pteronia elata B. NORD., sp. nov.

Orig. coll.: NORDENSTAM 1829, Cape Province, L. Namaqualand Div., Richtersveld, "Devil's Castle", c. 2 miles NE of Stinkfontein, 7.XI. 1962 (S holotype, BOL, K, M, NBG, PRE).

Illustr.: Fig. 1.

Frutex elatus modice ramosus; rami glabri striati, juniores brunneoli, vetustiores nigrocinerei. *Folia* opposita suberecta spathulata—anguste oblongo-obovata 1—2 cm longa 3—8 mm lata plana coriacea margine ciliolata. *Capitula* terminalia solitaria brevipedunculata 1—2 cm longa 0.5—1 cm lata 10—30-flora, ante anthesin apice obtusa. *Involucri squamae* 5—6-seriatae pallide aureae—stramineae apice saepe brunnescentes obtusae margine anguste membranaceae, exteriores oblongae vel ovato-oblongae, interiores spathulatae—oblanceolatae. *Corolla* lutea tubulosa 9—10.5 mm longa, lobi anguste ovati 2 mm longi. *Antherae* 4—4.5 mm longae. *Styli* lobi 2.5—3 mm longi. *Pappi* setae plures inaequilongae subferrugineae. *Achenium* obovato-turbinatum dense albosericeum.

A sparingly or moderately branching, gracile *shrub*, 1—2 m tall. *Branches* slender, ± straight, glabrous, striate; young branches light brown, older branches with thin ash-grey cortex. *Leaves* opposite in distant pairs (internodes often about equalling the leaves) or crowded on lateral short-shoots, suberect, spathulate—narrowly oblong-obovate, 1—2 cm long, 3—8 mm wide, flat, coriaceous, midveined (most prominently on the abaxial side), with distinctly white-ciliolated margins, otherwise glabrous; base half-clasping; apex rounded, obscurely apiculate. *Capitula* terminal, solitary, shortly pedunculate, somewhat campanulate, at length almost oblong-cylindric, 1—2 cm long, 0.5—1 cm broad, obtuse in bud. *Involucral scales* c. 25, about 5—6-seriate, coriaceous—cartilaginous, glabrous, pale golden yellow—straw-coloured (more greenish in bud), often brownish towards the tip, apically obtuse or rounded, inner ones more acute, with thin, membranous, somewhat fringed margins (less conspicuous in the outer scales); outer scales oblong or ovate-oblong, 4—7 mm long, 2—4 mm wide; middle scales narrowly oblong-obovate or spathulate, 8—11 mm long, 4—5 mm wide; innermost scales narrowly spathulate—oblanceolate, 10—12 mm long, 2—3 mm wide. *Receptacle* clavate, c. 4 mm high and wide; bractiferous sides shallowly alveolate, nude; floriferous top somewhat convex, paleate; paleae narrowly lanceolate-acuminate, somewhat lacerate, 4 mm long, whitish. *Florets* 10—30. *Corolla* yellow, tubular, 9—10.5 mm long, 1.5—2 mm wide near the apex, sparsely puberulous below the middle; lobes narrowly ovate, 2 mm long, 0.7—1 mm wide, with acute, cucullate tips and thickened margins. *Anthers* 4—4.5 mm long incl. the ovate, acute appendage. *Style* lobes lanceolate, 2.5—3 mm long, apically flattened, subacute. *Pappus* bristles c. 40, straight, 5—6 mm long, outer ones shorter, somewhat rusty, densely barbellate. *Achene* obovate-turbinate, 3 mm long, 1.5—1.8 mm wide, densely white silky-villous.

Flowering period: Oct.—Nov.

Cape Province, L. Namaqualand Div., Richtersveld: "Devil's Castle", c. 2 miles NE of Stinkfontein, 1962, NORDENSTAM 1829 (BOL, K, M, NBG, PRE, S) — Stinkfonteinberg, E. slopes below the S. peak, 1962, NORDENSTAM 1862 (K, M, MO, PRE, S).

This striking new species is very distinct, and I am unable to suggest any immediate allies. In the classification of HUTCHINSON and PHILLIPS (1917) the species would belong to sect. *Ciliatae* HUTCH. & PHILL. The key designed by these authors leads to *P. adenocarpa* HARV., a species of the Upper Karroo, distributed from Worcester to Victoria West and eastwards to Albany. This is a very different species, however, with much larger capitula and glandular, glabrous achenes. The new species may have closer affinities to *P. gymnocline* DC. and *P. lucilioides* DC., both of which are known from the Richtersveld. These two species differ from *P. elata* by their narrower, linear to oblanceolate leaves, which are not obligately opposite, and by the pointed tips of the young involucres. By characters of leaf pubescence these three species belong to three different sections in the essentially artificial scheme proposed by HUTCHINSON and PHILLIPS. The leaves are glabrous in *P. gymnocline* (sect. *Glabratae*), papillate in *P. lucilioides* (sect. *Papillatae*), and glabrous with ciliate margins in *P. elata* (sect. *Ciliatae*).

P. elata is known only from my two collections from the heart of the Richtersveld. In the modest vegetation of the desolate mountains near Stinkfontein (now: Ecksteinfontein), the tall and lanky shrubs of *P. elata* are a quite conspicuous feature.

Pteronia anisata B. NORD., sp. nov.

Orig. coll.: NORDENSTAM 1694, Cape Province, L. Namaqualand Div., Richtersveld, Cornell's Kop, N. slopes, 31.X. 1962 (S holotype, M).

Illustr.: Fig. 2.

Fruticulus ramosissimus aromaticus praeter axillas foliorum ciliatas glaber; rami juniores brunnei, vetustiores atrocinerei. *Folia* opposita flexuosa basi divaricata internodiis longiora lineari-filiformia 1—2 cm longa c. 1.5 mm lata subacuta. *Capitula* terminalia solitaria 7—8-flora sessilia vel subsessilia oblongo-cylindrica vel subcampanulata basi obtusa—rotundata. *Involucri squamae* 3—4-seriatae ovato-oblongae vel oblongae coriaceae stramineae apice fuscae venis tribus moniliformibus ornatae margine albomembranaceae, interiores usque ad 1 cm longae. *Corolla* lutea 7—7.5 mm longa, lobi triangulari-ovati 1 mm longi extus pauciglandulosi. *Antherae* 3 mm longae. *Styli* rami 2.5—3 mm longi extus biglandulosi. *Pappi* setae numerosae inaequilongae usque ad 1 cm longae dilute rufescentes basi connatae annulum distinctum supra achenium constrictum formantes. *Achenium* obovoideum indumento denso sericeo sordide albo vestitum.

A strongly aromatic, much-branched *shrublet,* 2—3 dm high, glabrous except in leaf-axils. Young *branches* brown, sulcate; older branches with sooty grey cortex. *Leaves* opposite, ± spreading, flexuous, longer than the internodes, linear-filiform, somewhat flattened or subtrigonous, 1—2 cm long, c. 1.5 mm thick, green, minutely papillate—colliculate with resin dots, subacute; leaf-base half-clasping, with a tuft of long weak hairs in the axil. *Capitula* terminal, solitary, 7—8-flowered, sessile or nearly so (uppermost leaves reduced and ± transitional to involucral scales, 2—5 mm long). *Involucre* oblong-cylindric or somewhat campanulate, c. 1 cm high, 5—6 mm wide, obtuse in bud, with rounded—obtuse base. *Involucral scales* 15—20, c. 3—4-seriate, oblong or ovate-oblong, coriaceous, straw-coloured and towards the tip brownish, obtuse, with three moniliform, brown, resiniferous lines, and with distinct, white, membranous margins; outermost scales short, thickish and subcarnose, somewhat greenish, c. 3 mm long and

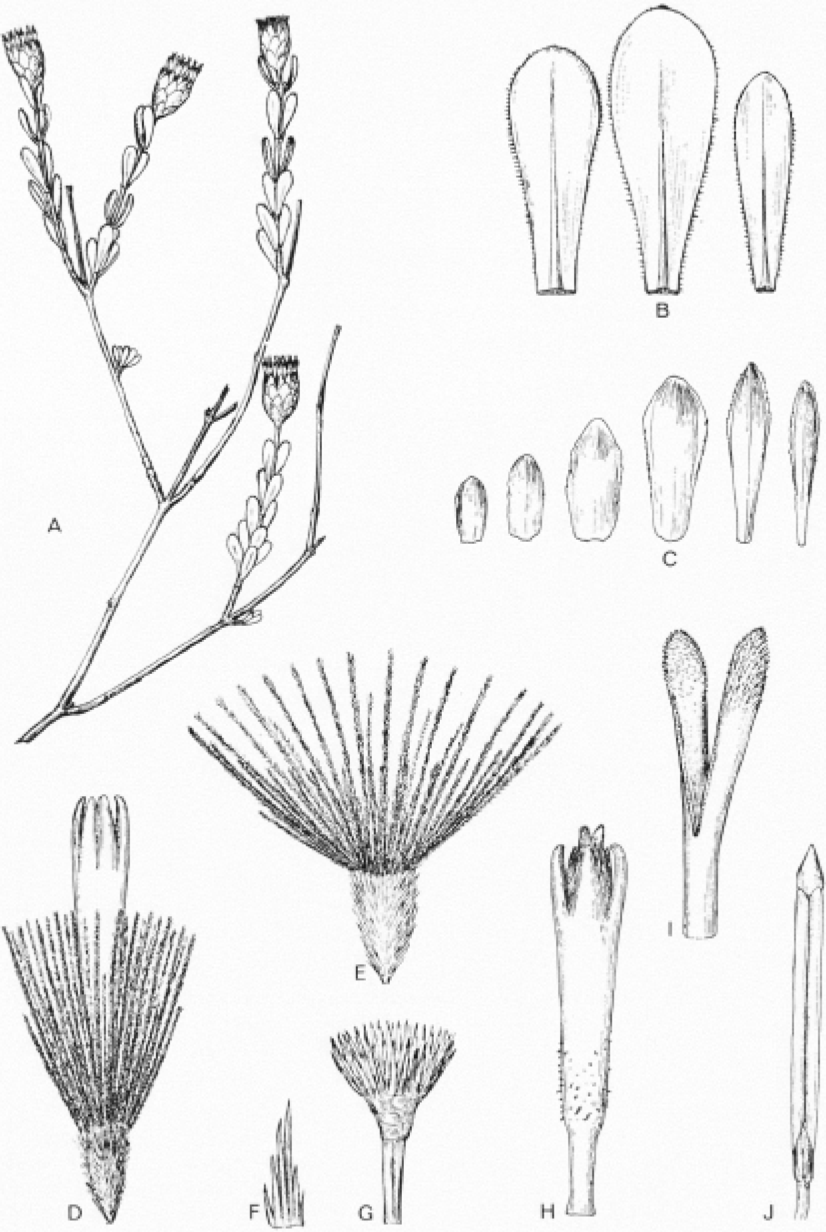


Fig. 1. *Pteronia elata* B. Nord. (Nordenstam 1829). — A: Portion of plant, ×0.5. — B: Leaves, ×2. — C: Series of involucral scales, from outermost (left) to innermost (right), ×2. — D: Floret, ×5. — E: Achene, ×5. — F: Receptacular scale, ×4. — G: Receptacle (phyllaries and florets removed), ×2. — H: Corolla, ×5. — I: Style branches, ×10. — J: Stamen, ×10. — Del. auct.

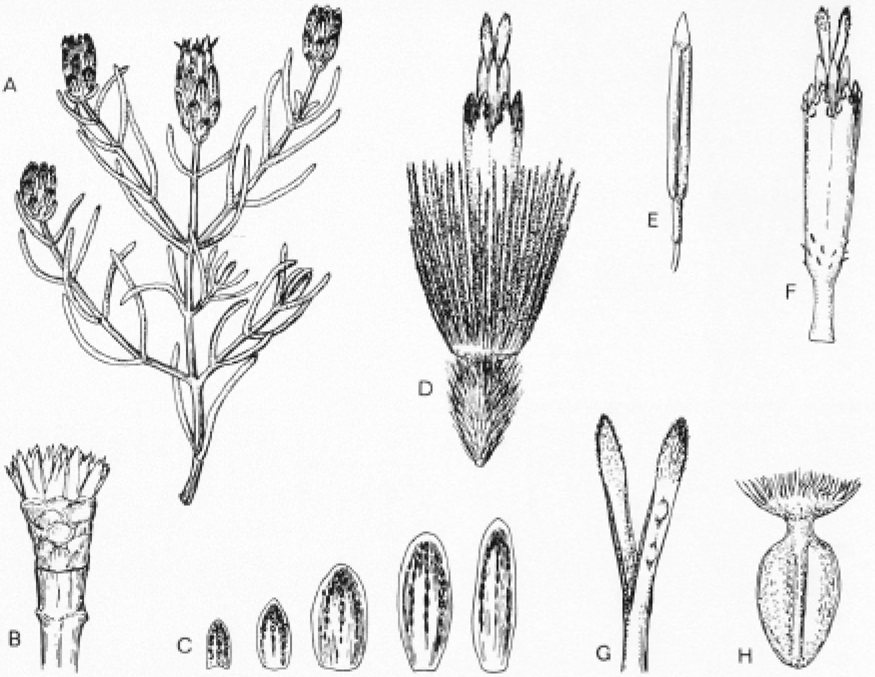


Fig. 2. *Pteronia anisata* B. NORD. (A—G: NORDENSTAM 1694; H: NORDENSTAM 1768). — A: Portion of plant, ×1. — B: Receptacle (phyllaries and florets removed), ×5. — C: Series of involucral scales (left: outer; right: inner), ×2. — D: Floret, ×5. — E: Stamen, ×10. — F: Corolla, ×5. — G: Style branches, ×10. — H: Achene (hairs and pappus except base removed), ×5. — Del. auct.

1.5 mm wide; innermost scales c. 1 cm long and 3—4 mm wide. *Receptacle* clavate, c. 2 mm high and wide (at the base 1.4 mm wide), glabrous, apically truncate and alveolate with 1—1.5 mm long, acutely lobed and fringed scales. *Corolla* yellow, 7—7.5 mm long; tube 2 mm long, 0.8 mm wide; limb cylindric, 5—6 mm long, 1.2—1.4 mm wide, sparsely puberulous towards the base; lobes triangular-ovate, 1 mm long, 0.6—0.8 mm wide, acute, with a few resin glands on the exteriors. *Anthers* 3 mm long incl. the narrowly ovate, acute appendage. *Style* branches 2.5—3 mm long, apically shortly hairy, flattened, subacute, with two resin glands on the exteriors. *Pappus* bristles numerous (c. 130—150), 5—6 (at length 10) mm long, coarse, straight, erect, light rufous, outer bristles shorter and more slender; bristles basally united into a distinct annulus 0.5 mm high, constricted above the top of the achene. *Achene* obovate, 3—4 mm long, 2 mm wide, densely sericeous with dirty white, straight hairs up to 4 mm long.

Flowering period: Oct.—Nov.

Cape Province, L. Namaqualand Div., Richtersveld: Cornell's Kop, N. slopes, 1962, NORDENSTAM 1694 (M, S) — Mountain between Numees and Hell's Kloof, 1962, NORDENSTAM 1768 (S).

I found this new species in two localities in the Richtersveld. In habit the species resembles *P. flexicaulis* L. f. and *P. adhaerens* COMPTON, but the plant is not viscid and the capitula are smaller with very different phyllaries.

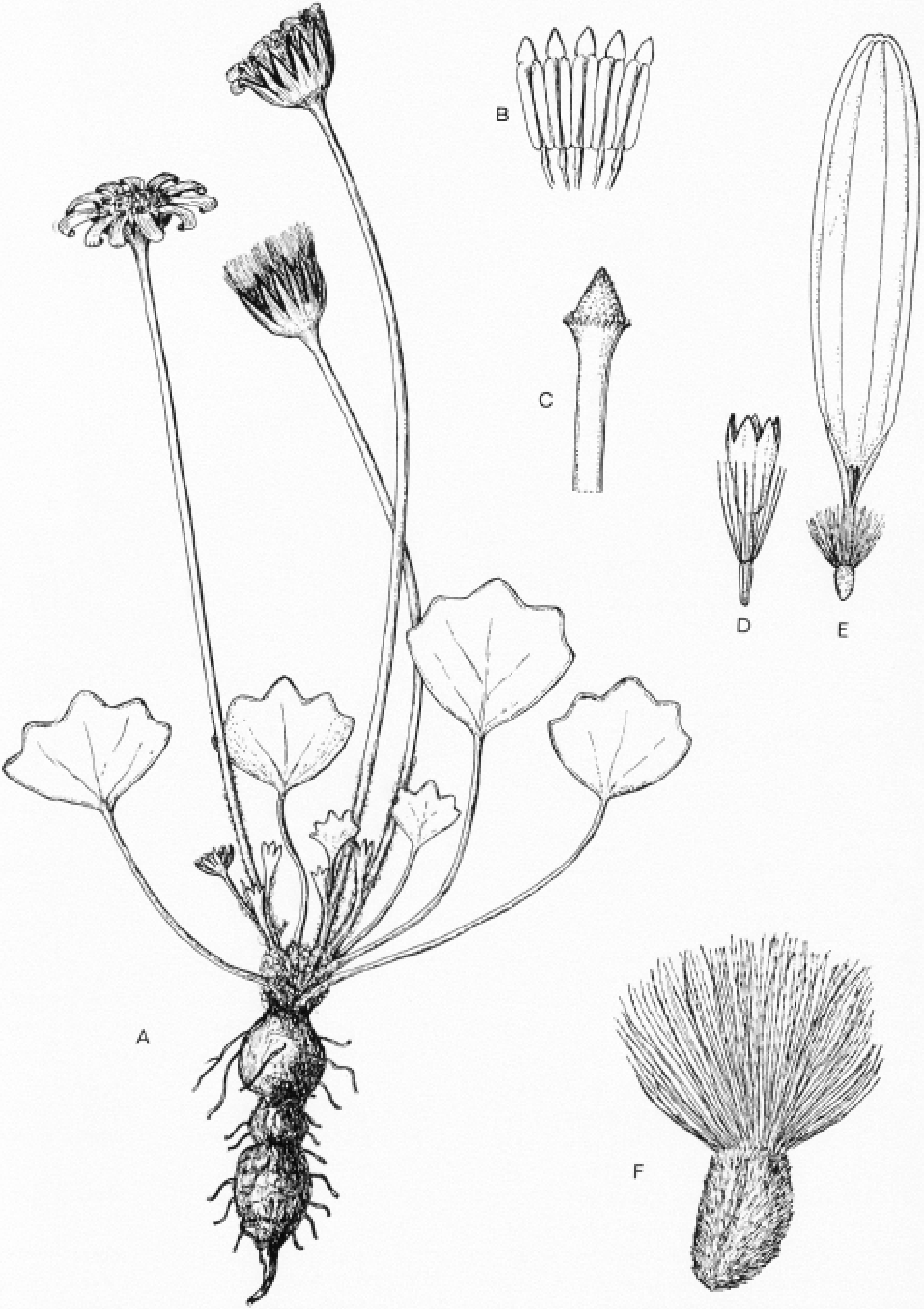


Fig. 3. *Othonna hederifolia* B. Nord. (Nordenstam 679). — A: Habit, ×1. — B: Stamens, ×10. — C: Style apex, from disc-floret, ×20. — D: Disc-floret, ×5. — E: Ray-floret, ×5. — F: Achene, ×5. — Del. auct.

The specific epithet chosen alludes to the aromatic smell, which is to my nose reminiscent of aniseed. The resin contents are noticeable in many parts of the plant, e.g. the papillate appearance of the leaves, the bead-like veins of the involucral scales, and the gland-like structures of corolla lobes and style branches.

Othonna hederifolia B. Nord., sp. nov.

Orig. coll.: Nordenstam 679, Cape Province, Calvinia Div., top of Van Rhyns Pass, in granitic sand on rocks, 19.VII. 1962 (S holotype, BOL, K, M, MO, NBG, PRE).

Illustr.: Fig. 3.

Radix tuberosa. *Folia* plura rosulata petiolata e collo brevi lanato exeuntia, petiolis elongatis lineari-filiformibus glabris, laminis transverse oblongis—depresse obovatis—late cuneatis planis verticaliter dispositis glabris coriaceis apice grosse dentatis. *Pedunculi* pauci—plures scapiformes interdum folio basali reducto instructi simplices monocephali erecti vel ascendentes glabri foliis saltem duplo longiores. *Capitula* radiata. *Involucrum* late campanulatum glabrum, bracteis 13 uniseriatis lanceolatis basi vel ad medium usque connatis acutis saepe atromarginatis. *Receptaculum* leviter conicum alveolatum glabrum. *Flores radii* feminei c. 13. *Corolla* lutea ligulata; lamina anguste oblonga 1—1.5 cm longa. *Stylus* fertilis bifidus. *Achenium* oblongo-obovatum 4 mm longum dense albovillosum. *Pappi* setae numerosae persistentes albae vel dilute stramineae achenio longiores. *Flores disci* feminei-steriles numerosi. *Corolla* lutea; tubus cylindricus; limbus anguste campanulatus. *Stylus* simplex sterilis apice appendice conica instructus. *Ovarium* abortivum glabrum. *Pappi* setae plures caducae albae corolla breviores.

Acaulescent perennial *herb*. *Root* tuberous, fusiform, oblong or seldom napiform, 2—10 cm long, 1—2.5 cm thick, sometimes with an elongated narrower apical portion, apically crowned by a woolly tuft, basally tapering to an elongated tap-root. *Leaves* rosulate, several—numerous, petiolate; petiole ascending (often buried in sand), 2—7 cm long, slender, c. 1 mm thick, glabrous, with a dilated, veined base; lamina flat, vertical, transversely oblong—depressedly obovate—broadly cuneate, apically coarsely and ± irregularly few-toothed with broadly triangular, obtuse or subacute lobes, basally cuneate or sometimes more rounded or truncate, coriaceous, dark green, glabrous, indistinctly veined, with slightly thickened margins. *Peduncles* few—several from the crown, simple, scapose (often with a reduced basal leaf), erect or ascending, 3—17 cm long, 1—1.5 mm thick, terete, normally about twice the length of the leaves, glabrous or somewhat woolly near the base. *Capitula* radiate. *Involucre* broadly campanulate, 1—1.8 cm in diam. *Involucral bracts* uniseriate, normally 13, connate to 1/3 or slightly more, lanceolate, 7—12 mm long, 1.5—2.5 mm wide, 3-veined, acute, often with blackish margins, some membrane-edged. *Receptacle* somewhat convex, shallowly alveolate. *Ray-florets* c. 13. *Corolla* yellow; tube c. 1.5 mm long, cylindric; lamina narrowly oblong, 1—1.5 cm long, 2.5—3 mm wide, 4-veined, obtuse. *Style* branches c. 1.2 mm long, obtuse. *Achene* oblong-obovate, c. 4 mm long and 2 mm wide, densely white-villous. *Pappus* bristles numerous—copious, persistent, ± straight, white or pale straw-coloured, finally 5—7 mm long. *Disc-florets* c. 50—100. *Corolla* c. 4 mm long, yellow; tube 1.3—1.5 mm long, cylindric; limb narrowly campanulate, c. 2.5 mm long; lobes triangular-ovate, 0.7 mm long, acute. *Anthers* 1.7 mm long incl. the ovate acute appendage. *Style* terete, simple, sterile, tipped by a 0.4 mm long cone with short sweeping-hairs at the base. *Ovary* narrowly oblong, 1.3 mm long, about 5-veined, glabrous, abortive. *Pappus* bristles c. 10—20, caducous, straight, erect, white, c. 3 mm long.

Flowering period: July—Sept. (—Oct.).

Chromosome number: 2n=20 (counted in root tips of Nordenstam 773, plants cultivated in greenhouse, Botanical Garden, Lund; modified Navashin's fixative, paraffin method, stain crystal violet).

Cape Province, Calvinia Div.: Top of Van Rhyns Pass, S of the road, 1962, NORDENSTAM 679 (BOL, K, M, MO, NBG, PRE, S) — Top of Van Rhyns Pass, N of the road, 1963, NORDENSTAM 2988 (S) — 6 miles E of Nieuwoudtville on Calvinia road, 1962, NORDENSTAM 773 (M, S) — Hantam Mountains, Tierhoek, below the mountain and also above the escarpment, 1962, NORDENSTAM 735 (S).

Further collections seen, all from Calvinia Div.: Van Rhyns Pass, STOKOE s.n. (SAM); NBG 460/53 leg. H. HALL (NBG); NBG 105/46 leg. SMITH (NBG) — 3 miles W of Nieuwoudtville, STOKOE & DAVIS s.n. (SAM); MAGUIRE 270 (NBG) — Willemsrivier, LEIPOLDT 763 (SAM).

This characteristic new species of sect. *Caulescentes* HARV. is recognized by its usually wedge-shaped and coarsely toothed leaf-blades (recalling those of some species of *Hedera*). The petioles are often buried in sand, and sometimes also the basal parts of the leaf-blades. The remainder of the leaves protrude above ground in vertical position. This typical feature adds a peculiar look to the plant, and it is probably an adaptation to reduce exposure to the sun.

Another species with wedge-shaped leaves is *O. cuneata* DC., which occurs in the lowlands of Vanrhynsdorp Division, mainly in quartzite areas. The two species are not likely to be confused, however, since *O. cuneata* has subcarnose and somewhat brittle leaves, branching peduncles, and smaller flowerheads.

O. hederifolia is a diploid with $2n = 20$, like *O. cuneata* and some other members of sect. *Caulescentes*. Hitherto known in this section are diploids, tetraploids, hexaploids, and octoploids, all with the basic number $x = 10$ (NORDENSTAM 1967, 1969).

The distribution of *O. hederifolia* is confined to sandy and clayey soils on top of the Bokkeveld escarpment in Calvinia Division, a region very rich in geophytes, including many Othonnas and monocots.

LITERATURE CITED

HUTCHINSON, J. & PHILLIPS, E. P. 1917. A revision of the genus Pteronia (Compositae). — Ann. S. Afr. Mus. 9 (5): 277—329.

NORDENSTAM, B. 1967. Chromosome numbers in Othonna (Compositae). — Bot. Notiser 120: 297—304.

— 1969. Chromosome studies on South African vascular plants. — Ibid. 122: 398—408.

Notes on the Flora of Angola

By Lars E. Kers

Institute of Botany,
University of Stockholm,
S-104 05 Stockholm, Sweden

ABSTRACT

Kers, L. E. 1971. Notes on the flora of Angola. — Bot. Notiser 124: 16—24.

Two new species are described from the Moçamedes district. *Stipagrostis vexillifera* spec. nov. is closely allied to *St. uniplumis* (Licht.) de Winter and *St. papposa* (Trin. & Rupr.) de Winter. Two collections of supposedly *Stipagrostis papposa* are discussed. One sample of *Aristida adscensionis* L. with gyrate awns is reported. *Hibiscus fritzscheae* Exell & Mendonça has hairy seeds, not glabrous as previously stated. A find of *Geranium ocellatum* Jacquem. ex Cambess. represents the first record of this genus in Angola. *Tribulus echinops* spec. nov. comes near to *T. zeyheri* Sond. but differs in its slender and numerous spines of the cocci. By its peculiar fruits the new *Tribulus* remarkably resembles an Australian species, namely *T. hystrix* R. Brown.

Stipagrostis vexillifera Kers, spec. nov.

Species nova *Stipagrostidi papposae* (Trin. & Rupr.) de Winter affinis, sed differt glumis aequilongis, panicula brevi, foliis patentibus et brevioribus, culmis multinodis (in *St. papposa* 2—4-nodis) basi geniculatis et superne 2—4 inflorescentias procreantibus. Species nova habitu cum *St. dregeana* Nees congruens, sed differt columna infra aristas plumosa et arista intermedia in apicem nudum excurrenti et culmis ramosis 5—7-nodis (in *St. dregeana* simplicibus 1—2-nodis).

Perennial grass, up to 40 cm tall, with a densely tufted base. *Culms* slender, branched, 5—7-noded, geniculated at the base and sometimes rooting from the lower nodes, upwards ascending—erect, the innovation shoots end in panicles, therefore about 2—4 inflorescences are produced from each main culm, the lower shoots vegetative or depauperate. *Internodes* terete, very faintly scabrid, 2.5—5 cm long, 0.5—1 mm thick. *Nodes* smooth, glabrous, somewhat thickened. *Leaf sheaths* smooth, striated, faintly scabrid, 1/3—1/2 as long as the internodes, the lower sheaths expanded, papery, straw coloured, 1—2 cm long and up to 3 mm in diameter, the upper sheaths tightly adpressed to the culms, thin, green, 1—4 cm long. *Ligula* of minute hairs, the auricles bearded. *Blade* short, 1—3 cm long, subulate or bristle-like, inrolled, ± rigid, spreading, often slightly recurved, smooth, faintly scabrid. *Panicles* extending beyond the upper leaf sheaths, open, short, 4—7 cm long (excluding the awns), with the awns 2—5 cm broad, branches thin, purplish, scabrid. *Spikelets* tinged with purple; pedicels thread-like, as long as the spikelets or shorter than these. *Glumes* equal in length, narrowly, lanceolate, gradually attenuating apically, membranaceous, 9—10 mm long, minutely scabrid on both sides, 3-nerved. *Lemma* 2—3 mm long (including the callus), finely dotted—scabrid, 3-nerved, articulated near the apex. *Callus* 0.5 mm long, bearded. *Column* 9 mm long, straw-coloured, with a tuft of hairs below the branching point of the awns, smooth at the base. *Awns* 3, rachis purplish coloured; central awn 3—4 cm long, upper part plumose, base smooth for about 5 mm, with an apical naked tip which is about 3—4 mm long; lateral awns smooth, about 1 cm long.

TYPUS SPECIEI: Kers 3663, 25.IV. 1968, Angola, Moçamedes district. Road Moçamedes — San Nicolau, 8 miles NE of the railway (S, holotype).

ICON.: Fig. 1.

This species is clearly allied to *Stipagrostis papposa* (Trin. & Rupr.) de Winter and *St. uniplumis* (Licht.) de Winter. It differs from the former species, of which the author has seen material from northern and central Africa, in its equal glumes, the presence of a distinctly elongated naked central awn tip, the geniculated growth of the culms and their numerous nodes. Besides this, the new species differs also in its markedly short panicles.

Stipagrostis vexillifera also comes close to *St. uniplumis,* a species which the author knows from S.W. Africa and southern Angola. However, they cannot easily be confused since the glumes are unequal in *St. uniplumis,* the central awn lacks a distinct naked tip, the culms are simple or few-branched and generally strictly erect from the very base.

By its short panicles, leaf-sheaths and leaves, its purplish glumes and short panicle-bearing culms, *Stipagrostis vexillifera* shows a superficial resemblance to *St. dregeana* (cf. Dinter 6344 in S). This species is readily distinguished from *St. vexillifera* because it lacks the tuft of hairs at the branching point of the awns and a naked central awn tip.

The author grows the new species in Stockholm from a single seed taken from the type (in the greenhouse at the Botanical Institute; voucher specimen: Kers 3694). This cultivated specimen corresponds in habit and in morphological details with the type specimen, except that the leaves are flat and not convolute.

This new species is fairly common within the coastal desert area to the northeast of Moçamedes. It is especially abundant on low hills and stony-gravelly elevations on the plains there. The short panicles are rather stiffly erect from the markedly thin culms and, when moved by the wind, their silvery awns are all directed horizontally and kept one-sided. The panicles with the awns thus resemble small flags flapping in the wind; hence the epithet *vexillifera* (cf. Fig. 1 A).

MATERIAL STUDIED: Angola: Moçamedes district: Gossweiler 11074, 27.V. 1937. From Luco to Mucongo, 200 m alt. (sub *Stipagrostis uniplumis*) (K). — Kers 3320, 25.IV. 1968. About 27 km NE of Moçamedes, along the road following the railway (S). — Kers 3663, 25.IV. 1968. Along the road Moçamedes—San Nicolau, 8 miles NE of the railway (S, holotype); Kers 3694, 3.IX. 1970. Specimen cultivated in Stockholm from seed of Kers 3663 (S).

Remarks on Stipagrostis papposa (Trin. & Rupr.) de Winter **and St. uniplumis** (Licht.) de Winter

Apart from the above mentioned material of *Stipagrostis papposa* from northern—central Africa, the author has also seen two collections of a *Stipagrostis* from Angola, which had been determined "*Aristida papposa* Trin. & Rupr." (Welwitsch 7355 and Gossweiler 11115, both in K). These two samples are supposedly conspecific with *St. papposa* var. *senegalensis* Trin. & Rupr., in spite of the fact that Henrard in his monograph did not list this species from southern Africa and gave no comment as regards the previous records of the species from Angola (Henrard 1929 pp. 25, 76; Rendle 1899 p. 205). Henrard in this case followed Trinius and Ruprecht's recognition of two geographically separated species, viz. *Stipagrostis papposa* and *St. uniplumis* (then as *Aristida*), distinguished mainly by the absence or presence of a naked central awn tip (Henrard 1927 p. 423). This treatment has obviously been accepted by subsequent authors (e.g. Devillers & Schnell 1953; de Winter 1965 p. 359 ff; Scholz 1969 p. 290).

Fig. 1. *Stipagrostis vexillifera* KERS, spec. nov. — A: General aspect of plant. Only two of the culms have been drawn. Note the small root emerging from one of the lower nodes. — B: Spikelet. — C: Flower. Only the basal portions of the filaments drawn. The palea is seen at the back of the ovary. — D: Glumes. Left: lower glume. Right: upper glume. — E: Lemma with the callus. — F: Grain seen from different sides. — (All drawings made from the type.)

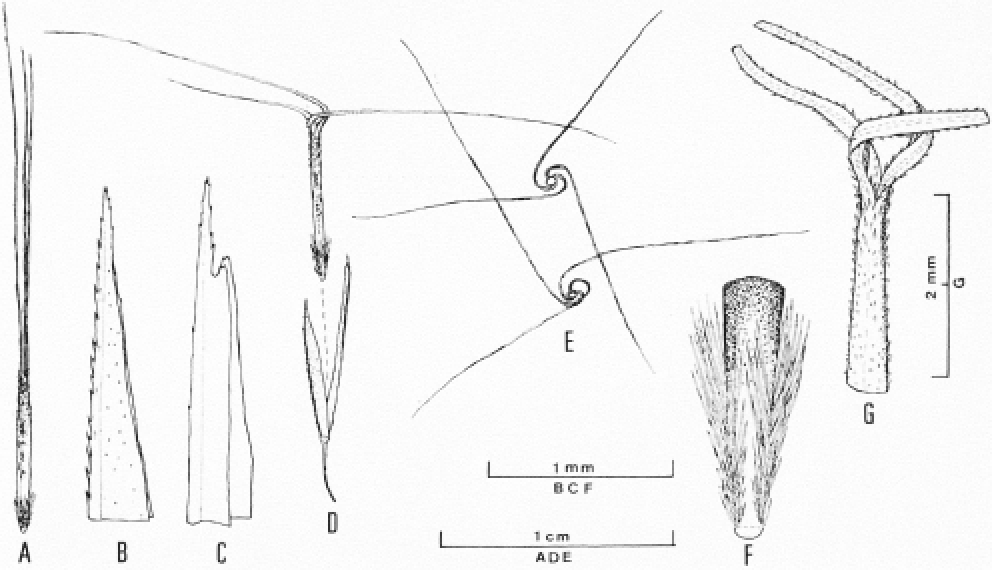


Fig. 2. *Aristida adscensionis* L. with gyrate awns. — A: Lemma (moistened) with the awns projecting straight from the body of the lemma. — B: Apex of the lower glume. — C: Apex of the upper glume. — D: Spikelet. The awns are twisted at the base and horizontally spread when dry. — E: Two 'fruits' seen from below showing the gyration of the awns. — F: Callus. — G: Body of the lemma (apical part) with the twisted bases of the awns. — (All drawings from Kers 3549.)

The present author, however, cannot find any essential difference between these two Angolan samples of supposedly *Stipagrostis papposa* and verified examples of this species from northern—central Africa. Thus, in the Angolan material too the central awns run out into a (minute) naked tip, which here is 0.75—1.5 mm long (0.5—2.5 mm measured in *St. papposa*). In details as in general habit, the material from both areas is identical or shows remarkable similarity.

Out of the material of *Stipagrostis* examined by the author, these two Angolan specimens of "*Stipagrostis papposa*" come especially close to *St. vexillifera*. The two specimens have culms which are branched upwards (3—4-noded) and the branches terminated by panicles, the specimens have short leaves and short yellowish papery sheaths, and the peripheral culms tend to spread though they are not distinctly geniculated or even rooting as in the new species. In their essential characters, however, they correspond to *St. papposa* because they have unequal glumes and only a minute naked tip of the central awns. Moreover, their panicles are a little longer (8—9 cm long) than in the new species.

Taking into consideration the rich variation in *Stipagrostis papposa* — *St. uniplumis* and the slight difference which separates them, it might be justifiable to unite the species. Their geographical separation on two distinct areas in Africa — that may not hold true — is of course not an argument for keeping them separate (Henrard 1927 p. 423). On the contrary, similar disjunct areas are often found in morphologically variable taxa from the arid or semiarid regions, e.g. *Stipagrostis ciliata, St. hirtigluma, St. obtusa, Cleome angustifolia* and many others (de Winter 1965 p. 305; Kers 1969 p. 30, Fig. 8).

MATERIAL OF STIPAGROSTIS PAPPOSA (TRIN. & RUPR.) DE WINTER: DRAR 207, Egypt, Gebel Elba (S); GILLETT 4460, Somaliland (S); A. LE JOLIS s.n., Gabon (S); SCHIMPER 2208, Ethiopia, Tacase pr. Gurrasarva (S); Without collector, s.n., Gabon, Guinée (S).

Gyrate Awns Observed in Aristida adscensionis L.

In *Aristida adscensionis* L. collected from the area north of Moçamedes, the awns were found to be spirally contorted at the base when dry (Fig. 2). The author has not found any previous report of gyrate awns in this species, nor in the very closely allied *Aristida curvata* (NEES) TRIN. & RUPR. A rich material of these two species has been studied (Herb. S), but the awns have shown no clear tendency to become twisted at the base. In these two species the ripe and dry awns normally spread in a V-shaped manner (at an angle of about 30—50°, occasionally up to 100°), and without torsion of the awn-bases or rarely with very slight torsion only (e.g. KERS 3576 from south of Moçamedes). Spirally contorted awns seem to be unknown in African *Aristida* (sensu DE WINTER 1965), but a number of species from the New World are characterized by this peculiarity (e.g. *Aristida brittonorum* HITCHC., *A. desmantha* TRIN. & RUPR., *A. gyrans* CHAPMAN, *A. mohrii* NASH., *A. neesiana* TRIN. & RUPR., *A. tenuispica* HITCHC., *A. tuberculosa* NUTTALL) (cf. HENRARD 1926, 1927, 1928).

The author considers this Angolan sample with gyrate awns to represent merely a local variant of the variable species *Aristida adscensionis*. It may also be noted that the author is unable to find any character clearly separating *A. adscensionis* L. coll. and *A. curvata* (NEES) TRIN. & RUPR. Thus, the sample mentioned here is just one of those from southern Angola and northern S.W. Africa which combine features said to characterize one or the other of these two species.

COLLECTION: KERS 3549, 25.IV. 1968, Angola, Moçamedes district. Gravelly-sandy water channels on rocky ground in the gorge down to the river Giraul. Road: Moçamedes—San Nicolau (S).

Hibiscus fritzscheae EXELL & MENDONÇA with Woolly Seeds

In their description of this species, the authors stated the seeds to be glabrous (EXELL 1936 p. 135). This feature is also mentioned as the key character against *Hibiscus castroi* BAK. F. & EXELL in EXELL and MENDONÇA 1937 p. 159. This statement is certainly an error; probably the fruits in the authors material were too young. On an isotype of *H. fritzscheae* in the Botanical Museum of Stockholm, the seeds are densely cottony with hairs up to 3 mm long. The author has collected this species in Angola and the seeds have hairs which are 3—4 mm long and white.

Hibiscus fritzscheae has beautiful dark red flowers and the species comes close to *H. elliottiae* HARV., which it also resembles in habit. *H. elliottiae* differs essentially from the allied species by lacking an epicalyx.

MATERIAL STUDIED: FRITZSCHE 163, 24. IV. 1904, Angola, Huila district, "Mossamedes—Humpata. Am Monino" (S, isotype). — KERS 3648, 26.IV. 1968, Moçamedes district, Road Moçamedes — San Nicolau, near the river Mucungo. Stony, gravelly soil on hill slope (S).

Geranium ocellatum JACQUEM. ex CAMBESS. New to Angola

The author found this species on the eastern margin of the Cheila Mountain plateau, about 20 km NW of Sá de Bandeira. This seems to be the first record of a *Geranium* from Angola (EXELL & MENDONÇA 1951 p. 257).

Although the fruit setting was good, very few specimens had expanded flowers. The author only managed to find two flowering specimens, and these each had one single flower. This peculiarity is explained by the fact that most flowers are cleistogamous. Only occasionally do some chasmogamous flowers develop in this species. This phenomenon has been observed also in those specimens which were grown in Stockholm from seeds of this Angolan collection. The cleistogamous flowers, dissected by the author, were found to have only five stamens. The occurrence of cleistogamous flowers in *Geranium* has previously been reported from the section *Lucida* R. KNUTH, to which section this species belongs, and in the section *Columbina* KOCH (KNUTH 1912 pp. 47, 60).

Geranium ocellatum is a wide-spread species showing a disjunct distribution. It is known from the Himalayas, Yemen and Africa. According to LAUNDON (1961 p. 68), the African range stretches from "Mt. Cameroon and the Bameda plateau in the west and extends from Sudan, Erithrea and Somalia to Southern Rhodesia in the east".

Geranium ocellatum apparently occurs in mountainous environments and at high elevations. With the new record from the Cheila Mtn, its bow-shaped range around the Congo basin has been completed.

COLLECTION: KERS 3298, 20.IV. 1968, Angola, Huila district, 20 km NW of Sá da Bandeira along the road to Tundevala. On the margin of the Cheila Mtn plateau (LISC, S). — KERS 3695, 6.IX. 1970, Specimens cult. from seeds of KERS 3298 in the greenhouse, Botanical Institute, Stockholm University (S).

Tribulus echinops KERS, spec. nov.

Species nova spinis fructuum longissimis numerosis puberulis bene distincta. — Herba annua caulibus prostratis ad 1 m longis, floribus 2—2.5 cm diametro, foliis 3—6-foliolatis, coccis valde spinosis, spinis acicularibus brunneis in cocco quoque c. 25 numerantibus. Species nova a *T. zeyheri* SOND. et a speciebus huius affinibus coccis magnopere differt. Ad *T. hystricem* R. BR. fructibus accedit sed differt stylo breviore, qui cum stigmate 1.5 mm longus est (stylus *T. hystricis* filiformis et ad 4 mm elongatus) et differt floribus minoribus, caulibus prostratis (non erectis).

Annual herb with herbaceous, prostrate stems which are up to 1 m long and about 3 mm thick, striated; indumentum of few long bulbous-based hairs (up to 2 mm long) and numerous minute hairs (up to 0.5 mm long); the hairs, especially those on younger parts, have a pale violet colour. *Leaves* 1—1.5 cm long, 3—6-foliolate. *Leaflets* ovate—oblong, mucronate at the apex, 5—10 mm long and 3—7 mm broad, densely pilose beneath, ciliated along the margin, almost glabrous on the upper surface. *Stipules* subulate to linear, acute, 3—5 mm long and 0.5—1 mm broad, pilose. *Pedicels* up to 2.5—3 cm long, rather stiff, striated, with indumentum of long and short hairs. *Flower buds* c. 0.5 cm long just before expanding. *Sepals* lanceolate, acute, 5—7 mm long and 2 mm broad in the expanded flowers, densely ciliated on the abaxial surface. *Petals* broadly cuneate, blunt at the apex, about twice as long as the sepals, 1—1.25 cm long and broad, yellow, glabrous. *Stamens* 10, as long as the pistil or a little shorter; filaments 2—5 mm long, the epipetal stamens about 1/3 as long as the others, yellow, flat, somewhat broadening at the base; anthers oblong—obovate, 1—2 mm long, thecas yellow, connective tissue pale violet. *Pistil* 3.5 mm long in the expanded flower, stigma pyramidal, 1.25 mm long and about three times as long as the style, ovary densely covered with erect bristle-like bulbous-based hairs. *Intrastaminal glands* united to form a shallow, crown-shaped cup at the base of the ovary. *Ripe fruits* of five cocci which are 2.5—3 cm across (incl. the spines) dark brown and densely puberulous, each coccus armed with about 25 very long spines, which are slender and needle-shaped, 1—2 mm thick at the base and 0.4—1.4 cm long.

TYPUS SPECIEI: KERS 3543, 25.IV. 1968, Angola, Moçamedes district, at Saco do Giraul c. 10 km N of Moçamedes, just N of the river Giraul. Sandy-gravelly desert plain between rock outcrops (S, holotype).

ICON.: Fig. 3.

This species, at first view and especially if the fruits are lacking, may easily be

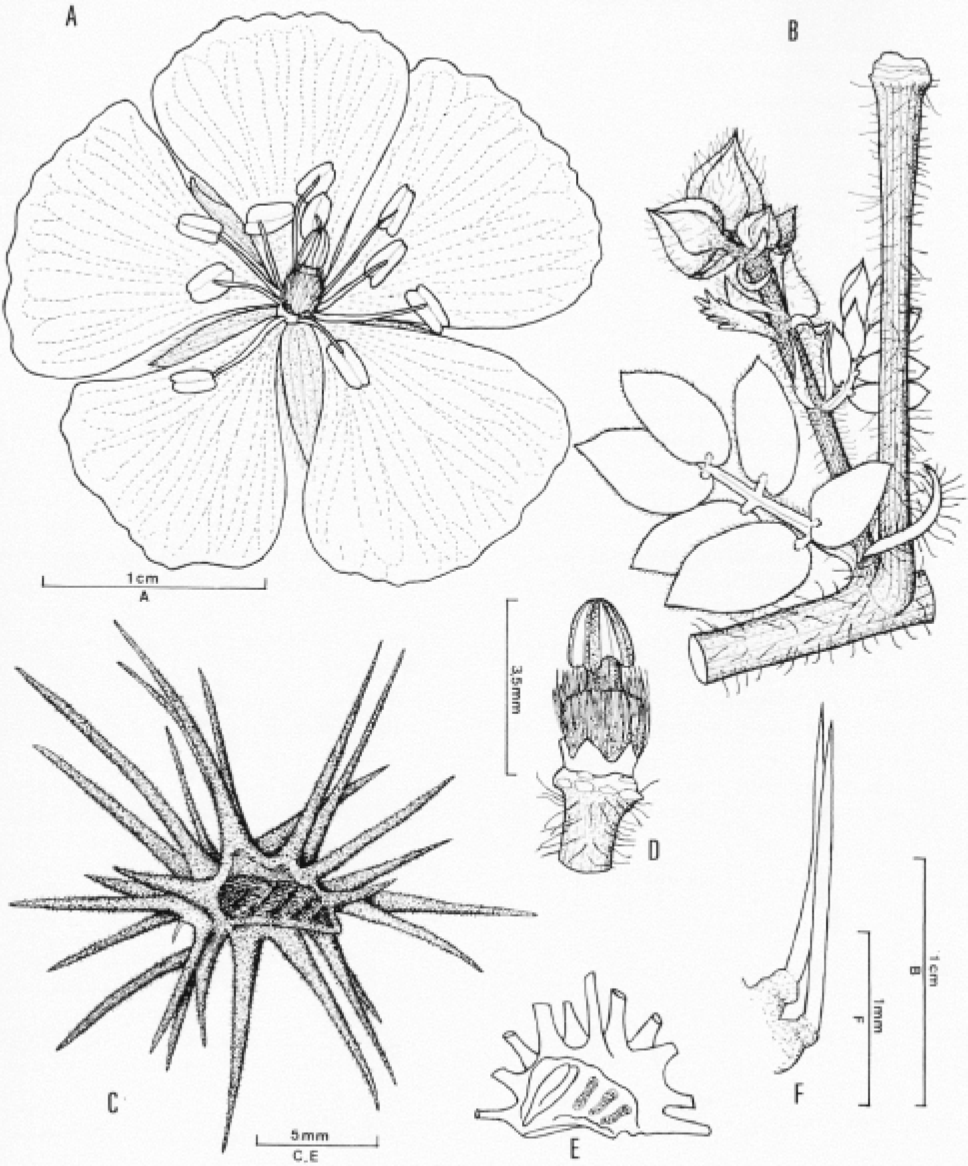


Fig. 3. *Tribulus echinops* Kers, spec. nov. — A: Flower. — B: Portion of stem with pedicel and axillary branch. — C: Coccus. — D: Gynocium. — E: Coccus, dissected to show the four seeds of which only one is viable. — F: Bulbous-based hairs from the wall of the ovary. — (All drawings made from the type.)

mistaken for *Tribulus zeyheri* SOND., a species which is widely spread in southern Africa up to Angola. Although the vegetative parts are similar, the fruits are so strikingly different that the author has found it necessary to give the new taxon specific rank.

Students of *Tribulus zeyheri* have found it advisable to use a rather broad circumscription for this species (SCHWEICKERDT 1937; EXELL & MENDONÇA 1951; SCHREIBER 1966). The species is variable indeed, including both erect perennial forms and prostrate annual ones. The degree of hairiness also varies within the species. The fruits, however, display the most apparent variation: they may be almost spineless or markedly spiny (cf. SCHWEICKERDT 1937 pp. 176—177, Figs. 3, 6). The synonymy of *T. zeyheri* includes a number of species and varieties which were recognized by the combination of different morphological features, e.g. habit, duration, spinescence of the fruits, hairiness etc. (cf. SCHREIBER 1966 pp. 6—7). By its peculiar fruits the new species differs markedly from any of the forms recognized within *T. zeyheri*. In the spiny forms of *T. zeyheri* the cocci may have at most 4—6 well developed spines in addition to some minor ones, and the spines are very stout and conical as they taper apically from a distinctly broad base. In the new species the spinescence is quite different as the spines are needle-shaped and slender, densely puberulous and their number about 25 on each coccus.

In its fruits, the new species resembles remarkably two Australian species, viz. *Tribulus hystrix* R. BR., and *T. occidentalis* R. BR., which show a similar spinescence of the cocci (cf. MOORE 1920 p. 159 ff & Plate 11). According to MOORE's description of *T. hystrix*, the new species differs from it in the smaller flowers (2.2 cm in diam. against 5 cm) and smaller fruits (c. 2.4 cm in diam. against 3.5 cm), as well as in the prostrate growth (erect in *T. hystrix*). *Tribulus occidentalis* has flowers smaller than in *T. hystrix* (2.5 cm in diam.), hereby resembling *T. echinops*, but the spines are almost equal and shorter than in *T. echinops* (cf. MOORE 1920 p. 161 & Plate 11). I have examined the Australian material of *Tribulus* at Kew, and found that the new species is not identical with *T. hystrix*, *T. occidentalis* or any other Australian species, and thus certainly does not represent an Australian introduction into Angola. I am inclined to suggest the similarity between the Angolan *T. echinops* and the Australian *T. hystrix* and *T. occidentalis* as a case of parallel evolution.

ACKNOWLEDGEMENTS

I wish to express my sincere thanks to the Curator of the Kew Herbarium for the material of *Tribulus* and *Stipagrostis* which was kindly sent to me on loan. I am also much indebted to Fil. lic. Miss ADELAIDE STORK, Stockholm who corrected the Latin diagnoses. The author's visit to Angola in 1968 was made possible by travel grants and economical support from the Swedish Natural Science Research Council and from the Swedish Academy of Sciences (S. J. ENANDER's Fond).

LITERATURE CITED

DEVILLERS, M. A. & SCHNELL, R. 1953. Icones Plantarum Africanarum. II, no. 44 (Aristida papposa Trin. & Rupr.). — Ifan-Dakar.

EXELL, A. W. 1936. Notes on the flora of Angola. III. — Journ. Bot. (London) 74: 132—140.

— & MENDONÇA, F. A. 1937. Conspectus Florae Angolensis. 1 (1). — Lisboa.

— — 1951. Conspectus Florae Angolensis. 1 (2). — Lisboa.

HENRARD, J. T. 1926. A critical revision of the genus Aristida. I. — Meded. Rijks Herb. Leiden. 54.

— 1927. A critical revision of the genus Aristida. II. — Ibid. 54 A.

— 1928. A critical revision of the genus Aristida. III. — Ibid. 54 B.

— 1929. A monograph of the genus Aristida. I. — Ibid. 58.

— 1932. A monograph of the genus Aristida. II. — Ibid. 58 A.

KERS, L. E. 1969. Studies in Cleome. II. Cleome angustifolia Forssk. s. lat. and Cleome semitetrandra Sond. — Svensk Bot. Tidskr. 63: 1—48.

KNUTH, R. 1912. Geraniaceae. — In ENGLER, Das Pflanzenreich 53 (IV, 129) — Leipzig.

LAUNDON, J. R. 1961. Notes on Geranium in Africa and Arabia. — Bol. Soc. Brot, 35: 59—73.

MOORE, S. LE M. 1920. A contribution to the flora of Australia. — I. On two species of Tribulus described by Robert Brown. — Journ. Linn. Soc. London (Bot.) 45: 159—162.

RENDLE, A. B. 1899. Catalogue of the African plants coll. by Dr. Friedrich Welwitsch in 1853—61. 2 (1): 135—257. — London.

SCHOLZ, H. 1969. Bemerkungen zu einigen Stipagrostis-Arten (Gramineae) aus Afrika und Arabien. — Österr. Bot. Zeitschr. 117: 284—292.

SCHREIBER, A. 1966. Zygophyllaceae. — In MERXMÜLLER, Prodromus einer Flora von Südwestafrika. 65: 1—19. — Lehre.

SCHWEICKERDT, H. G. 1937. An account of the South African species of Tribulus Tour. ex Linn. — Bothalia 3: 159—178.

DE WINTER, B. 1965. The south African Stipeae and Aristideae (Gramineae). An anatomical, cytological and taxonomic study. — Bothalia 8: 201—404.

Studies in the Gesneriaceae I

Morphology and Embryology of Platystemma violoides Wall.

By R. D. Adatia

M. V. College of Science,
Andheri, Bombay,
India

Y. B. Sharma and M. R. Vijayaraghavan

Department of Botany,
University of Delhi, Delhi 7,
India

ABSTRACT

Adatia, R. D., Sharma, Y. B. and Vijayaraghavan, M. R. 1971. Studies in the Gesneriaceae I. Morphology and embryology of Platystemma violoides Wall. — Bot. Notiser 124: 25—38.

The morphology and embryology of *Platystemma violoides* has been investigated. Flowers are bracteate, bracteolate, tetracyclic and hypogynous. Androecium consists of 4 fertile stamens and one staminode. Gynoecium is bicarpellary and syncarpous. Anther wall comprises epidermis, endothecium, one middle layer and tapetum. The tapetum is of the secretory type. Meiotic divisions in the microspore mother cell are of the simultaneous type. Both tetrahedral and decussate tetrads are formed. The anther dehisces by a horizontal groove and the pollen grains are shed at the 2-celled stage.

Numerous tiny ovules are borne on two massive parietal placentae. The ovules are anatropous, unitegminal and tenuinucellar. The innermost layer of the integument organizes into an endothelium. A feebly developed hypostase is seen specially after fertilization. In the young nucellus a single hypodermal archesporial initial differentiates and directly functions as the megaspore mother cell. Meiotic divisions in the megaspore mother cell result in the formation of a linear tetrad. Only the chalazal megaspore functions to form an 8-nucleate embryo sac of the Polygonum type.

The primary endosperm nucleus divides much earlier than the zygote. Its division results in the formation of a micropylar and a chalazal chamber. Subsequent divisions are confined to the micropylar chamber. The uppermost pair of the derivatives cut off in the micropylar chamber organizes into a micropylar haustorium. The chalazal chamber directly functions as a 2-nucleate haustorium. The development of the endosperm is Cellular and follows the Brunella type. The embryogeny conforms to the Onagrad type. At maturity the seed comprises only two layers. Prior to fertilization the pericarp is composed of 5—7 layers. During maturation of the fruit, the cells of the pericarp elongate tangentially. Those of the outer epidermis and 3 or 4 subjacent layers accumulate tannin. The inner epidermis shows uniform thickening.

INTRODUCTION

Unlike most other dicotyledonous plants which possess well-developed vegetative organs, the family Gesneriaceae presents a group of morphological curios. For example, *Platystemma violoides* is reported to bear a 'solitary' leaf throughout its life cycle. Many other genera are characterized by such interesting features like (1) the absence of a plumule-radicle axis in the embryo (*Streptocarpus polyanthus*; WILLIS 1931) and (2) the continued growth of one of the cotyledons representing the entire plant, or from which a rosette of leaves or a well-developed shoot might arise (WILLIS 1931; JOSHI 1938). Features like the presence of handsome and often velvety leaves, bearing of tubular or bell-shaped, gaudy flowers and a remarkable capacity for vegetative propagation have bestowed the gesneriads a special place among the best ornamentals.

Considering the large size of the Gesneriaceae, the number of taxa embryologically investigated is relatively small. The existing literature reveals that the earlier workers dealt mainly with the development of endosperm. No detailed information is available on the ontogeny of microsporangium, microsporogenesis, male gametophyte, the structure and development of seed coat and pericarp. Megasporogenesis, megagametogenesis, and embryogenesis have been studied only in a few species. Thus an investigation on the life history of *Platystemma*, *Aeschynanthus* and *Rhynchoglossum* was undertaken. The present paper is the first in the series and concerns the embryology of *Platystemma violoides*.

MATERIAL AND METHODS

The material of *Platystemma violoides* was collected from Mussoorie, India. Formalin-acetic-alcohol was used for fixing the buds, flowers and fruits. For proper penetration of the fixative, calyx and corolla were removed from old buds, and mature fruits were trimmed laterally. The material was dehydrated in ethyl alcohol-xylol series and imbedded in paraffin wax following customary methods.

To facilitate sectioning, the paraffin-imbedded material was partially exposed and then soaked for 4 to 6 days in Gifford's acetic acid-alcohol modified by the addition of glycerine (GIFFORD 1950). Depending upon the age of the material, serial transverse and longitudinal sections were cut between 6 and 18 microns. The sections were stained either with iron-haematoxylin or safranin-fast green.

OBSERVATIONS

External Morphology

Platystemma violoides is a delicate erect herb which is distributed in the temperate Western Himalayas at an altitude of 1800—2700 metres (COLLETT 1921). The plant body is divisible into two regions — the subterranean and the aerial parts (Fig. 1 A). The leaf is sessile, exstipulate and simple. The reproductive shoot arises as a solitary peduncle from the region where the lamina is attached to the stem (Fig. 1 A). The peduncle is terminated in a cyme which generally bears 1—4 flowers. Rarely as many as 11 flowers were observed.

The flowers are bracteate, pedicellate, bracteolate, tetracyclic and hypogynous. The bracts form an involucre which is deciduous. The calyx is gamosepalous, campanulate and forms a short tube (Fig. 1 B—E). The calyx persists in the fruit (Fig. 1 J). The corolla is violet to dark blue. It is gamopetalous (Fig. 1 E—F) and the lobes are connate forming a short tube. The androecium consists of four fertile, epipetalous stamens. The fifth member is reduced to a tiny club-like staminode. The stamens are inserted at the throat of the corolla tube (Fig. 1 F). The filament is short and dilated at the base (Fig. 1 G). The anthers are dorsifixed, and running across the ventral surface is a groove which divides the anther into a large upper and a small lower lip (Fig. 1 H). The dehiscence of the anther occurs through a horizontal groove (Fig. 1 I). The gynoecium is bicarpellary and syncarpous. Numerous tiny ovules develop on two massive parietal placentae. The ovules are anatropous, unitegminal and tenuinucellar (Fig. 3 A—D). The style is long and inflexed in the bud (Fig. 1 K). The fruit is a capsule and is partially enclosed by the persistent calyx (Fig. 1 J).

Microsporangium

The archesporial cells (Fig. 2 A) divide periclinally to form an outer layer of

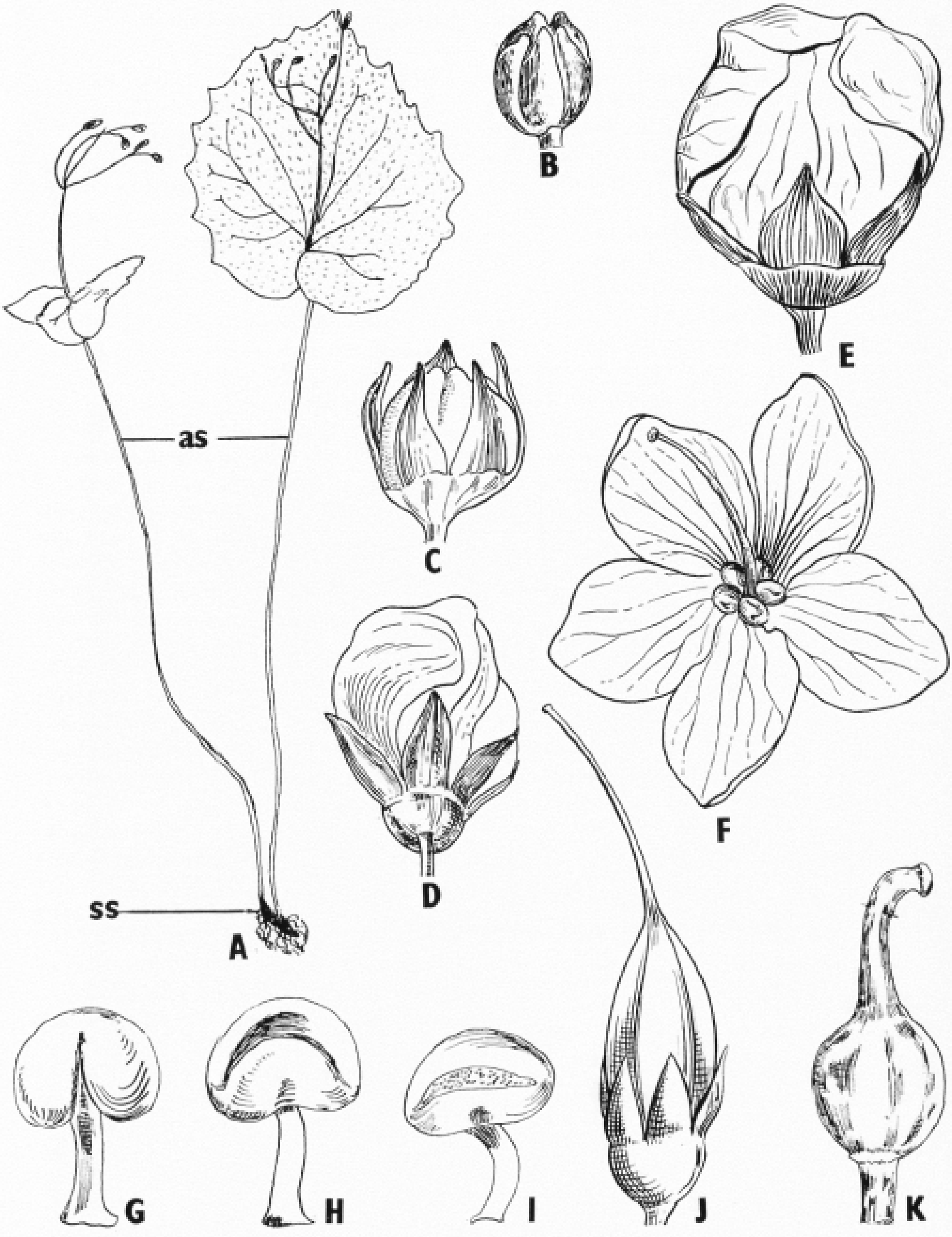


Fig. 1. *Platystemma violoides* (*as*, aerial stem; *ss*, subterranean stem). — A: Entire plant with subterranean stem. — B—E: Flower buds of different ages. — F: Single flower. — G—H: Abaxial and adaxial views of stamen. — I: Anther at dehiscence. — J—K: Pistils of different ages, note the persistent calyx in J. — A ×0.45, B—F, K ×4.0, G—I ×7.8, J ×4.5.

primary parietal cells and an inner primary sporogenous layer. The parietal cells undergo periclinal divisions and give rise to two layers of which the inner forms the tapetum (Fig. 2 B). The outer layer contributes to the middle layer and the endothecium (Fig. 2 B—D). Thus, in transection a young anther shows an epidermis, an endothecium, middle layer, tapetum and sporogenous layer. The development of anther wall conforms to the Dicotyledonous type (DAVIS 1966). The cells of the sporogenous layer undergo repeated divisions and differentiate into microspore mother cells (Fig. 2 C). During the development of the anther the epidermal cells divide anticlinally and become greatly stretched (Fig. 2 D). At the time when the microspore tetrads are formed the middle layer is compressed, the tapetal cells become binucleate and the endothecium lacks fibrous thickenings (Fig. 2 D—E). However, at the time of shedding of the pollen, the endothecium attains its maximum development and its cells develop fibrous thickenings (Fig. 2 F).

The tapetum is of the secretory type. Nuclear division and fusion in the tapetal cells are common (Fig. 2 D—E). Ultimately the tapetal nuclei degenerate and in the mature anther no trace of the tapetal cells is seen and the anther wall is represented by the epidermis and the endothecium (Fig. 2 F).

Microsporogenesis

The microspore mother cells enlarge, become rounded and divide meiotically (Fig. 2 G—L) to form microspore tetrads. The tetrads are generally tetrahedral (Fig. 2 M) and occasionally decussate (Fig. 2 N). The young microspore has a centrally situated nucleus and dense cytoplasm (Fig. 2 O). Subsequently, the nucleus moves towards the periphery and the microspore divides so as to produce a small generative and a large vegetative cell. Mature pollen grains are 2-celled (Fig. 2 P).

Megasporogenesis and Female Gametophyte

In the ovular primordium usually a single hypodermal archesporial cell differentiates in the young nucellus much earlier than inception of the integument (Fig. 3 A). It does not cut off a parietal cell and directly functions as the megaspore mother cell (Fig. 3 A—D). Although, twin megaspore mother cells occur occasionally no instance of twin embryo sacs was observed. The megaspore mother cell considerably elongates and undergoes meiosis I to form a dyad. Meiosis II is simultaneous in both the dyad cells (Fig. 3 E) and results in a linear tetrad of megaspores (Fig. 3 F—H). Only rarely the division in the chalazal dyad precedes that in the micropylar one. Irrespective of the sequence in degeneration of the three micropylar megaspores, only the chalazal member of the tetrad functions (Fig. 3 G—H).

The functional megaspore by mitotic divisions produces 2, 4 (Fig. 3 I—J), and 8 nucleate embryo sacs. By the time 2-nucleate female gametophyte is formed the nucellus is almost obliterated and the embryo sac is directly bordered by the integumentary tapetum. During further development, the embryo sac extends at the micropylar end and the endothelium ensheaths only the narrow region of the gametophyte.

The organized embryo sac shows an egg apparatus, two polar nuclei and three antipodal cells (Fig. 3 K). The antipodal cells are uninucleate and are usually arranged in a T-shaped fashion (Fig. 3 L) and rarely in a linear row (Fig. 3 K). Double fertilization occurs. At the time of entry of the pollen tube one of the synergids degenerates.

Endosperm

The primary endosperm nucleus lies in the centre of the embryo sac (Fig. 4 A) and divides prior to the zygote. Its division is followed by a transverse wall resulting in the formation of a micropylar and a

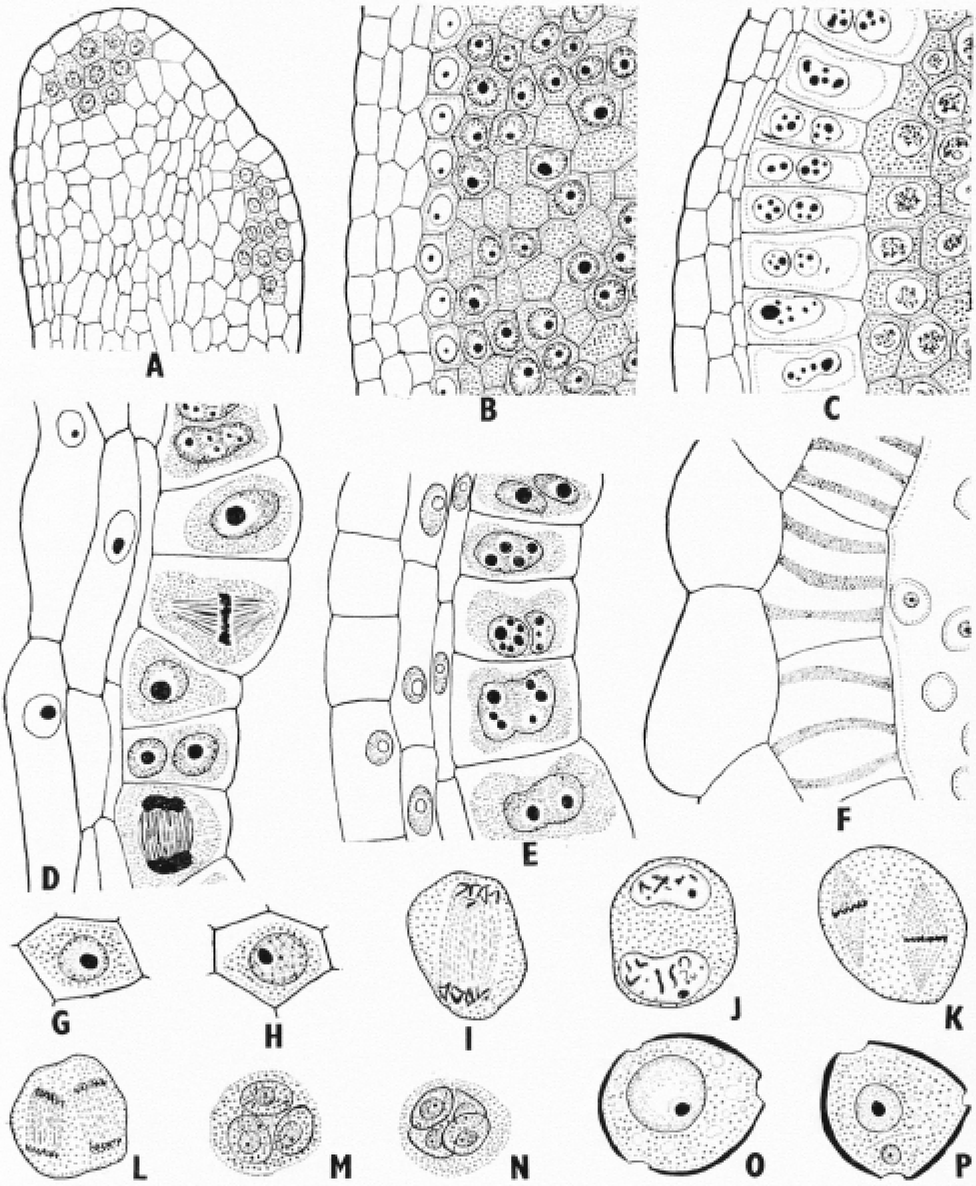


Fig. 2. *Platystemma violoides.* — A: Longisection of young anther showing two groups of hypodermal archesporial cells; that at the top represents the abaxial and that on the right the adaxial sporangium. — B—C: Portion of transections of anther showing wall layers and microspore mother cells. — D—F: Transections of portion of anthers at successively older stages, the tapetal nuclei are in division in D and fusion in E; in F note the well-developed endothecium. — G—N: Stages illustrating meiosis and cytokinesis in microspore mother cells. — O—P: One and two-celled pollen grains. — A ×425, B—C ×530, D—E ×1065, F ×530, G—P ×1065.

chalazal chamber (Fig. 4 B). Subsequent cell divisions are confined to the micropylar chamber wherein the first division is vertical (Fig. 4 C). The chalazal chamber directly functions as a 2-nucleate haustorium (Fig. 4 C—E). At this stage the endosperm comprises three cells arranged in two tiers — the micropylar tier with two juxtaposed cells and the chalazal tier which is a binucleate cell (Fig. 4 C). The micropylar tier undergoes many transverse divisions (Fig. 4 D—F). The uppermost pair of derivatives cut off towards the micropyle organizes into micropylar haustorium (Fig. 4 D—F). All the other derivatives of the micropylar chamber constitute the endosperm proper (Fig. 4 E—F).

The chalazal haustorium is the first to be organized (Fig. 4 C). Its nucleus divides once and the haustorium remains binucleate throughout its life. The nuclei are hypertrophied and lie imbedded in dense cytoplasm (Fig. 4 C—E). Morphological details suggest that the chalazal haustorium is less aggressive than the micropylar; it remains confined to the region of the hypostase. Unlike the micropylar haustorium, the chalazal haustorium is also the first to become disorganized, whereas the former remains distinct for a longer period and its cell are uninucleate. The remnants of the micropylar haustorium persist in mature seed (Fig. 4 G). The development of the endosperm is Cellular and conforms to the Brunella type (SCHNARF 1931).

Embryogeny

The zygote (Fig. 5 A) divides transversely resulting in a terminal cell *ca* and a basal cell *cb* (Fig. 5 B). The terminal cell divides vertically (Fig. 5 C) and the resultant *q* comprises either two juxtaposed cells (Fig. 5 D, F) or two overlapping cells (Fig. 5 E). The basal cell *cb* undergoes a transverse division (Fig. 5 E) giving rise to the tiers *m* and *ci* (Fig. 5 F).

Each of the two derivatives of the terminal cell *ca* divides vertically at right angles to the common wall between them to give rise to the quadrant *q* (Fig. 5 G). The four cells of the quadrant now divide transversely engendering the octant (Fig. 5 H—I). The cells of the octant are disposed in two tiers namely *l* and *l'* resulting in a group of peripheral and a group of inner cells. The peripheral cells organize into the dermatogen, whereas the inner cells function as the initials of the periblem and plerome (Fig. 5 J—L). All these eventually produce the hypocotyl. A similar histogenic development follows also in the terminal tier *l* (Fig. 5 K). Its derivatives give rise to the cotyledons and the epicotyl. The tier *m* derived from the basal cell *cb* cuts off a hypophysis initial and it undergoes two vertical divisions at right angles to each other forming a tier of four cells (Fig. 5 I—J). Further development results in the formation of a peripheral layer of cells and a group of four inner cells. The inner cells wedge in between the lower flanks of the globular embryo (Fig. 5 K) and organize the initials of the central cylinder of the root. The suspensor is derived from the tiers *n* and *n'* (Fig. 5 G—M). The mature embryo is dicotyledonous and the embryogeny conforms to the Onagrad type (JOHANSEN 1950).

Fig. 3. *Platystemma violoides* (*pt*, pollen tube). — A: L.s. ovular primordium showing hypodermal archesporial cell. — B—D: Longisections of ovules showing mode of curvature during growth and development of integument; ovule becomes completely anatropous at megaspore mother cell stage. — E: Dyad cells showing simultaneous division. — F—H: Megaspore tetrads; note the functional chalazal megaspore in H. — I—J: Four-nucleate embryo sacs, in J the nuclei are in telophase. — K—L: Longisections of the ovules showing organized embryo sacs; antipodal cells show linear arrangement in K whereas it is T-shaped in L. — A—L ×730.

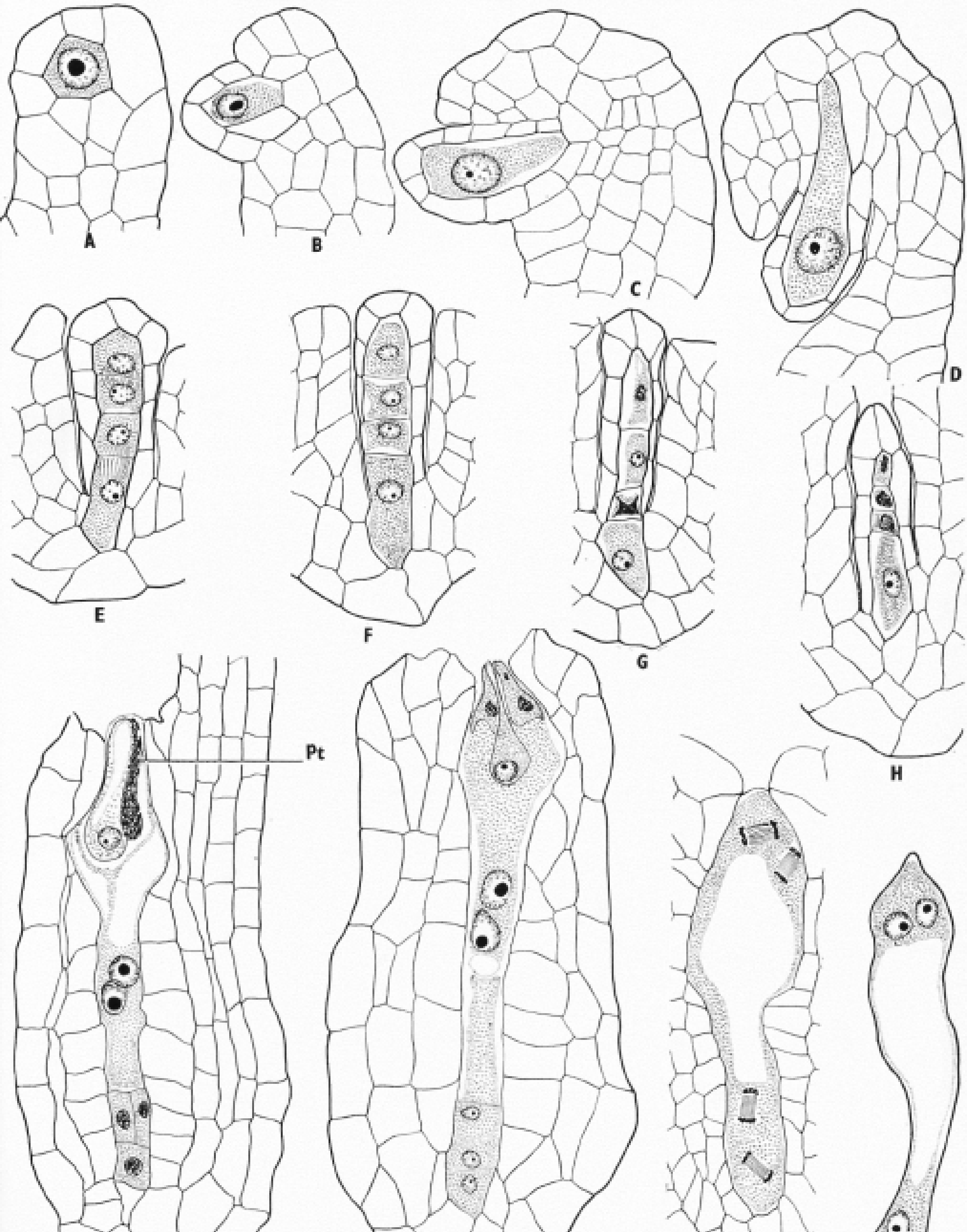


Fig. 3.

Testa and Pericarp

In the young ovule the integument consists of two or three layers of parenchymatous cells. When the embryo sac is 2-nucleate the seed coat comprises three layers (Fig. 6 A, D). The cells of the inner epidermis of the only integument become richly cytoplasmic and differentiate into an endothelium. The cells of the outer epidermis and those of the middle layer contain prominent nuclei and show vacuolation (Fig. 6 D). However, they remain quiescent so that in the developing seed also the integument is only 3-layered. By the time the embryo sac is organized, the cells of the outer epidermis elongate tangentially and those of the middle layer are compressed. The development of the integumentary tapetum does not keep pace with the rapid elongation of female gametophyte and thus becomes restricted to the narrow chalazal region of the embryo sac (Fig. 6 B, E).

Following fertilization, the epidermis of the integument and the endothelium elongate considerably in the tangential plane. The epidermal cells develop slight thickening on their outer tangential wall. The middle layer degenerates and is completely obliterated. The cells of the endothelium are highly vacuolated and occasionally show prominent nuclei (Fig. 6 C, F).

Prior to fertilization the pericarp is composed of 5—7 layers of cells. Those of the outer epidermis are isodiametric, whereas the inner epidermal cells are longer than broad. The cells inbetween these two layers have irregular outline and scanty cytoplasm (Fig. 6 G).

During maturation of the fruit, the cells of the pericarp elongate tangentially. The outer epidermis and three or four subjacent layers accumulate some tannin. The cells of the inner epidermis show almost uniform thickening (Fig. 6 H).

DISCUSSION

MICROSPORANGIUM AND MICROSPOROGENESIS. The structure of the microsporangium is uniform in the Gesneriaceae. Four wall layers namely epidermis, endothecium, middle layer and tapetum are formed. According to DAVIS (1966) the development of anther wall in the Gesneriaceae conforms to the Dicotyledonous type. Present study on *Platystemma* also reveals the same pattern. The tapetal cells enlarge considerably and become multinucleate. In *Didymocarpus tomentosa* 2- to 5-nucleate tapetum was observed (THATHACHAR 1942). In *Klugia notoniana* (AREKAL 1961) the tapetal cells later become 2- or 3-nucleate whereas in *Epithema carnosum* (PADMANABHAN 1961) they remain only 2-nucleate. In the tapetal cells nuclear fusion has been observed in *Platystemma violoides* (present work) as well as in *Didymocarpus tomentosa* (THATHACHAR 1942), *Epithema carnosum* (PADMANABHAN 1961) and *Klugia notoniana* (AREKAL 1961).

Fig. 4. *Platystemma violoides* (*cc*, chalazal chamber; *ch*, chalazal haustorium; *emb*, embryo; *end*, endosperm; *hy*, hypostase; *mc*, micropylar chamber; *mh*, micropylar haustorium; *pemb*, proembryo; *pen*, primary endosperm nucleus; *s*, synergid; *z*, zygote). — A: Longisection of part of the ovule showing zygote and primary endosperm nucleus; note the persistent synergid. — B: Two-celled endosperm, showing the formation of micropylar and chalazal chambers. — C: L.s. ovule showing 2-celled micropylar chamber and 2-nucleate chalazal chamber. — D: Advanced stage of endosperm showing 3 tiers of 2 cells each in micropylar chamber and 2-nucleate chalazal haustorium. — E—F: Longisections of seeds at more advanced stages; endosperm haustoria and endosperm proper are well-developed; note the highly elongated zygote in E, 2-celled proembryo in F, and hypostase in both. — G: L.s. mature seed, testa is 2 or 3-layered at places, endosperm is relegated to the periphery, embryo is dicotyledonous; remnant of micropylar haustorium is also seen. A—D ×610, E ×300, F—G ×170.

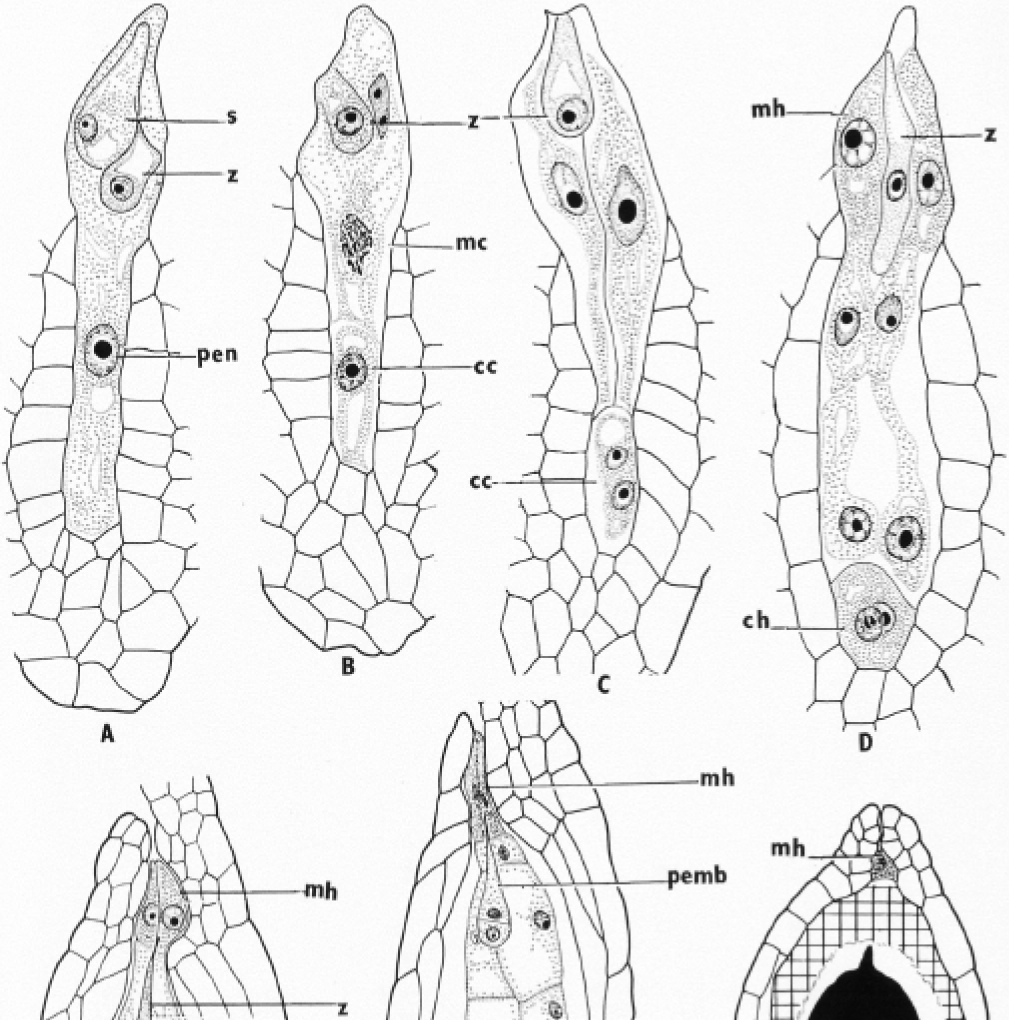

s
z
pen
A
z
mc
cc
B
z
cc
C
mh
z
ch
D
mh
z
ch
hy
E
mh
pemb
ch
hy
F
mh
emb
end
G

Fig. 4.

MEGASPORANGIUM, MEGASPOROGENESIS AND FEMALE GAMETOPHYTE. In the Gesneriaceae the ovules are anatropous, unitegminal and tenuinucellar. A single hypodermal archesporium is formed which produces a linear tetrad of megaspores. This is also true of *Aeschynanthus ramosissima* (unpublished observation). ABEKAL (1961) reported occasional occurrence of two megaspore mother cells and two megaspore tetrads in *Klugia notoniana* but no twin embryo sacs were observed by him. On the contrary, GLIŠIĆ (1928) observed two embryo sacs in *Haberlea rhodopensis*. The devolopment of embryo sac in the Gesneriaceae conforms to the Polygonum type except for *Rhytidophyllum crenulatum* and *R. tomentosum* where COOK (1907) gave a description suggestive of Adoxa type. On the basis of some of the illustrations presented by him, MAHESHWARI (1946) doubted his observations and suggested a reinvestigation.

An extra-micropylar development of embryo sac was reported for *Monophyllaea horsfieldii* (OEHLKERS 1923) and *Roettlera* (GLIŠIĆ 1934). In all the other genera so far investigated including *Platystemma violoides* the embryo sac presents no tendencies for an extra-micropylar development. The synergids and antipodal cells degenerate after fertilization. However, persistence of one of the synergids has been recorded for *Rhynchoglossum obliquum* (THATHACHAR 1943) and *Klugia notoniana* (AREKAL 1961). In *P. violoides* one of the synergids is destroyed at the time of entry and impact of the pollen tube and the other degenerates after fertilization.

ENDOSPERM. The primary endosperm nucleus divides to give rise to micropylar and chalazal chamber. On the basis of the mode of formation of the 3-celled condition, the development of endosperm in this family has been classified into two categories. In the first, the micropylar chamber divides transversely to form a linear row of three cells. Such a feature is reported for *Klugia zeylanica* (SCHNARF 1921), *Ramondia nathaliae* and *R. serbica* (GLIŠIĆ 1924). The second is characterised by a vertical division in the micropylar chamber. To this belong *Corytoloma cyclophyllum* (LAURENT 1923), *Haberlea rhodopensis* (GLIŠIĆ 1928), *Rottlera* sp. (GLIŠIĆ 1934), *Ramondia pyrenaica* (CRÉTÉ 1942), *Didymocarpus tomentosa* (THATHACHAR 1942), *Rhynchoglossum obliquum* (THATHACHAR 1943), *Chirita lavandulacea* (CRÉTÉ 1949), *Alloplectus sanguineus* (CRÉTÉ 1955), *Epithema carnosum* (PADMANABHAN 1961), *Klugia notoniana* (AREKAL 1961) and *Platystemma violoides* (present paper).

A feature common to both the categories of endosperm development is the organization of a micropylar as well as a chalazal haustorium. The presence of a 2-celled micropylar haustorium is common to a large majority of the taxa investigated including *Platystemma violoides*. However, a 4-celled condition is reported to be of regular occurrence in *Ramondia nathaliae* and *R. serbica* (GLIŠIĆ 1924), and as a rare phenomenon in *Haberlea rhodopensis* GLIŠIĆ 1928). Irrespective of the number of cells constituting the haustorium, the cells were invariably uninucleate, a character also observed in *P. violoides*. An extra-micropylar development of the micropylar haustorium has been reported for *Didymocarpus tomentosa* (THATHACHAR 1942) but such a phenomenon was not observed in *P. violoides*.

Fig. 5. *Platystemma violoides* (*cot*, cotyledons; *sus*, suspensor). — A: Zygote. — B—C: Two-celled proembryo, the terminal cell (*ca*) shows vertical division. — D—E: Three-celled proembryo, in E the basal cell *cb* is in late anaphase. — F: Four-celled proembryo. — G: Proembryo showing the formation of tiers *q*, *m*, *n*, and *n'*. — H—I: Octant stage. — J—K: Advanced stage of proembryos showing the demarcation of histogens. — L—M: Heart-shaped and dicotyledonous embryos. — A—K ×610, L—M ×305.

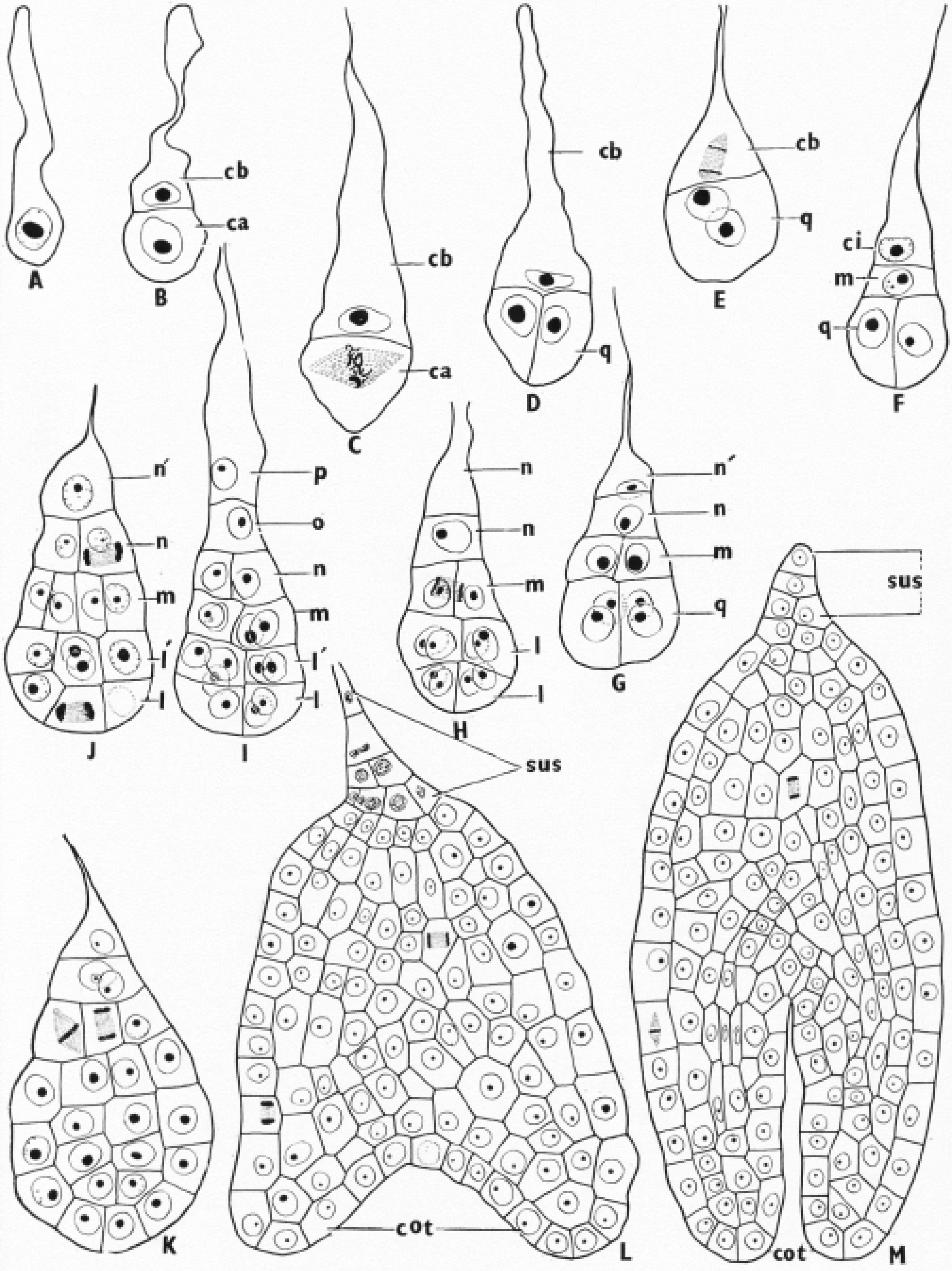


Fig. 5.

A uninucleate chalazal haustorium has been recorded for *Klugia zeylanica* (Schnarf 1921), *Ramondia nathaliae* and *R. serbica* (Glišić 1924) and *Rhynchoglossum obliquum* (Thathachar 1943). In *Klugia notoniana*, Arekal (1961) observed that the chalazal haustorium is binucleate during early stages of development and eventually becomes uninucleate owing to the fusion of the two free nuclei. He further observed the uninucleate chalazal haustorium to extend laterally and upward in the subepidermal region of the integument consuming the integumentary cells lying between the endothelium and the outer epidermis.

Binucleate chalazal haustorium is a characteristic feature of several gesneriads, like *Didymocarpus tomentosa* (Thathachar 1942), *Chirita lavandulacea* (Crété 1949), *Alloplectus sanguineus* (Crété 1955), *Epithema carnosum* (Padmanabhan 1961) and *Platystemma violoides* (present paper).

Occasionally, the chalazal haustorium is bicelled and uninucleate in *Haberlea rhodopensis* (Glišić 1928) but it is completely absent in a hybrid of *Streptocarpus* (Crété 1942).

EMBRYOGENY. In *Rhytidophyllum crenulatum* Cook (1907) observed a couple of instances where the embryo was elongated, lacked cotyledons and even differentiation of the histogens. *Ramondia pyrenaica* (Crété 1942) is exceptional in having elongated and multinucleate suspensor cells. None of these abnormalities reported above was observed in *Platystemma violoides*.

TESTA. Our information on the structure of seed coat in the Gesneriaceae is meagre. Some data are available only in *Epithema carnosum* (Padmanabhan 1961) and *Klugia notoniana* (Arekal 1961). In both these species integuments comprise four layers but in *P. violoides* only three layers have been observed.

ACKNOWLEDGEMENTS

We are indebted to the late Professor P. Maheshwari F. R. S. for suggesting the problem and providing the material; to Professor B. M. Johri for encouragement and suggestions. Sincere thanks are due to Dr. N. S. Rangaswamy, Dr. N. N. Bhandari, and Dr. K. M. M. Dakshini for valuable discussion.

LITERATURE CITED

Arekal, G. D. 1961. Embryology of Klugia notoniana. — Bot. Gaz. 123: 144—150.

Collett, H. 1921. Flora simlensis. — Calcutta.

Cook, M. T. 1907. The embryology of Rhytidophyllum. — Bull. Torrey Bot. Club 34: 179—184.

Crété, P. 1942. Recherches histologiques et physiologiques sur l'embryologie des Labiatiflores. Contribution à l'étude des formations haustoriales. — Paris.

— 1949. Recherches embryologiques sur les Gesnériacées. Développement de l'albumen et de l'embryon chez le Chirita lavandulacea Stapf. — Bull. Soc. Bot. France 96: 234—235.

— 1955. L'origine du sac embryonnaire et le développement de l'albumen chez l'Alloplectus sanguineus Mart. (Gesnériacées). — Bull. Soc. Bot. France 102: 205—208.

Davis, G. L. 1966. Systematic embryology of the angiosperms. — New York.

Fig. 6. *Platystemma violoides* (*emb*, embryo). — A—C: Longisections of ovules and seed. — D: Magnified view of the portion marked *d* in A to show 3-layered testa. — E: Enlarged view of the region marked *e* in B; the epidermal cells have elongated tangentially and show scanty cytoplasm; middle layer is compressed, endothelium borders mainly the chalazal region of the embryo sac. — F: Magnified view of the region *f* in C showing only the epidermis and endothecium; the middle layer is obliterated. — G—H: Portion of the pericarp before and after fertilization respectively. — A—B ×380, C ×90, D—F ×960, G—H ×480.

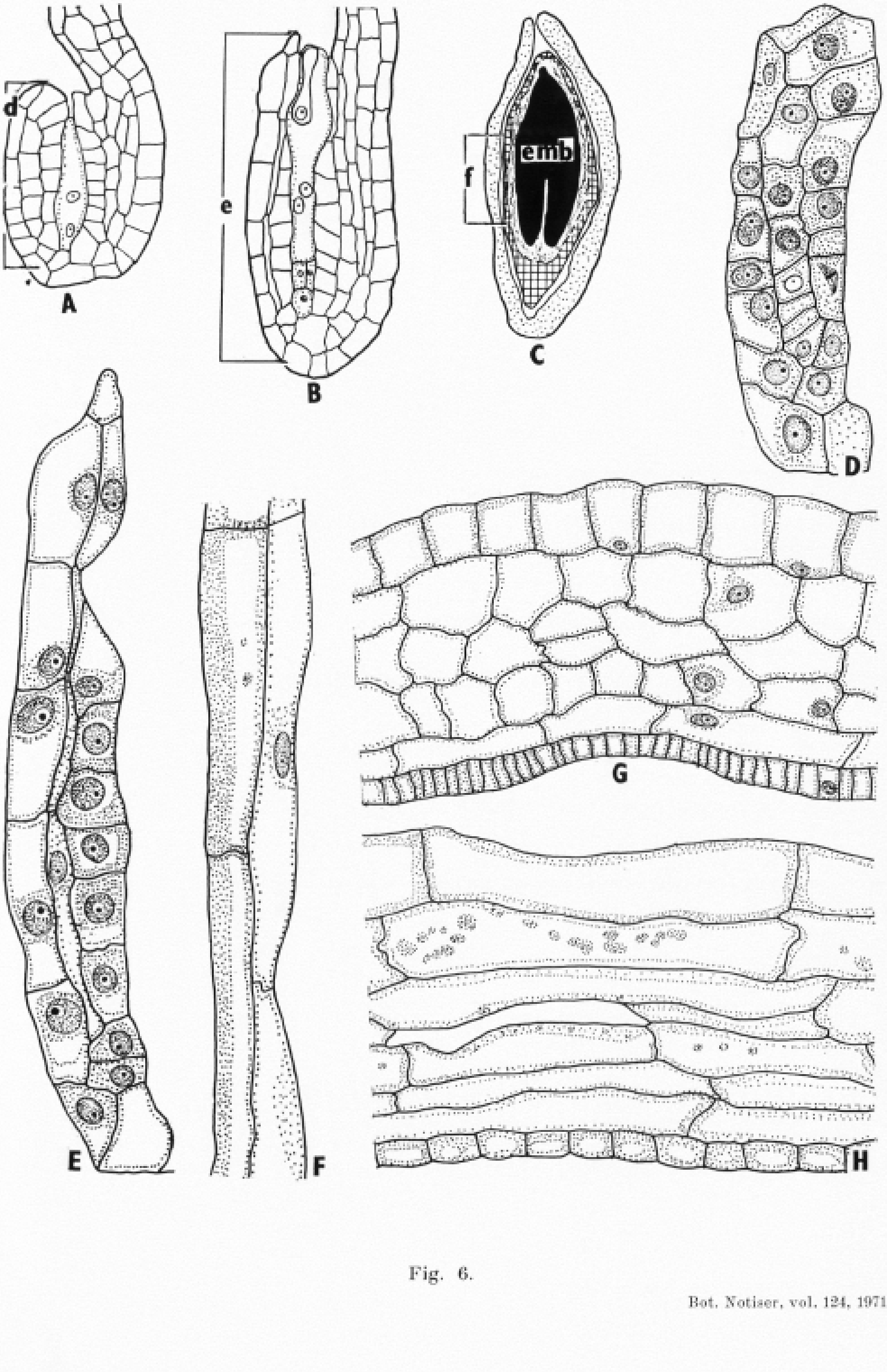


Fig. 6.

GIFFORD, E. M. 1950. Softening refractory plant material embedded in paraffin. — Stain Techn. 25: 161—162.

GLIŠIĆ, L. M. 1924. Development of the female X-generation and embryo in Ramondia. — Belgrade.

— 1928. Development of the female gametophyte and endosperm in Haberlea rhodopensis Friv. — Bull. Inst. Jard. Bot. Univ. Beograd. 1: 1—13.

— 1934. Zur Kenntnis der Samenentwicklung der Gesneriaceen. Über die Endosperm- und Haustorienbildung von Roettlera. — Bull. Inst. Jard. Bot. Univ. Beograd. 3: 94—111.

JOHANSEN, D. A. 1950. Plant embryology. — Waltham.

JOSHI, A. C. 1938. Evolution of the vegetative form in the Gesneriaceae. — Curr. Sci. 7: 234—236.

*LAURENT, V. 1923. Zur Entwicklungsgeschichte von Corytoloma cyclophyllum Dus. n. sp. ined. — Svensk Bot. Tidskr. 17: 165—174.

MAHESHWARI, P. 1946. The Adoxa type of embryo sac: A critical review. — Lloydia 9: 73—113.

*OEHLKERS, F. 1923. Entwicklungsgeschichte von Monophyllaea Horsfieldii. — Beih. Bot. Zentralblatt 39: 128—151.

PADMANABHAN, D. 1961. A contribution to the embryology of Epithema carnosum. — Journ. Madras Univ. 31 B: 37—46.

SCHNARF, K. 1921. Kleine Beiträge zur Entwicklungsgeschichte der Angiospermen. II. Klugia zeylanica. (R. Brown) Gardn. — Österr. Bot. Zeitschr. 70: 255—261.

— 1931. Vergleichende Embryologie der Angiospermen. — Berlin.

THATHACHAR, T. 1942. Studies in Gesneriaceae. Gametogenesis and embryogeny of Didymocarpus tomentosa Wt. — Journ. Indian Bot. Soc. 21: 185—193.

— 1943. Studies in Gesneriaceae. Development of seed in Rhynchoglossum obliquum Bl. — Journ. Indian Bot. Soc. 22: 51—57.

WILLIS, J. C. 1931. A dictionary of the flowering plants and ferns. — Cambridge.

---

*Not seen in original.

Anatomy of the Inflorescence of some Euphorbiaceae

With a Discussion on the Phylogeny and Evolution of the Inflorescence including the Cyathium

By C. Venkata Rao

Department of Botany,
Andhra University Post Graduate Centre,
Guntur 5, India

ABSTRACT

Venkata Rao, C. 1971. Anatomy of the inflorescence of some Euphorbiaceae. With a discussion of the phylogeny and evolution of the inflorescence including the cyathium. — Bot. Notiser 124: 39—64.

The anatomy of the inflorescence in some members of Euphorbiaceae has been studied, viz. *Acalypha indica, Dalechampia roezliana, Synadenium grantii, Monadenium leave, M. schubei, Euphorbia nivulia, E. dracunculoides, E. thymifolia, E. rothiana, E. hirta, Poinsettia pulcherrima, P. geniculata, P. heterophylla,* and *Pedilanthus tithymaloides.* The results are correlated with observations on the morphology of the inflorescence and floral anatomy, and in the light of the findings the phylogeny and evolution of the inflorescence in the family are discussed.

The inflorescence in Euphorbiaceae evolved mainly by reduction, which occurred synchronously with that in vegetative parts and floral structure. From a primitive type represented by *Jatropha curcas,* evolution is traced in three directions, towards simple types, condensed types and reduced types (cyathia). Along the first line, reduction occurred in the main and lateral axes and in the number of flowers borne on them along with a shift from terminal to the axillary position. This led to the evolution of the panicle, pseudoraceme, raceme, spike, head, fascicle and the solitary axillary flower.

In the evolution of the condensed (*Dalechampia*) type of inflorescence, the terminal female flower becomes suppressed; one lateral cyme of female flowers, four male glomerules and several foliaceous bracts persist and the axis undergoes some condensation.

By combining the most primitive features noticed in the cyathia of living genera, the inflorescence ancestral to the cyathium is reconstructed. This is supposed to be amentoid with a terminal female flower, several male glomerules and foliaceous bracts below, all arranged in a 2/5 spiral; the male glomerules had numerous male flowers in each and the male flower had perianth and at least two stamens; the bracts bore a pair of marginal glands. This ancestral type resembles closely the inflorescence noticed in *Acalypha indica.*

INTRODUCTION

Euphorbiaceae is a large family with about 283 genera and 6800 species (Pax & Hoffman 1931). In his recent treatment of the family, Hutchinson (1969) divides it into 40 independent tribes as against the 11 tribes and two sub-families of Pax and Hoffman (1931). These tribes are arranged in a phylogenetic sequence based on his concepts of evolution in the family. The series begin with Glochideae and Caletiae; the Euphoribieae take the pride of place as "the climax group".

The inflorescence in Euphorbiaceae shows much variation ranging from large terminal dichasia and panicles to small condensed clusters and solitary axillary flowers. Some of the tribes (e.g., Acalypheae, Crotoneae, Codiaeae, Dalechampieae etc.) are characterised by definite types of inflorescence. The cyathium, a "super-evolved inflorescence" the like of which is not noticed in any other angiosperms, marks the culmination of reduction, condensation and specialisation and is characteristic of the tribe Euphorbieae. *Euphorbia*, the largest genus of the tribe, is considered to be a heterogeneous assemblage both on morphological and cytological (PERRY 1943) grounds. Groups of species or even single species have been given generic status by different taxonomists (cf. SCHMIDT 1907; MILLSPAUGH 1913, 1914; CROIZAT 1938; DRESSLER 1961). Since this treatment is not accepted by all taxonomists, there is much variation in the number of genera recognised. HUTCHINSON (1969) lists only ten genera under the tribe and DRESSLER (1961) fourteen. However, if all the genera recognised by various taxonomists are pooled, they would make up 17, viz. *Agaloma, Anthostema, Calycopeplus, Chamaesyce, Cubanthus, Dichostemma, Diplocyathium*[1], *Elaeophorbia, Euphorbia, Euphorbiodendron, Monadenium, Neoguillauminia, Pedilanthus, Poinsettia, Stenadenium, Synadenium* and *Tithymalus*.

There is some difference of opinion regarding the taxonomic position of *Anthostema*. BAILLON (1858) excludes this genus from Euphorbieae and places it in Hippomaieae since he believed that the female flower is placed laterally in the inflorescence and not centrally as in the cyathia of other Euphorbieae. However, other taxonomists (PAX & HOFFMAN 1931; CROIZAT 1940; HUTCHINSON 1969) favour its inclusion in Euphorbieae.

PREVIOUS WORK

A perusal of the literature on Euphorbiaceae shows that there is no comprehensive account on the phylogeny and evolution of the inflorescence in the family. HUTCHINSON (1969) bases his conclusions regarding the evolutionary trends in the family mainly on floral morphology and does not express any opinion on the primitive (ancestral) inflorescence in the family or the evolutionary trends in it.

The phylogeny and evolution of the cyathium have been the most difficult of interpretation and so far they have defied the attempts of botanists. HABER (1925) has studied the anatomy of the cyathium of several species of *Euphorbia* but made no attempt at tracing its phylogeny. HABER interprets each gland of the cyathium as a "pair of modified secondary (male) branches of a lateral inflorescence branch fused with which are parts of adjacent involucral bracts", thus virtually supporting the view originally expressed by N. E. BROWN (quoted from THISELTON-DYER 1909).

CROIZAT (1936, 1937) first postulated that the cyathium is derived by vertical condensation of an elongated inflorescence with a longstalked terminal female flower below which were found several glomerules of male flowers distributed around the axis. However, since he could not find any inflorescence with such an arrangement of flowers in the living Euphorbiaceae, he (CROIZAT 1940) made the alternative suggestion that the closed, radially symmetrical (*Euphorbia* type) cyathium with a central female flower is derived from the open, zygomorphic inflorescence with a lateral female flower (such as is found in *Dalechampia*). Later CROIZAT (1942) even went beyond the limits of Euphorbiaceae and tried to derive the cyathium from the inflorescence types in Malvales. However, these suggestions are dismissed by DRESSLER (1957) as being "imaginative and lacking support from any evidence". CROIZAT (1940) himself is

---

[1] Sir GEORGE TAYLOR (Royal Botanic Gardens, Kew) writes in a personal letter (May, 1969) that *Diplocyathium* is nothing more than a bad genus based on a species (*Euphorbia capitulata* REICHB.) with a perpetuated cyathial monstrosity.

conscious of the shortcomings of his hypotheses and despairs that the problems may never be solved except through the collective endeavours of students of various botanical disciplines.

Though much literature has accumulated on the morphology of the cyathium, no satisfactory explanation has so far been offered by taxonomists as to its phylogeny. The homologies of the female flower, the male glomerules and their associated "bracteoles", the morphology of the involucral bracts and glands remain unexplained. An attempt is made in the following pages to explain the various problems on the basis of studies in morphology and anatomy of the inflorescences in some taxa.

MATERIALS AND METHODS

Morphological and anatomical observations have been made on the inflorescence in some taxa of Euphorbiaceae. Herbarium materials as well as those fixed in formalin-acetic-alcohol were studied. For microtoming, the herbarium material was first soaked in distilled water for 2—3 days and put in 1 % solution of caustic soda and kept in paraffin bath at 60°C overnight. Then the material was washed thoroughly and treated like fixed material. The materials were dehydrated in alcohol series, cleared in xylol and infiltrated and embedded in paraffin of 60°C m.p. Microtome sections were cut from 6—12 μ in thickness and stained in Delafield's haematoxylin.

OBSERVATIONS

Acalypha indica L.

Acalypha belongs to the tribe Acalypheae. The inflorescences in *A. indica* are elongated axillary pseudoracemes found on the main as well as lateral branches of the plant. The peduncle shows three flower-bearing regions (Fig. 8 E): (*1*) towards the base of the axis are found 5—12 large foliaceous bracts disposed in 2/5 spiral; each bract subtends a cyme of three female flowers which mature in basipetal succession (Fig. 1 B); (*2*) after a short interval 6—10 glomerules of male flowers are found also disposed spirally around the axis; each cluster bears 6—10 flowers which show common as well as individual floral bracts (Fig. 1 C); (*3*) the main axis elongates considerably beyond the region of male flowers and terminates in a 3-lobed structure (Fig. 1 D). This is described by GAMBLE (1967) as a "tuft of sterile flowers", but is actually found to be a fertile female flower which sets a viable seed (Fig. 1 E).

Each female flower of the basal cymes shows an individual bract, a short pedicel, 3-lobed perianth, a pistil of three uniovulate carpels and three stylar branches with bilobed stigmas. The male flowers are pedicellate; the pedicel has a joint in the middle which shows that each flower may be the sole survivor of a cyme (Fig. 1 C). The flower shows a perianth of four segments and 8 stamens slightly connate at base. The stalk of the terminal female flower is merely a continuation of the peduncle; the flower itself is sessile and ebracteate (Fig. 1 E). It shows a perianth of 3 or 4 connate lobes. The structure of the pistil differs from that of the female flowers lower down. The three carpels are divergent and arranged in the form of Y. The proximal carpel is fertile and the two distal ones sterile and empty (Fig. 1 E). The fertile carpel shows a single stylar branch towards the base with several filiform segments. The attachment of the ovule in the carpel towards the base shows that this is the morphologically apical region and that the carpel has rotated and become parallel to the inflorescence axis.

The peduncle below the region of the foliaceous bracts shows a siphonostele. Below the bract the main stele gives off a lateral stele from which 7—9 bract traces depart (Fig. 1 A). These function as the midrib and marginals. All these bundles branch and the branches anastomose and give a leaf-like venation to the bract. Each female flower is fed by a branch from the lateral stele. This gives off a trace into the bract of the flower, one trace into each of the three tepals and three dorsals and three pairs of ventrals into the pistil. The pair of ventrals of each carpel come together in the region of the placenta and give off a single ovular trace which branches slightly in the chalaza. Each dorsal bundle extends into one stylar branch.

The pedicel of the male flower receives 6—8 bundles. After giving off one trace into each of the tepals, the floral stele forms 8 staminal bundles which feed the stamens. Above the level of attachment of the male glomerules, the vascular bundles of the main axis continue their course as such. At the base of the female flower one trace is given off into each of the tepals after which the stele forms a single dorsal and a pair of ventrals (Fig. 1 F). The dorsal bundle branches in a pinnate manner; these bundles, after traversing beneath the ridges of the fertile carpel extend into the sterile carpels (Fig. 1 I). The two ventrals fuse and give off the ovular trace after which the common ventral extends into the stylar branch (Fig. 1 G, H).

Some non-vascular glands are found on the margin of the foliaceous bract subtending the female cymes.

Dalechampia roezliana Mull.

The inflorescence of *D. roezliana* shows two pairs of decussating bracts at base, of which the outer pair is larger, petaloid with leaf-like venation and the inner pair smaller and membraneous (Fig. 2 A). To the inside of one bract of the inner pair is found a small bract with a cyme of three collaterally placed female flowers in its axil; all the flowers are at the same stage of development (Fig. 2 F). Each flower is pedicellate and provided with 5—6 tepals, a pistil of three uniovulate carpels, and a simple stout style which is slightly three lobed at the apex (Fig. 2 B). The inflorescence axis elongates beyond the level of attachment of the female flowers into an internode and bears two pairs of empty membraneous bracts (Fig. 8 O). This shows that the female flowers are not terminal as Croizat (1940) believes but lateral and basal. The axis then expands into a convex receptacle on which four clusters of male flowers are distributed at different levels, each cluster arising in the axil of a common bract. Three of the clusters bear three flowers each and the fourth has two flowers (Fig. 2 H). A few sterile bracts are found at the summit of the axis which indicate that some more male flowers have been suppressed. Both the fertile and sterile bracts are laciniate and the ultimate segments are metamorphosed into elongated glands (Fig. 2 D). There are no sterile male flowers in the inflorescence of *D. roezliana* as Willis (1948), Good (1956) and Hutchinson (1969) believe. The male flower shows a joint in its pedicel as is noticed in *Acalypha indica*. It has a gamophyllous 4-lobed perianth and 12—15 stamens which are connate below into a column (Fig. 2 C).

The peduncle shows a dictyostele of numerous bundles. From this three traces emerge into each of the four basal bracts. The common bract subtending the cyme of female flowers also receives three traces which branch further (Fig. 2 F). Each female flower receives one stele from which one trace departs to the individual floral bract and each of the tepals (Fig. 2 G).

Fig. 1. *Acalypha indica*. — A: T.s. peduncle of lateral cyme below a foliaceous bract showing the origin of bract traces. — B: L.s. cyme of female flowers. — C: L.s glomerule of male flowers. — D: Terminal female flower. — E: L.s. terminal female flower. — F—I: T.s female flower from base upwards. — D ×11; rest ×39. (*bt*=bract traces; *fbr*=foliaceous bract; *p*=perianth; *fb*=floral bract; *cb*=common bract; *s*=seed; *n*=nucellus; *en*=endosperm; *em*=embryo; *stb*=stylar branch; *dct*=dorsal carpellary trace; *vct*=ventral carpellary trace; *fsb*=filiform stigmatic branches; *cv*=common ventral; *cw*=carpellary wall; *sc*=sterile carpel; *fc*=fertile carpel).

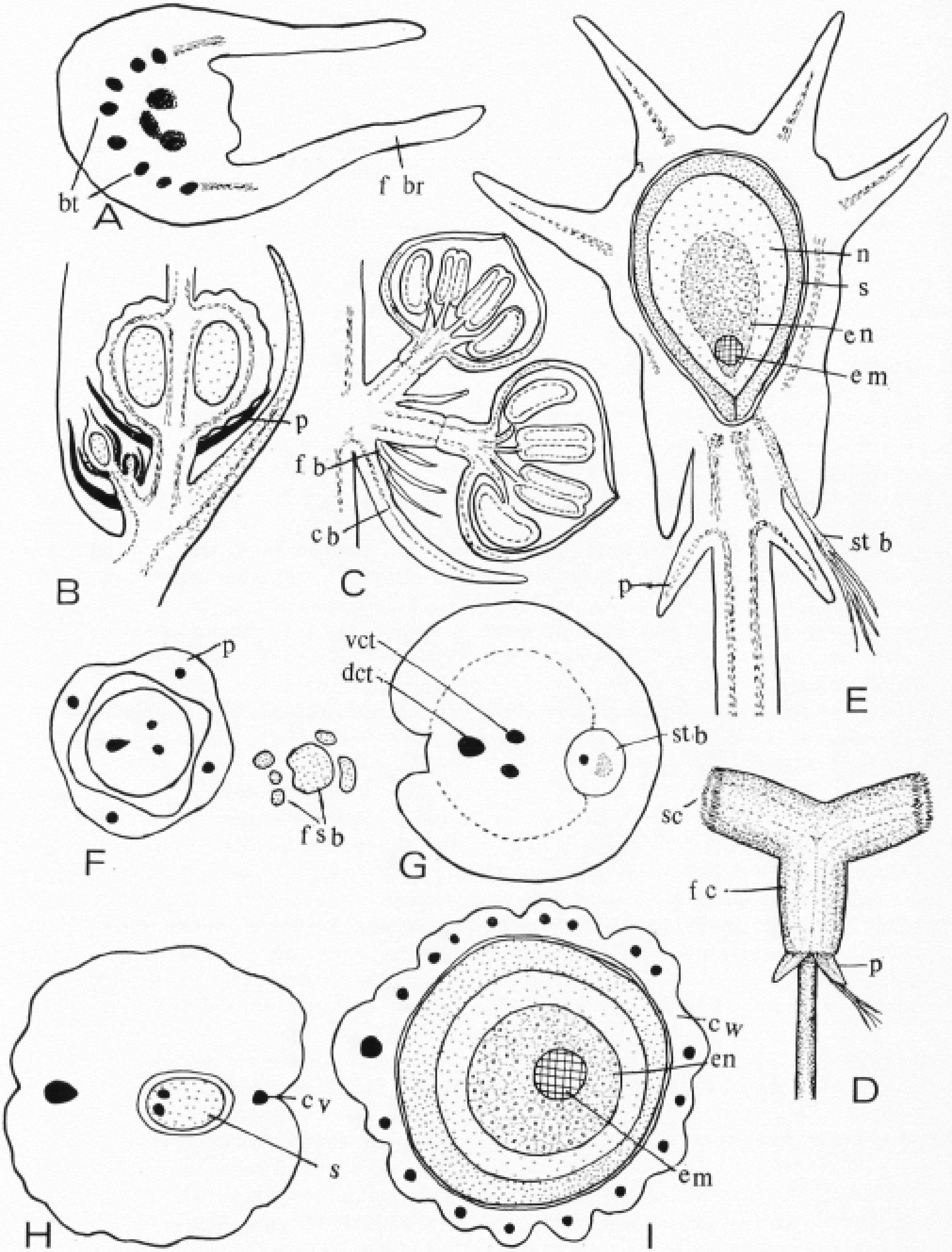

bt
f br
A
p
B
f b
c b
C
n
s
en
em
st b
p
E
p
F
f s b
vct
dct
st b
G
sc
f c
p
D
c v
s
H
c w
en
em
I

Fig. 1.

The traces divide into three bundles each which traverse as midrib and marginals. The remaining bundles vascularise the pistil as in *A. indica* (Fig. 2 F). Some nonvascular glands are found on the margins of the tepals (Fig. 2 G).

From the stele of the internode above the level of attachment of the female flowers, three traces are given off into each of the four sterile bracts which subtend the male glomerules. Then the stele gives off 11 rings of bundles one for each male flower, and some traces for the fertile and sterile bracts. The pedicel of the male flower shows a ring of 8 bundles. The tepals are 3-traced; eight traces are given off from the floral stele of which the antero-posterior and lateral traces are the tepal midribs and the alternate ones are the conjoint tepal marginals. The latter divide radially and demarcate the laterals of adjacent tepals. The floral stele then breaks up into 12—15 staminal bundles. The traces of fertile and sterile bracts branch repeatedly and form numerous strands which extend into the nectaries. Each gland consists of richly protoplasmic cells of which the epidermal cells are radially elongated (Fig. 2 E).

Synadenium grantii Hook.

Synadenium and other genera described hereafter belong to the tribe Euphorbieae. The cyathia in *S. grantii* occur in terminal panicles. Each cyathium is shortly peduncled and slightly bent at the top. The involucre is biseriate and consists of superposed series of bracts which are adnate in the lower part (Fig. 3 B). The bracts of the outer series are succulent and form a truncate, saucershaped structure which bears a ring-like nectary at its top (Fig. 3 A). The inner series of bracts are membraneous; their involute margins are connate and form five compartments around the axis inside which the male glomerules are situated. Each glomerule consists of 6—8 *Euphorbia*-like male flowers which are associated with ribbon-like or laciniate 'bracteoles' (Fig. 3 C, G). The female flower is long-stalked and provided with a rudimentary or 3-lobed perianth and a pistil of three uniovulate carpels with three bifid styles (Fig. 3 B).

The peduncle of the cyathium shows a siphonostele (Fig. 3 D). At the base of the cyathium, two abortive cyathia are found laterally concealed by their respective bracts. Two branch steles depart from the stele of the peduncle for these cyathia and their bracts (Fig. 3 E). Close to the emergence of the above steles, five steles depart from the main stele all round, while the remaining bundles continue their course in the axis. Each lateral stele first gives off three traces for the involucral bract and functions as the stele for the male glomerule (Fig. 3 F). This breaks up into 8 concentric bundles which enter the stalks of the stamens (Fig. 3 G). Since the part of the stalk below the joint is considered to be homologous to the pedicel, these bundles must be regarded as 'pithless' steles. The ring of bundles in the main axis gives off three vestigial traces into the three perianth parts; the remaining bundles vascularise the ovary as in *Acalypha indica*.

The bract traces traverse without branching in the lower part of the involucre. At about the middle of its height, the bract marginals branch slightly in a radial manner while the midrib bundles remain undivided. Higher up the marginal bundles divide tangentially and form arcs of bundles to the outside. The bract midribs and some marginal bundles bend inside and traverse the inner series of bracts. The arcs of bundles enter the outer series of bracts which begin to separate from the inner. The bundles first divide radially and form a ring of closely placed bundles (Fig. 3 H); then these branch repeatedly and form several concentric rings of strands which traverse the broadening zone of glandular tissue. The glandular cells first appear around a linear schizogenously formed space (Fig. 3 I). These spaces enlarge higher up so that the zone becomes

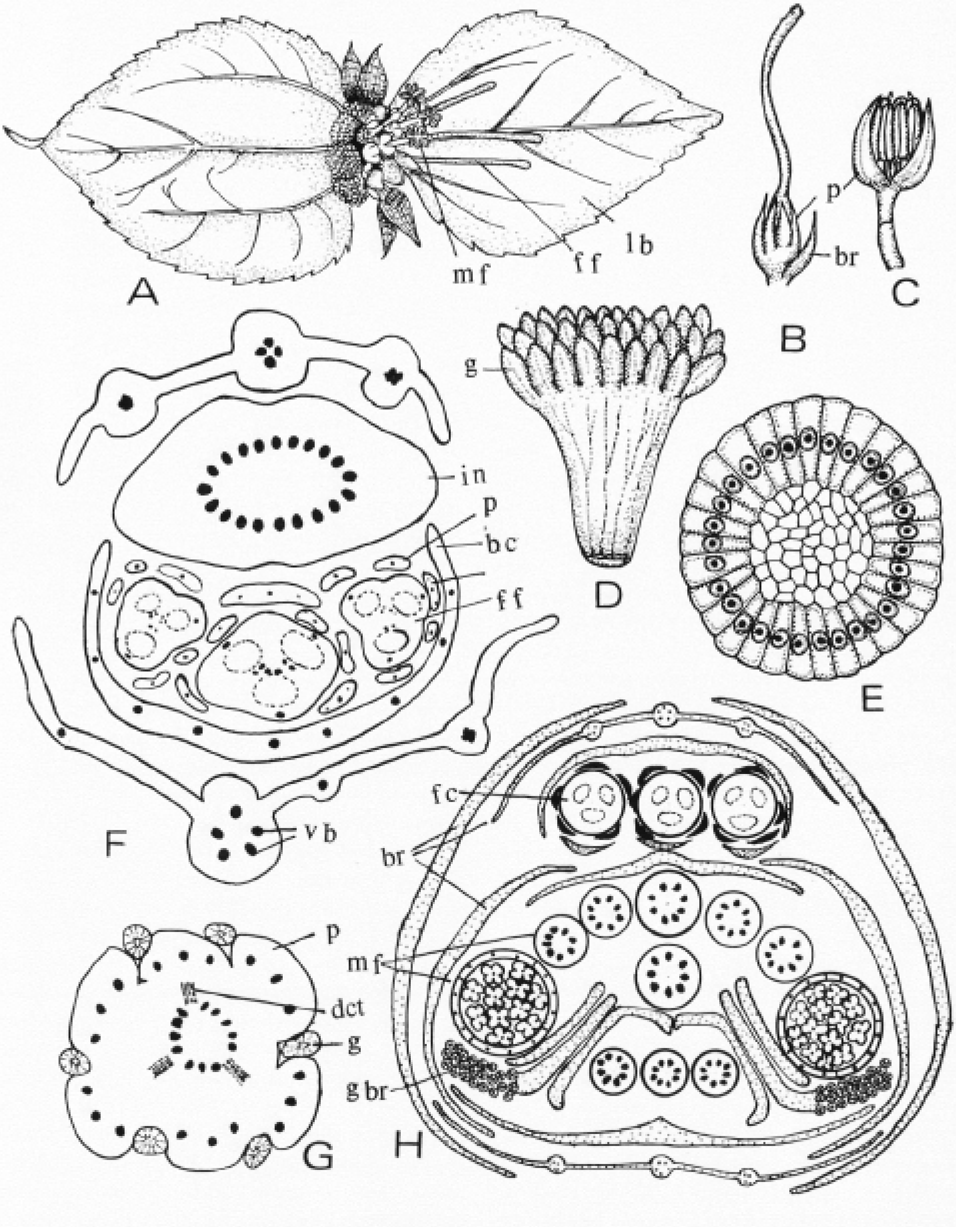


Fig. 2. *Dalechampia roezliana.* — A: An inflorescence, ×1. — B: A female flower, ×3. — C: A male flower, ×3. — D: A sterile bract with glands, ×6. — E: T.s. gland, ×200. — F: T.s. inflorescence above the level of attachment of the female cyme, ×28. — G: T.s. base of female flower showing glands on tepals, ×39. — H: Diagrammatic transverse section of the inflorescence. (*mf* = male flower; *ff* = female flowers; *lb* = lower bract; *g* = gland; *br* = bract; *p* = perianth; *in* = internode; *bc* = bract of the female cyme; *fc* = female cyme; *dct* = dorsal carpellary trace; *gbr* = gland tipped sterile bract; *vb* = vascular bundles of the bract midrib — note the stele-like arrangement of the bundles).

mesh-like in appearance with glandular cells lining each space (Fig. 3 K).

Monadenium laeve Stapf and **M. schubei** (Pax) N. E. Brown

The cyathium in *Monadenium* resembles that of *Synadenium* in its biseriate involucre and differs mainly in its involucre being open on one side to or below the middle due to incomplete connation of bracts. The cyathium in both species of *Monadenium* is subtended by a large, foliaceous bract which is fused with the base of the involucre (Fig. 4 A, B). The bracts of both series are adnate and form a symmetrical cup at base. The outer involucre is more succulent and bears a gland at its top as in *Synadenium*, which is interrupted at the opening. The inner involucre consists of five membraneous, laciniate bracts. Their involute margins are connate laterally so as to form partitions between the male glomerules. Four (*M. schubei*) or 5—6 (*M. laeve*) *Euphorbia*-like male flowers are found in each glomerule associated with 'bracteoles' (Fig. 4 C, 4 H). The female flower is long-stalked and becomes exserted as its peduncle bends out through the opening of the involucre. It shows a reduced 3-lobed perianth, and a tricarpellary pistil with three bilobed stigmas (Fig. 4 B, 4 D).

Microtome sections at the base of the cyathium of *Monadenium* reveal two lateral cyathia as in *Synadenium* concealed inside common bract (Fig. 4 F, 4 H). The stele of the main peduncle first gives off traces to the foliaceous bract and the bract surrounding the abortive cyathia (Fig. 4 E). Then two steles depart for the lateral cyathia which are organised in a plan essentially similar to the main cyathium though all the flowers are abortive (Fig. 4 G). A little above the emergence of the steles for the lateral cyathia, five steles depart from the stele of the main axis for the five male glomerules and their subtending bracts. Three traces depart from each stele for the bracts after which it forms 4—6 traces for the male flowers (Fig. 4 F, 4 K). The bundles of the axial stele, after traversing the peduncle, give off three traces into the three lobes of the perianth and then vascularise the pistil as in *Acalypha indica* (Fig. 4 D). Thus, though the cyathium is externally zygomorphic, it is cup-like and radially symmetrical at base; this fact shows that it has evolved from an actinomorphic ancestral type. The nectary is fed by numerous strands formed by the radial division of the bundles of the outer involucre (Fig. 4 I).

Euphorbia L.

The cyathium in species of this large genus is typically regular with a uniseriate, cup-like involucre; minor variations are noticed in the number of flowers in each glomerule, presence or absence of 'bracteoles' and number of glands, and their size and shape. In *E. prostrata* only 4 or 3 glands are present; in *E. hirta* the glands are small and spherical; in *E. nivulia* they are large and cushion-shaped (Fig. 5 A, 5 H) and in *E. marginata* flat and cup-like. Some taxonomists place species which show petaloid (*E. marginata*) or horn-like (*E. dracunculoides*) appendages for the nectary in a separate genus *Agaloma* (Fig. 5 F). The number of male flowers ranges from numerous to one (12—8 in *E. nivulia;* 4—3 in *E. dracunculoides;* 2 in *E. thymifolia;* and one in *E. prostrata* and *E.*

Fig. 3. *Synadenium grantii.* — A: An entire cyathium, ×6. — B: L.s. cyathium, ×6. — C: A male flower and its bract, ×11. — D—G: T.s. cyathium at various heights, ×39. — H—K: T.s. gland at different levels, ×39. (*ii*=inner involucre; *oi*=outer involucre; *n*=nectary; *mf*=male flower; *ff*=female flower; *sac*=stele of abortive cyathium; *lst*=lateral stele of the male glomerule; *ac*=abortive cyathium; *tib*=traces of involucral bract; *nb*=nectary bundles; *brl*=bracteoles; *pf*=peduncle of female flower; *gc*= glandular cells).

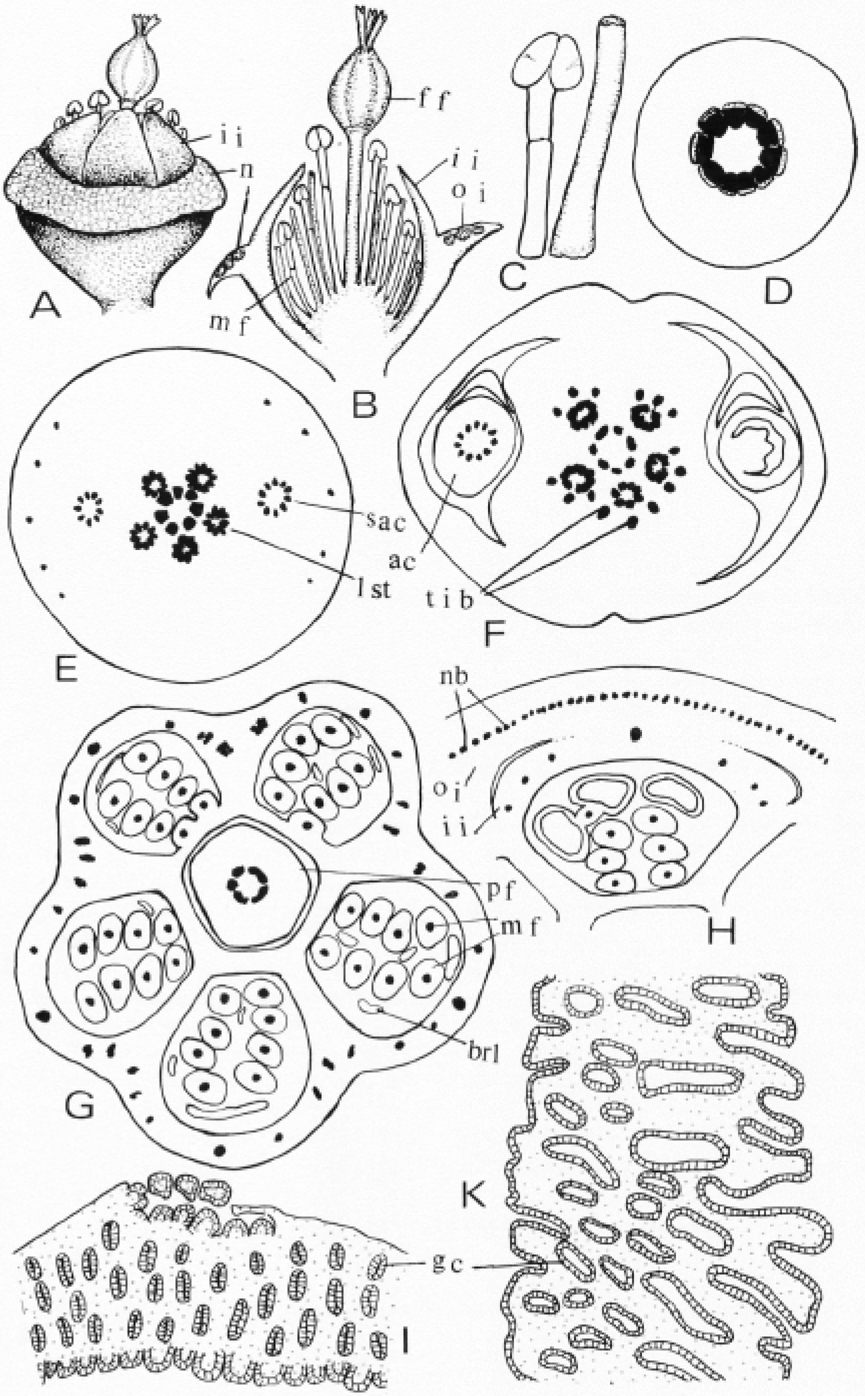


Fig. 3.

hirta); these may (*E. nivulia*) or may not be associated with bracteoles (Fig. 5 C, 5 H). The male flowers are monandrous and naked; the female flowers are mostly naked; in some (*E. marginata*) they show a vestigial, disc-like perianth. In *E. nivulia* the cyathia become male by abortion (Fig. 5 K).

Haber (1925) studied the anatomy of the cyathium in several species of *Euphorbia* and found that its vascular plan is remarkably uniform. So the anatomy of only a few species is studied here and the important features are highlighted.

E. nivulia is an arborescent, broad-leaved species; such species are supposed to be the most primitive and transitional between *Euphorbia* and other genera like *Synadenium* and *Monadenium*. Transverse sections at the base of the cyathium show two lateral abortive cyathia each covered by its own bract (Fig. 5 I). Similar cyathia but which are fertile are noticed in *E. rothiana* (Fig. 5 L). These lateral cyathia are fed by branch steles which depart from the stele of the peduncle. The origin and emergence of traces for the bract and male flowers of the glomerule in species of *Euphorbia* resemble those in *Monadenium* and *Synadenium*. After giving off the three bract traces the inner vascular tissue of each stele breaks up into as many bundles as there are male flowers in a glomerule. The 'bracteoles' present in *E. nivulia* are non-vascular. The bundles of the main stele extend to the base of the female flower; here they form three dorsal traces and three pairs of ventrals for the three carpels (Fig. 5 E). In *E. nivulia,* a few vestigial bundles are left after the emergence of the five lateral steles which fade out in the pistillode.

The vasculature of the nectaries varies with their size and shape. In *E. hirta* in which they are small and spherical, the bundles remain concentric and unbranched and fade out at the base of the gland (Fig. 5 D). In *E. dracunculoides* the laterals of adjacent bracts branch and form numerous strands which traverse the nectary; some strands situated at the extreme margins extend into the appendages of the gland (Fig. 5 G). Where the glands are cup-like (*E. marginata*) the nectary bundles form an open ring. The vascularisation of the nectaries in *E. nivulia* recalls that in *Synadenium*. The bract laterals give off strands to the outside which divide radially to form a ring of closely placed strands in the lower succulent region of the involucre while the bract midribs and some laterals enter the bracts. Higher up the ring-like region breaks up into five thick, cushion-like glands which stand alternate to the lobes of the involucre. The bundles which enter each gland branch further within the gland (Fig. 5 K, 5 M).

Poinsettia (Grah.) House

The anatomy of the cyathium of *P. pulcherrima* (Willd.) Grah., *P. heterophylla* (L.) Kl. & Gke., and *P. geniculata* (Ort.) Kl. & Gke. was studied. The cyathia in *Poinsettia* occur in pleiochasial or dichasial clusters the branches of which show a monochasial tendency. The involucre is uniseriate and symmetrical. It bears only one cup-like lateral nectary making the cyathium slightly zygomorphic (Fig. 6 A). In cyathia of *P. geniculata* situated at the centre of the pleiochasium 8—10 glands are noticed (Croizat 1942) while in similar cyathia of other species five glands are noticed on the involucre (Dressler 1961). This shows that the cyathium of *Poinsettia*

Fig. 4. *Monadenium.* — A: Entire inflorescence of *M. laeve,* ×3. — B—I: *M. schubei.* — B: Entire inflorescence, ×3. — C: A male flower and its bract; ×11. — D: T.s. female flower, ×39. — E—I: T.s. cyathium at various heights; — G ×39; rest ×22. — K: T.s. cyathium of *M. leave,* ×25. (*bc*=bract of the cyathium; *g*=gland; *bt*=bract traces; *ff*=female flower; *p*=perianth; *ac*=abortive cyathium; *tib*=traces of involucral bract; *smg*=stele of male glomerule; *nb*=nectary bundles; *oi*=outer involucre; *ii*=inner involucre; *brl*=bracteoles).

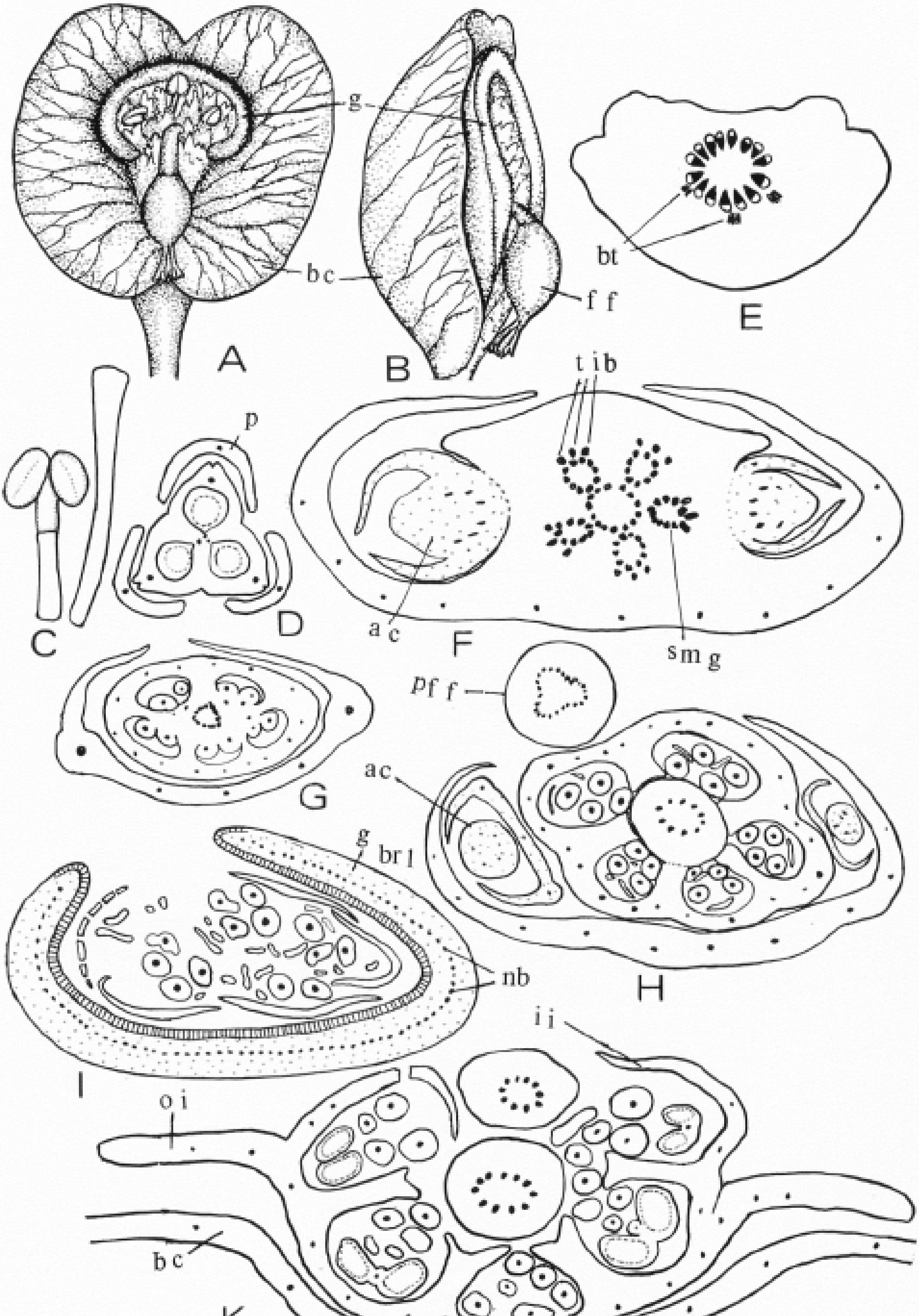


Fig. 4.

is derived by reduction from an ancestral, actinomorphic 5-glanded (*Euphorbia*-like) cyathium. This conclusion is also borne out by the present studies in *P. pulcherrima* in which four vestigial, non-vascular glands are noticed in addition to the functional one (Fig. 6 F, 6 G).

The vasculature of the organs of the cyathium of *Poinsettia* resembles that of *Euphorbia* closely (Fig. 6 B, 6 C). The number of male flowers in a glomerule ranges from 17—15 in *P. pulcherrima* to 6—4 in *P. heterophylla* and *P. geniculata* (Fig. 6 C, 6 D). Bracteoles are found in association with male flowers in *P. pulcherrima*. While the bract laterals on other sides remain unbranched, those on the side of the functional nectary first form two V-shaped arcs of bundles by their division. These run together and form a compressed ring of closely placed bundles. These give off some strands towards the centre. While the bundles of the ring traverse the thick succulent wall of the nectary, those at the centre extend to the floor of the gland or slightly to the inner margin of the cup (Fig. 6 E, 6 G).

Pedilanthus tithymaloides (L.) Poit.

The morphology of the cyathium of *Pedilanthus* is very difficult to interpret. Though Ridola (1903), Michaelis (1924) and Troll (1928) described the development and structure of the cyathium, it remained incompletely understood till the publication of Dressler's (1957) monograph which is illustrated by drawings and photographs of cleared preparations. The arguments and figures presented by Dressler (1961 p. 80) for deriving the strongly zygomorphic cyathium of *Pedilanthus* from the actinomorphic cyathium of *Euphorbia* are quite convincing.

The cyathia of *Pedilanthus* occur in terminal and axillary dichasial or monochasial clusters. Each main cyathium is subtended by two "cyme bracts", in the axils of which potentially fertile cyathia are found. The involucre in *Pedilanthus* is uniseriate. It is rounded and cup-like at base as in *Monadenium* where it is formed by the fusion of five bracts of equal width. Higher up the bracts become dissimilar due to unequal growth and consequently mature cyathia become oblique (Fig. 7 A, 7 B). The most important characteristic of the cyathium is the development of a spur ("appendix" of older terminology). This is a compound structure which involves all the bracts though not in equal degree. In the full grown cyathium, two bracts are anterior, two lateral and one median and posterior, overlying a fissure. The posterior bract is massive and two-lobed and forms a chamber inside which four free glands are enclosed (Fig. 7 B, 7 I). Since the spur above the region of attachment of the glands is formed always by four lobes, Dressler (1957) homologises the spur lobes to the appendages of the glands similar to those found in *Agaloma*. The male flowers of *Pedilanthus* are naked and monandrous and female flower long-stalked, naked and provided with a pistil of three uniovulate carpels, a simple stout style which is slightly 3-lobed at the apex. Abnormal cyathia in which each gland is replaced by a pair of structures are reported.

Fig. 5. *Euphorbia*. — A—E: *E. hirta*. — A: Inflorescence opened on one side, ×11; — B, C, E: T.s. cyathium at different heights, ×39. — D: T.s. base of gland, ×50. — F, G: *E. dracunculoides*. — F: Entire cyathium, ×17. — G: L.s. cyathium, ×22. — H—L: *E. nivulia*. — H: Entire cyathium, ×3. — I: T.s. base of cyathium showing abortive lateral cyathia, ×22. — K: L.s. part of cyathium, note pistillode, ×22. — L: T.s. base of cyathium of *E. rothiana* showing fertile lateral cyathia, ×28. — M: T.s. part of cyathium of *E. nivulia* at the level of glands, ×22. (*ff* = female flower; *mf* = male flower; *g* = gland; *br* = bract; *bt* = bract traces; *nb* = nectary bundles; *ag* = appendaged gland; *p* = pistillode; *ac* = abortive cyathium; *smg* = stele of male glomerule; *brl* = bracteole; *lc* = lateral cyathium; *pmc* = peduncle of main cyathium).

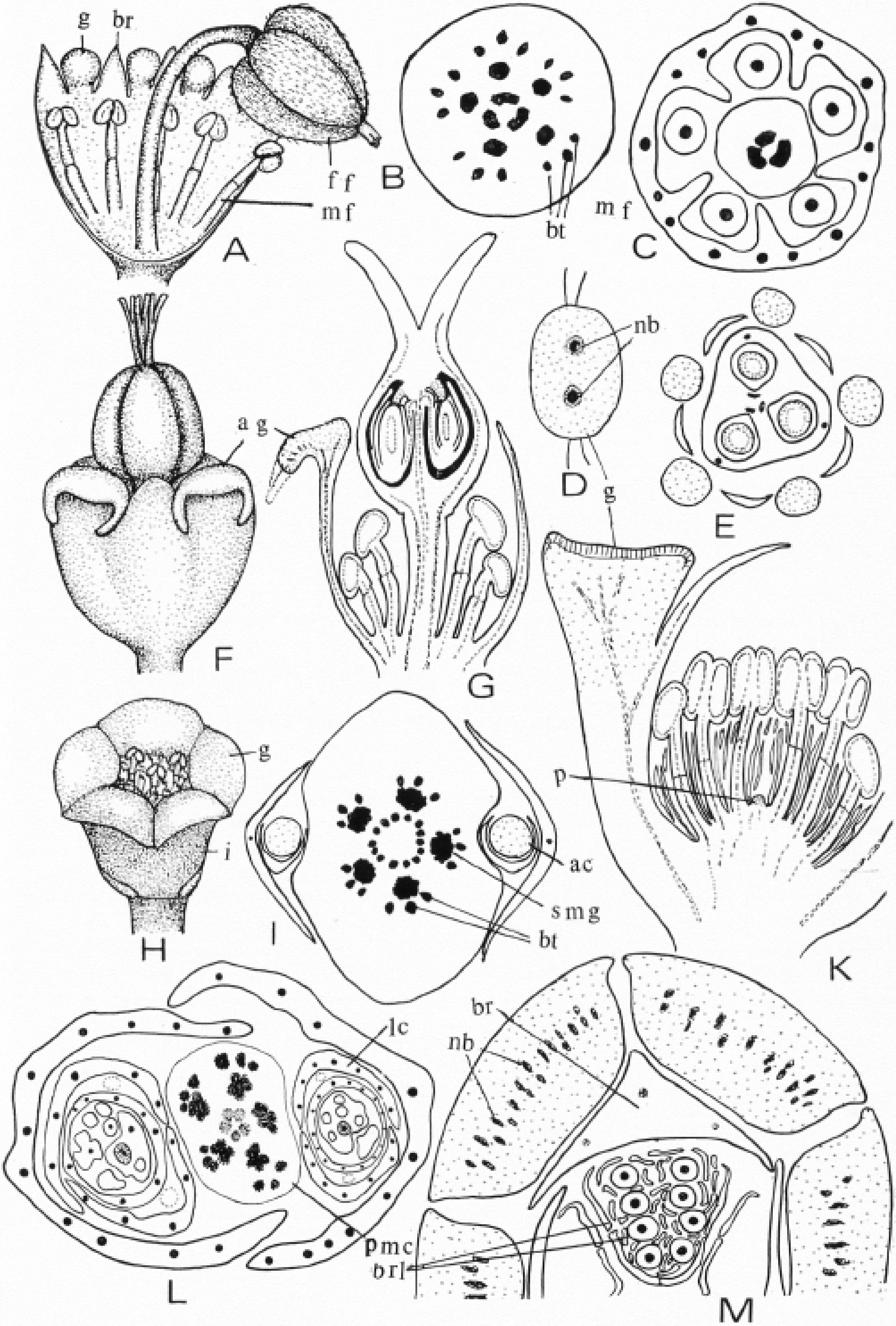

g
br
ff
mf
A
B
bt
mf
C
nb
D
E
ag
g
F
G
g
i
H
p
ac
smg
bt
I
K
br
nb
lc
pmc
brl
L
M

Fig. 5.

The origin and emergence of traces for the bracts and male flowers in *Pedilanthus* are similar to those of *Euphorbia* (Fig. 7 D). The traces for each bract traverse as its midrib and marginals. The midrib gives off a few branches but these do not enter the glands. Each gland is a double structure as in *Euphorbia* and is fed by marginals of adjacent bracts. The lateral pair of glands are supplied by the upper marginals of the anterior pair of bracts and the lower marginals of the lateral pair; the median pair are vascularised by the upper marginals of the lateral pair and the marginals of the posterior bract (Fig. 7 H, 7 I). This shows that the gland on the anterior side is suppressed. The bract bundles continue their course in the lobes of the spur. The vasculature of the female flower resembles that of *Euphorbia*.

DRESSLER (1957) remarks that the zygomorphy of the cyathium of *Pedilanthus* is evident also in the variation in the number of male flowers in the different glomerules of the same inflorescence. In the present studies it was noticed that in one cyathium, four glomerules showed 4—5 male flowers while one had only one flower (Fig. 7 C). It was also noticed that there is a tendency towards suppression of one or two male glomerules, so that in cyathia with five involucral bracts, four or three male glomerules were noticed. This disturbs the numerical and structural relation between the bracts and male glomerules and accentuates the zygomorphy. In such cases, the sterile bracts received their vascular supply from adjacent lateral steles (Fig. 7 E—G).

The vasculature of the female flower resembles that of *Acalypha indica* (Fig. 7 K).

DISCUSSION

Two different views have been expressed regarding the phylogeny and evolution of the inflorescence in angiosperms: (*1*) that the solitary axillary flower is the simplest ancestral type and that the elaborate and complex forms are derived from it by aggregation and condensation (PARKIN 1914); and (2) that the complex types like the panicle (ČELAKOVSKY 1892; NÄGELI 1884; PILGER 1922) or the dichasium (WOODSON 1935; RICKETT 1944) represent the most primitive types and that the simpler as well as condensed forms are derived by reduction. However, as VENKATA RAO (1965) has pointed out, evolution of the inflorescence may not have progressed in the same set patterns in all families and may have occurred differently and sometimes along more than one line in different families. The trends of evolution in any particular group can be visualised only by intensive comparative studies of the inflorescence in the existing members.

For an understanding of the phylogeny of the inflorescence in any family two things are essential: (*a*) reconstruction of the ancestral type of inflorescence and (*b*) formulation of the evolutionary trends in it. Though the inflorescence in Euphorbiaceae shows such a range of variation as is noticed in few other angiospermous families, reconstruction of the ancestral inflorescence is not a difficult task because, as in the case of evolution of the flower (VENKATA RAO & RAMALAKSHMI 1968), in the inflorescence also, reduction seems to be the keynote of evolution. One interesting feature noticed in Euphorbiaceae is that reduction in the inflorescence has progressed synchronously in vegetative and reproductive parts of the different taxa.

A comparison at this stage of the course of evolution in Euphorbiaceae with that in the other two families which show cactoid habit (Asclepiadaceae and Cactaceae) is bound to be interesting. In Asclepiadaceae reduction is evident from the leafy to the leafless condition (Stapelieae) and from the paniculate and dichasial inflorescences to the solitary axillary flower. But the flower itself has remained remarkably constant in structure and has suffered little reduction. On the other hand, it has even undergone bizarre enlargement as in some Stapelias. In Cactaceae, reduction is noticed from leafy, elaborate vege-

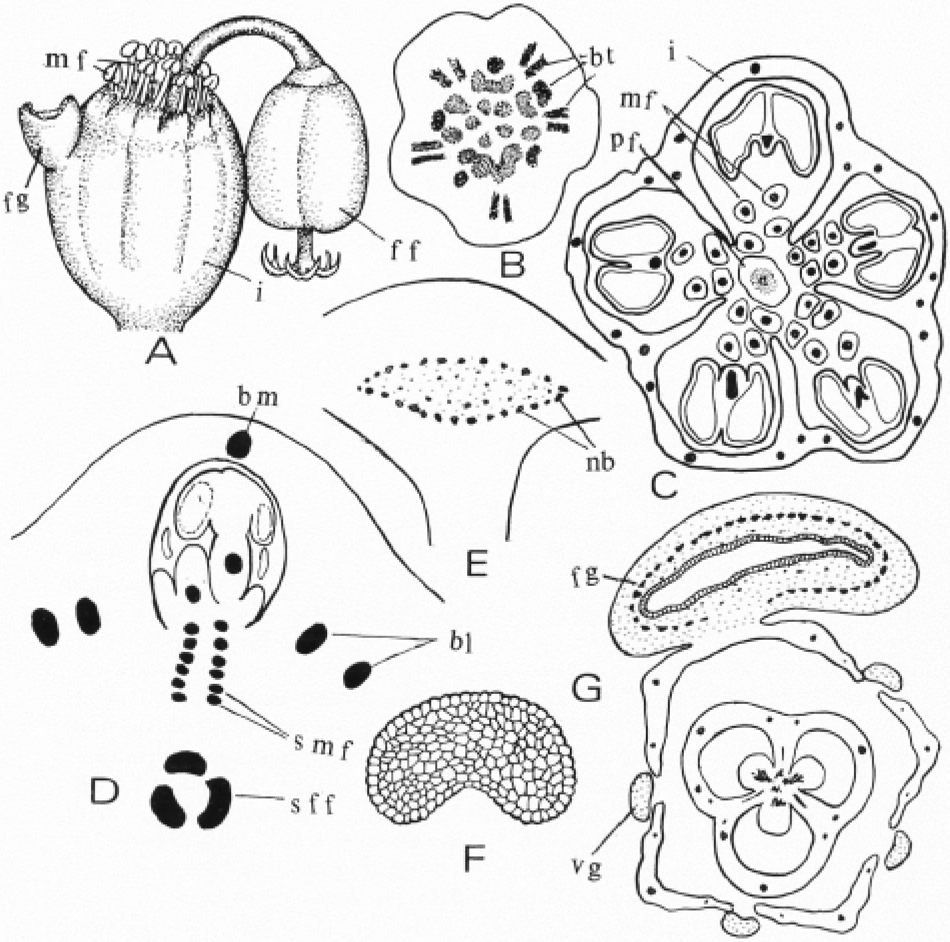


Fig. 6. *Poinsettia*. — A: Entire cyathium of *P. pulcherrima*, ×3). — B—C: T.s. cyathium of *P. geniculata*, ×34. — D—G: *P. pulcherrima*. — D: T.s. part of cyathium showing bract midrib, bract marginals and steles of male and female flowers, ×22. — E: T.s. part of involucre in the region of the functional nectary showing branching of the bract laterals, ×22. — F: T.s. vestigial nectary, ×45. — G: T.s. cyathium at the level of the nectary, ×10. (*mf*=male flowers; *fg*=functional glands; *ff*=female flower; *i*=involucre; *bt*=bract traces; *pf*=peduncle of female flower; *nb*=nectary bundles; *bl*=bract laterals; *bm*=bract midrib; *sff*=stele of female flower; *smf*=steles of male flowers; *vg*=vestigial gland).

tative body and paniculate inflorescences (Pereskioideae) to leafless stunted form and solitary axillary flowers (Opuntioideae and Cereoideae) but the flower remained complex and elaborate in structure. In Euphorbiaceae on the other hand, reduction in size of the plant body, leaf, inflorescence and flower have progressed synchronously and consistently in the various taxa. All stages of reduction are noticed from forms showing arborescent habit, large compound leaves, elaborate inflorescences and complex flowers to those showing herbaceous and cactoid habit, reduced inflorescences and extremely reduced flowers. So by correlating the various features, the ancestral type of inflorescence can be easily reconstructed.

For the sake of convenience, evolution of the inflorescence in Euphorbiaceae is described under three heads: (*a*) evolution of the simple types; (*b*) evolution of the condensed types; and (*c*) evolution of the reduced types (cyathia).

a. Evolution of the Simple Types of Inflorescence

The inflorescence of *Jatropha curcas* (Jatropheae) is a large terminal dichasium. Dichasia of male flowers also occur in *Hyaenanche globosa* of the tribe Hymenocardieae (HUTCHINSON 1969). In *J. curcas*, a hermaphrodite flower occurs at the lower dichotomies while higher up the flowers become male by abortion and show pistillodes. The hermaphrodite flowers are dichlamydeous, heterochlamydeous, pentacyclic (obdiplostemonous) and pentamerous in all floral whorls except the gynoecium; they also show alternipetalous glands. These are the most elaborate flowers in the living Euphorbiaceae. Since these flowers are found in association with arborescent habit, and large palmately compound or lobed leaf, the Jatropheae seem to deserve the first place in the phylogenetic sequence of the tribes though HUTCHINSON (1969) gives it the 18th rank. However, the dichasium of *J. curcas* cannot be taken as the ancestral type for the family because reduction has already occurred in floral structure (and in the number of ovules to one per carpel). It can, however, be taken as the nearest approach to the ancestral type found among the living taxa.

By combining the floral structure of *Wielandia* (which has pentacarpellary pistil) and *Jatropha*, VENKATA RAO and RAMALAKSHMI (1968) have shown that the ancestral flower of Euphorbiaceae was hermaphrodite and pentamerous in all floral whorls [$K_5C_5A_{5+5}G_{(5)}$]. The presence of glands and the typically obdiplostemonous condition of the androecium in these flowers show that the ancestral Euphorbiaceae are nearer to the Geraniales rather than to Tiliales as HUTCHINSON (1969) thinks. By combining the most primitive flower with the most primitive inflorescence we can now visualise the ancestral inflorescence of Euphorbiaceae as a dichasium in which all flowers were hermaphrodite, pentacyclic and pentamerous in all the floral whorls. From such a type, all kinds of inflorescence including the peculiar pseudoraceme of *Acalypha indica* type with a truly terminal female flower can be derived mainly by reduction. During the course of evolution, reduction occurred in the length of the main and lateral axes of the inflorescence, in the number of flowers borne on them and in the pedicels of flowers; a shift also occurred from the terminal to the axillary position of the inflorescence.

The panicle seems to be the nearest approach to the dichasium and derived from it by less regular and more diffuse branching. Terminal and axillary panicles are noticed in several taxa, viz. *Ricinus communis, Chrozophora rottleri, Upaca huedelotii, Drypetes afzelli, Hevea braziliensis, Mallotus philippinensis* etc. Often

---

Fig. 7. *Pedilanthus tithymaloides*. — A: Entire cyathium, ×3. — B: L.s. cyathium, ×3. — C—G: Transverse sections of cyathia at the base (cut in plane A—A) showing origin of bract traces and steles of male flowers, ×22. — C: Cyathium with five male glomerules of which one bears only one male flower. — D—E: Cyathium with four male glomerules. — F—G: Cyathium with three male glomerules. — H: Vertical section towards base of appendix (cut at level B—B), ×22. — I: Vertical section cut higher up, ×22. — K: T.s. female flower, ×22. (*pb* = posterior bract; *lb* = lateral bract; *ab* = anterior bract; *g* = gland; *mf* = male flower; *ff* = female flower; *bt* = bract traces; *nb* = nectary bundles; *smg* = stele of male glomerule; *sf* = stele of female flower; *dcb* = dorsal carpellary bundle; *ml* = median lateral; *vcb* = ventral carpellary bundle).

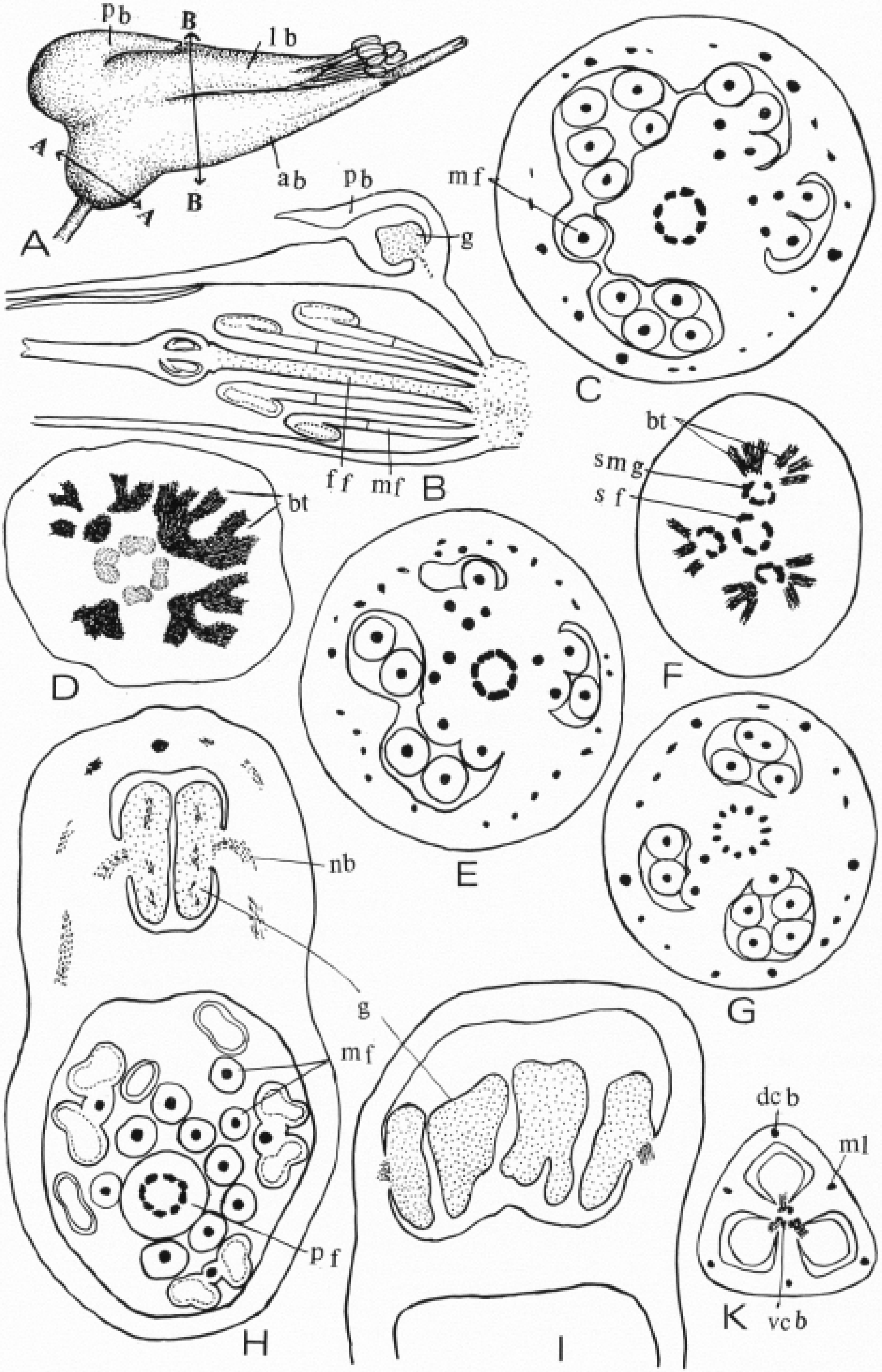

pb
B
lb
A
A
ab
B
A
pb
g
mf
ff
mf
B
C
bt
smg
sf
D
bt
E
F
G
nb
g
mf
pf
H
I
dcb
ml
vcb
K

Fig. 7.

these plants are arborescent and show compound or lobed leaves. The flowers have become monochlamydeous and unisexual but in some taxa the male flowers show numerous stamens (*Ricinus*).

In the pseudoraceme of *Acalypha indica* type, the hermaphrodite flower which occurs at the first dichotomy of the ancestral dichasium seems to have persisted and formed the long-stalked terminal female flower. Reduction in the lateral axes resulted in the formation of clusters of unisexual flowers lower down. The pseudoraceme of *Croton* type (in which a few female flowers occur at base and some male glomerules above), can be derived from *Acalypha indica* type by elimination of the terminal female flower. In all other types of inflorescence also except the cyathium, the terminal female flower is suppressed.

The uniaxial racemes and amentoid spikes noticed in *Excoecaria agallocha, Hymenocordia acida,* and species of *Acalypha* (e.g., *A. wilkersiana*) and *Codiaeum* seem to be derived from the panicle by suppression of the lateral branches. In some taxa the flowers occur either in sessile clusters (*Excoecaria*) or cymules (some Codiaeae) showing clearly that they are derived from paniculate inflorescences. Since the main axis of the inflorescence has not suffered much reduction in the above types, the inflorescences remain amentoid.

When reduction occurs of the main axis of the inflorescence (with reduction in pedicels) the inflorescences become short spikes or strobilate clusters or globose heads as are noticed in *Hasskarlia didymostemon* and some members of Hippomanieae. Complete reduction of the main axis, not accompanied by a reduction in pedicels, would result in dense axillary fascicles as are noticed in *Erismanthus sinensis* of Codiaeae and some members of Mercurialideae. Progressive reduction in the number of flowers in a cluster leads to the few-flowered fascicles (*Phyllanthus niruri, Agyneia bacciformis*) and ultimately to the solitary axillary flower (*Phyllanthus emblica, Breynia rhamnoides*) which marks the culmination of reduction in this line. The last two types are found in association with herbaceous habit, small simple leaves, short (dwarf) branches of limited growth and small, unisexual monochlamydeous, few-stamened flowers.

The writer's views regarding the evolution of the simple types of inflorescence are shown in Fig. 8 A—N.

One feature noticed in this line of evolution is the absence of an organ (involucre) which integrates the flowers of an inflorescence even when they are clustered. The development of an involucre is characteristic of the other two lines of evolution.

b. Evolution of the Condensed Types of Inflorescence

An important feature noticed in the evolution of the inflorescence in several angiospermous families (Umbelliferae, Rubiaceae, Compositae, Proteaceae etc.) is the tendency towards reduction in the flower-bearing region of the peduncle and the consequent aggregation of the flowers into flower-like clusters or pseudanthia. This is accompained by the aggregation

Fig. 8. Diagrammatic representation of the evolution of inflorescence in Euphorbiaceae (other than cyathium). — A: Hypothetical ancestral dichasium with all hermaphrodite flowers. — B: Dichasium of *Jatropha curcas* with hermaphrodite flowers at basal dichotomies and male flowers higher up. — C: Floral diagram of a hermaphrodite flower. — D: Panicle. — E: Pseudoraceme of *Acalypha indica*. — F: Pseudoraceme of *Croton* type. — G: Racemes of *Codiaeum* sp. — H: Catkin of *Acalypha* sp. — I: Globose head of Hippomanieae. — J: Dense axillary fascicle of *Erismanthus* sp. — K: Two-flowered axillary fascicle of *Phyllanthus niruri*. — L: Solitary axillary flower of *Breynia rhamnoides*. — M, N: Floral diagrams of female and male flowers of *Breynia*. — O: L.s. inflorescence of *Dalechampia roezliana* (*ff*=female flower; *bb*=basal bracts; *in*=internode; *gsb*=gland-tipped sterile bract; *mf*=male flower).

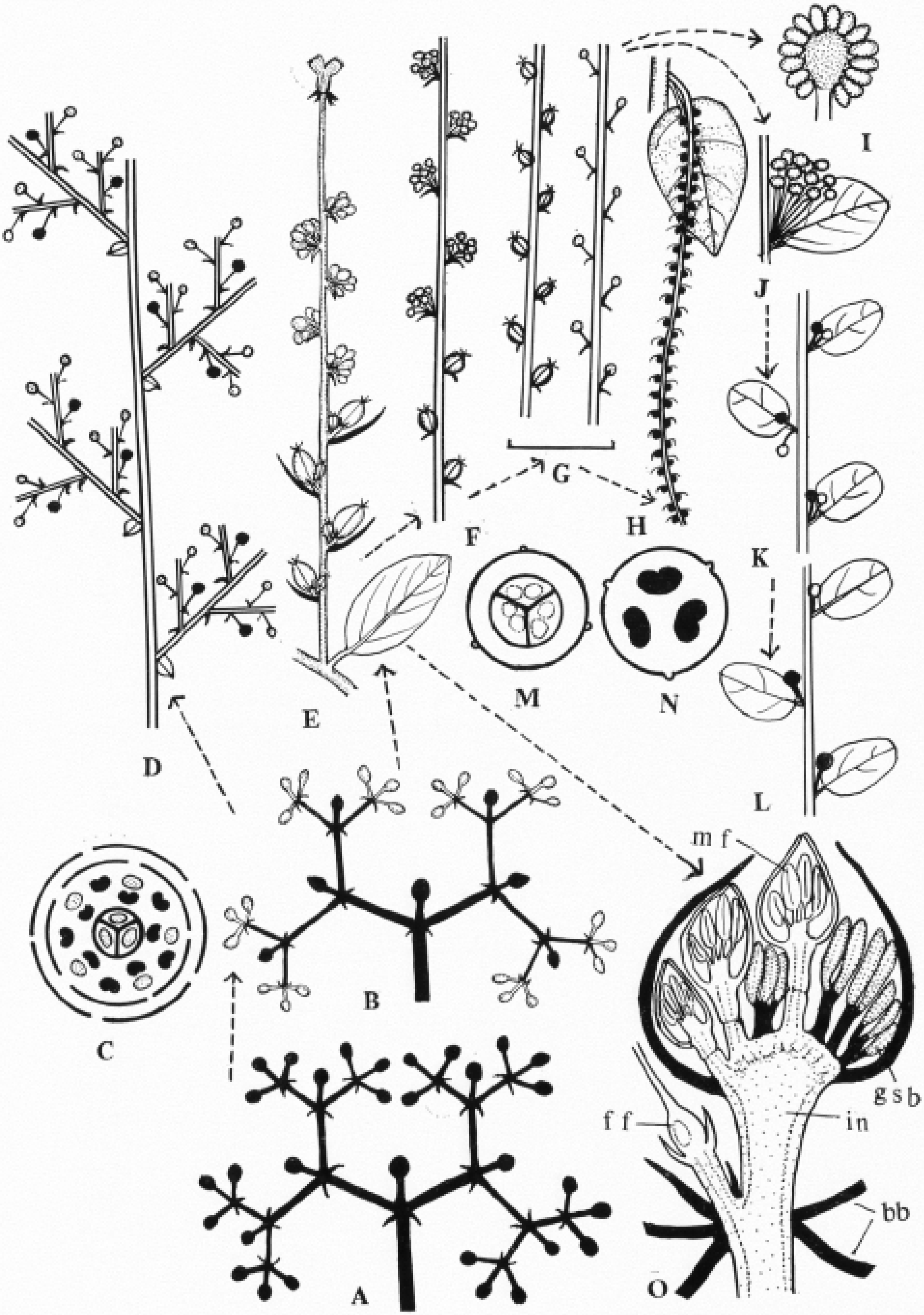


Fig. 8.

of the bracts of the circumference flowers into one or more series forming the involucre. As GOOD (1956) remarks, the involucre is the most important single ingredient which integrates all the component flowers of an inflorescence. Once the pseudanthium is established, it shows evolutionary trends which are similar to those noticed in the evolution of the flower, viz. connation, adnation, reduction and amplification of organs as well as their traces, and progress towards zygomorphy and unisexuality. These trends are noticed in the evolution of both condensed as well as reduced types of inflorescence of Euphorbiaceae. These two types, however, cannot be derived from each other; both of them seem to be derived from a common ancestral (*Acalypha indica*) type of inflorescence.

The inflorescence of *Dalechampia* has been described by several botanists as "remarkable" in Euphorbiaceae on account of its conspicuousness and aggregation of the flowers. In *D. roezliana* it is a condensed panicle. It shows close resemblance to the inflorescence of *Acalypha indica* in the perianthed male and female flowers, in polyandrous condition of the male flowers and even in the presence of a joint in their pedicels. The inflorescence of *D. roezliana* seems to be derived from that of *A. indica* by: elimination of the terminal female flower, retention of four male glomerules, several foliaceous bracts of which only one is fertile and bears a cyme of female flowers, and by some condensation of the main axis. Some of the structural features show that the inflorescence is at a low level of organisation. Though the bracts form an incipient involucre they show decussate arrangement and not the whorled condition characteristic of the typical involucres. The presence of an internode between female and male flowers, the attachment of the male glomerules at different levels on the axis, the pedicellate nature of the male and female flowers, the retention of some empty bracts and the convex nature of the receptacle are primitive features which show that it is a far cry from the inflorescence of *Dalechampia* to the cyathium. There is nothing in the inflorescence of *Dalechampia* to justify the statement of CROIZAT (1940) that it marks the "culmination of the structural possibilities of the cyathium". The lateral position of the female flowers in the inflorescence of *Dalechampia* shows that the cyathium cannot be derived from it.

The inflorescence of *Anthostema senegalensis* was available only for morphological studies. It shows an involucre of four bracts each of which bears a flat, rhomboidal gland. Inside this involucre are found four involucels of male flowers "spread out in a semi-circle in front of a solitary female flower" (THISELTON-DYER 1909). Each male involucel contains an outer series of four larger bracts and one or two inner series of smaller bracts which surround 8—12 male flowers. The male flower is monandrous and shows a cup-like, 4—5-lobed perianth at the joint of its stalk (Fig. 9 A—C). The female flower is perianthed and shows a pistil of three uniovulate carpels and a simple, stout style which is slightly 3-lobed at the apex as in *Dalechampia*.

It is difficult to say decisively without anatomical studies whether or not the female flower of *Anthostema* is central (terminal). From morphological studies, it seems to be lateral. The inflorescence seems to be derived from *Dalechampia* type by further reduction. The involucral bracts have become whorled and the male glomerules and female flower are brought nearly to the same level. Only one female flower out of the cyme seen in *Dalechampia* seems to persist. The presence of several series of bracts around the male clusters and the cup-like perianth in the male flowers show that reduction has not advanced far when compared to the typical cyathium.

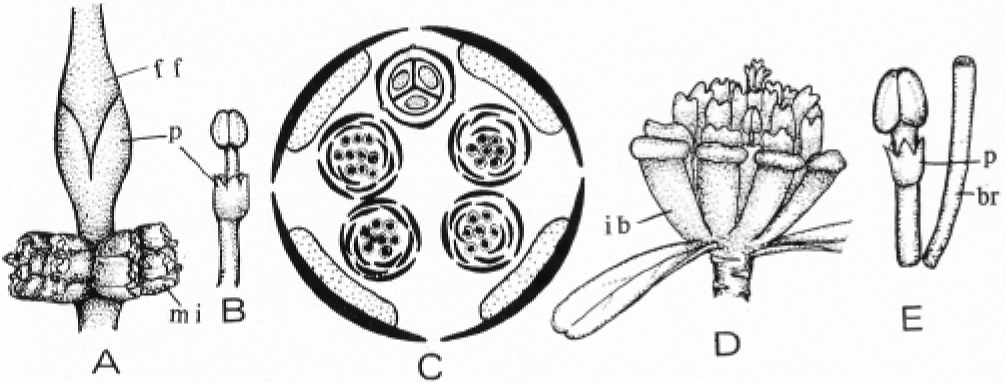


Fig. 9. *Anthostema senegalensis*. — A: An inflorescence (without involucral bracts), ×3. — B: A male flower, ×11. — C: Plan of the inflorescence. — D: inflorescence of *Diplocyathium* sp., ×3. — E: A male flower of *Dichostemma* sp., ×11. (*p*=perianth; *ff*=female flower; *mi*=male involucel; *ib*=involucral bract; *br*=bract).

c. Evolution of the Reduced Types of Inflorescence (Cyathia)

The earlier taxonomists regarded the cyathium as a hermaphrodite flower. Later, as suggested first by LAMARCK (1788) (quoted from DRESSLER 1957), it is now accepted by all botanists as a condensed involucrate cluster of unisexual flowers in an advanced stage of reduction (for literature cf. SCHMIDT 1907; HABER 1925; SCHOUTE 1937; CROIZAT 1936, 1937). The term cyathium is used here for an inflorescence which is actinomorphic (at least in the basal region) and in which the central female flower is surrounded symmetrically by 4—5 clusters of male flowers, all of which are subtended by an involucre of one or more series of bracts which bear glands. So, there are five ingredients in the cyathium, viz. (*1*) the inflorescence axis, (*2*) the female flower, (*3*) the male glomerules and associated bracts, (*4*) the involucre and (*5*) the glands.

As already pointed out, the first task towards the understanding of the phylogeny of the cyathium is the reconstruction of the ancestral inflorescence. This can be done by synthesising the primitive features noticed in the organs of the cyathia of the living genera.

The uniformity in the organisation of the cyathium as a whole as well as in the structural features of its organs, especially male and female flowers, and even in the less important features like the presence of two lateral (functional or abortive) cyathia associated with the main cyathium, show that the cyathium is monophyletic as some previous investigators also believed.

The cyathium is now accepted as a vertically shortened inflorescence axis; so the ancestral inflorescence must have been amentoid. Since the organs of the cyathium surround the female flower symmetrically, the ancestral inflorescence must have been radially symmetrical.

The female flower is always central even when the cyathium is externally zygomorphic as in *Monadenium*, *Stenadenium*, *Pedilanthus* and *Cubanthus*. Its stalk is merely the continuation of the main peduncle (so the term gynophore should not be applied to it). So there must have been a female flower (which itself seems to be sessile) terminating the main axis of the ancestral inflorescence. The fact that the emergence of the pistil outside the involucre is conductive first to pollination and then to seed dispersal seems to have led to the retention of the long stalk in nearly all genera of Euphorbieae. (*Elaeophorbia* is the only genus in which the female flower is sessile; this genus has drupaceous fruit). In *Synadenium, Monadenium, Dichostemma* and *Cubanthus* the female flower shows a 3—4 lobed perianth, while in other genera this is either vestigial or completely absent. So in the ancestral condition, the female flower seems to have been perianthed. The protection afforded by the involucre seems to have led to the complete reduction of the perianth (cf. reduction of the calyx in flowers of Compositae).

The male flowers are monandrous in most genera, the only evidence that they are flowers and not stamens being provided by a joint in the stalk. The part below the joint is considered to be homologous to the pedicel and that above to the filament. Evidence for this is given by a cup-like membraneous perianth at the joint in the male flowers of *Dichostemma* (Fig. 9 E). In *Calycopeplus* which shows the most primitive male flowers among Euphorbieae, two stamens are found within the cup-like perianth (Croizat 1940). So it is evident that in the ancestral condition the male flowers were pedicellate, perianthed and provided with two or more stamens. Numerous male flowers are found in the glomerules of some taxa like *Poinsettia pulcherrima* and *Euphorbia nivulia* which shows that there were numerous male flowers in the glomerules of the ancestral inflorescence. The presence of membraneous bract which subtends a glomerule and 'bracteoles' which are interspersed among the male flowers shows that in the ancestral condition there were individual and common bracts for the male flowers. Due to the protection given by the involucre, the bracts as well as the perianth of the male flowers became completely reduced. Though the male glomerules are commonly whorled, in some taxa (like *Poinsettia pulcherrima)* they are placed in a spiral manner which fact has been commented upon by several investigators. Croizat (1938) dismisses this fact lightly remarking "it is wholly irrevalent in my judgment whether or not the male flowers in *Euphorbia* show a spiral ratio amenable to fractional expression because the cyathium is a shortened floral axis and not a foliate branchlet". However, in view of the fact that a whorl is a condensed spiral, this evidence is very significant in showing that the male glomerules in the ancestral inflorescence were disposed in a 2/5 spiral on the elongated axis below the female flower. Anatomical studies have shown that the male flowers in each cluster are arranged in a dichasial cyme the branches of which show a monochasial tendency. This arrangement seems to be reminiscent of the ancestral dichasium of the family.

While the structure of the female and male flowers of the cyathium in the different Euphorbieae is relatively uniform, considerable variation is noticed in the number and arrangement of the bracts in the involucre. This not only shows that the involucre has evolved at different rates in the different genera but that its evolution progressed independent of that of other organs of the cyathium. So the involucre should provide important clues to the phylogeny of the cyathium, the relative evolutionary status and the inter-relationships among the different cyathium bearing genera.

Since the involucral bracts subtend the male glomerules and since the vascular supply of both the organs is common, it is generally supposed that the involucral bracts belong to the male clusters. But factual evidence disproves such a conclusion: *Firstly* one of the "bracteoles" of the male flowers usually subtends the whole glomerule and appears to be the common bract; this shows that the involucral bracts do not belong to the male glomerules; *secondly* in size as well as texture, the fleshy, foliaceous, persistent, vascularised involucral bracts appear quite different from the scaly, membraneous, non-vascular bracteoles; *thirdly* the involucre in some genera is multiseriate or biseriate; even if the bracts of the innermost series are taken as the bracts of the male flowers, the homology of the supernumerary bracts of the outer series still requires explanation. These facts point to the existence of several accessory, free, foliaceous bracts below the region of male glomerules in the ancestral inflorescence, which were also disposed in a 2/5 spiral like the male glomerules themselves. Probably these bracts were fertile in the ancestral condition and therefore fleshy and persistent, and became sterile with specialisation into the involucre. Condensation of several cycles of the spiral in which the bracts were disposed would give rise to multiseriate involucre of several superposed, free bracts as are noticed in *Diplocyathium* (Fig. 9 D). This genus therefore seems to represent the most primitive involucre among the living Euphorbieae. (Even if it is a bad genus and does not deserve a generic status, its involucre can be taken as atavistic representing the ancestral condition). With progressive reduction and condensation, the original spiral would give place to the whorled condition and the involucre would become bi- and uniseriate. When these processes occur synchronously in the male glomerules and involucral bracts, the glomerules would become axillary to the bracts as both are disposed in a continuous spiral. Since it is usual for the vascular traces of closely superposed organs to become fused, the vascular supply of the male glomerules and the involucral bracts would become adnate.

A perusal of the literature on the morphology of the nectary in angiosperms shows that there is a tendency on the part of botanists to read more meaning into it than is actually present. This has led to some confusion in the interpretation of floral morphology especially in Monochlamydeae in which the nectaries are interpreted as modified sepals, petals, stipules, stamens, carpels and organs *sui generis*. The same tendency is noticed in the interpretation of the glands of the involucre. Some botanists regard them as foliar enations while others consider them ramular. Glands occur on various plant parts in Euphorbiaceae, as pairs of extra-floral nectaries on the top or base of the petiole; on margins of fertile bracts (*Acalypha indica*), on sterile bracts (*Dalechampia*), on the thalamus (*Jatropha*) and on tepals (*Dalechampia*). It is quite unlikely that structures which show such diverse positions could represent modifications of any plant parts; they seem to be only enations of the respective organs. However, ignoring the evidence of comparative morphology, HABER (1925) interprets each gland on the involucre of *Euphorbia* as a pair of sterile male clusters which have fused with the bract tissue. This explanation has been accepted by CROIZAT (1942) and EAMES (1961). HABER's interpretation is based on the fact that each gland is fed by two lateral bundles of adjacent bracts and these bundles sometimes (*Poinsettia pulcherrima*) divide radially and form a stele-like ring of bundles. However, the vasculature of the gland shows much variation in different genera according to its size and shape and therefore by itself cannot offer any explanation as to its homology. The stele like division of the nectary bundle also does not indicate its ramular nature; a similar division is noticed in the midrib bundle of the lower bracts of *Dalechampia* (cf. Fig. 2 E). The present studies have shown that the bracts in all genera studied are 3-bundled and that the bundles feeding each gland are only the laterals of adjacent bracts. So the glands of the involucre seem to be foliar enations as DRESSLER (1957) also believes.

In this connection, the occurrence of pairs of extra-floral nectaries at the top of the petiole in several tribes of Euphorbiaceae (Chrozophoreae, Gelonieae, Macarangeae, Hureae, Ricineae, Crotoneae and Hippomanieae of HUTCHINSON) appears to be particularly significant. The foliaceous bracts which subtend the female flowers must be regarded as modified vegetative leaves. With reduction in the petiole of such bracts, it can be supposed that the glands assumed a marginal position on the lamina. These glands were probably non-vascular in the ancestral condition and later became vascularised with specialisation, as is noticed in Proteaceae (VENKATA RAO 1967). So in the ancestral inflorescence each involucral bract must have borne two marginal glands. Increasing connation between the bracts after they become whorled must have led to the fusion of the glands belonging to the adjacent bracts in pairs. This conclusion is supported by the anatomical evidence (presented above) and also by teratological evidence. In some abnormal cyathia of *Euphorbia, Poinsettia* and *Pedilanthus*, each gland was replaced by a pair of organs so that the involucre showed 8—10 glands instead of the usual four or five. *Neoguillauminia* seems to show the most primitive type of nectary in Euphorbieae. Five pairs of glands are noticed in the cyathium. These, however, do not occur on the rim of the involucre but as pairs of structures which radiate from the central female flower. It can be supposed that the involucral bracts in *Neoguillauminia* are 3-lobed and that the lateral lobes which bear the glands are involute, a condition commonly noticed in several other genera.

Now, by combining the primitive structural features of the different organs of the cyathia enumerated above, the characteristics of the inflorescence ancestral to the cyathium can be given as follows: It is an amentoid structure with a long-stalked, terminal, perianthed female flower, several glomerules of male flowers below disposed in 2/5 spiral on the axis, each containing numerous bracteate, pedicellate, perianthed male flowers with two or more stamens, and several cycles of foliaceous bracts below the region of male clusters, which are also disposed in 2/5 spiral, each bract bearing a pair of glands on its margin. It is interesting to notice that all the above listed features (except some details of structure of the terminal female flower) are found in the inflorescence of *Acalypha indica*. However, this itself cannot be taken as the ancestral inflorescence because (*a*) the terminal female flower has suffered some reduction and does not conform to the type commonly noticed in cyathia and (*b*) the lower foliaceous bracts are fertile and bear cymes of female flowers. But it can still be regarded as the nearest approach to the ancestral inflorescence found among the living Euphorbiaceae and as the ideal starting point for the derivation of the cyathium.

From this ancestral type of inflorescence, evolution seems to have occurred along different lines mentioned above viz. connation, adnation, reduction, amplification of organs as well as their traces and progress towards zygomorphy and unisexuality.

Condensation of the axis and reduction in number of bracts led to the whorled, multiseriate, biseriate and uniseriate types of involucre. When this is associated with complete (*Synadenium*) or incomplete (*Stenadenium, Monadenium*) connation and adnation, completely cup-like or incompletely cup-like, open involucres would result. Evolution in the male glomerules consisted in the elimination of bracts, reduction in perianth, in the number of stamens to one per flower and in the number of flowers to one per glomerule. The terminal female flower itself suffered little reduction, the only feature of evolution noticed in it being the loss of its perianth.

Evolution in the glands consists in the connation of the original nectaries in pairs so that their number first equalled that of the involucral bracts. Then reduction occurred to four (*Pedilanthus*), 4—3 (*Euphorbia prostrata*) or to one (*Poinsettia*). In *Cubanthus* one gland becomes suppressed and the surviving four fuse in pairs. Amplification of the nectaries as well as their vascular supply is also noticed in some taxa due to the development of petaloid (*E. marginata*) or horn-like (*E. dracunculoides, Agaloma*) appendages. In

Poinsettia the single nectary becomes large and cup-like and shows abundance of vascular bundles.

Coincident with reduction in number of the organs of the cyathium a general reduction occurs in its size and the size of the involucral bracts from large succulent (*Poinsettia*) to small membraneous structures (*Euphorbia hirta, E. prostrata*). Evolution is noticed from radial to zygomorphic symmetry which is brought about either by (*a*) incomplete union of the involucral bracts (*Monadenium, Stenadenium*), or (*b*) structural modification of the bracts, or (*c*) suppression of some members of different whorls, viz. male glomerules, and glands (*Pedilanthus, Poinsettia, Cubanthus*). *Pedilanthus* and *Cubanthus* show the most strongly zygomorphic cyathia among Euphorbieae. In some taxa like *Dichostemma* and some species of *Euphorbia* (*E. nivulia*) the cyathia become male by abortion. Taking into account all evolutionary trends, the small cyathium of *E. prostrata* with membraneous bracts, 3—4 glands, 5 monandrous male flowers and a naked female flower seems to mark the culmination of evolution in the cyathium; it resembles a small monochlamydeous flower with $P_5\ A_5\ \underline{G}_{(3)}$.

The inter-relationships among the various cyathium bearing genera can now be briefly considered. The genus *Diplocyathium* stands out from the other genera in its multiseriate involucre of free gland-tipped bracts which seems to represent the most primitive condition. However, in the structure of male and female flowers, the genus has attained the level of *Euphorbia*. This illustrates clearly that the different organs of the cyathium evolved at different rates and independent of each other.

The three genera *Synadenium, Monadenium* and *Stenadenium* resemble each other and differ from other genera in their biseriate involucre. They differ from each other in varying degrees of connation and adnation of the involural bracts.

Neoguillauminia and *Dichostemma* have uniseriate perianth but the glands occur radial to the female flower. The simple thick glands of *Dichostemma* seem to be derived by connation of the pairs of glands found in *Neoguillauminia*.

All genera with symmetrical uniseriate involucre and glands situated on the involucre seem to form one line of evolution, viz. *Calycopeplus, Euphorbia, Elaeophorbia, Euphorbiodendron, Agaloma, Chamaesyce*, and *Poinsettia*.

The genera with zygomorphic cyathia which show structural modification of the involucral bracts and suppression and fusion of glands viz. *Pedilanthus, Cubanthus* and *Tithymalus* form another line which is an offshoot of the *Euphorbia*-line.

ACKNOWLEDGEMENTS

I am thankful to the Director, Royal Botanic Gardens, Kew, for kindly loaning some herbarium materials of cyathium-bearing taxa, to the Director, National Botanic Gardens, Kirstenbosch, for herbarium material of two species of *Monadenium*, and to the Director, National Botanic Gardens, Lucknow, for fixed material of *Dalechampia*. I am thankful to Prof. P. G. JORDAAN for kindly supplying some literature on the South African Euphorbieae.

LITERATURE CITED

BAILLON, H. 1858. Étude générale du groupe des Euphorbiacées. — Paris.

ČELAKOVSKY, L. J. 1892. Gedanken über eine zeitgemässe Reform der Theorie der Blütenstände. — Bot. Jahrb. 16: 33—51.

CROIZAT, L. 1936. On the classification of Euphorbia. I. How important is the cyathium? — Bull. Torrey Bot. Club 63: 525—532.

— 1937. On the classification of Euphorbia. II. How should the cyathium be interpreted? — Bull. Torrey Bot. Club 64: 523—537.

— 1938. Notes on the Euphorbiaceae with a new genus and a new subtribe of the Euphorbieae. — Phillip. Journ. Sci. (Bot.) 64: 397—412.

— 1940. On the phylogeny of the Euphorbiaceae and some of their presumed allies. — Rev. Univ. (Chile) 15: 205—220.

— 1942. Peculiarities of the inflorescence in the Euphorbiaceae. — Bot. Gaz. 103: 771—779.

Dressler, R. L. 1957. The genus Pedilanthus (Euphorbiaceae). — Contr. Gray Herb. Harvard Univ. No. 182.

— 1961. A synopsis of Poinsettia. Ann. Missouri Bot. Gard. 48: 329—341.

Eames, A. J. 1961. The morphology of angiosperms. — New York.

Gamble, J. S. 1967. The flora of Madras Presidency. II. — Calcutta.

Good, R. 1956. Features of evolution in flowering plants. — London.

Haber, J. M. 1925. The anatomy and the morphology of the flower of Euphorbia. — Ann. Bot. 39: 657—707.

Hutchinson, J. 1969. Tribalism in the family Euphorbiaceae. — Amer. Journ. Bot. 56: 738—758.

Michaelis, P. 1924. Blütenmorphologische Untersuchungen an den Euphorbiaceen. — Bot. Abhandl. 3: 1—150.

Millspaugh, C. F. 1913. The genera Pedilanthus and Cubanthus and other American Euphorbiaceae. — Publ. Field Mus. Nat. Hist. Bot. Ser. 2: 353—377.

— 1914. Contributions to North American Euphorbiaceae. V. — Publ. Field Mus. Nat. Hist. Bot. Ser. 2: 383—397.

Nägeli, C. W. von 1884. Mechanisch-physiologische Theorie der Abstammungslehre. — München.

Parkin, J. 1914. The evolution of the inflorescence. — Journ. Linn. Soc. London (Bot.) 42: 511—563.

Pax, F. & Hoffman, K. 1931. Euphorbiaceae. — In Engler & Prantl, Die natürlichen Pflanzenfamilien (Ed. 2) 16 c: 11—232. — Leipzig.

Perry, B. A. 1943. Chromosome numbers and phylogenetic relationships in the Euphorbiaceae. — Amer. Journ. Bot. 30: 527—543.

Pilger, R. K. F. 1922. Über Verzweigung und Blütenstandsbildung bei den Holzgewächsen. — Biblioth. Bot. 23: 1—38.

Rickett, H. W. 1944. The classification of inflorescences. — Bot. Rev. 10: 187—231.

Ridola, F. 1903. Interpretazione morphologica del ciazio di Pedilanthus. — Boll. Orto Bot. Napoli 1: 415—418.

Schmidt, H. 1907. Über die Entwicklung der Blüten und Blütenstände von Euphorbia L. und Diplocyathium n. g. — Beih. Bot. Centralblatt 12 (1): 21—69.

Schoute, J. C. 1937. On the aestivation in the cyathium of Euphorbia fulgens with some remarks on the morphological interpretation of the cyathium in general. — Rec. Trav. Bot. Neerl. 34: 168—181.

Thiselton-Dyer, W. T. 1909. Flora of Tropical Africa. II. — London.

Troll, W. 1928. Organisation und Gestalt im Bereich der Blüte. — Berlin.

Venkata Rao, C. 1965. Studies in the Proteaceae. V. Evolution of the inflorescence. — Journ. Ind. Bot. Soc. 44: 244—270.

— 1967. Morphology of the nectary in the Proteaceae. — New Phytol. 66: 99—108.

— & Ramalakshmi, T. 1968. Floral anatomy of some Euphorbiaceae. I. Non-cyathium taxa. — Journ. Ind. Bot. Soc. 47: 278—300.

Willis, J. C. 1948. Dictionary of flowering plants and ferns. Ed. 6. — Cambridge.

Woodson, R. E. Jr. 1935. Observations on the inflorescence of Apocynaceae. — Ann. Missouri Bot. Gard. 22: 1—48.

Some Sources of Error in the Determination of Arm Ratios of Chromosomes

By B. Bentzer, R. v. Bothmer, L. Engstrand,
M. Gustafsson and S. Snogerup

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

Bentzer, B., v. Bothmer, R., Engstrand, L., Gustafsson, M. and Snogerup, S. 1971. Some sources of error in the determination of arm ratios of chromosomes. — Bot. Notiser 124: 65—74.

Four different reasons for arm ratio variation are discussed:

1. Unsynchronized contraction of chromosome arms.
2. Different ways of measuring chromosomes, i.e., on drawings and photos, respectively.
3. Different ways of treating received data.
4. The human factor, i.e., different persons independently measuring and calculating arm ratios from the same chromosomes.

INTRODUCTION

In cytological investigations it is often desirable to identify and describe individual chromosomes. The two chromosome characters most commonly employed are relative length, i.e., the length of an individual chromosome in per cent of the total length of the haploid complement, and arm ratio (arm index, r-index), i.e., long arm/short arm ratio. During cytological routine work the present authors have found that the arm ratio may be a somewhat ambiguous characteristic. The present paper is intended to illustrate some of the main problems involved. Concerning centromeric positions, the nomenclature recommended by Levan et al. (1965) is followed.

PREVIOUS OBSERVATIONS

Several authors have discussed the problem of chromosome diagnostics (cf. Bothmer 1970). The observable chromosome morphology is influenced by a number of factors, both biological and technical. Svärdson (1945) found that in Salmonidae the long chromosomes are contracted more rapidly than the short ones between prophase and metaphase. Wickbom (1949) obtained the same results in Anurans and Urodelians. The results of Svärdson and Wickbom may be generalized to apply to individual chromosome arms. However, in living material of *Haemanthus* and *Leucojum*, Bajer (1959) found that all chromosomes are shortened in a similar way in all stages between late prophase and telophase, independently of their dimensions.

Sasaki (1961) observed in colchicine treated mammalian material that long chromosomes vary more in relative length than short ones. Long chromosomes are usually more contracted by colchicine treatment than short ones. This applies also to long versus short cromosome arms, which means that the arm ratio is more or less modified by colchicine treatment. SYBENGA (1959) showed in *Secale* that different pretreatments, e.g., oxyquinoline, bromnaphthalene, and colchicine, influence the chromosome set in similar ways. He also pointed out that different squashing pressures frequently affect the chromosome length as well as the arm ratio.

Comparing some different methods of measuring chromosomes, SYBENGA found that direct measurements with an ocular screw micrometer or measurements on photos, both at high magnification (100× oil immersion lens), are the most accurate. Measurements on photos taken at a lower magnification (40× dry lens) were considered less exact.

SIMAK (1962) and MATÉRN & SIMAK (1968, 1969), working on *Larix*, paid special attention to the problem of reversal of order, i.e., confusion of non-homologous chromosomes. They also discussed arm reversals, i.e., confusion of the arms of more or less *m* (metacentric) chromosomes, which will tend to increase the arm ratio, since this is *a priori* defined as long arm/short arm ratio. MATÉRN & SIMAK (1968) found that reversals of order can not be disregarded if the difference in length between two chromosomes is less than 11 per cent. To avoid arm reversals they estimated that the mean difference in arm length must be more than 20 per cent. ESSAD et al. (1966) called attention to the fact that if four similar chromosomes are artificially grouped two and two on the basis of arm ratios, the differences between the pairs might well be significant and thus incorrectly tend to confirm the initial distinction. They also presented a method, based on comparisons of variances, to calculate the degree of fidelity with which the individual chromosomes of a set can be identified (also presented by MATÉRN & SIMAK 1968, 1969).

LEWITSKY (1931) emphasized the error obtained by measuring chromosomes lying not quite horizontally but in an oblique position. However, this source of error is to some extent eliminated when using squash technique instead of sectioning.

AIMS, MATERIAL AND METHODS

The present investigation attempts to elucidate two main problems:

1. How large are the differences in arm ratio when homologous chromosomes are measured in different stages of contraction? Are these differences dependent on the centromeric position?

2. How large are the variations in arm ratios obtained by different persons independently measuring the same chromosomes, a) in camera-lucida drawings, and b) in photographs? Are these variations dependent on the centromeric position?

To answer the first question, material of *Fritillaria erhardii* BOISS. & ORPH. (Greece, Northern Sporades, Pelagos) was used. Three pairs of marker chromosomes with different arm ratios were measured in ten cells at different stages of contraction in the same root tip. The total length of the measured chromosomes was used to express the degree of contraction. The arm ratios were calculated from measurements on camera-lucida drawings.

To answer the second question, material of *Tulipa cretica* BOISS. (Greece, Kikladhes, Naxos) was used (Fig. 1). The authors independently drew and measured five marker chromosomes in 10 cells from the same root tip. The same cells were photographed (magnification 3100 and 8100 diameters, respectively) and the arm ratios were calculated from measurements on the photos. For technical reasons, chromosome no. 5 was omitted when measuring the photographed cells. When chromosomes were drawn with the aid of a camera-lucida, special attention was paid to:

1. Keeping the mirror at a constant angle.

2. Adjusting the position of the preparations so that the images of all chromosomes were drawn at the same spot.

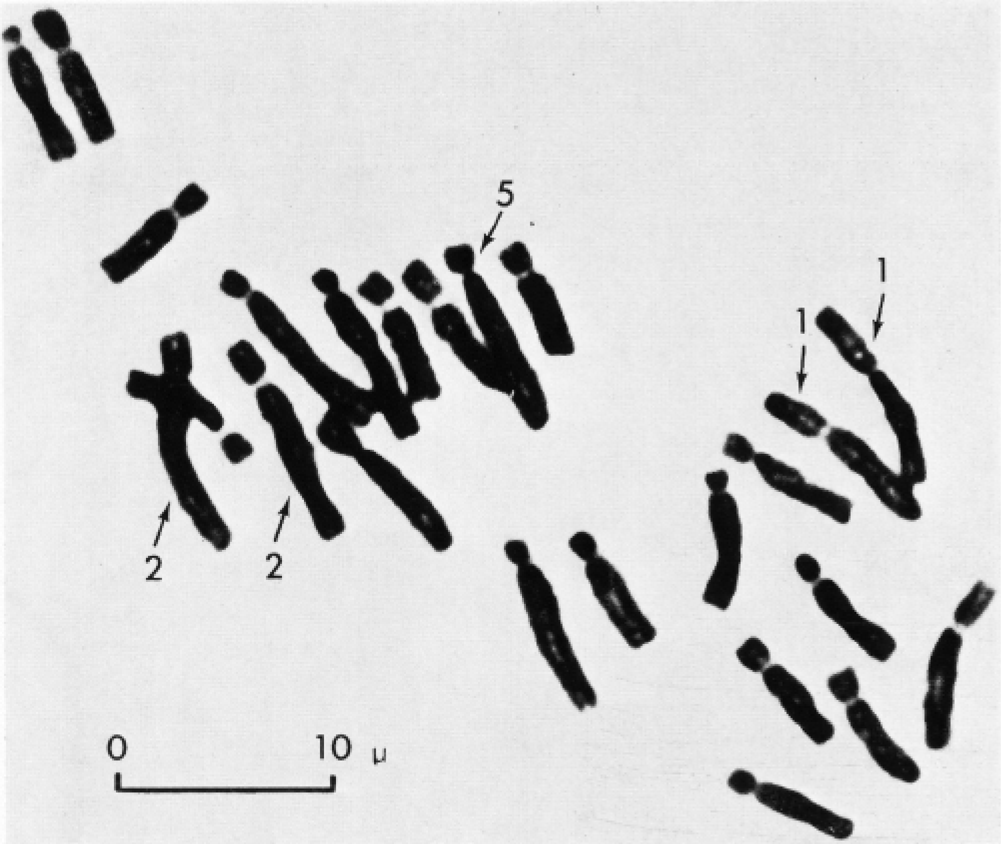


Fig. 1. Photo of a somatic metaphase plate of *Tulipa cretica* BOISS., 2n=24. The arrows indicate the different chromosomes used in the present investigation.

The measurements were carried out with an accuracy of 0.5 mm. To illustrate the chromosomal variation, 95 % confidence limits (m ± 2sE) were used in the diagrams. When two lines do not overlap, the difference between the mean values is significant at approximately the 1 % level.

Before fixation the plants were manured with a nutriment solution and placed under strong light. Root tips were pretreated in a 1 : 1 mixture of 0.3 % colchicine and 1 mM 8-hydroxyquinoline for two hours and fixed in Acetic alcohol (1 : 3). The squash technique described by ÖSTERGREN and HENEEN (1962) was followed. After staining with Feulgen, the root tips were treated in a c. 5 % water solution of pectinase for about two hours.

RESULTS

1. Variation Caused by Measuring Chromosomes in Different Stages of Contraction

Measurements on differently contracted marker chromosomes of *Fritillaria* revealed that *m* chromosomes (nos. 1 and 2) retain a ± constant arm ratio, whereas

nr	long arm	short arm	satellite	arm ratio
1	32.0	22.0	--	1.45
2	35.0	23.0	--	1.52
3	29.0	3.0	6.0	3.22
4	31.0	2.0	5.5	4.15
5	34.0	4.5	1.5	5.67
6	31.5	4.5	2.0	4.85

1	34.0	25.0	--	1.36
2	35.0	24.0	--	1.46
3	34.5	3.5	6.5	3.45
4	35.0	4.0	7.5	3.04
5	43.0	4.0	2.0	7.17
6	40.0	3.5	1.5	8.00

1	47.5	34.5	--	1.38
2	46.0	32.5	--	1.42
3	54.0	7.0	11.1	3.00
4	51.0	4.5	9.5	3.64
5	78.0	6.0	2.0	9.75
6	76.0	7.0	2.0	8.44

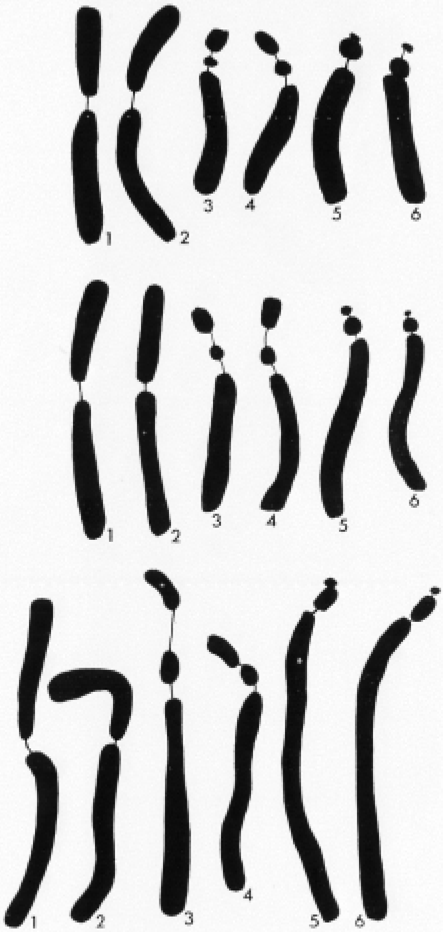


Fig. 2. Variation in arm ratios in three pairs of marker chromosomes at different stages of contraction (*Fritillaria erhardii*).

st — subtelocentric — (nos. 3 and 4) and *stt* — subtelocentric to telocentric — (nos. 5 and 6) chromosomes show a decreasing variability of arm ratio with increasing degree of contraction (Figs. 2 & 3). This is presumably not caused by errors in the measurements, since in that case an opposite trend would be expected (see Figs. 3 and 4). It seems likely that homologous chromosomes are not completely synchronized with respect to contraction. This applies particularly to the long arms of *stt* chromosomes (cf. BOSE 1956). The result obtained corresponds rather well to those of SVÄRDSON (1945) and WICKBOM (1949).

It was also found that in *st* and *t* chromosomes the arm ratio decreases with increasing degree of contraction (cf. Fig. 3). This result would be expected if the arms are contracted at different rates. The more terminal centromeric position a chromosome has, the more pronounced is this effect. In *msm* chromosomes it is negligible. When the arm ratio exceeds c. 3 special care should be taken that the

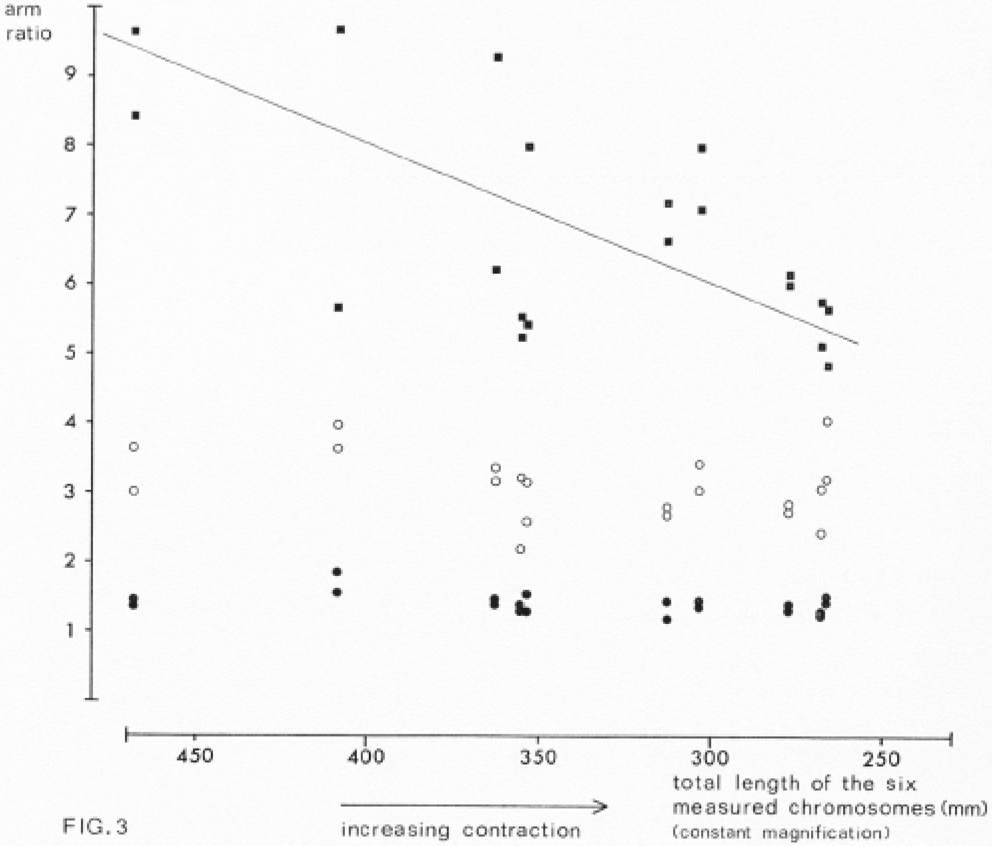


FIG. 3

Fig. 3. Arm ratios of three pairs of chromosomes plotted versus degree of contraction (ten cells measured). Each homologous chromosome indicated separately. Dots = *m* chromosomes, rings = *st* chromosomes, squares = *t* chromosomes (*Fritillaria erhardii*).

measurements are carried out on chromosomes at the maximum degree of contraction.

2. Errors Caused by Technical Difficulties

When arm ratios were measured and calculated by several persons independently, differences were found in *st* (pair no. 2) and *t* (chromosome no. 5) chromosomes. In *msm* chromosomes (pair no. 1), on the other hand, the results obtained by different persons were very similar. Figs. 5, 6 & 7 give the arm ratios measured for two pairs of chromosomes and one single SAT chromosome. The measurements were carried out on, *1*) camera-lucida drawings, 2) photographs with a medium magnification (×3100), and *3*) photographs with a high magnification (×8100). The following conclusions can be drawn from the data obtained:

1. msm chromosomes (Fig. 5): The different methods of measuring gave almost the same results. The variation in arm ratios obtained by different persons was very moderate.

2. st chromosomes (Fig. 6): Less variation was found in measurements from

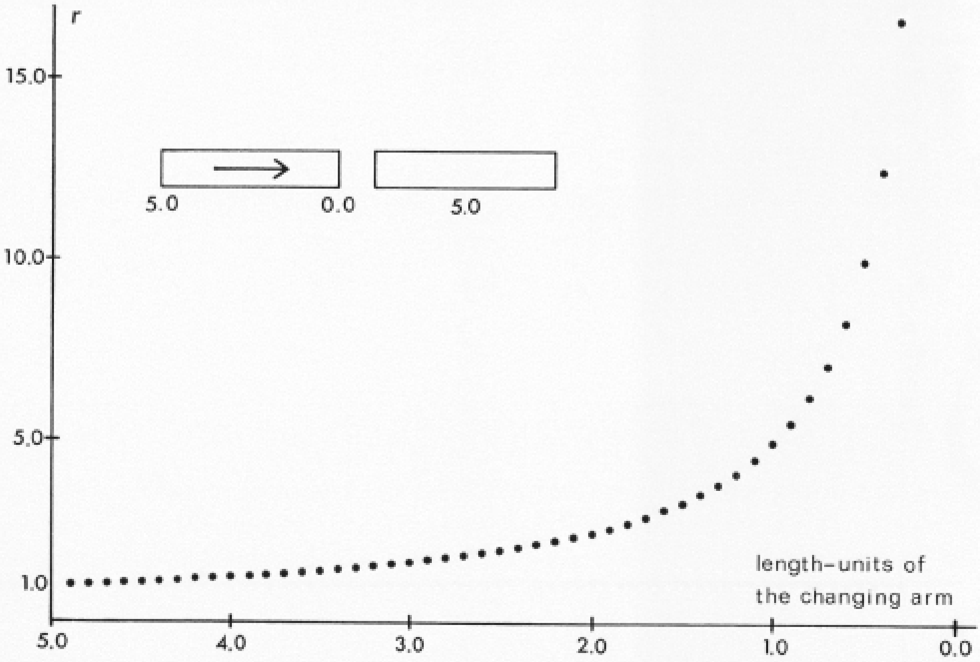


FIG. 4

Fig. 4. Diagram indicating how arm ratios increase (vertical axis) when the length of one chromosome arm is supposed to decrease (horizontal axis) and the other is kept at a constant length. Originally the chromosome is supposed to be metacentric with both arms 5 length units.

photographs than from drawings (the same chromosome drawn by each person independently). In some cases the arm ratios obtained from drawings by different persons showed significant differences. It thus appears preferable to measure from photographs, more or less independently of magnification.

3. t chromosomes (Fig. 7): Only measurements from drawings were available. Considerable variation was found in the drawings by different persons. Arm ratios of *t* chromosomes should consequently be given with rather wide limits. Probably the wide variation depends partly on differences in drawing technique.

The confidence limits are generally wider the higher the arm ratios are. The measurements made by different persons on drawings varied more than those made on photographs. It is possible to make a rough estimation of the magnitude of errors originating from the process of drawing by comparing 1, 2 and 3 in Figs. 5 and 6. The variation increases with increasing arm ratio; this applies to measurements from both drawings and photographs. However, the tendency is more evident in the drawings. The reason for the confidence limits to be wider when the arm ratios increase is at least partly illustrated in Fig. 4. The diagram indicates that a very small mistake in measuring the short arm of an *stt* chromosome affects the arm ratio considerably.

In order to obtain a more accurate value of arm ratio it is necessary to measure more than 5, probably 10 cells from

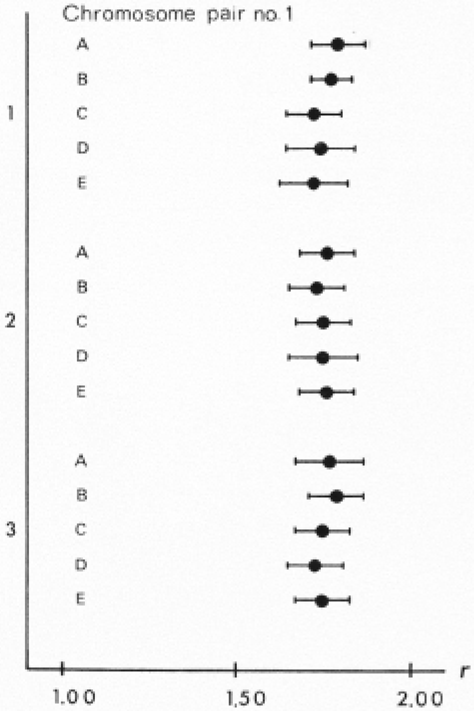


FIG. 5

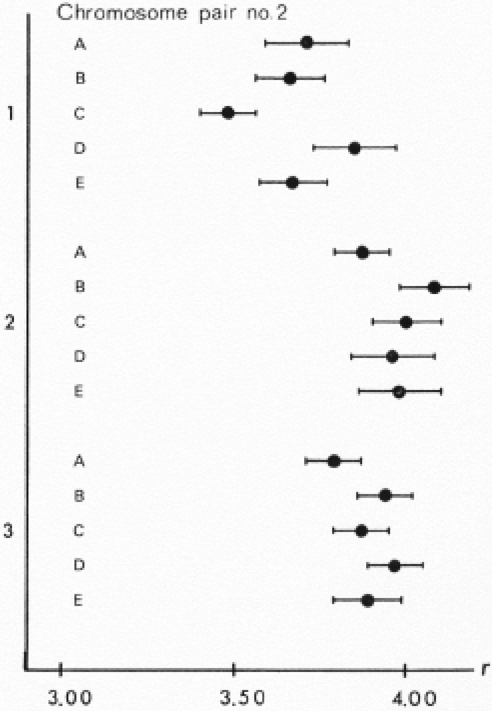


FIG. 6

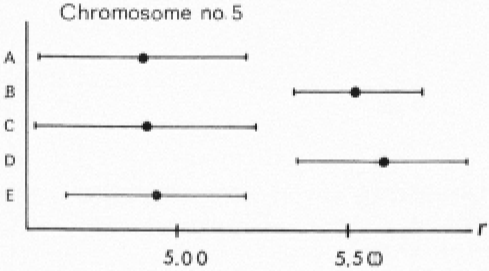


FIG. 7

Figs. 5—7. Confidence limits for arm ratios (r) based on measurements from *1*) drawings, *2*) photos ×3100, and *3*) photos ×8100. A, B, C, D, and E indicate measurements made by different persons. — Fig. 5: Chromosome pair no. 1. — Fig. 6: Chromosome pair no. 2. — Fig. 7: Chromosome no. 5. Confidence limits based on measurements from drawings only.

each individual (cf. Figs. 8 and 9). In each cell the arm ratios of the two homologous chromosomes of pair no. 1 and pair no. 2 were separated into two classes (high values and low values, respectively; cf. Figs. 12 and 13). In pair no. 1 this arrangement gave rise to significant differences between the homologous chromosomes. In pair no. 2 the difference between the high and low classes was somewhat less obvious. The differences found in chromosome pair no. 1 may indicate structural heterozygosity, but may also depend on the combined effects of other sources of variation.

Figs. 10 and 11 illustrate confidence limits for the arm ratio mean value of chromosome pairs nos. 1 and 2 in the ten cells studied. The data indicate that there

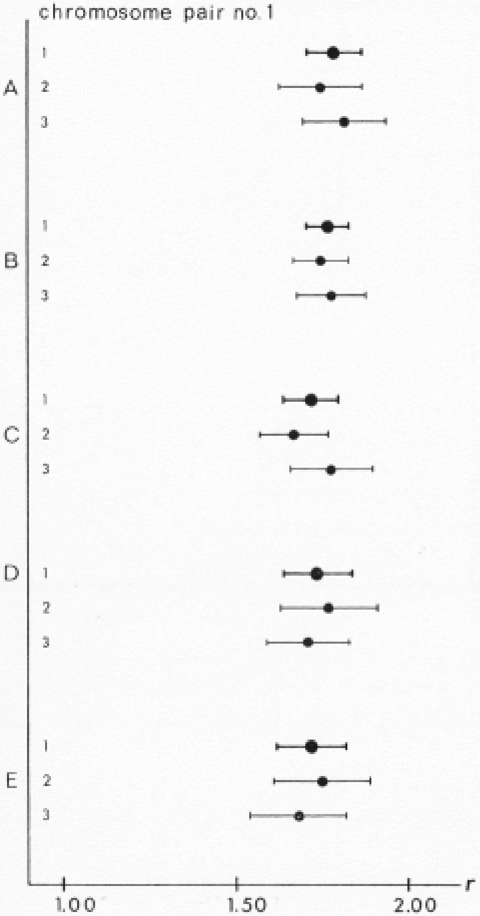


FIG. 8

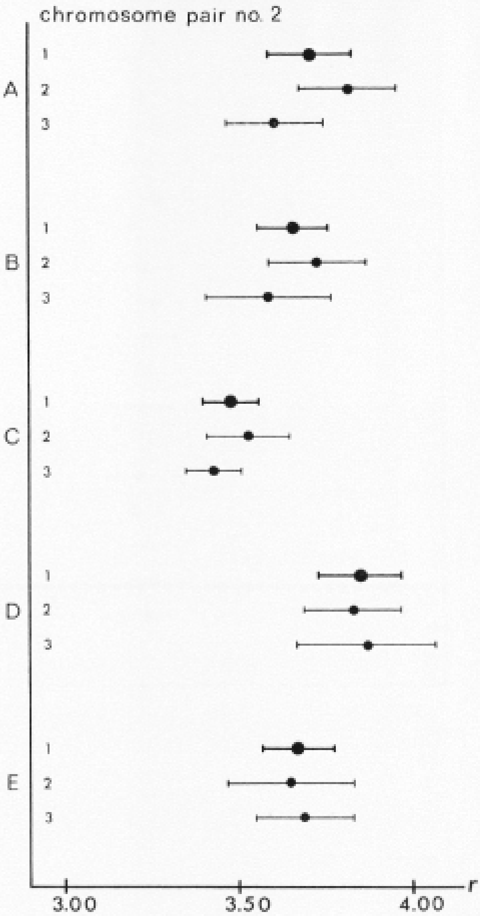


FIG. 9

Figs. 8—9. Confidence limits for arm ratios (r) based on photos (×8100). Interval 1: calculations from 10 measured cells. Intervals 2 and 3: calculations from 5 measured cells each. A—E are measurements made by different persons. — Fig. 8: Chromosome pair no. 1. — Fig. 9: Chromosome pair no. 2.

are true differences between cells with respect to arm ratios of the same chromosomes. Chromosome pairs nos. 1 and 2 give similar results. Thus there are apparently true differences between cells with respect to the contraction of individual chromosome arms or parts of them.

CONCLUSIONS

In order to restrict the errors in arm ratio determination as much as possible, the following requirements should be met:

1. The degree of contraction of the chromosomes must be uniform and as high as possible. The absolute length of the chromosomes in cells compared should not differ by more than c. 10 %.

2. At least ten chromosome sets should be measured from each individual.

3. Arm ratios cannot be given with the

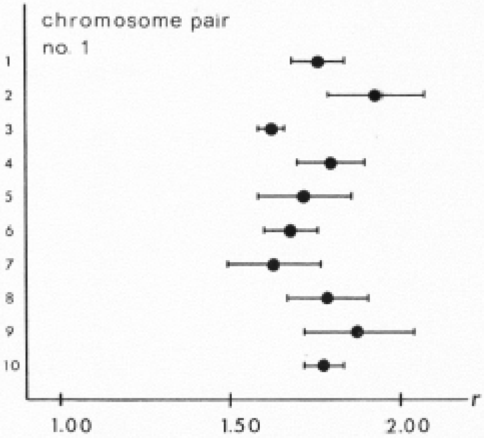


FIG. 10

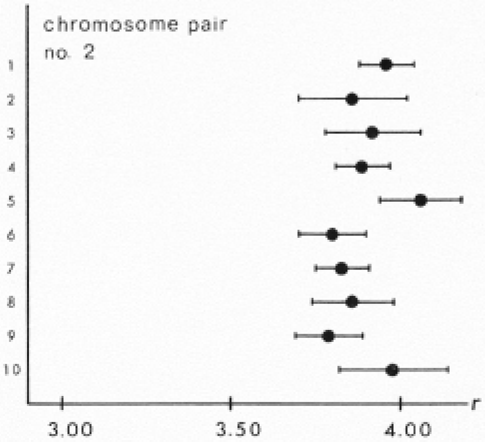


FIG. 11

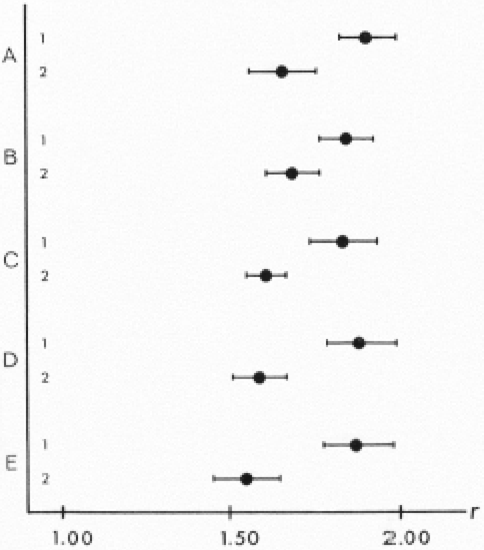


FIG. 12

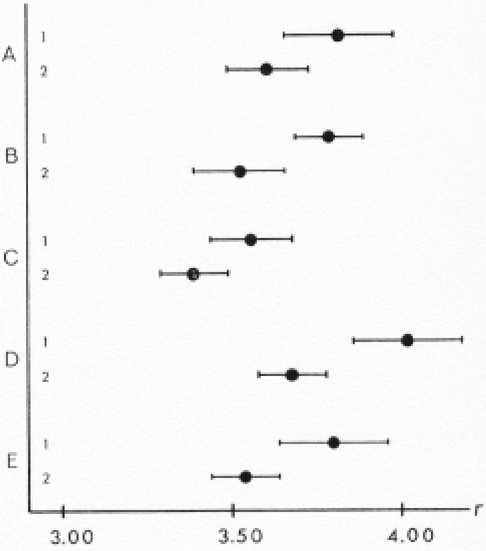


FIG. 13

Figs. 10—11. Confidence limits for arm ratios (r) based on photos (×8100) from ten cells (1—10). — Fig. 10: Chromosome pair no. 1. — Fig. 11: Chromosome pair no. 2.

Figs. 12—13. Confidence limits for arm ratios (r) calculated from photos (×8100). Interval 1 includes the five highest r values obtained by one person and interval 2 the five lowest. A—E are calculations made by different persons. — Fig. 12: Chromosome pair no. 1. — Fig. 13: Chromosome pair no. 2.

same accuracy for *st* and *t* chromosomes as for *m* chromosomes.

4. In the course of an investigation all measurements and/or drawings should be made by the same person.

5. Structural heterozygosity can be revealed by measurements only if the differences exceed 20 %.

LITERATURE CITED

Bajer, A. 1959. Change of length and volume of mitotic chromosomes in living cells. — Hereditas 45: 579—596.

Bose, S. 1956. Aberrations in the nucleolar chromosome of inbred rye. — Hereditas 42: 263—292.

Bothmer, R. von 1970. Cytological studies in Allium I. Chromosome numbers and morphology in sect. Allium from Greece. — Bot. Notiser 123: 519—551.

Essad, S., Arnoux, J. & Maia, N. 1966. Contrôle de validité des caryogrammes. Application au caryotype de Lolium perenne L. — Chromosoma 20: 202—220.

Levan, A., Fredga, K. & Sandberg, A. A. 1965. Nomenclature for centromeric position on chromosomes. — Hereditas 52: 201—220.

Lewitsky, G. A. 1931. The morphology of chromosomes. — Bull. Appl. Bot. Pl.-Breed. (Leningrad) 27: 19—173.

Matérn, B. & Simak, M. 1968. Statistical problems in karyotype analysis. — Hereditas 59: 280—288.

— 1969. On some statistical problems connected with the identification of chromosomes. — Res. Notes Dep. Forest Biometry, Roy. Coll. Forestry (Stockholm) 1: 1—81.

Östergren, G. & Heneen, W. K. 1962. A squash technique for chromosome morphological studies. — Hereditas 48: 332—341.

Sasaki, M. 1961. Observations on the modification in size and shape of chromosomes due to technical procedure. — Chromosoma 11: 514—522.

Simak, M. 1962. Karyotype analysis of Larix decidua Mill. from different provenances. — Meddel. Stat. Skogsforskningsinst. 51: 1—22.

Svärdson, G. 1945. Chromosome studies on Salmonidae. — Meddel. Stat. Försöksanst. Sötvatt.-fiske 23: 1—151.

Sybenga, J. 1959. Some sources of error in the determination of chromosome length. — Chromosoma 10: 355—364.

Wickbom, T. 1949. The time factor of chromosome spiralization. — Hereditas 35: 245—248.

Potentilla Goulandrii, Dianthus Stamatiadae, Onosma psammophilum, drei neue Arten der griechischen Flora

Von K. H. Rechinger

Naturhistorisches Museum
Botanische Abteilung
A-1014 Wien, Österreich

ABSTRACT

Rechinger, K. H. 1971. Potentilla Goulandrii, Dianthus Stamatiadae, Onosma psammophilum, drei neue Arten der griechischen Flora. — Bot. Notiser 124: 75—81.

Potentilla Goulandrii is described from Mt. Vourinos in W. Macedonia. It is a very large-flowered species resembling members of the *P. recta* group in habit, but differing, e.g., in its leaves, calyx, and shape of the style.

Dianthus Stamatiadae, collected near Servia in W. Macedonia, is a distinct species slightly resembling *D. Balbisii* in habit. It is characterized by very short sheaths, and flowers in 3—6-flowered heads with lanceolate, almost entirely herbaceous epicalyx-scales.

Onosma psammophilum from maritime sand near the mouth of the river Strymon in E. Macedonia has a strong, woody, branched stem, and elongated, leafy floriferous branches. It is prominently heterophyllous. Taxonomically it appears to be rather isolated.

Potentilla Goulandrii Rech. f., sp. nov. — Fig. 1 & 2.

Perennis, pluricaulis. Caules floriferi 25—35 cm alti, ascendentes vel suberecti, purpurascentes, pilis longis albis rectis antrorsis ± appressis laxiuscule usque densiuscule obsiti, foliati, in tertia vel quarta circiter parte superiore corymbose ramosi et floriferi. Folia basalia et caulina infima petiolo laminam circiter aequante suffulta; petiolus pilis albis antrorsis ± rectis simplicibus obsitus; lamina digitata; foliola plerumque 7-na, crasse herbacea, viridia, longitudinaliter plicata, nervatura tenuissima reticulata oculo nudo vix visibili, oblongo-cuneata, marginibus integerrima, apice rotundato-truncata et inciso-tridentata, 10—22 mm longa, antice in statu explicato usque ad 7 mm lata; folia caulina inferiora stipulis magnis usque ad 16 mm longis, inferne usque ad 5 mm latis, omnino herbaceis, e basi semiovata subsensim caudato-attenuatis, supra glabris margine longe antrorse ciliatis provisa; petiolus lamina brevior; lamina e foliolis 7 composita, foliolis quam in foliis basalibus proportione longioribus, angustioribus, linearibus, usque ad 35 mm longis, 4 mm latis, marginibus subparallelis, obsolete remote serratis usque subintegris, antice truncatis et brevissime tridentatis, pilis longis rectis antrorsis imprimis secus costam medianam et margine sparse obsitis, ceterum glabris; folia caulina superiora et ramealia decrescentia, stipulis autem non reductis, lamina ad lacinias paucas lanceolatas acutas reducta. Rami inflorescentiae stricti, virides, quam caulis foliaque ± densius pilosa; praeter pilos longos simplices antrorsos glandulae nonnullae stipitatae minutissimae evolutae. Calycis laciniae ovato-lanceolatae, acutae, sub anthesi increscentes, usque ad 15×6 mm, herbaceae, facie glabrae, mar-

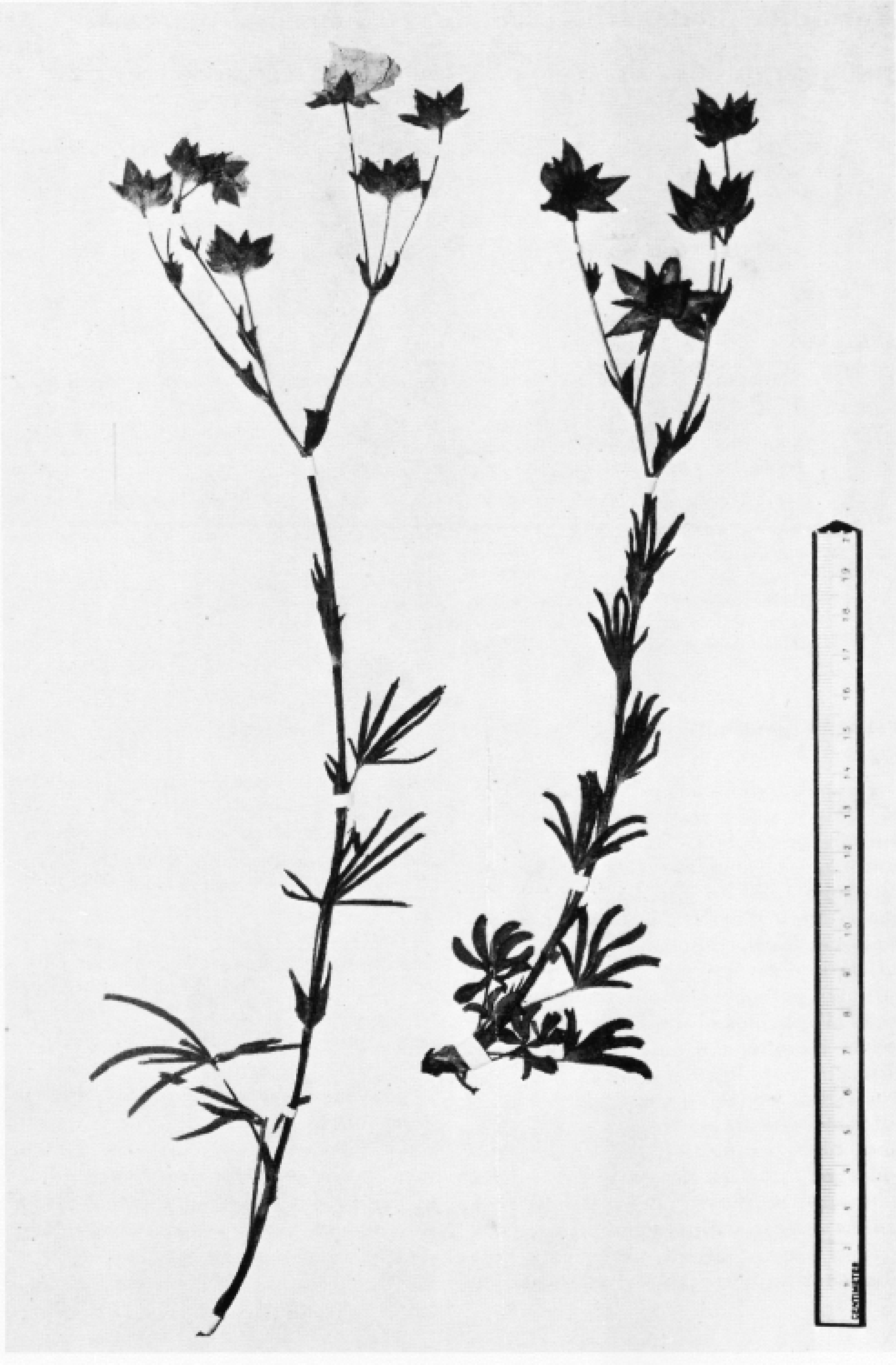


Fig. 1. *Potentilla Goulandrii* Rech. f. Habitus.

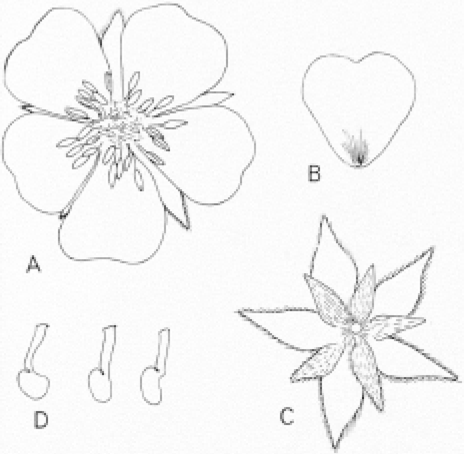


Fig. 2. *Potentilla Goulandrii* Rech. f. — A: Blüte. — B: Kronblatt. — C: Kelch. — D: Fruchtknoten mit Griffel. — A—C natürliche Größe, D ×3.

gine longe antrorse albo-ciliatae; epicalycis laciniae lanceolatae, acutae, usque ad 8×3 mm, facie longe antrorse albo-pilosae. Petala ±15×15 mm, late cordata, flava, antice leviter late emarginata. Stamina 2—3 mm, antherae ±2 mm longae, flavescenti-virentes. Stylus subterminalis, basi valde constrictus, tota longitudine aequa fere crassitudine; stigma vix distinctum. Fructus ignotus.

Graecia: Macedonia occidentalis: Mons Vourinos, "Tsamia (rocky area underneath the Chapel of Hagios Panteleimon, limestones), alt. 1250—1300 m". Stamatiadou in Herb. Goulandris 9619 (holotypus W, isotypus herb. Goulandris).

Die neue Art ist dem Begründer des Botanischen Museums Goulandris in Kifissia bei Athen, Herrn Angelos Goulandris, gewidmet.

P. Goulandrii ist habituell am ehesten mit dem Formenkreis der *P. recta,* und zwar wegen des weitaus überwiegend aus langen, einfachen Haaren bestehenden Induments mit *P. hirta* zu vergleichen. Die längsgefalteten, schmalen, an den Seiten streng ganzrandigen, nur vorne kurz 3-zähnigen Blättchen der Grundblätter, die noch schmäleren, parallelrandigen, an den Seiten nur ganz entfernt kleingesägten Blättchen der Stengelblätter sowie die über die oberen Stengelblätter und die Blätter der Infloreszenzregion fast gleitend in die ungewöhnlich großen Kelchblätter überleitende Blattfolge, lassen *P. Goulandrii* sofort als eine von allen bisher beschriebenen weit verschiedene neue Art erkennen. Diese Auffassung wird bestätigt, wenn man die Griffelmerkmale mit in Betracht zieht; man vergleiche diesbezüglich Wolf, Bibl. Bot. 16: 43 (1908) fig. 2 oder Hegi, IV, 2: 810 (1922) fig. 1109. Die Griffelgestalt der *P. Goulandrii* deckt sich mit keiner der dort dargestellten Griffeltypen. Der Griffel der neuen Art ist fast endständig, am Ansatz stark eingeschnürt, dann aber aufwärts fast gleich dick; die Narbe ist flach, kaum breiter als der Griffel. Immerhin läßt sich diese Griffelform am natürlichsten als eine besondere Modifikation des Griffeltypus der *Conostylae* interprätieren. Dafür spricht die Endständigkeit und die basale Einschnürung. Dagegen spricht freilich die von der basalen Einschnürung bis zur Narbe ganz oder fast gleichbleibende Dicke des Griffels, wie sie sonst meines Wissens nirgends realisiert ist.

Ohne hier auf phylogenetische Spekulationen einzugehen, spricht die systematisch isolierte Stellung der *P. Goulandrii* für eine Deutung der Art als Paläoendemit.

Dianthus Stamatiadae Rech. f., sp. nov. — Fig. 3.

Perennis, dense caespitosus, multicaulis, florendi tempore rosulae steriles foliorum et caules floriferi emortui anni praeteriti adsunt. Folia rosularia graminea, 4—6 cm longa, 2 mm lata, viridia, subtus subglaucescentia, tota longitudine costa mediana tenui sed prominente et marginibus calloso-incrassatis percursa, acutissima, margine papilloso-scabridula, recta vel subfalcata. Caules floriferi ±20 cm alti, erecti vel subarcuati, herbacei, obtuse quadran-

Fig. 3. *Dianthus Stamatiadae* Rech. f. — A: Habitus. — B: Infloreszenz.

guli, papilloso-scabriduli, a nodo sexto plerumque breviter stricte pauciramosi et floriferi. Folia caulina basi vagina brevi membranacea caulis diametro non longiore coalita, basalibus similia, paulo breviora, subangustiora, erecta vel cauli fere appressa. Flores plerumque 3—6-ni conferti. Folia florum fasciculos fulcrantia graminea, ima basi tantum subdilatata, ibique ± scariosa vel scarioso-marginata, ceterum herbacea, foliisque caulinis omnino similia, elevate plurinervia, magis scabrida. Squamae calycinae 4, e basi ovato-lanceolata pallide scariosa subsensim in mucronem foliaceum stricte erectum quam basis scariosa circiter duplo longiorem attenuata acutissima, quam calyx paulo tantum breviora, elevate multinervia, scabra. Calyx c. 20 mm longus, subtubulosus, in vel infra medium paulo dilatatus, superne attenuatus, elevate multinervosus, papilloso-scabridus, nervis in parte inferiore pallide scariosa ± evanescentibus, in parte superiore herbacea distinctis; calycis dentes acutissimi, 7—8 mm longi. Petalorum lamina supra purpurea, subtus pallida, c. 8×7 mm, late obovato-cuneata, margine argute sinuato-dentata, basi barbata.

Graecia: Macedonia occidentalis: "On the road from Larissa to Kozani, 5 km before the town of Servia (along the public road on soft limestone cliffs), 18. VI. 1970", E. STAMATIADOU 9628 (holotypus W, isotypus herb. GOULANDRIS).

D. Stamatiadae ist Frau E. STAMATIADOU, der Entdeckerin zweier der drei hier beschriebenen Novitäten, gewidmet.

D. Stamatiadae ist ausgezeichnet durch dicht rasigen, vielstengeligen, ausdauernden Wuchs, sehr kurze Blattscheiden und am Grund kaum verbreiterte, nur am Rand schwach häutige, sonst durchaus krautige, grasartige Hochblätter, die an Länge fast die Kelchlänge erreichen und durch purpurne, kurz gezähnte, am Grund gebärtete Platte der Petalen. Dadurch kommt ein Vergleich mit *D. Balbisii* SER. in DC. in Betracht, mit dem tatsächlich ein gewisse habituelle Ähnlichkeit besteht. *D. Balbisii* hat jedoch lockeren Wuchs, breitere Blätter, vor allem aber viel längere Blattscheiden, die an Länge den doppelten Stengeldurchmesser erreichen. Kurze Blattscheiden hat *D. Stamatiadae* mit *D. trifasciculatus* KIT. in SCHULT. gemeinsam, der jedoch viel längere und breitere Blätter hat, ganz abgesehen von den weitgehenden Verschiedenheiten in den Kelchschuppen und den viel kürzeren Kelchen. Damit erscheint *D. Stamatiadae* als eine systematisch recht isoliert stehende Art.

Onosma psammophilum RECH. f. & RIEDL, sp. nov. — Fig. 4.

Suffrutex, c. 40 cm altus, crebre irregulariter ramosus; rami floriferi elongati, 10—20 cm longi, arcuati, saepe diffusi, flexuosi, florendi tempore praeter ramos floriferos rosulas foliorum vel ramos inferne nudos superne folia subrosulatim congesta proferentes emittens. Indumentum caulis e setis nonnullis patentibus pilis brevibus stellatim dispositis cinctis et pube brevissima, crispula. Folia in margine, supra pro maxima parte et subtus secus nervum medianum setis patentibus vel appressis tuberculis in facie superiore tantum plerumque distinctis stellatim pilosis insidentibus, subtus et pro parte supra pilis stellatim dispositis in facie inferiore densissimis seta centrali valde reducta et iis simillima tecta, ceterum glabra. Folia caulina basi semicordata sessilia, 2—3×1—1.5 cm, prope basin latissima, apice ± rotundata, margine subincrassato-subrevoluta, costa mediana subtus prominente, supra immersa. Folia ramorum floriferorum numerosa, regulariter disposita, quam folia caulina pluries minora iis ceterum similia, in bracteas transeuntia. Bracteae parvae, tertiam partem calycis attingentes, e basi subcordata triangulari-oblonga. Inflorescentia demum elongata. Calyx florifer 5—6 mm longus, laciniis late linearibus usque ad basin liberis, obtusiusculis, setis nonnullis pilis

Fig. 4. *Onosma psammophilum* Rech. f. & H. Riedl. — Habitus.

stellatim dispositis cinctis et pube brevi primo subappressis, demum patentibus vestitis, fructiferis usque ad c. 10 mm accrescentibus. Corolla pallide flava, ± 18 mm longa, sursum sensim paulo ampliata, laciniis brevissimis latis, breviter revolutis, extra puberula, intus glabra. Nectarium annuliforme basale glabrum. Antherae ± 6 mm longae, anguste lineares, basibus cohaerentes, apice sterili brevi obsolete bidentato incluso. Filamenta 12—13 mm longa, 2/3 longitudinis corollae adnata, ± 2.5 mm supra basin corollae inserta, lineares, tota longitudine fere subaequilata, in parte superiore plicata. Stylus 2—3 mm longus, quam corolla sublongior. Nuculae plerumque singulae, nigrescenti-brunneae, albo-marmoratae, nitidae, 2.5—3 mm longae, ovoideae, subrostratae, obtusae, in ventre obtuse carinatae.

Graecia: Macedonia orientalis: In arenosis litoreis compactis ad sinum Orphani maris Aegaei ab ostiis Strymonis fluvii occidentem versus, 21. VII. 1970. Rechinger 39000 (holotypus W).

Onosma psammophilum ist habituell sehr auffällig. Das starke Verholzen, die ausgeprägte Heterophyllie, die ungewöhnlich stark verlängerten, reichlich beblätterten Blütenzweige und die Neigung, aus den verholzenden Sproßabschnitten Blattrosetten oder kurze, sterile Seitensprosse zu bilden, machen die Eigenart des *O. psammophilum* in vegetativer Hinsicht aus. Ökologisch ist das Vorkommen auf kompaktem Sand bemerkenswert.

Es läßt sich keine unmittelbare Beziehung zu irgendeiner bisher bekannten Art angeben. Habituell bestehen am ehesten Übereinstimmungen mit haplotrichen Arten, wie *O. rostellatum* und *O.* (Subgen. *Podonosma*) *orientale* L., mit denen aber sonst keine engere Verwandtschaft angenommen werden kann. Damit ist erneut bestätigt, was sich bei jeder Beschäftigung mit dieser Gattung zeigt: es ist eine Gliederung in monotypische oder aus einigen wegigen Arten bestehende Gruppen möglich, die zusammen alle erdenklichen Kombinationen von Merkmalen verwirklichen, und meist eine sehr enge geographische Verbreitung haben, doch sind die Beziehungen zwischen diesen Gruppen kaum mit Sicherheit anzugeben. Im Blütenbereich besteht das hervorstechendste Merkmal des *O. psammophilum* in den im Verhältnis zur Länge der Korollen sehr kurzen Kelchen, wie sie auch für die Arten um *O. echioides* L. und *O. Aucherianum* DC. charakteristisch sind, die aber im übrigen keinerlei habituelle Ähnlichkeit mit *O. psammophilum* aufweisen. Die Wuchsform ist wie auch die isolierte systematische Stellung ein Hinweis darauf, daß es sich um eine recht altertümliche Sippe handeln dürfte.

Wegen des Namens und wegen des Vorkommens — am Sandstrand bei Makri etwa 180 km östlich vom Fundort des *O. psammophilum* — drängt sich ein Vergleich mit *O. heterophyllum* Griseb. auf. Dieses hat jedoch laut Originalbeschreibung viel längere Korollen und Kelche — 25 gegen 18 mm bezw. 5—10 gegen 12—13 mm — intensiver gelb gefärbte Korollen und schwächer ausgeprägte Heterophyllie.

Tapeinia Comm. ex Juss. (Iridaceae) and the Rediscovery of Galaxia obscura Cav.

By D. M. Moore

Department of Botany,
University of Reading,
Reading RG1 5AQ, England

ABSTRACT

MOORE, D. M. 1971. Tapeinia Comm. ex Juss. (Iridaceae) and the rediscovery of Galaxia obscura Cav. -- Bot. Notiser 124: 82—86.

The genus *Tapeinia* COMM. ex JUSS. (Iridaceae) has hitherto been considered to contain one species, the correct name for which is shown to be *T. pumila* (FORST. f.) BAILLON. *Galaxia obscura* CAV., which has not been seen since its collection by COMMERSON, has been rediscovered in South Chile and Tierra del Fuego. A description, illustrations and a distribution map are provided and the species is shown to comprise a second member of *Tapeinia*, for which the new combination *T. obscura* (CAV.) D. M. MOORE is made.

THE GENUS TAPEINIA

Historical Survey

During December and January, 1767—68, when BOUGAINEVILLE's expedition was exploring the Estrecho de Magellan, COMMERSON collected a small iridaceous plant which was later described as *Ixia magellanica* LAM. No details of the type locality are given other than that the habitat was "maritime rocks". This specimen, which is in the Paris herbarium, was used by JUSSIEU (1789) to erect the monotypic genus *Tapeinia*. Whilst COOK's second expedition was in Tierra del Fuego from 20 December 1774 to 3 January 1775 the FORSTERS collected a plant to be described as *Ixia pumila* FORST. f.; the collecting locality was either Seno Navidad, at the west end of Isla Hoste, or the Islas Año Nuevo, north of Isla de los Estados.

WILLDENOW (1797) considered the LAMARCK and FORSTER species to be synonymous and, despite uncertainty as to the correct genus, there has never been any doubt about this among subsequent authors, a view confirmed by examination of the type specimens. HOOKER (1874) took up the name *Tapeinia magellanica* (LAM.) J. F. GMEL., which has been widely applied to the species by later workers, although some people have used the combination *T. pumila* (FORST. f.) BAILLON. The reason for this confusion is that the two available basionyms, *Ixia magellanica* LAM. and *I. pumila* FORST. f., were both published in 1789. The part of LAMARCK's Encycl. Méth. Bot. in which the former name appeared was issued in October, 1789 (RICKETT & STAFLEU 1961), while the Comment. Soc. Reg. Sci. Götting. 9 (for 1787—1788), containing on pp. 13—45 G. FORSTER's 'Fasciculus Plantarum Magellanicarum', in which *I. pumila* was described, was reviewed as a whole in Göttingische Anzeigen 1789 (83): 833 issued on 23 May 1789 (W. T. STEARN, personal communication). This is conclusive evidence that the FORSTER name was published during or before May, 1789 and accordingly must be the valid basionym for this species. The appropriate details are as follows:

Tapeinia pumila (FORST. f.) BAILLON, Hist. Pl. 13: 149 (1894).

Ixia pumila FORST. f., Comment. Götting., ser. 2, 9: 21, t. 2 (May 1789).
I. magellanica LAM., Encycl. Méth. Bot. 3: 334 (Oct. 1789) — P!
Tapeinia magellanica (LAM.) J. F. GMEL., Syst. Veg. 2: 108 (1791).
Moraea magellanica (LAM.) WILLD., Sp. Pl. ed. 4, 1: 241 (1797).
Witsenia magellanica (LAM.) PERS., Syn. Pl. 1: 42 (1805).
W. pumila (FORST. f). VAHL, Enum. Pl. 2: 48 (1805).
Echthronema pumila (FORST. f.) HERBERT, Bot. Reg. 29: misc. 85 (1843).

TYPUS: Tierra del Fuego. Dec.—Jan. 1774—75. J. R. & G. FORSTER (BM!).

Distribution and Affinity

Tapeinia pumila, which occurs from Isla de los Estados through southern and western Fuegia and along the Chilean coast to its northern limit in the Cordillera Celada, Prov. Valdivia (REED s.n., Jan. 1872, BM), is a fairly common species of wet maritime heath and tussocky sedgeland, most often coastal but attaining an altitude of 400 m on Isla Desolación (DUSÉN 1900) and c. 1100 m in the Cordillera Pelada. The genus *Tapeinia,* of which until now *T. pumila* is considered to be the sole representative, comprises small, caespitose, perennial herbs with crowded, distichous leaves and is closely related to *Sisyrinchium* L. from which, in addition to its habit, it is distinguished by its 1-flowered, terminal spathe and by the ovules and seeds being restricted to the lower part of the loculi.

GALAXIA OBSCURA

Original Collection

Whilst the BOUGAINEVILLE expedition was exploring the Estrecho de Magellan west from Cabo Froward COMMERSON collected another small iridaceous plant in the mountains behind Puerto Galant. This plant was apparently sent to A. L. DE JUSSIEU, as was much of COMMERSON's material (GODLEY 1965), and forwarded to CAVANILLES who based on it a new species, *Galaxia obscura* CAV. described as follows: "G. foliis subulatis canaliculatis, tubo corollae brevi. Planta Sisyrinchio affinis. Commerson herb. magellanico. Radix bulbosa. Folia imbricata, subulata, canaliculata, acutissima. Flores solitarii. Corolla monopetala sexfida ochroleuca, laciniis obtusis refusis. Staminum tubus corolla duplo brevior, filamentis tribus brevissimis terminatus, antheriferis. Germen inferum suboratum. Stylus vaginatus staminum longitudine. Fructus deest. Habitat haec plantula vix sesquipollicaris in monte prope portum Galant in freto Magellanico, ubi eam reperit Commerson." (CAVANILLES 1788). It has not proved possible to trace the type specimen of this species, which is not with the CAVANILLES collections, and the drawing prepared by CAVANILLES (1788 pl. 189, fig. 4) must therefore be so designated. Most subsequent authors have placed *Galaxia obscura* in synonymy with the species now known as *Tapeinia pumila.* The only exceptions being VAHL (1805), who considered them to be different species, and POEPPIG (1833), who gave *G. obscura* as a synonym of his *Sisyrinchium frigidum,* described from Volcán Antuco in Prov. Bío-Bío, Chile.

The Rediscovery of Galaxia obscura

In 1968 I collected a small, white-flowered, iridaceous plant on an unnamed mountain (54°53′ S, 66°53′ W) near the headwaters of the Río Chico, some 4 km inland from Estancia Moat on the north shore of the Canal Beagle. The plant was growing in a damp gravelly area beside a stream, together with *Caltha sagittata* CAV. and *Viola tridentata* MENZ.; only one population, of about twelve individuals, was seen. Although superficially similar to

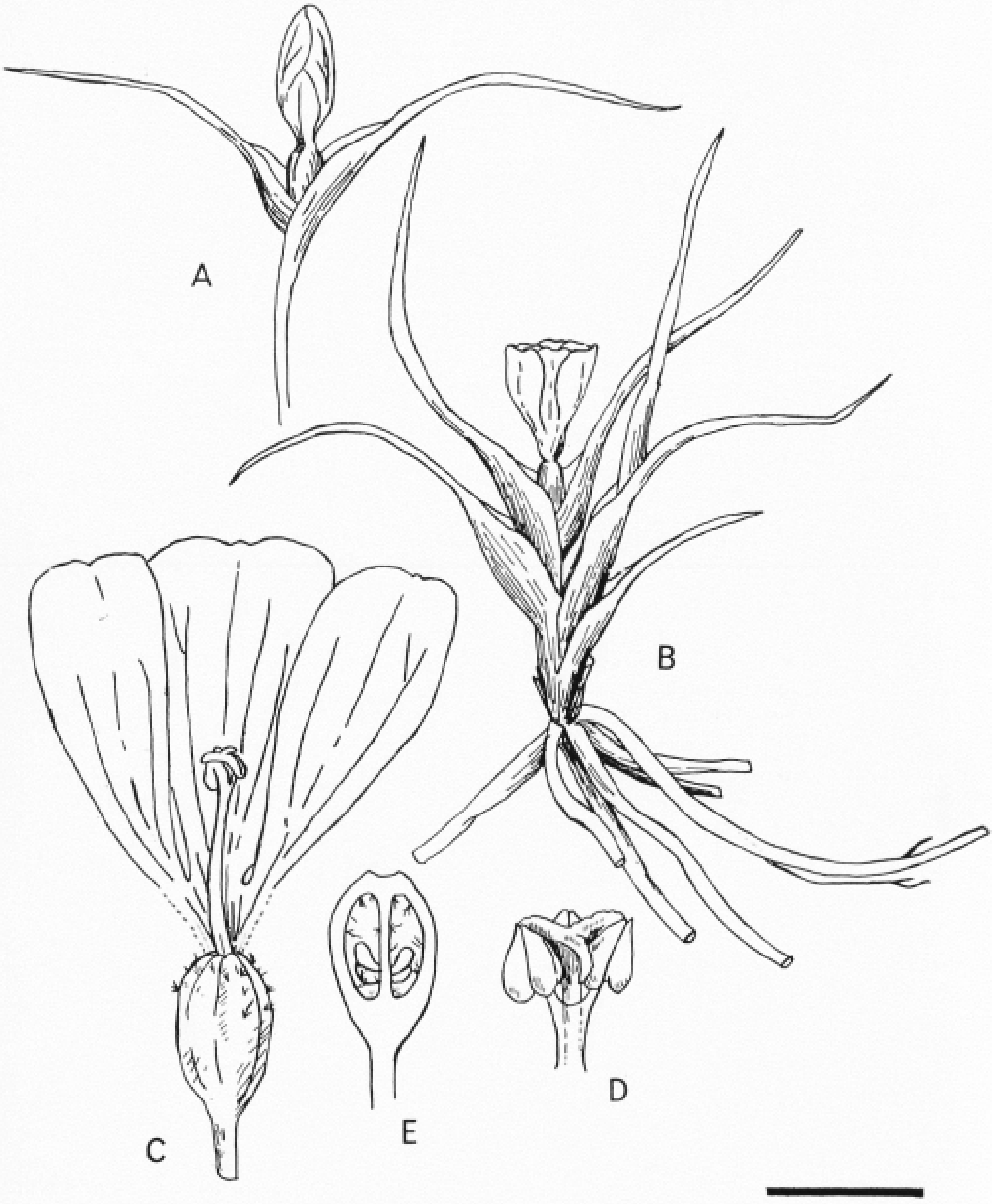


Fig. 1. *Tapeinia obscura* (Cav.) D. M. Moore. — A—B: Habit. — C: Opened flower. — D: Stigma and anthers. — E: Vertical section of ovary. — Scale = 12 mm for A & B, 4 mm for C & E, 2 mm for D. Drawn from Moore 1625 (LTR).

Fig. 2. *Galaxia* Cav. Photograph of type illustration in Cavanilles' 'Monadelphiae Classis Dissertationes decem', plate 189, fig. 4 D.

Tapeinia pumila, the plant obviously differed in its much less caespitose habit, less pungent leaves with prominent basal sheaths and larger flower. This plant (Fig. 1) is clearly identical with Cavanilles' drawing of *Galaxia obscura* (Fig. 2) and there is no doubt that these are the same species. I have subsequently had the privilege of studying collections from S. Chile and Tierra del Fuego made by Dr. E. J. Godley, botanist with the Royal Society of London Expedition in 1958—59, and have found three further sheets of this same species, all collected at high elevations. Without doubt, therefore, Commerson collected two similar species of small Iridaceae along the Estrecho de Magellan, the well known, widespread, usually coastal *Tapeinia pumila* and the alpine *Galaxia obscura,* which has not been collected since until its rediscovery by Dr. Godley and myself.

Galaxia obscura Transferred to Tapeinia

Galaxia Thunb., as it is currently delimited, comprises about four species and is restricted to South Africa. Amongst other distinguishing characters the plants have a tunicate corm and a slender perianth-tube, and the genus is therefore usually included in the tribe Croceae. Clearly, therefore, Cavanilles was incorrect in placing his new species in *Galaxia,* since it has a very short perianth-tube and possesses a very short rhizome. These characters, together with its undivided style-branches, place the species in the tribe Sisyrinchieae, where it is obviously close to *Sisyrinchium* and *Tapeinia.* As noted earlier, *Tapeinia* is very closely related to *Sisyrinchium,* from which it is distinguished by its habit, its 1-flowered, terminal spathe and by the ovules and seeds being restricted to the lower part of the loculi. Although of somewhat different habit, *Galaxia obscura* possesses all the above characters of *Tapeinia* and must be referable to that genus. Unlike the type species it has the filaments connate almost throughout their length, less crowded leaves with prominent basal sheaths, a slightly or unbranched stem and larger flowers (<9 mm in *T. pumila*). None of these characters suggests the necessity for erecting a new genus, particularly since *Sisyrinchium* possesses a comparable variability in such characters, and it seems clear that *Galaxia obscura* must be included in *Tapeinia,* the appropriate combination being as follows:

Tapeinia obscura (Cav.) D. M. Moore comb. nov.

Galaxia obscura Cav., Monad. Class. Diss. Dec. 341, t. 189 fig. 4 (1788).
? *Sisyrinchium frigidum* Poepp., Fragm. Syn. Pl. Phan., 1 (1833).

Plant 3—6 cm; stem simple or with 1—2 branches arising in axils of lower leaves, usually solitary, enclosed by leaf-basis, with very short vertical rhizome bearing rather stout roots. Leaves 2—8, alternate, distichous, up to 30×1 mm, linear-subulate, acuminate, usually arcuate, glabrous, widening at base into an open, pale scarious sheath 8—18×4—9 mm. Flower solitary, terminal, exceeded by upper leaves. Perianth 8—14 mm, campanulate-infundibuliform, but frequently unopened and ellipsoidal, white or very pale yellowish; segments 2.5—4.5 mm wide, the inner slightly narrower than the outer, oblanceolate, obtuse to truncate, shallowly emarginate, mucronulate, imbricate, connate for basal 1/7—1/6. Anthers ovoid, at same level as stigma; filaments connate almost to apex. Style up to 4 mm, filiform, 3-lobed, the stigmatic lobes undivided; ovary c. 4 mm, obovoid—ellipsoidal, glabrous or with small tufts of minute hairs in upper part, 3-locular, with ovules in lower half of each loculus. Mature fruit not seen.

DISTRIBUTION: Fig. 3. Open ground obove timberline (515—720 m) on mountains along Canal Beagle and north along the Chilean coast to Isla Wellington (49° 80′ S). Perhaps further north.

TYPUS: Chile, Magallanes, mountains behind Puerto Galant. xii—i. 1767—68. Commerson s. n. (Cavanilles, Monad. Class. Diss. Dec. t. 189, fig. 4).

MATERIAL SEEN: Tierra del Fuego. Isla Grande: Estancia Moat, mountain at head of Rio Chico (54°53′ S, 66°53′ W), damp ground beside stream, c. 1700 ft., 26. i. 1968, Moore 1625 (BAB, K, LTR); Isla Navarino: Puerto Williams, open tableland, c. 2100 ft., 7. i. 1959, Godley 887 (CHR, K). — Chile. Magallanes: Peninsula Muñoz Gamero, Seno Aguila, open ground high on mountain, 27. xii. 1958, Godley 802 (CHR, K); Isla Wellington: Puerto Eden, high altitude, 16. xii. 1958, leg. Kuschel, Godley 702 (CHR, K).

ACKNOWLEDGEMENTS

I am grateful to the Royal Society of London for the award of a government grant-in-aid which enabled me to carry out the field work, and to Dr. E. J. Godley for permitting me to study his South Chilean and Fuegian collections. I am indebted to Dr. W. T. Stearn for providing me with the information on the publication date of G. Forster's 'Fasciculus' and to Mrs. R. N. Goodall, who prepared the drawing on which Fig. 1 is based. Professor V. H. Heywood kindly examined the type of *Ixia magellanica* in Paris.

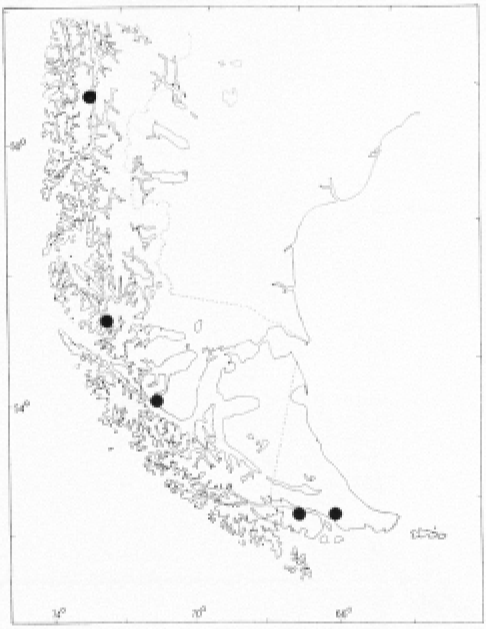


Fig. 3. Distribution of *Tapeinia obscura* (Cav.) D. M. Moore.

LITERATURE CITED

Cavanilles, A. J. 1788. Monadelphiae Classis Dissertationes decem, pp. 267—354. — Madrid.

Dusén, P. K. H. 1900. Die Gefässpflanzen der Magellansländer. — In: Wiss. Ergebn. schwed. Exped. Magellansländ. 3 (5): 77—266.

Godley, E. J. 1965. Botany of the southern zone: exploration to 1843. — Tuatara 13 (3): 140—181.

Hooker, J. D. 1847. Botany of the Antarctic voyage. Vol. 1: Flora Antarctica. Pt. 2: Botany of Fuegia, The Falklands, Kerguelen's Land, etc. — London.

Jussieu, A. L. 1789. Genera plantarum secundum ordines naturales disposita, . . . — Paris.

Poeppig, E. F. 1833. Fragmentum Synopseos Plantarum Phanerogamarum. — Leipzig.

Rickett, H. W. and Stafleu, F. A. 1961. Nomina generica conservanda et rejicienda spermatophytorum. VIII. Bibliography. — Taxon 10 (4): 111—121.

Vahl, M. H. 1805. Enumeratio plantarum . . . 2. — København.

Willdenow, C. L. 1797. Species Plantarum. Ed. 4. 1 (1): 1—495. — Berlin.

Studies in Montia L., Claytonia L. and Allied Genera V

The Genus Montiastrum (Gray) Rydb.

By Örjan Nilsson

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

Nilsson, Ö. 1971. Studies in Montia L., Claytonia L. and allied genera V. The genus Montiastrum (Gray) Rydb. — Bot. Notiser 124: 87—121.

The genus *Montiastrum* (Gray) Rydb. (subfam. Montioideae, Portulacaceae) is circumscribed and its relations to the genera of the *Montia* group are discussed. Its main characteristics are: *1.* perennial or annual, small herbs; 2. leaves alternate, ± linear and sessile, sheathing at the base; *3.* stomata on both leaf-sides, subsidiary cells often four; *4.* inflorescences terminal or pseudo-lateral, pedunculate, common axis elongate, bract normally one; *5.* involucre longer than capsule, usually distinctly parallel-veined; *6.* tepals five, shortly petiolate, almost free; *7.* stamens five or three; *8.* capsule dehiscing almost to the base; *9.* seeds (normally) three, usually distinctly keeled, attachment plate in a depression, strophiole very minute, testa smooth; *10.* pollen grains pantocolpate, spherical, tholate.

The genus comprises four species: *M. vassilievii* (Kuzen.) Ö. Nilss., *M. bostockii* (Porsild) Ö. Nilss. comb. nov., *M. dichotomum* (Nutt.) Rydb., and *M. lineare* (Dougl.) Rydb. *M. vassilievii* is a poorly known endemic in easternmost Siberia, while the remainders are North American. *M. dichotomum* and *M. lineare* are annuals concentrated to the Columbia River System in NW. United States, the latter extending to southern California and central British Columbia. *M. bostockii* is a perennial, endemic in a small area between Alaska and SW. Yukon Territory.

The branching habit and its evolutionary trends are discussed. The anatomy of leaves and stem, the phyllotaxy, the morphology of cotyledons, leaves, bracts, and inflorescences are described. Floral structures, pollination mechanisms, and breeding systems are considered. The perennial species have large allogamous, protandrous flowers with five stamens. In the autogamous annuals, homogamic flowers with reductions in size and number of stamens occur. The unique pollen grains have spiniferous tholi effective in the aggregation of the grains. They are presumed to have evolved in response to insect-pollination. Function and efficiency of seed dispersal are considered.

The reproductive systems of annual and perennial species are compared. *M. bostockii* reproduces sexually by outbreeding, and is also propagated vegetatively. The annuals are predominantly inbreeding and are characterized by a high and regular seed set. Their reduced genetic variability is partly compensated by a high phenotypic plasticity.

M. dichotomum is a winter annual with insignificant infraspecific variation. In *M. lineare* the occurrence of winter annual and summer annual forms are discussed. The latter is presumed to have evolved from the former.

INTRODUCTION

The difficulties in generic delimitation in the subfamily Montioideae (sensu Pax & Hoffman 1934 p. 257) have been emphasized in previous papers (Nilsson 1966, 1967, 1970). The *Claytonia*—*Montia* complex has been interpreted in at least three different ways in recent literature (cf. Bogle 1969 pp. 585—589).

The present author favours a splitting

of the complex into several genera. Most of these were established by Rydberg and with a few exceptions correspond to previously recognized sections of *Montia* or *Claytonia*. The present study is intended to give the genera more definite and natural circumscriptions and attempts are made to elucidate the evolutionary relationships in the group.

The subfam. Montioideae was divided by Nilsson (1970 p. 120) into two main groups, the *Claytonia* group and the *Montia* group. The former contains only the genus *Claytonia* L. itself (and probably *Lewisia* Pursh) sensu Swanson (1966) and Nilsson (1967). The *Montia* group comprises eight genera, among them *Montiastrum* (Gray) Rydb. which deviates in several respects, however, and seems to represent a separate evolutionary line (cf. p. 90).

MATERIAL AND METHODS

The descriptions are based on herbarium specimens. Material from the following herbaria has been studied: BM, C*, CAN, E*, F, GB, GH*, JEPS*, K*, LA*, LD*, LE, M, MO, MT, NY*, ORE*, OSC*, PRC, S*, SMU, UBC*, UC, UPS, US, V*, WS*, WTU* (in herbaria marked with * the entire *Montiastrum* material has been examined; the abbreviations follow Index Herbariorum, Ed. 5, 1964).

Montiastrum lineare and *M. dichotomum* have been cultivated in the Lund Botanical Garden. In addition to the collections listed in Nilsson (1966 pp. 464—466) some material has been raised from seeds of the following herbarium specimens: *M. dichotomum*: Idaho, Latah Co., W. H. Baker 7353; *M. lineare*: British Columbia, E of Oliver, K. Bearmish & F. Vrughtman 60098; Oregon, Wallowa Co., G. Mason 6192; Oregon, Jefferson Co., Black Butte, J. M. Johnson 398.

To avoid mechanical injury of floral structures, emasculation was performed by filling buds or young flowers with water which kills the pollen grains almost instantly by osmotic shock. The water containing the pollen was sucked up by means of a thin pipette. The stigmas may be examined under the microscope to check whether any pollen grains remain. The flower was left for one day before artificial pollen application. If self-pollination has taken place before the water treatment, the tepals will fade and the flower does not open the next day (p. 110).

Germination of pollen grains and growth of pollen tubes were studied in living flowers. After artificial pollination *in situ*, the pistil was cut off and fixed in Carnoy 1 : 1. The preparation was carefully rinsed in water, transferred to a c. 10 % pectinase solution for one to two hours, stained in lacto-phenol and gently squashed. The slides can be studied under the microscope after two to five hours. It is essential to apply as few pollen grains as possible to be able to follow the individual pollen tubes in the style tissue.

Anatomical preparations and pollen preparations according to the acetolysis method were mainly made from herbarium specimens. Dry pollen grains for the scanning electron microscopy preparations were shadowed with palladium vapour in high vacuum. The studies were performed with a Cambridge Electro-Scanning microscope; Kodak Plus-X Pan film was used for the photographs. Electromicrographs of sectioned pollen grains and some of the acetolysed pollen preparations were made at the Palynological Laboratory, Solna, Sweden (cf. Erdtman 1969 p. 402).

The sticky substances covering the surface of the pollen grains were studied. Living or recently dried pollen grains were placed on a slide in safranin coloured water (cover slip should not be applied). The oily substances then form minute transparent, globules adhering to the grains. The globules are almost uniform in size, and by counting them along the periphery of the grain the amount of sticky substances can be roughly estimated.

The illustrations of some organ details are camera lucida drawings made from preparations in which the vascular system was stained with safranin. The surrounding tissue was often made transparent with lactic acid. Dry material was soaked in water before the treatment. Some of the illustrations, e.g., those of inflorescences and branching systems, are simplified and diagrammatic.

TAXONOMY

Montiastrum (Gray) Rydberg, Fl. Rocky Mts., Ed. 1. 265, 1061 (1917), emend. Ö. Nilsson.

Claytonia L. p.p. in Hooker 1833 p. 224; *Claytonia* [sect.] *Naiocrene* Torrey & Gray 1838 pp. 201—202 p.p.; *Claytonia* [sect.] *Montiastrum* Gray 1887 pp. 283—284 p.p.; *Claytonia* sect. *Pseudo-Claytonia* v. Poellnitz 1932 pp. 281—282 p.p. ("*Pseudo-Montia*" p.

284); *Claytonia* sect. *Microclaytonia* KUZENEVA in KOMAROV 1936 p. 383, not validly published. (*Claytonia* § *Limnia* **** *Montiastrum* GRAY 1887 pp. 280—284.)

Montia L. p.p. in GREENE 1891 p. 180; *Montia* [sect.] *Montiastrum* (GRAY) ROBINSON 1897 p. 276 p.p.; *Montia* sect. *Montiastrum* (GRAY) PAX & HOFFMANN 1934 p. 259 p.p.; ditto sensu SWANSON 1966 p. 232.

Type species: *Montiastrum lineare* (DOUGL.) RYDB. (cf. RYDBERG 1932 p. 296).

Perennial or annual, somewhat succulent, glabrous, small-sized herbs. *Stems* terete, sometimes with adventitious roots at least at the basal nodes, erect, ascending or repent, usually 5—15 cm, short-lived, ± branched or simple. *Leaves* simple, alternate, often somewhat crowded at the base, entire, flat to semiterete with a ± concave abaxial side, sessile or sometimes indistinctly petiolate, linear, linear-spathulate or very narrowly oblanceolate, narrowly obtuse to acute, often 3-veined with a ± sunken median vein; leaf base much dilated with scarious margins, half-clasping, shortly sheathing. *Stomata* on both sides of the leaf, usually somewhat sparser on the abaxial side, often slightly sunken; subsidiary cells ± distinct, 2—4 (often 4), parallel to the guard cells; guard cells with distinct external and internal ledges; epidermal cells with straight or ± undulating side walls, cuticle thick, often distinctly wrinkled. *Inflorescences* one to many on floriferous shoots, terminal (or pseudo-lateral), scorpioid cymes with a few to many flowers (usually 3—10); and normally a single comparatively large, usually ovate, half-clasping, papery and ± green bract opposite the lowermost pedicel; axis usually erect and elongate; peduncle ± erect, elongate. *Pedicels* after anthesis recurved from the base like a bow, or ascending and hooked in the distal part. *Involucral leaves* two, opposite, almost equal, very broadly obovate or rounded, obtuse, truncate or slightly emarginate, the outer laterally clasping the inner, usually growing considerably after anthesis, becoming distinctly longer than the capsule, usually with distinct ± parallel veins, persistent, often turning reddish when dry. *Tepals* five, almost free, equal, or the three opposite the stamens somewhat smaller and narrower, 1—3 times as long as the involucre, obovate to narrowly spathulate, obtuse to slightly emarginate, shortly clawed; tepal limb patent to ascending from an almost erect claw, veins in the distal part of the limb often strongly undulate. Flowers protandrous or homogamic, in the annual species sometimes cleistogamous and much reduced. *Stamens* five or three, opposite the tepals, about 2/3—1/2 of the tepal length, free from each other but filaments at the base dilated, flattened and adnate to the tepals, anthers two-celled, extrorse to laterorse. *Style* as long as the ovary or up to about twice as long, thin, distinctly set off from the ovary and after anthesis falling off from a distinct point; *style branches* three, rather long, diverging and recurved when receptive, stigmatic area confined to the adaxial surface, papillae thin and crowded. *Ovary* broadly obovoid to pear-shaped, indistinctly stipitate; ovules three. *Capsule* ± broadly obovoid, often somewhat triangular and trisulcate at the base, with a rather distinct apical point formed by the style base; valves three, dehiscing almost to the base, becoming reflexed and involute. *Seeds* often three, lens-shaped to obovoid and compressed with a lateral, usually distinct keel, attachment plate in a depression, strophiole very minute, brownish, and not protruding; testa smooth with rounded cells on the central areas and oblong ones along the keel, black. *Pollen grains* pantocolpate, spherical, and tholate (cf. NILSSON 1967 pp. 354—355).

The genus *Montiastrum* has four species, the perennial *M. vassilievii* (KUZEN.) Ö. NILSS. and *M. bostockii* (PORSILD) Ö. NILSS., and the annual *M. dichotomum* (NUTT.) RYDB. and *M. lineare* (DOUGL.) RYDB. In vegetative characters *M. vassilievii* and the two annual species show some affinity (p. 104), while *M. bostockii* is more different. The flowers of the two perennial species are similar and not reduced. In floral morphology the annuals are divergent and more advanced. In view of the perennial habit and unreduced flowers, *M. bostockii* and *M. vassilievii* may be regarded as more primitive.

Montiastrum differs notably in several characters from other genera in the *Montia* group, and its relations to them are uncertain. Some of the distinguishing features are in common with one or a few of the other genera, but the combination of characters gives *Montiastrum* a distinct and natural circumscription.

Historical Survey

Hooker (1833 p. 224) placed the first described species of *Montiastrum*, *M. lineare*, in *Claytonia*. Torrey and Gray (1838 pp. 201—202) described *C. dichotoma*, which together with *C. linearis*, *C. parvifolia*, and *C. diffusa* were placed in the "section" *Naiocrene*. In 1887 the "section" *Montiastrum* of *Claytonia* was established by Gray. It included *C. linearis*, *C. dichotoma*, and *C. diffusa*. The section *Pseudo-Claytonia* (v. Poellnitz 1932 p. 313) included *C. linearis*, *C. dichotoma*, and *C. howellii*. Some annual species of *Claytonia* (including *C. linearis*) were transferred to *Montia* by Greene (1891 p. 180).

The section *Montiastrum* (of *Claytonia* or *Montia*) has, beside the species *M. linearis* and *M. dichotoma*, also included other species of the *Montia* group which belong to different genera according to the present treatment. Swanson (1966 p. 232) restricted the section *Montiastrum* (of *Montia*) to include *M. linearis* and *M. dichotoma*.

In 1917 Rydberg established the genus *Montiastrum* with the single species *M. lineare*. Later Rydberg (1932) included also *M. dichotomum* and *M. howellii* in the genus. Rydberg's generic concept has been followed here, but in a modified form. *M. howellii* is excluded and two perennial species are added.

Swanson (1966) divided the genus *Montia* into four sections (cf. Nilsson 1970 p. 123). The section *Montiastrum* was distinguished, e.g., by the following characters: strictly annual, basal rosette lacking, cauline leaves alternate, acicular-linear with a sheathing base, inflorescences simple racemes terminating each branch, adventitious roots lacking, and pollen grains tholate. Swanson's description of the section was adapted to the annual species only, and thus it cannot be directly applied to the genus *Montiastrum* in the circumscription given here.

Montiastrum was placed in the *Montia* group of the subfamily Montioideae by Nilsson (1970 p. 120) but it was emphasized that the genus is deviating. *Montiastrum* has been retained in the group primarily because of agreement in floral and inflorescence features and in anatomy.

KEY TO THE SPECIES

1 A. Perennials. Stamens 5. Tepals twice as long as the involucre or longer .... 2.
1 B. Annuals. Stamens normally 3. Tepals less than twice as long as the involucre ... 3.
2 A. Caespitose, with no repent stems. Flowering shoots with one upper leaf. All leaves linear, sessile. Tepals about twice as long as the involucre. Bract broadly ovate .... 1. *M. vassilievii* p. 90
2 B. Stems repent with ascending floriferous, many-leaved shoots. Basal leaves narrowly oblanceolate, ± distinctly petiolate. Tepals about three times as long as the involucre. Bract ovate .... 2. *M. bostockii* p. 92
3 A. Seeds broadly obovoid, flattened, 0.8—1.2 mm long, dull to somewhat shining. Inflorescences usually 5—16 per plant, with often 7—13 flowers each. Involucre broadly pitcher-shaped, often c. 2 mm long .... 3. *M. dichotomum* p. 95
3 B. Seeds orbicular, lens-shaped, 1.4—2.5 mm long, highly shining. Inflorescences usually 1—8 per plant, often with 3—8 flowers each. Involucre cup-shaped, often 4—5 mm long .... 4. *M. lineare* p. 98

1. **Montiastrum vassilievii** (Kuzen.) Ö. Nilss. Grana Palynol. 7 (2): 360 (1967).

Claytonia Vassilievii Kuzeneva in Komarov 1936 pp. 383, 880.

ORIGINAL COLLECTION: USSR, basin of Anadyr, at Mt. Irgunej in the Raritkin mountain ridge, 1933, V. Vassiliev 1661. (LE holotype; cf. Kuzeneva in Komarov 1936 p. 880. The collector was incorrectly named Bacumjef in Nilsson 1967 p. 360.)

The following description is partly com-

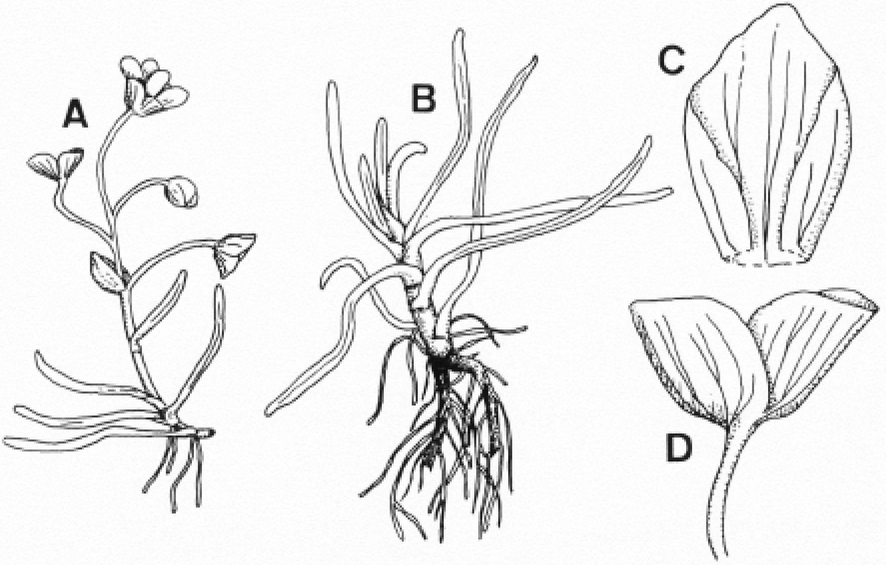


Fig. 1. *Montiastrum vassilievii.* — A: Habit of a floriferous shoot. — B: Habit of a vegetative shoot. — C: Bract. — D: Involucre.

piled according to KUZENEVA in KOMAROV 1936 p. 880, VOLKOVA 1964 pp. 1760—1762, and ALIOSHINA 1963 pp. 1195—1196. The limited material, a single sheet, does not permit a complete description.

Dwarfish, perennial and probably caespitose. *Subterranean stem* ± vertical, rather long, slender, with fibrous adventitious roots particularly at the nodes, branched with aerial floriferous and vegetative shoots. *Vegetative shoots* with 3—11 very short internodes and crowded leaves (Fig. 1 B). *Flowering stem* 2—4 cm long, c. 1 mm thick, erect to ascending, with 3—5 very short basal internodes (c. 2—5 mm) the upper one or two internodes longer (c. 1 cm), stem-base with crowded leaves, the upper part of the stem with only one leaf (Fig. 1 A). *Leaves* linear, subterete, erecto-patent, sessile, the basal ones 1.5—3 cm long, 1—2 mm broad, the upper one c. 1 cm long and 1 mm broad, subacute to obtuse; leaf base almost amplexicaul with broad scarious margins. *Inflorescence* terminal, 2—5-flowered, axis up to 2 cm long. *Peduncle* c. 1 cm long. *Bract* one, comparatively large, broadly ovate, 4—6 mm long, 3.5—5 mm broad, subacute, semi-membranous with distinct parallel veins (Fig. 1 C). *Pedicels* 10—15 mm long at anthesis, later somewhat elongate and recurved. *Involucral leaves* very broadly obovate, 3—4 mm long and c. 5 mm broad, truncate to broadly obtuse, with a very distinct parallel veining, becoming reddish when dry (Fig. 1 D). *Tepals* of almost equal size and shape, 6—8 mm long, obovate, obtuse, all laterally united at the base for about 1/3 of their length, white. *Stamens* five, of about equal length, 3—4 mm long, distinctly shorter than the tepals, at the base adnate to the tepals for half the length of the filaments. Pistil and capsule not known. *Seeds* almost orbicular, lens-shaped. *Pollen grains* 52—60 μ in diam. excluding the tholi; tholi 8—24, 8—10 μ high and 13—16 μ wide; spinulae 1.2 μ long, 0.6 μ wide at the base.

DISCUSSION

Originally the species was referred to *Claytonia* (Kuzeneva in Komarov 1936 p. 880), but in a section of its own, *Microclaytonia* Kuzen. Some characters like the sessile, alternate leaves, the "single" leaf of the flowering stem, and the large bract at the base of the inflorescence were emphasized as important to distinguish *Microclaytonia* from the other three sections of the genus represented in the Siberian flora.

Alioshina (1963 p. 1193) noted that *Claytonia vassilievii* differed markedly from other *Claytonia* and resembled species of *Montiastrum* in its pollen morphology. Although retaining the species in *Claytonia*, she indicated that it might well be transferred to *Montiastrum* on account of this character.

In the study of the *Claytonia* species of the USSR, Volkova (1964 pp. 1761—1762) realized that *C. vassilievii* did not fit well in the genus. The pollen morphological affinities to *Montiastrum* pointed out by Alioshina were considered, but since *C. vassilievii* has five stamens and the *Montiastrum* species known at that time only three, Volkova suggested instead that it might be placed in a new section of the genus *Montia*. She did not, however, make the necessary nomenclatural changes.

Pollen morphology and several gross morphological characters indicate a close relationship between this species and the North American members of the genus *Montiastrum*, and it seems natural to treat the species within this genus. In habit it somewhat resembles small specimens of *M. lineare* (p. 103).

DISTRIBUTION AND HABITAT

Montiastrum vassilievii is a local endemic known only from the original locality in the Anadyr Basin in northeastern Siberia. The Siberian occurrence of this species gives the genus *Montiastrum* a distribution which is somewhat similar to that of the genus *Claytonia* (p. 118).

The species grows in wet and clayey places on bare soil on steep mountain slopes.

FLOWERING PERIOD: August.

2. **Montiastrum bostockii** (Porsild) Ö. Nilss. comb. nov.

Claytonia Bostockii A. E. Porsild 1951 pp. 160—161, 362.

ORIGINAL COLLECTION: Canada, Dawson Range, south of Selkirk near source of Klaza River, approximate lat. 62°20′N. and long. 137°30′W., muskeg on north-facing slope, elevation 4200 feet, 1933, H. S. Bostock 19 (CAN holotype; cf. Porsild 1951 p. 161.)

Perennial, forming loose mats by supraterranean runners. *Stems* repent with ascending to erect floriferous shoots; *repent stems* (stolons) 5—15 cm long, 0.5—1 mm thick, very delicate, leafy at least in the apical part, sparsely or not ramified, sometimes with a few fibrous adventitious roots mainly in the distal part, internodes often 5—12, 5—15 mm long, hibernating but short-lived, usually with flowering shoot in or near the distal part; *floriferous stem* 6—12 cm high, c. 1 mm thick, unbranched, with 3—7 leaves mainly at the base; basal internodes 0.3—1.5 cm, uppermost 2—3.5 cm (Fig. 2 A, B). *Leaves* ± erect to erecto-patent, linear to very narrowly oblanceolate or linear-spathulate, 0.8—4 cm long, 1.5—3 mm broad, obtuse to subacute, sessile or the basal leaves often petiolate; "petiole" ± distinct, up to 3.5 cm long, "blade" 1—1.5 cm long. Epidermal cells of the leaf "blade" large, irregular in shape with strongly undulating side walls, those of the upper stem leaves smaller with almost straight side walls. *Inflorescence* single, terminal, axis 0.5—2 cm, occasionally one or two internodes not developing, flowers 2—6. *Peduncle* 2—6 cm, erect. *Bract* usually one (very rarely two), 4—7 mm long, 3—4 mm broad, usually ovate, acute—obtuse, semi-membranous or sometimes resemb-

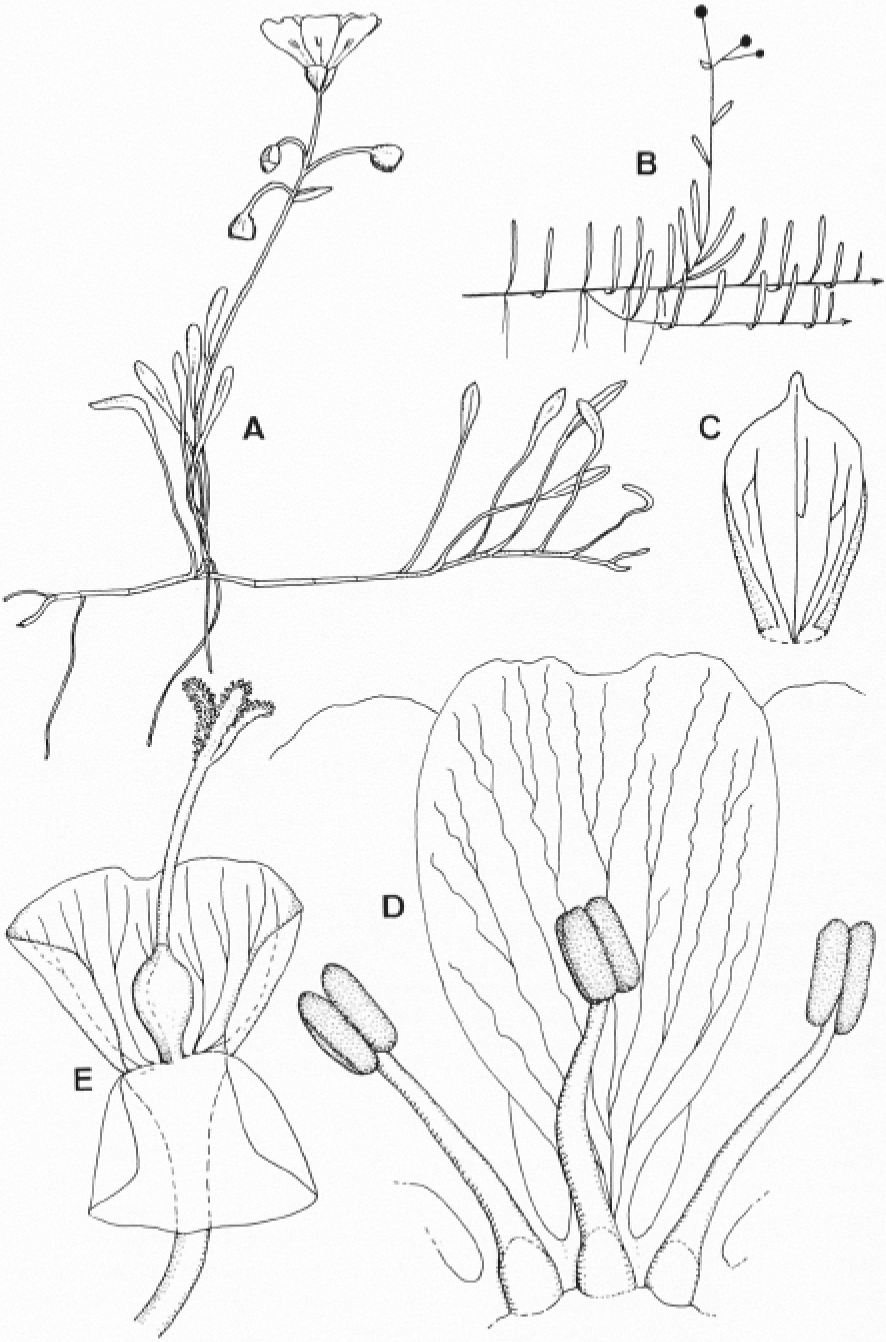


Fig. 2. *Montiastrum bostockii.* — A: Habit of a plant. — B: Diagrammatic drawing of a plant showing the type of branching, the arrows indicating lateral shoots. — C: Bract. — D: Involucre and pistil, the upper involucral leaf is the outer one. — E: Part of the perianth with stamens.

ling small, normal leaves (Fig. 2 C). *Pedicel* 4—11 mm at anthesis, after anthesis recurved and somewhat elongate, up to 20 mm. *Involucral leaves* very broadly obovate, 3.5—4.5 mm long at anthesis, up to 5.5 mm after anthesis, obtuse to retuse, somewhat longer than the capsule, green or reddish with a narrow white scarious margin, veins ± parallel, not very distinct (Fig. 2 E). *Tepals* equal, about 3 times as long as the involucre, 10—13 mm long, 5—7 mm broad, obovate, obtuse to slightly emarginate, flat, shortly (1.5—3 mm) clawed, laterally united at the base for c. 1 mm, white (or pink) with a yellowish claw and sometimes with distinct pink veins (Fig. 2 F). *Stamens* five, equal, 5—7 mm long, about half as long as the tepals; filament base adnate to the tepals for 1—1.5 mm; anther 1.5—1.8 mm long, c. 1 mm broad, versatile, ± extrorse, yellow (Fig. 2 F). Flowers protandrous. *Style* slender, c. 3 mm long at the beginning of anthesis, elongating to c. 5.4 mm at the end of anthesis; *style branches* 0.8—1.3 mm, elongating and diverging during the "female" phase of the flower, with rather short papillae. *Ovary* 1.7—1.9 mm long, 0.8 mm wide, obovoid to pear-shaped (Fig. 2 E). *Capsule* broadly obovoid, smooth, slightly triangular at the base, 3.8—4.5 mm long. *Seeds* (not entirely ripe) broadly obovate to almost orbicular, lens-shaped, laterally much flattened, keeled almost all around, 1.5—1.7 mm long, shining. *Pollen grains* 40—55 μ in diam.; colpi 7.6—9.0 μ long, about 60—65 colpi delimiting 20—28 rather regular hexagons or often pentagons, some colpi not developing; tholi 20—28, often 24, 12—16 μ in diam., 9—13 μ high; basal areas 11—14 μ, spinulae on each tholus 12—22, rather coarse and blunt, 2—2,5 μ long; tholi and basal areas distinctly punctate (p. 111, Fig. 9).

DISCUSSION

The species was placed in *Claytonia* by Porsild (1951 pp. 160—161) and kept in that genus by Davies (1966 p. 302) and Hultén (1968 p. 406). Previously an Alaskan collection (Murie 190) which belongs to this species was referred to as *Claytonia* sp. by Hultén (1944 pp. 543—544). He considered the species to be closely related to *C. vassilievii* Kuzen., a judicious supposition.

The flowers of *Montiastrum bostockii* resemble those of some perennial *Claytonia* species, e.g., *C. sarmentosa* C. A. Mey. and *C. arctica* Adams. The flowers are comparatively large and regularly pentamerous, with ± emarginate, almost free tepals. They are evidently protandrous (p. 108) with extrorse and versatile anthers and a long style.

The perennial *Claytonia* species have six ovules, however, while *Montiastrum bostockii* has three, and the seeds differ in shape. The *Claytonia* species have rosulate leaves and a pair of opposite leaves on the floriferous branches. The inflorescences are borne on specialised lateral branches on a usually very short, long-lived main stem. In *Montiastrum bostockii* the leaves are all alternate and borne all along the stem; the inflorescence is single and terminal and the repent stems are elongated and short-lived (p. 102). The pollen grains of *Claytonia* are tricolpate of an ordinary type, but the pollen grains of *Montiastrum* are tholate (p. 111).

When the pollen grains of *M. bostockii* were found to be tholate the species filled an evolutionary gap. The two annual species which were studied first are autogamous with reduced flowers. Therefore it was of great interest that there existed a recent, perennial and allogamous species with the same pollen type. This pollen type is supposed to have evolved in an insect-pollinated flower (p. 111).

Gross morphology and pollen morphology makes it natural to treat the species in the genus *Montiastrum*. If compared with the annual species, *M. bostockii* shows several morphological features which seem to be more primitive, e.g., the perennial habit, the actinomorphic large flower with five stamens, and a long style.

There is little variation in the examined material (cf. Appendix). The flowers of one collection (Schofield & Crum 8048) are more deeply pink than the others.

The similarity between *M. bostockii* and *M. vassilievii* was pointed out by Hultén (1944). Both are perennial and have unreduced flowers of considerable size. They occur in the northernmost part of the distribution area of the genus, but on different sides of the Bering Strait. Their present area does not overlap that of the annual species in the south (p. 118).

DISTRIBUTION AND HABITAT

Montiastrum bostockii is probably restricted to a small area in the borderland between southern Alaska and the Yukon Territory. The area is located north of the Wrangell Mts. in the highland of the upper Yukon River. The species is known from one locality in Alaska and from about six in the Yukon Territory. It grows on wet, often north-facing slopes at 1200—1500 m, and on wet alpine tundras.

A specimen from Manitoba collected by P. A. Taverner certainly belongs to this species (cf. Porsild 1951 p. 161), but the collection needs confirmation as indicated by Hultén (1968 p. 406). A similar disjunction does occur, however, in *Crunocallis chamissoi* (Nilsson 1970 p. 137).

3. **Montiastrum dichotomum** (Nutt.) Rydberg, N. American Fl. 21 (4): 296 (1932).

Claytonia dichotoma Nuttall in Torrey & Gray 1838 p. 202; *Claytonia dichotoma* Nutt. sensu Gray 1887 p. 284 p.p. (includes "*Montia Howellii* S. Wats.").

Montia dichotoma (Nutt.) Howell 1893 p. 36.

Claytonia spathulata Dougl. in Hooker 1847 p. 230; *Claytonia linearis* Dougl. p.p. sensu Davies 1952 p. 275; *Claytonia linearis* Dougl. var. *dichotoma* W. H. Baker 1956 p. 35.

ORIGINAL COLLECTION: [USA, Oregon] Columbia f. Wahlamet plains (Nuttall; BM lectotype, isotypes in NY, and perhaps also in GH and K, but in the latter two the locality is Oregon; cf. Piper 1906 p. 251. "Type locality: In wet places on rocks, near the junction of the Wahlamet with the Oregon. Collected by Nuttall.").

Annual, dwarfish herb. *Primary root* very thin, persistent with fibrous lateral branches, occasionally with additional adventitious roots from the basal nodes. *Cotyledons* linear, 1.2—2.4 cm long. *Stem* 2.0—9.5 cm long (usually 3.5—6 cm), 0.8—1.2 mm thick, erect to ascending, usually much branched, at least at the base, main stem usually not distinct (p. 104), branches often many-leaved; basal internodes usually very short, 0.5—2.0 mm, upper internodes longer, the uppermost 0.4—1.6 cm (Figs. 3 A, B; 7 A). *Leaves* usually numerous on flowering plants (occasionally only 3—6), the basal linear to linear-spathulate, crowded and sometimes withered at anthesis, 0.3—4.5 cm long (usually 1.5—3.5 cm), 0.8—2.0 mm broad, abruptly subacute, almost semiterete, patent to ascending or diffusely spreading, sessile, shortly sheathing. *Stomata* of the leaves often in longitudinal rows, on the abaxial side distinctly sunken; subsidiary cells not always distinct; guard cells 35—42 μ long. *Inflorescences* 2—several (usually 5—16), unilateral, terminal or sometimes pseudolateral, each with 3—17 flowers (usually 7—13), axis usually elongate, 1.0—3.5 cm long (Fig. 7 A). *Peduncle* 0.2—1.6 cm long, usually shorter than the leaf. *Bract* one or occasionally two, 1.8—6.0 mm long, 1.5—3.6 mm broad, ovate to narrowly ovate, half-clasping at the base, obtuse, with very narrow, white scarious margins and usually three ± parallel veins (Fig. 3 C). *Pedicel* 1—4 mm long at anthesis, later elongating, usually recurved from the base and often hook-like at the distal end. *Involucral leaves* broadly ovate—almost circular, 1.2—1.7 mm long at anthesis, green with a very narrow, white margin, after anthesis becoming 1.6—2.5 mm long and 1.5—2.3 mm broad (often 2.0×2.2 mm), distinctly longer than the capsule, obtuse to truncate, with 4—6 somewhat elevated veins; involucre broadly pitcher-shaped, often becoming reddish when dry (Fig. 3 F). *Flower* homogamic, predominantly autogamous (Fig. 3 D), sometimes cleistogamous and then considerably reduced. *Tepals* five, two somewhat larger, obovate to spathulate, 1.6—2.8 mm long and 0.6—1.3 mm broad, about 1.1—1.5 times longer than the involucre (in cleistogamous flowers somewhat shorter than the involucre) ascending to suberect at anthesis, obtuse, claws indistinct, 0.3—0.6 mm long, united for up to c. 0.4 mm, greenish white (Fig. 3 E). *Stamens* normally three, very rarely four or five, 1.2—1.8 mm long, about 2/3 of the tepal length, filaments adnate for c. 0.3 mm anther yellow, medifixed, not versatile, ovoid, 0.2—0.5 mm long, 0.2—0.4 mm broad, ± laterorse (Fig. 3 E). *Ovary* pear-shaped, 0.6—0.8 mm long, 0.5—0.7 mm broad, usually with a short stipe, c. 0.1 mm long. *Style* somewhat shorter than the ovary, 0.3—0.6 mm (Fig. 3 H); *style branches* 0.2—0.3 mm long, diverging, with comparatively long papillae. *Capsule* broadly pear-shaped to obovoid, 1.4—1.8 mm long, 1.2—1.5 mm broad, slightly trisulcate at the base (Fig. 3 G). *Seeds* broadly obovoid, somewhat flattened, 0.8—1.2 mm long (Fig. 10), 0.7—0.9 mm broad, 0.3—0.6 mm thick, usually with a narrow, sharp, but not always distinct keel, dull to somewhat shining (Fig. 3 I). *Pollen grains* 45—49 μ in diam., colpi 35—45, tholi 15—20, 8.5—10.5 μ in diameter, 7.0—8.2 μ high, basal plates c. 2 μ broad, spinulae 8—11 per tholus. *Chromosome number* 2n = 14.

DISCUSSION

Originally this species was described under *Claytonia* (NUTTALL in TORREY & GRAY 1838). It was presumed to be "very nearly related to *C. linearis,* but much smaller in all its parts"; in particular the small flowers and seeds were emphasized. HOWELL (1893 p. 36) transferred the species to *Montia*. HOOKER (1847 p. 230) confused it with *Claytonia spathulata* DOUGL. (but misnamed it *C. linearis* on the label; GEYER, K), and GRAY (1887 p. 284) united it with *Montia howellii* S. WATS. — at least its smallest and most depressed forms he found to agree with NUTTALL's type material (p. 95). *Claytonia dichotoma* was included in *C. linearis* by DAVIES (1952 p. 275), and treated as a variety of *C. linearis* by BAKER (1956 p. 35).

The similarity between *Montiastrum dichotomum* and *M. lineare* has been pointed out by several authors. The smaller size of the former species has been emphasized, and HOLM (1913 p. 8) added that the species was more branched and many-flowered. In the extensive herbarium material examined, surprisingly few sheets were incorrectly determined, and no true intermediates were met with.

Important features of *M. dichotomum* (in addition to the key characters) are the small size, rich and pseudo-dichotomous branching, many-flowered, usually unilateral and numerous inflorescences, and the diploid chromosome number which is reflected in the size of guard cells and pollen grains.

In greenhouse cultivation *M. dichotomum* develops in a way which indicates that it is a winter annual. After germination the plants become rosulate and remain so for up to three months before flowering. In the garden germination takes place in September to October, and flowering in April (cf. Table 3 and p. 114).

The infraspecific variation of *M. dichotomum* seems insignificant and mainly modificative. Plants of dry and sunny sites often become reddish in the vegetative parts. In well-developed specimens a few flowers may have five stamens (p. 108).

The plasticity of the species was studied experimentally. Ten plants raised from seeds of a self-pollinated individual (M. C. MELBOURN) were placed in different environments; five were sparsely and five were well watered. The former developed on the average six inflorescences with

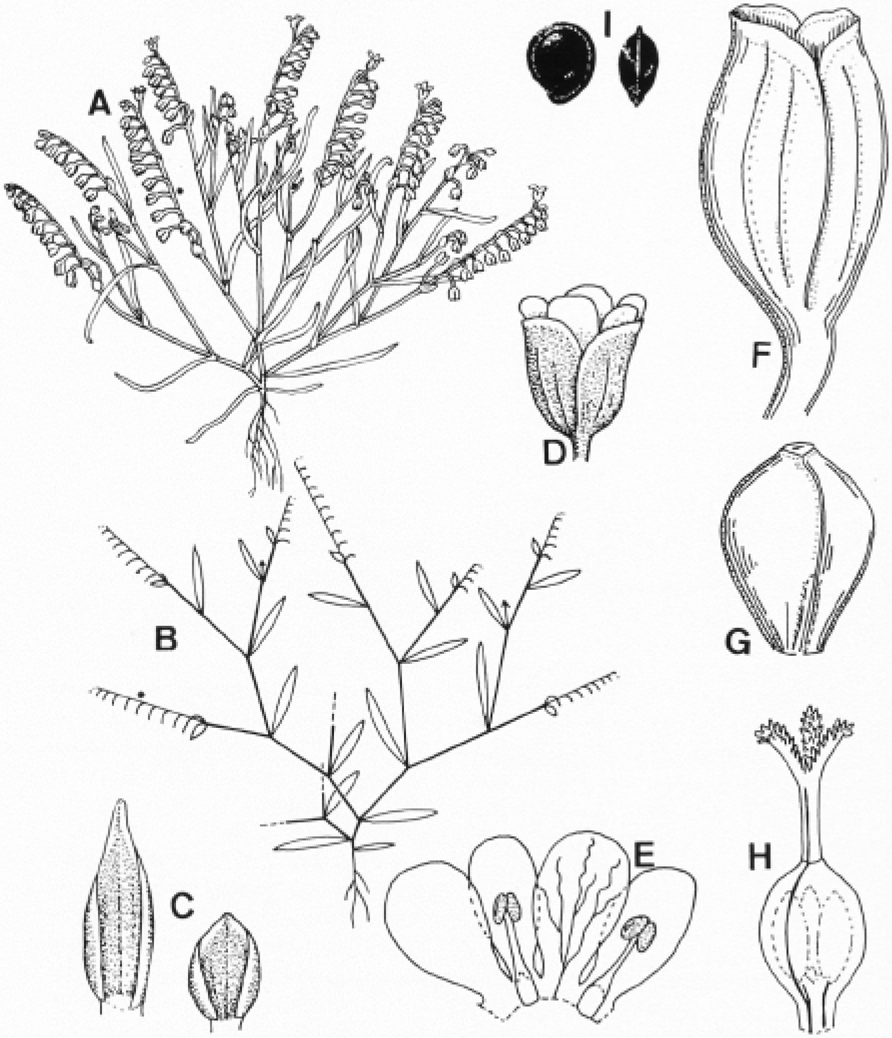


Fig. 3. *Montiastrum dichotomum.* — A: Habit of a plant; * shows the first inflorescence of the main stem. — B: Diagrammatic drawing of a part of A showing the type of branching; * see A, arrows indicate lateral shoots and broken lines omitted parts. — C: Two bracts. — D: Flower. — E: Part of the perianth with stamens. — F: Involucre. — G: Capsule. — H: Pistil. — I: Seeds, the left in lateral view.

nine flowers each, and the latter sixteen inflorescences with twelve flowers each; the latter plants were also large, with longer leaves and branches. When three of the sparsely watered plants were later well watered, new lateral branches with longer leaves and some more rich-flowered inflorescences developed.

Specimens of the same herbarium collection are usually very similar. Two collections have been cultivated (p. 88), and these show only slight differences although they originate from different localities. The species is almost obligately autogamous.

DISTRIBUTION AND HABITAT

Montiastrum dichotomum occurs in western North America and is mainly restricted to the Columbia River System and to the Klamath River (Fig. 6 A). The distribution area falls within that of *M. lineare*, but is considerably smaller.

The species is found on low or moderate elevations, in the Arid Transition and Upper Sonoran Zones, from about 100 m to 700 m. *M. dichotomum* generally occurs on lower elevations than *M. lineare*. It is probably not common anywhere, but it has been collected rather frequently in the Coeur d'Alene area in northern Idaho, along the lower course of the Columbia at Pullman, and near Victoria on Vancouver Island (See Appendix).

M. dichotomum grows in wet or at least in temporarily moist habitats, around muddy springs, banks of streamlets, vernal pools, and moist cliffs. Some of these localities have a shallow soil and become dry in the summer. The species prefers open habitats usually with a flora of vernal annuals in open yellow pine woods, oak woodlands and *Pinus poderosa* grassland. Like *M. lineare* the species sometimes occurs in disturbed habitats, e.g., in roadside ditches and moist grassy fields. It seems to be only occasionally a ruderal.

FLOWERING PERIOD: April to May, extending to the end of June.

4. **Montiastrum lineare** (Dougl.) Rydberg, Fl. Rocky Mts., Ed. 1. 265, 1061 (1917).

Claytonia linearis Douglas in Hooker 1833 p. 224; *Montia linearis* (Dougl.) Greene 1891 p. 181. [*Claytonia linearis* Dougl. p. p. sensu Davies 1952 p. 275; *Montiastrum lineare* (Dougl.) Heller 1907 in Herb. US p. 109.]

ORIGINAL COLLECTION: [USA, Washington] common on the rocks of the Kettle Falls also on the Great Falls, 200 miles from the ocean (in the Columbia River VII. 1826), Douglas. (K lectotype, isotypes in BM and perhaps in E and GH; cf. Piper 1906 p. 251, "Type locality: Moist rocky places; on the Great and Little Falls of the Columbia, abundant. Douglas.")

In the original description of the species "Great and Little Falls of the Columbia" was given as localities. These are then later cited as the type locality. Little Falls is probably an error for Kettle Falls which is the name on the label of the original collection.

Annual. *Primary root* thin, persistent with fibrous lateral branches, sometimes additional adventitious roots from the basal nodes. *Cotyledons* linear, 2—4.5 cm long, sometimes persistent until flowering (Fig. 4 E). *Stem* 3.5—22 cm long (usually 7—13 cm), 1.5—3 mm thick, sometimes reddish, erect or ascending, simple to much branched, branches usually with one to a few leaves, some basal internodes very short, 0.1—2 cm; thus basal leaves often crowded (sometime withered at anthesis), upper internodes longer, the uppermost 0.8—4.5 cm (Figs. 4 A—D; 7 B). *Leaves* 4 to numerous on flowering stems patent to suberect, linear, sessile, shortly sheathing, 1.5—9.5 cm long (usually 2.5—4.5 cm), the basal ones longest, 1—2.5 mm broad, almost semiterete, the abaxial side usually ± flat or slightly concave (Fig. 7 D), the uppermost leaf usually somewhat broader and flatter than the remainder; apex acute to narrowly obtuse; midrib distinct. *Stomata* of the leaf usually in longitudinal rows; subsidiary cells 2—4, on the abaxial side always 4, usually distinct; guard cells 45—52 μ long; epidermal cells of the upper leaf-side with straight or slightly undulating side walls, those of the lower side very long with straight side walls, cuticle smooth on the central part of the abaxial side of the leaf, on the remaining part wrinkled with distinct, minute, longitudinal ridges, 2—9 on each cell. *Inflorescences* 1—10 (—25), often terminal, sometimes unilateral, (2—) 3—8 (—14)-flowered, axis normally elongate, about 2—11 cm long, erect; occasionally a few internodes not developing or varying in other

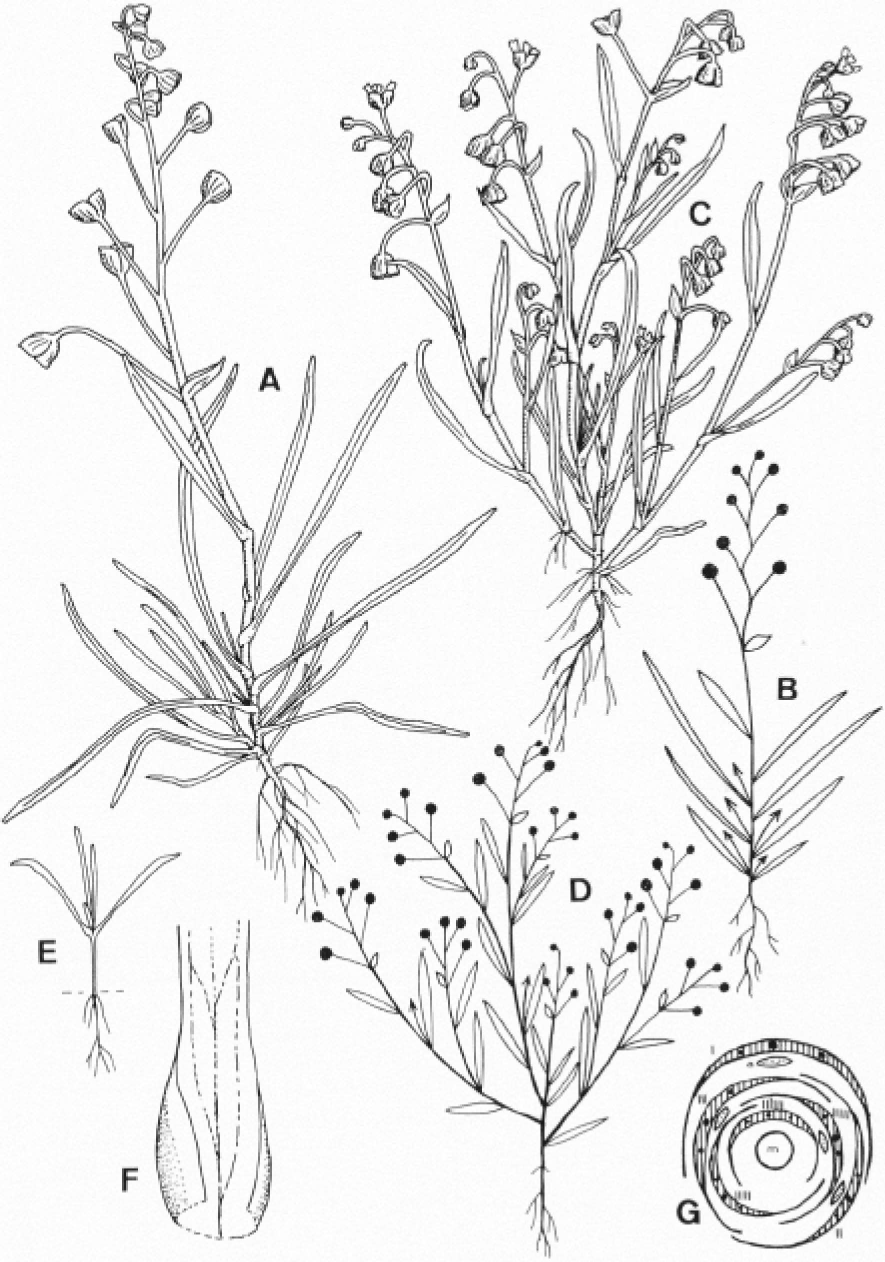


Fig. 4. *Montiastrum lineare.* — A: Habit of a summer annual plant. — B: Diagrammatic drawing of A, showing the type of branching; the arrows indicate lateral shoots. — C: Habit of a winter annual plant. — D: Diagrammatic drawing of C, see B. — E: Seedling with cotyledons, the broken line marks the ground. — F: Leaf base. — G: Diagrammatic drawing of a cross-section of a stem (m) with leaves (I—IIIIII) showing the position and succession of the leaves and the lateral shoots (a).

ways (Fig. 8 A—O and p. 107); usually one flower per inflorescence at anthesis per day. *Peduncle* 0.5—4.5 cm long, usually becoming longer than the leaf. *Bract* one or very occasionally two to five, 2—16 mm long, 2—5.5 mm broad, ovate to broadly ovate, acute to obtuse, or obtuse-apiculate, papery and green at anthesis, with white scarious margins and 3—5 distinct ± parallel veins (Fig. 5 A). *Pedicels* 0.2—1.1 cm long at anthesis, after anthesis up to 3 cm, usually somewhat reflexed or recurved from the base and often hook-like at the distal end. *Involucral leaves* very broadly ovate to rounded, 1.7—3.5 mm long at anthesis, green with narrow white margins, after anthesis enlarged to 2.5—6.5×2.5—9.0 mm (often 4.5×5.0 mm), obtuse to retuse or sometimes with a short apical slit, usually with 6—12 very distinct veins, often becoming reddish when dry, involucre cup-shaped (Fig. 5 C). *Flowers* homogamic, predominantly autogamous, chasmogamous (Fig. 5 B) but also cleistogamous (the description of floral structures refers to the former; the latter are generally smaller and more reduced). *Tepals* five, the two non-staminate ones usually somewhat larger than the remainder (in cleistogamous flowers the size difference is more obvious), obovate to shortly spathulate, 4.0—6.5 mm long, 1.2—2.1 mm broad, about 1.3—1.8 times longer than the involucre (in cleistogamous flowers often somewhat shorter than the involucre), ascending to almost erect at anthesis, obtuse to slightly emarginate, distinctly petiolate, petioles 0.8—1.2 mm long, c. 0.3 mm broad, connate for up to 0.2 mm, white to faintly lavender (Fig. 5 D). *Stamens* normally three, occasionally five or four (in cleistogamous flowers always three), 2.8—3.8 mm long, about 2/3 of the tepal length, adnate to about the middle, anther yellow, medifixed, not versatile, ovoid, 0.5—0.9 mm long, 0.3—0.6 mm broad, ± laterorse (Fig. 5 D). *Ovary* obovoid, 1.2—1.6 mm long. *Style* narrow, usually about as long as the ovary but sometimes up to almost twice as long; *style branches* 0.7—0.9 mm long, diverging, with rather closely set, rather long papillae. *Capsule* broadly pear-shaped to obovoid, 2.6—3.9 mm long, 2.3—3.5 mm broad, trisulcate at the base; groves about 1/3 of the capsule length (Fig. 5 F). *Seeds* ± orbicular in outline, lens-shaped, diam. 1.4—2.5 mm (usually 1.7—2.1 mm; Fig. 10), about 0.8—1.0 mm thick, usually with a sharp keel, up to 0.3 mm broad, almost all around, very shining (Fig. 5 G). *Pollen grains* 57—68 μ in diam., colpi 80—90, tholi 28—34, 10—10.5 μ in diameter and c. 8 μ high, basal plates c. 15 μ in diameter, spinulae 10—16 per tholus. *Chromosome number* 2n=28.

DISCUSSION

Like *Montiastrum dichotomum, M. lineare* has been treated under both *Claytonia* and *Montia*. RYDBERG (1917) established the genus *Montiastrum* with the single species *M. lineare*. However, HELLER used this name on printed herbarium labels already in 1907. His combination has not been regarded as valid.

M. lineare is a rather variable species. It modifies in about the same way as *M. dichotomum*. Specimens cultivated in greenhouses often become very different from those collected in natural habitats.

M. lineare is predominantly autogamous (p. 110). In cultivation the individuals of the same collection (population sample) are almost identical. Also the specimens of the same herbarium collection are usually very similar.

The infraspecific variation of *M. lineare* cannot entirely be explained as modificative. A summer annual and a winter annual form can be distinguished. These are discussed in detail on pp. 116—118.

DISTRIBUTION AND HABITAT

Montiastrum lineare occurs in the western part of North America with a centre in the elevated plains of the Columbia River Basin in Oregon, Washington and

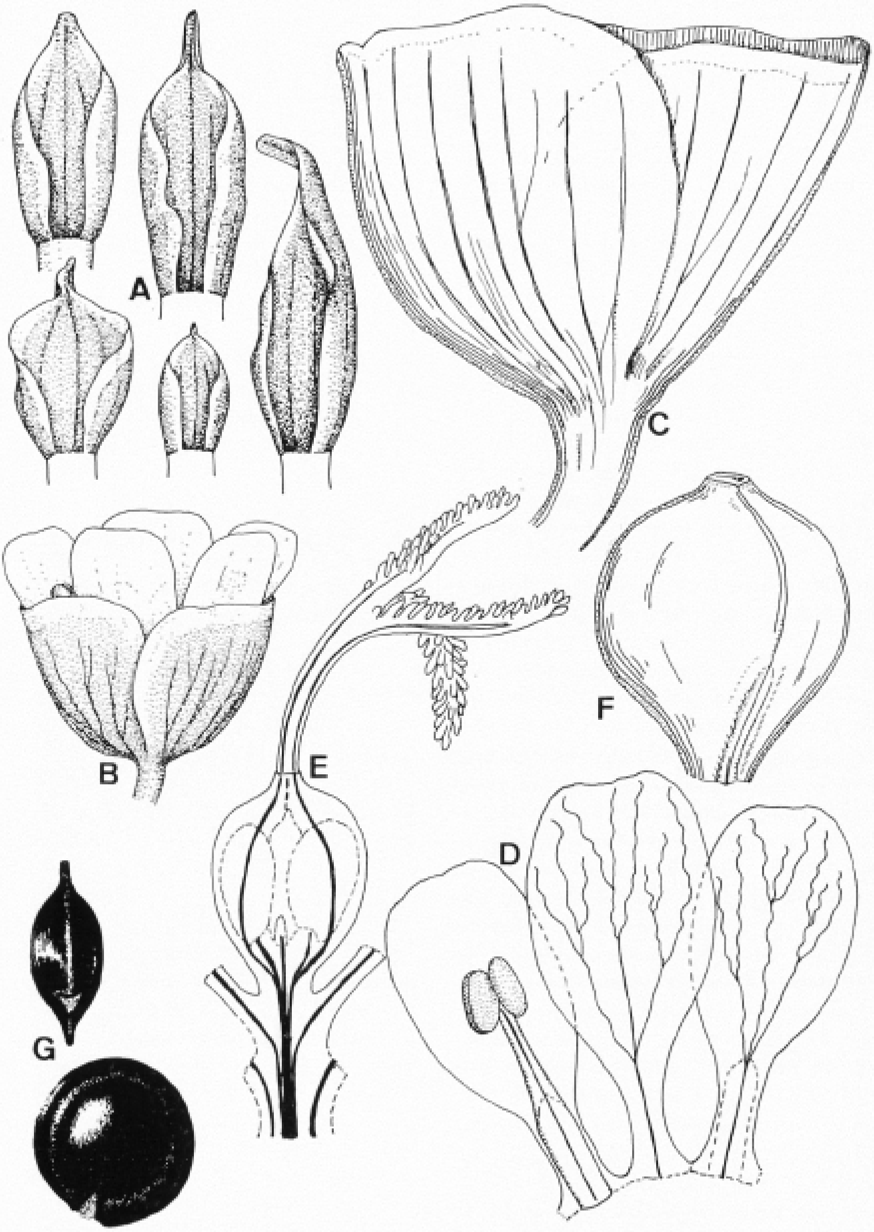


Fig. 5. *Montiastrum lineare.* — A: Five bracts, showing variation in size and shape. — B: Flower. — C: Involucre. — D: Part of the perianth with a stamen. — E: Pistil. — F: Capsule. — G: Seeds, the lower in lateral view.

Idaho, extending northwards into adjacent parts of British Columbia (Vancouver Island and along the lower Frazer River), and south to the Sierra Nevadas and the coastal strip of N. California. It is also recorded from Utah, Nevada and from westernmost Alberta in Canada with outlying occurrences in central British Columbia, in the Yellowstone area in Montana, and in the San Jacinto and San Bernardino Mountains in Southern California (cf. ABRAMS 1964 p. 126; RYDBERG 1932 p. 296; HITCHCOCK et al. 1964 pp. 240—241; Appendix and Fig. 6 B).

The species occurs mainly in valleys, foothills and plains within the Transition Zone; in northern California usually between 700 and 2000 meters, and in Washington between 200 and 1500 meters.

M. lineare is the commonest species of the genus and has the widest distribution. Its distribution area has no close parallel in the *Montia* group but some of the annual species of *Claytonia* have similar distributions, though their centers are generally more southern.

The habitats are predominantly wet or at least temporarily moist; usually gravelly, silty or sandy often bare soils or rocks with a thin soil cover, e.g., on stream banks, ditches, hillsides, moist meadows, vernal pools and grassy clearings. The species prefers open habitats. It may grow in open yellow pine woods or Ponderosa pine—grassland, in Douglas fir—maple, and black oak forests in the *Purshia—Amelanchier* assocation. The species often grows together with *Collinsia parviflora, Draba* spp., *Nemophila menziesii, Ranunculus occidentalis, Saxifraga integrifolia, Claytonia arenicola, C. perfoliata* agg., and other spring-blooming annuals. Occasionally it has been collected together with *Montiastrum dichotomum.*

Besides in these natural and probably native habitats the species also often grows in cultivated or waste land. In some areas in British Columbia (cf. MULLIGAN in BAKER & STEBBINS 1965 p. 130), Washington, Oregon, and Idaho it shows evident weedy tendencies, and occurs in gardens, orchards, wet fields with sweet clover, grass or grains, roadsides and cuts, and other disturbed places. In such sites it may cover large areas, often quite densely. It seems probable that the species has reached some localities as a weed, and in that way widened its distribution.

FLOWERING PERIOD: Usually from the end of March to the end of June. In higher elevations flowering may continue till the end of July. Generally the summer annual form starts flowering somewhat later than the winter annual. The latter has been collected in flower as early as January.

MORPHOLOGY AND REPRODUCTIVE BIOLOGY

Stems and Branching Habit

The branching of *Montiastrum* is sympodial which is most evident in the annual species, where the main stem and branches are usually terminated by inflorescences and the growth is continued by lateral branches (cf. HOLM 1905 p. 29). Buds may develop in every leaf axil (Fig. 4 G), and the branching is usually not restricted to any defined regions of the plants, although basal branching often prevails.

In *M. bostockii* the main branch turns erect and ends with an inflorescence, while the lateral branches are persistently spreading. After fruiting the flowering shoot dies. The plant is rather sparingly branched and forms long, narrow stolons which may root at the nodes. The internodes of the repent stems are rather long, while the basal ones of the flowering shoot are short (Fig. 2 A—B). The repent stems hibernate.

The branching of *M. vassilievii* is incompletely known because of the scanty material. Probably it has a rather short perennial stem which is partly subterranean with short internodes and adventi-

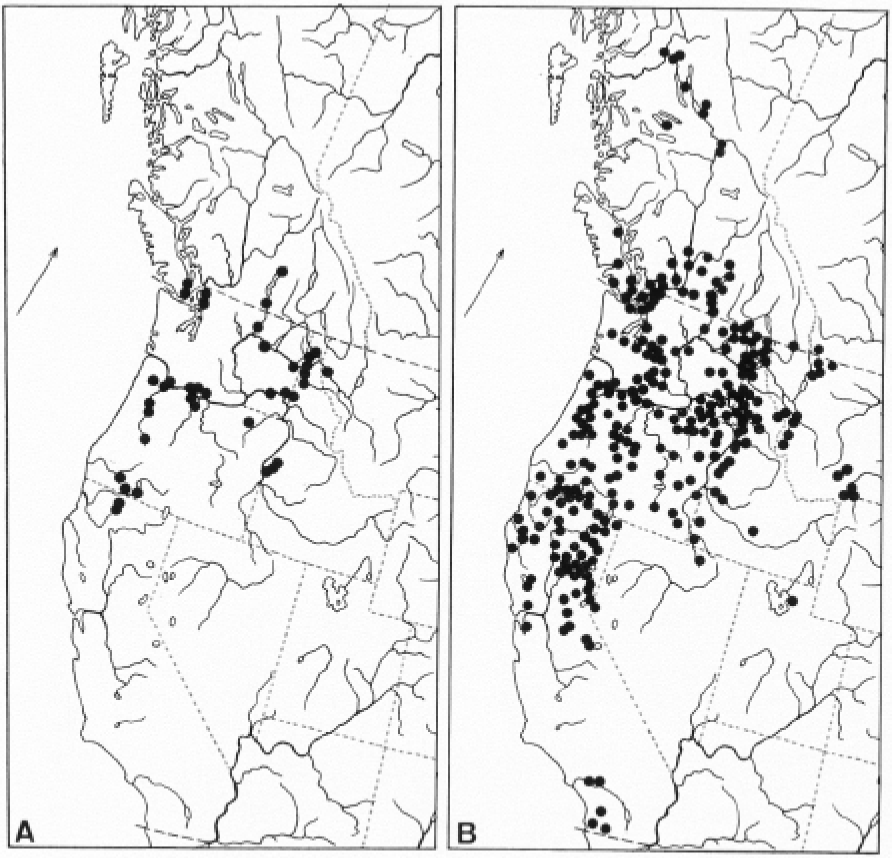


Fig. 6. The distribution in western North America of A: *Montiastrum dichotomum* and B: *Montiastrum lineare*. The maps are based on available herbarium material.

tious roots. This "main" stem terminates with an inflorescence. Lateral leafy, short branches develop in the leaf axils. They hibernate (hemicryptophyte) and continue growth and flowering in the following year. This gives the plant a loose caespitose habit. The branching resembles that of the winter annual form of *M. lineare*, but the flowering of the main shoot and the lateral ones takes place in different seasons.

The summer and winter annual forms of *M. lineare* (p. 116) differ from each other in mode of branching. The summer annual form is characterized by a rapidly growing main shoot, which terminates by an inflorescence and has rather long internodes. Usually, lateral branches do not appear before anthesis. Sometimes they fail to appear at all or are poorly developed. One or a few of them may flower, but then usually after the main inflorescence (Fig. 4 A—B). The suppression of the lateral branches seems to be an adaptation for rapid growth and flowering, which must be advantageous in a spring-blooming, summer annual with short time for development (p. 117).

In the winter annual form the main shoot is slow-growing in the autumn and forms very short internodes. Lateral branches develop early, usually before hibernation. In the spring an inflorescence ends the main shoot. At the same time the lateral branches develop and often overtop the main shoot. Their anthesis is almost synchronous with the "main" inflorescence and then they often branch further. Thus the lateral branches constitute the predominant part of the plant and the total flowering time is prolonged (p. 117; Fig. 4 C—D). The lateral branches are usually ascending, and adventitous roots sometimes develop at their basal nodes.

M. dichotomum is also a winter annual and resembles the corresponding form of *M. lineare*. The branching is usually more regular, however, and follows the diagrammatic model of Fig. 3 B. Usually the stem is branching at every node and the branching appears dichotomous. The branching system is a sympodium where the branches seem to follow in a 2/5 phyllotaxy. The lateral, often diffusely spreading branches constitute the predominant part of the plant.

The branching type of *Montiastrum* does not quite agree with any other genus of the *Montia* group, but *M. dichotomum* corresponds in several respects with *Limnalsine* Rydb. The branching system of *M. vassilievii* and the two forms of *M. lineare* seem to form a continuous evolutionary series. It is interesting in the alternative development of the lateral branches adapted to different life forms. The branching system of *M. bostockii* differs in being principally repent and adapted to vegetative reproduction.

Swanson's (1966 pp. 230—233) description of the branching system of "*Montiastrum*" and his habit diagram are too vague to be discussed, especially since the perennial species are not considered.

Anatomically the stem agrees in most respects with other genera of *Montia* group, in particular with those having alternate leaves. Mutually the species of *Montiastrum* are very similar (*M. vassilievii* not studied). The epidermis cells are very long with more or less straight side walls. Usually they are somewhat higher than broad with a distinctly thickened inner wall. The stomata seem to be rather frequent. The cuticle is thick and wrinkled, especially the lateral wrinkles are prominent (Fig. 7 F). Inside the epidermis is a thick, rather open, parenchymatous cortex (cf. Franz 1908 p. 41). The cortex is assimilatory and consists of cells rounded in transverse section. Just under the epidermis the cortical cells are often reddish. The cortical tissue of the repent stems of *M. bostockii* may sometimes be starch-storing. The starch occurs in a compact layer, a few cells thick, under epidermis. The endodermis cells are very thin-walled with marked Casparian dots. The xylem part of the stele forms a continuous cylinder with broad leaf gaps below the nodes. The leaf traces are usually three of which the central is the thinnest (Fig. 7 G). In branched stem parts the vascular tissue to the branch is set off below the node. Inside the xylem is a narrow, parenchymatous pith which is usually not hollow. The phloem cells are generally very thin-walled but under the endodermis there is usually a continuous

Fig. 7. A: *Montiastrum dichotomum*. B—G: *M. lineare*. — A—B: Part of stem, leaves and inflorescences, showing the branching and the vascular system (somewhat simplified); 1. peduncle, 2. bract, 3. pedicel, 4. axis. — C: Leaf-epidermis from the adaxial face with stoma in cross-section. — D: Cross-section of a leaf just below the middle, spotted areas indicate the assimilatory tissue, the white area surrounded by a broken line marks a parenchymatous tissue almost lacking chloroplasts. — E: Part of the abaxial leaf-epidermis with stomata, the guard cells are spotted. — F: Stem-epidermis in cross-section. — G: Stem stele in cross-section just above the middle of an internode; at the node above one leaf; 1. endodermis, 2. cells with thickened walls (pericycle), 3. xylem, 4. pith.

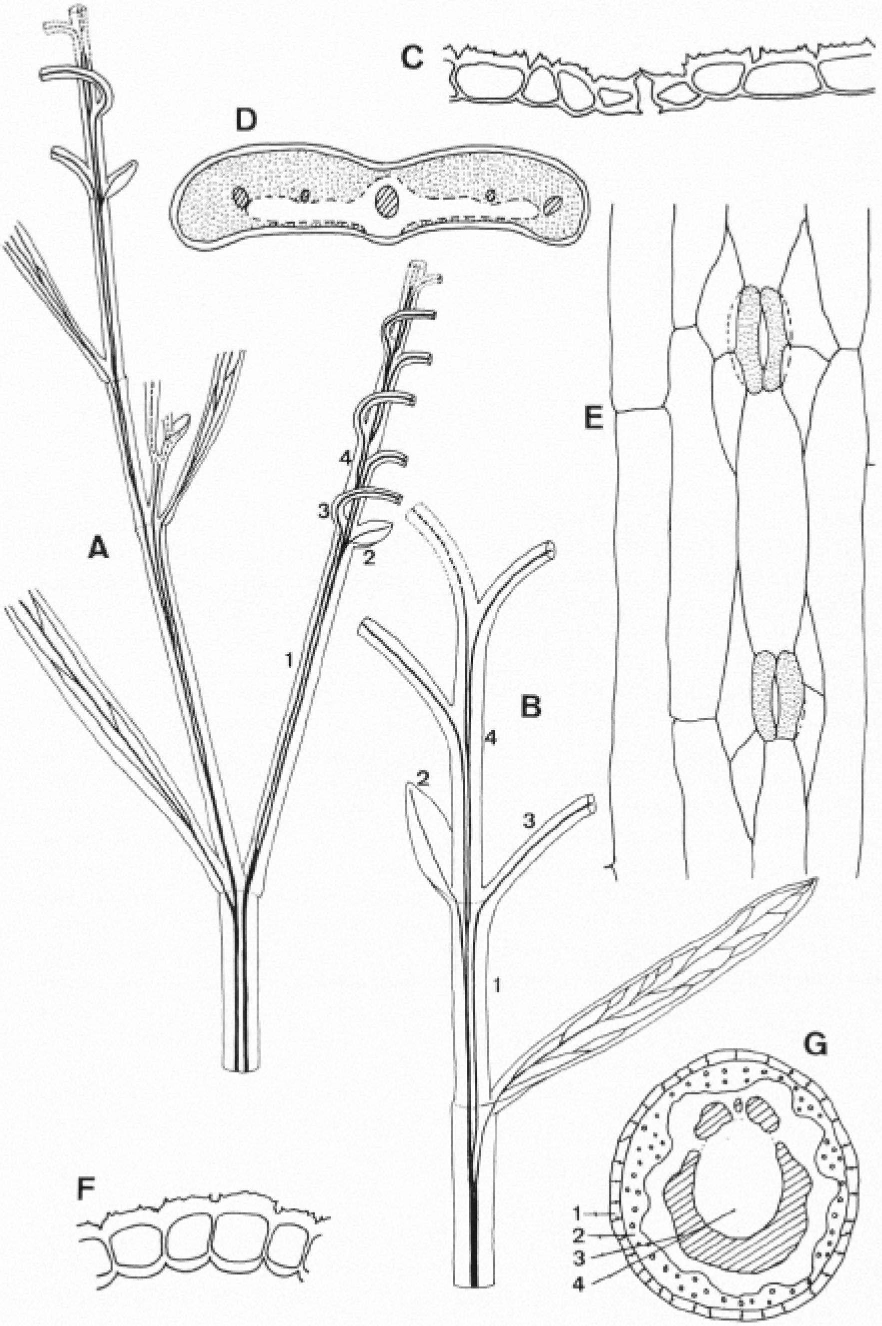


Fig. 7.

layer varying in thickness with thick-walled, fibre-like cells (pericycle). The limit between the phloem and these thick-walled cells is usually not distinct. No intraxylary phloem occurs. The stem lacks mechanical tissues and in the annuals it withers rapidly after fruiting.

The description of stem anatomy of the subfamily Montioideae given by FRANZ (1908 p. 40) is not directly applicable because it primarily deals with the anatomy of the inflorescence-bearing branches of *Claytonia perfoliata* DONN. s. lat.

Cotyledons and Leaves

The two epigeic cotyledons of the annual species are isomorphic, glabrous, and linear (Fig. 4 E). After germination they grow rapidly and may reach final size within four to six days. The testa of the seed is often attached to the top of one of them, or occasionally to both. The cotyledons often persist till flowering in the summer annual form of *M. lineare* (p. 117).

The cotyledons of the annual *Montiastrum* species are similar to those of *Neopaxia* Ö. NILSS. but different from those of *Montia, Naiocrene* (TORR. & GRAY) RYDB., *Crunocallis* RYDB., and some annual *Claytonia* species. In these the cotyledons are differentiated in a blade and a more or less distinct petiole.

Some leaves are usually crowded at the stem base. In the winter annual form of *M. lineare* and in *M. vassilievii* the basal leaves are more or less rosulate. The last-mentioned species has only one leaf on the floriferous shoot, while the remaining species have a few to many scattered cauline leaves. All the leaves of the annual species and those on vertical shoots of *M. bostockii* alternate in a 2/5 spiral (Fig. 4 G), and are spreading to erecto-patent. In *Claytonia* and *Montia* the phyllotaxy is different. The leaves of the creeping shoots of *M. bostockii* have an altered arrangement and are erect.

The leaf base is much widened with broad membranous margins. Usually it is almost amplexicaul and forms a short sheath which may enclose the short apex or lateral buds (Fig. 4 F).

The cauline leaves are more or less linear and almost sessile in all species. The basal leaves of *M. bostockii,* however, may be narrowly spathulate and are often differentiated in a short blade and a long, but not always distinct petiole. In *M. lineare* the uppermost leaf of the stem or branches is often broader and flatter than the others. The leaves are flat or may even be almost semiterete with a convex adaxial and a ± flat abaxial face. The degree of succulence may vary and seems modificative. Specimens of open and dry places have the thickest leaves. In such places the leaves and other vegetative parts of the plants often turn reddish.

The veining of the leaves may be characterized as camptodrome. The midrib is distinct and usually somewhat sunken. The lateral two veins are thin and often indistinct. On the adaxial side near the leaf apex the midrib ends in a hydathode, which may be more or less distinct and usually darkens on dry specimens.

The epidermis is comparatively thick, and thickest on the abaxial side. The side walls of the cells are almost straight on the abaxial side but ± undulating on the opposite side. The cuticle is rather thick and evidently wrinkled longitudinally on both sides, usually with the exception of the central part of the abaxial side which is smooth. Two lateral wrinkles on each cell are particularly large (Fig. 7 C). Stomata occur on both leaf-sides, but usually sparser on the abaxial side where they are often arranged in longitudinal rows. The stomata are elliptical and usually somewhat sunken. The guard cells are provided with large outer and inner ledges, the outer being the largest. The subsidiary cells may vary from two to four (usually four) and are lateral. Usually they are distinct and smaller than the surrounding epidermal cells (Fig. 7 E).

In *Montia* the stomata are almost confined to the adaxial leaf-side; they lack subsidiary cells, and the guard cells have only a thin outer ledge.

The mesophyll is usually differentiated in a compact, chlorophyllose adaxial tissue and an open tissue almost free from chlorophyll. The limit between the two tissues is often diffuse. A chlorophyllose tissue consisting of a single layer of cells also occurs on the abaxial side. It is absent, however, below the midrib (Fig. 7 D). Two rather wide lacunes may occur laterally. The vascular bundles have a distinct endodermis. No mechanical tissue occurs in the leaf.

Some features in leaf anatomy show that the lateral parts of the abaxial leaf-side differ from the central and are similar to the adaxial side which may indicate a "displacement" during ontogeny.

Inflorescences

The inflorescences terminate the main stem or lateral branches. There is only one inflorescence on the flowering shoots of the perennial species, while the number may vary in the annual species. In much branched specimens of the latter some inflorescences obtain a pseudo-lateral position because of overtopping of a lateral branch in the sympodium (Figs. 7 A and 3 A, B).

The inflorescence is a scorpioid cyme of the type that prevails in the *Montia* group (cf. HOLM 1905 p. 28). It is pedunculate with normally one papery to membranous bract opposite the lowest pedicel (Fig. 7 A, B). *M. bostockii* has occasionally bracts which form transitions to ordinary leaves. In *M. lineare* the bract is often provided with a green ± large, apical part which probably represents the reduced leaf blade, while the remaining part corresponds to the leaf base (cf. HOLM 1913 p. 8; Fig. 5 A). The genus *Montiastrum* is characterized by its comparatively large bracts.

The number of flowers per inflorescence varies. The flowers are more numerous in the annual species than in the perennial.

The "common" axis of the inflorescence (cf. NILSSON 1970 p. 134) is straight and elongate. Its terminal part is coiled when in bud. The pedicel is straight and erect at anthesis and fruit maturity, but recurved or hooked in bud and when the fruit ripens. In *M. dichotomum* and to some extent in *M. lineare* all pedicels curve in the same direction and the inflorescence becomes ± "one-sided" (Fig. 3 A).

Abnormal inflorescences are rather common in *M. lineare* (particularly in overfed cultivated plants) but very rare in *M. dichotomum*. Some examples in *M. lineare* are illustrated in Fig. 8. Similar divergent inflorescences may occur in other genera of the *Montia* group (NILSSON 1970 pp. 134—135). The commonest irregularities in the inflorescence of *Montiastrum* involve reductions of one to several internodes of the common axis or the development of one to several additional bracts. Rarely vegetative parts with ordinary leaves may be inserted (Fig. 8 N—O). When additional bracts appear, it is a common feature that they only occur at every second flower (Fig. 8 E).

The ancestral inflorescence in the group (now only represented in the genus *Neopaxia*; cf. NILSSON 1966 pp. 275—277) was probably pedunculate with an elongate common axis and several flowers with a bract opposite each flower.

Flowers and Pollination Mechanisms

SWANSON (1966 p. 231) emphasized the uniformity of the flowers in Montioideae. From a general point of view his statement is justified. Reduced and slightly zygomorphic flowers occur in some species of the *Montia* group, however (cf. ALMQUIST 1884, STRANDMARK 1887, EICHLER 1878 pp. 125—128).

Franz (1908 pp. 22—27) compared the reduced and the unreduced ("standard") flower types of the subfamily. The "standard" flower was described as having an actinomorphic perianth of a single whorl of five tepals and one whorl of epitepalic stamens. The different degrees of syntepaly were also discussed by Franz.

Particular attention has been paid to the unique bifoliate involucre of the family, which has often been referred to as a calyx. Its origin and orientation is somewhat uncertain and will not be further discussed here. In *Montiastrum* it is longer than the fruit and often distinctly parallel-ribbed, which is a useful generic character.

Allogamous flowers agree with the "standard" flower of Franz, and probably resemble the ancestral type of the group. Autogamous flowers are more or less reduced and may be regarded as derived. In *Montiastrum*, species with both allogamous and autogamous flowers occur, which renders the genus a particular interest with regard to floral evolution.

M. bostockii and *M. vassilievii* are allogamous (the latter is insufficiently known). The tepals are more or less coloured, almost free, subequal (Nilsson 1970 p. 136), and up to about three times longer than the involucre (Fig. 2 A). Nectaries occur at the pistil base. The five stamens are equal with long filaments and comparatively large, somewhat versatile anthers which are almost extrorse (Fig. 2 D). The stamens are ascending and excurve during anthesis. The pollen production is rather large; cf. Table 1. The style is long with recurved branches, richly papillate on their adaxial face (Fig. 2 E).

Very occasionally, e.g., in *Crunocallis chamissoi* (cf. Nilsson 1970 p. 136) small flowers of poorly developed specimens may have somewhat unequal tepals and only three stamens. This condition constitutes a transition to the autogamous flower type.

The flowers of *M. bostockii* are protandrous with separate "male and female" phases. During the "male" phase the pollen is exposed outwards and the style is short with firmly convergent branches. During the "female" phase the style grows considerably, the style branches diverge and become recurved, exposing the expanding papillae on the stigmas (Fig. 2 E). In this phase the stamens start fading, and sometimes the anthers drop. Autogamy appears to be almost eliminated.

In inflorescences of *M. bostockii* two flowers are often in anthesis simultaneously — the upper one in "male" and the lower in "female" phase. Pollination results in a rapid withering of the flower.

M. lineare and *M. dichotomum* are predominantly autogamous. In the latter the autogamy seems almost obligate. The tepals are white or greenish white, and usually only slightly longer than the involucre (sometimes shorter, e.g., in cleistogamous flowers; cf. Figs. 3 D; 5 B). The tepals opposite the three stamens are smaller than the two others (Holm 1913 p. 8).

Normally the stamens are three, occasionally five or very rarely four. Pentastaminate flowers may occur in the lowest part of the inflorescences in well-developed specimens. The accessory stamens are often smaller than the others and have minute anthers, often with undeveloped pollen grains. Very occasionally flowers with five perfect stamens may occur.

In the autogamous flower the stamens are short and the anthers small, medifixed and laterorse. The pollen production per

Fig. 8. *Montiastrum lineare*, variation in inflorescences, highly simplified. — A: the "normal" type. — B—C: Some or all internodes of the axis reduced. — D—E: Additional bracts. — F—M: Branched inflorescences with different types of coalescence, between the peduncle and the axis of the terminal and lateral inflorescences, and with different length of the internodes (cf. the text). — N—O: Inflorescences with inserted vegetative parts. (First flower of the terminal inflorescences is indicated with a cross.)

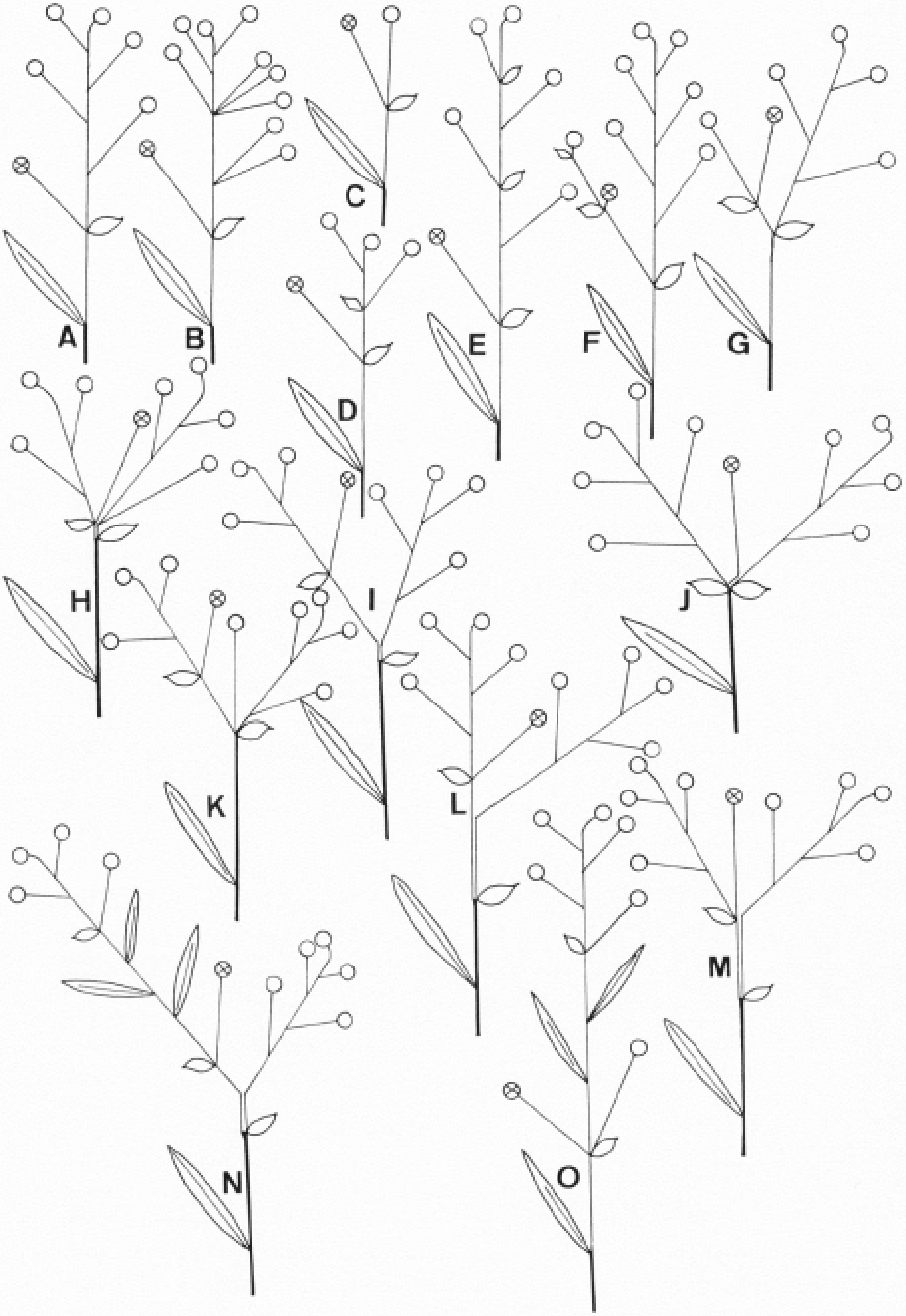


Fig. 8.

Table 1. Approximate seed and pollen production in three *Montiastrum* species; one allogamous, *M. bostockii*, and two autogamous, *M. lineare* (summer and winter annual forms) and *M. dichotomum*. The seed production has been calculated from the mean values of the number of flowers per plant or flowering shoot; there are three ovules per flower all of which have been assumed to develop into seeds (10 specimens of *M. bostockii*, 20 of the remainder, were examined). The pollen production was calculated from counts of pollen grains in 5 flowers of each species; the figures are given in round numbers (cf. the text).

Species	Number of pollen grains/flower	Number of seeds/ plant or flowering shoot
M. bostockii	1780—2170	12
M. lineare	240— 380	87 (126) *
M. dichotomum ..	110— 160	312

* the figure refers to five specimens of the winter annual form.

flower is low; cf. Table 1. The style is rather short or sometimes the style branches are almost sessile (Fig. 3 H). The length and position of the three stamens permit contact with the recurving style branches.

The flowers of *M. lineare* and *M. dichotomum* are homogamic with no tendency to protandry. The flowers may be chasmogamous. Cleistogamy is most common in *M. dichotomum*. Under similar external conditions chasmogamous flowers seem to be more frequent in the summer annual form of *M. lineare* than in the winter annual (p. 117). In chasmogamous flowers opening takes place 2—3 hours after sunrise and closing 1—3 hours after noon. When closed the flower does not open again and it withers rapidly. However, emasculated flowers of *M. lineare* (p. 88) may remain open for up to three days or until they are artificially pollinated.

Bud pollination is common and usually takes place the day before the flower opens. Particularly in the summer annual form of *M. lineare* bud pollination sometimes fails to take place and the flowers may open unpollinated.

Cleistogamy which may be regarded as a type of prolonged bud pollination occurs particularly in rainy and cloudy days when the temperature is low. The uppermost flowers of an inflorescence or those of late inflorescences are almost exclusively cleistogamous.

The two types of flowers in the *Montia* group may be characterized as follows:

ALLOGAMOUS FLOWER TYPE: Tepals five, ± equal, large, often coloured. Nectar and scent usually present. Stamens five, equal; filaments long, excurving; anthers large, ± extrorse, versatile; pollen production high. Style long with long recurving branches. Protandrous with separate "male and female" phases. Chasmogamous.

AUTOGAMOUS FLOWER TYPE: Tepals five (or two), unequal, small, often greenish white. Nectar and scent lacking. Stamens three, filaments short, curving inwards; anthers small, ± laterorse, nonversatile; pollen production low. Style and style branches short. Homogamic. Chasmogamous or cleistogamous, bud pollination frequent.

Transitions between the two types may occur, but they are rare and often nonconsistent. The allogamous type occurs mainly in perennial species and the autogamous in annual.

In the *Claytonia* group species occur with allogamous or autogamous flowers. Those with allogamous flowers are mainly perennials and their floral structures follow the above scheme. The autogamous species are annuals with floral reductions which in some points are different from those of the *Montia* group. Some annual, autogamous species of *Calandrinia* have floral reductions which almost exactly follow the autogamous scheme of the *Montia* group (FRANZ 1908 pp. 20—21). The autogamous *Calandrinia* species belong to a group characterized by pantocolpate pollen grains (NILSSON 1967 p. 283).

Pollen Grains

The pollen grains of *Montiastrum* represent a unique type, the morphology of which was described by NILSSON (1967). The pollen grains are multi-pantocolpate. The centres of the mescocolpate areas (the basal plates) are much vaulted and form the characteristic, spiniferous tholi.

It is reasonable to assume that this pollen type has evolved from the 12-pantocolpate type which is represented in some genera of the *Montia* group, e.g., *Crunocallis*, *Montia* and *Maxia*. This supposed relationship is one of the reasons for placing the genus in the *Montia* group. No transitional pollen types are known, however.

The pollen grains of *Limnalsine* have a distinctly thickened part in the centre of the mesocolpate areas (NILSSON 1967 pp. 352—353). ALIOSHINA (1963) believed them to be of a transitional type. She assumed that the tholate type had evolved from a pollen type resembling that of *Limnalsine*. However, in *Limnalsine* the elevated centre of the mesocolpate area is formed by a much thickened sexine which is in firm contact with the nexine. In *Montiastrum*, on the contrary, sections of the tholi show that they are hollow. The sexine is separated from the nexine, vaulted, and not particularly thickened. The elevated central parts of the mesocolpate areas thus appear to have evolved in different ways in the two genera and there seems to be no reason to accept the straightforward evolutionary relationship proposed by ALIOSHINA. Furthermore, the tholate pollen grains diverge in their mode of germination. The entire basal plate flakes off and forms an opening for the protruding pollen tube. On the whole, the basal plates (mesocolpate areas) tend to drop very easily from the tholate grains, a condition never observed in any other pantocolpate grains (NILSSON 1967).

The mechanical and biological function of the tholate pollen grains has not been considered previously. Sticky substances covering the pollen grains (so-called tryphine; cf. ERDTMAN 1969 p. 243), were found in an often considerable amount in most species in the subfamily (p. 88). The tryphine causes the grains to stick together, forming masses of variable size. On the grains of *Montiastrum* (*M. bostockii*, *lineare*, and *dichotomum*) the tryphine is almost lacking. Nevertheless the pollen forms masses usually containing 14—32 grains which are often firmly held together. The coherence of the grains in masses is caused by the tholi which fit into the interspaces between the tholi of adjacent grains. The spines on top of the tholi and the rough surface of the tectum (large puncta) contribute to strengthen the adherence (Fig. 9 E—H).

It is very probable that the development of the tholi is an adaptation which increases the coherence between the grains. It is a common condition that pollen grains of insect-pollinated flowers stick together (KNOLL 1930), which permits a transfer of pollen in masses. Usually this is caused by a sticky or spiny surface of the grains — in *Montiastrum* the tholi have this function. It is therefore probable that the tholate pollen grains originally evolved in insect-pollinated flowers. In the genus there is one (sufficiently known) recent species, *M. bostockii*, with flowers of a type suggesting insect pollination (p. 108). The tholate pollen grains strongly indicate that the allogamous species of *Montiastrum* come closer to the ancestral forms than the autogamous ones, which must be regarded as derived.

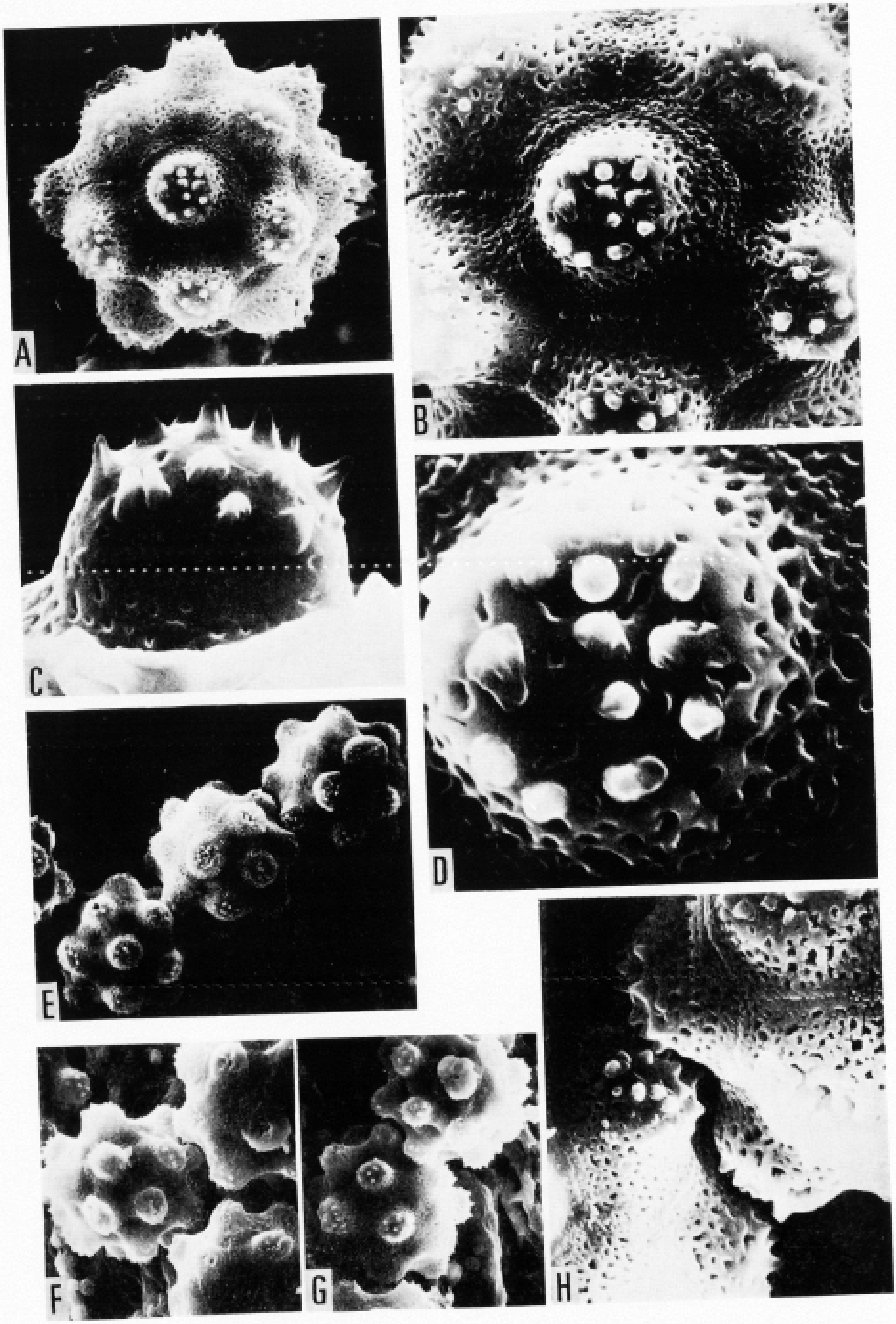


Fig. 9.

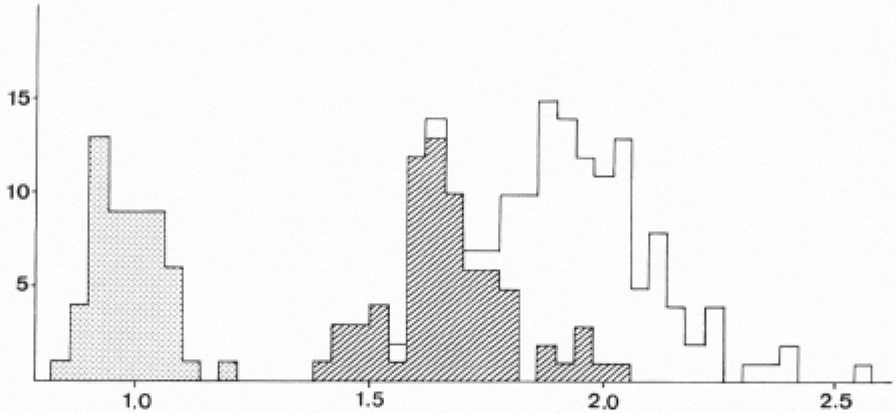


Fig. 10. Histogram of seed length in *Montiastrum*. Number of specimens examined on the vertical axis; length in mm on the horizontal axis. Mature seeds have been measured, 5 per collection. — Spotted columns=*M. dichotomum*; hatched and white columns=*M. lineare*, hatched columns the winter annual form, white the summer annual; the histogram is cumulative, because the values have been added upon the columns, to show the variation in seed length of *M. lineare* as a unit (further explanation in the text).

Seeds, Dispersal, and Reproduction

All genera of the *Montia* group have three ovules. The seeds have a smooth testa, are laterally flattened, and usually distinctly keeled. The attachment plate is in a lateral depression and the strophiole is minute and not protruding. According to Brandegee (1895 p. 87) the cotyledons of *M. lineare* are accumbent in the seed. They are similar in *M. dichotomum* and *M. bostockii*.

The seeds of the annual species ripen rapidly. In the same inflorescence flower and mature capsules may be present simultaneously. The time from flowering to seed maturity is normally 6—8 days. The corresponding time for the perennial species is insufficiently known, but examined capsules of *M. bostockii* indicate a slower ripening.

At maturity the seeds are actively thrown off by a mechanism found in the entire subfamily (Willis 1892 pp. 382—383; Franz 1908 p. 36). At dehiscence the three valves of the capsule become strongly involute and somewhat reflexed. The rolling inwards is caused by lignified, transverse ribs in the side walls of the longitudinally directed epidermal cells. By the sudden movements of the valves the seeds are liberated, pressed strongly against each other, and thrown off. The mechanism does not operate perfectly if one or two seeds are missing (cf. below). In greenhouse the seeds of *M. dichotomum* may be thrown away up to 2.5 m, and those of *M. lineare* up to 2.0 m. The seeds lack other adaptations for dispersal.

The living material available for germination experiments has been too meagre

Fig. 9. *Montiastrum bostockii*. Scanning electromicrographs of the pollen grains. — A: One pollen grain, a tholus in the centre with a pentagonous basal plate (×c. 1100). — B: The frontal area of A showing the tholi, basal plates and colpi; the colpi have become very narrow because of shrinkage (×c. 2300). — C: A tholus in lateral view (×c. 5500). — D: A tholus from the top (×c. 5500). — E—H: The photographs intend to show how the grains aggregate by means of the tholi which fit into free interspaces of adjacent grains, and how the spines on the top of the tholi make the fixation stronger (E—G ×c. 600, H ×c. 2300).

to permit detailed conclusions, and continuous observations have only been performed during one year. The seeds of the annual species usually need a resting period of about four to six weeks before germination can take place. Some seeds seem to have a prolonged dormancy. Only occasionally do the seeds germinate simultaneously, even if they originate from the same self-pollinated plant and are sown under similar conditions. Usually 55—65 % of the seeds germinate within two weeks. The remaining seeds may be dormant until the soil is stirred or germinate at certain periods (cf. below).

Half a year old seeds of cultivated specimens of *M. dichotomum*, and of the winter and summer annual form of *M. lineare* were sown at two different occasions (April and September; 50 seeds of each taxon at both occasions; in greenhouse 18—20°C; the seeds were covered with sand). The seedlings were then counted before and after stirring of the soil, and summed up. The following figures were obtained: *M. dichotomum* 35 (April) and 34 (September), *M. lineare* winter annual form 39 and 42, *M. lineare* summer annual form 21 and 12. After pre-chilling (0° to —3°C) 36 seeds of the summer annual form (50 seeds sown in October) germinated; the chilling treatment does not affect the germination of the winter annual taxa in a corresponding rate.

The seeds of the winter annual form of *M. lineare* may be viabel up to c. 10 years when preserved under herbarium conditions, and three to four year old seeds have about the same germination capacity as one year old ones.

The seeds of both annual species can be sown at any time of the year and germinate. However, observations on dormant seeds indicate that the summer annual form of *M. lineare* has a periodic germination, with the highest rates in spring (late February to April). In the winter annual form of *M. lineare* and in *M. dichotomum* such a distinct periodicity does not seem to occur, although there are germination "peaks" in autumn (September to October) and spring (February to March).

The seedlings grow rapidly. In the summer annual form of *M. lineare* the first flowers usually appear about 35 to 45 days after germination (p. 117). The winter annual *M. lineare* and *M. dichotomum* flower distinctly later than the summer annual, if sown at the same time.

The seed production seems to be low and irregular in the perennial, allogamous *M. bostockii*. In examined ovaries one to three ovules are sometimes stunted and shrunken, which may indicate failing or ineffective pollination. The calculated seed production per flowering shoot is shown in Table 1. The calculation has been made on the assumption that all ovules develop into seeds; the actual number is probably lower.

The low seed production of *M. bostockii* is partly compensated by the effective vegetative reproduction by supraterranean runners. The sexual reproduction is probably slow and irregular in this species which means that the individuals are long-lived and mainly reproduce asexually. Cross-pollinaiion presumably predominates in sexual reproduction.

The seed set in the two annual species is almost perfect, and the self-pollination mechanism thus seems very effective. The mean number of seeds per capsule per specimen (40 specimens from different collections of each species were examined) was 3.00 in *M. dichotomum* and 2.94 in *M. lineare*. The calculated annual seed production per plant of the two species is shown in Table 1. The annual seed production in *M. dichtomum* is higher than in *M. lineare*, but both have distinctly higher values than *M. bostockii*.

Six generations of the winter annual form of *M. lineare* and five of *M. dichotomum* were raised in succession, each generation being self-pollinated. No inbreeding degeneration was observed. The plants remained fully vital and the seed set was high and regular. Artificial cross-pollination was performed in *M. lineare* (winter annual form). It had no unfavourable consequenses, and the plants obtained were perfectly fertile, but showed an individual variation which does not occur among inbred plants.

High and regular seed set is essential for the survival of the annual species which often occur in rather unstable habitats. The reduction of genetic variability is partly compensated by a high phenotypic plasticity. The seed production follows the development of the individual plants. Seasonal reductions or even losses in the seed production are probably balanced by dormant seeds. A regular formation of three seeds per capsule is also important for the function of the dispersal mechanism (p. 113). It one or two seeds are missing the mechanism does not operate effectively.

The reduced genetic variability in the local populations is reflected in the herbarium material. Most collections consist of very similar individuals, and plants raised from such collections tend to be almost identical.

Cytology and Crossing Experiments

The chromosome numbers of *Montiastrum dichotomum* and *M. lineare* are 2n=14 and 2n=28, respectively (Nilsson 1966 p. 466; Fig. 11 A, B). The karyotype differs in some respects from *Montia*, *Naiocrene*, and *Neopaxia*. The chromosomes are larger, the centromere is subterminal to submedian, and the satellite is very thin (Nilsson 1966 p. 467). Morphologically, the chromosomes show a closer resemblance to some annual *Claytonia* species than to the *Montia* group. In *Claytonia* Lewis and Suda (1968 pp. 64—66) found that the annuals, which were regarded as advanced, have somewhat smaller chromosomes than the "less specialized" perennials. The diploid *Montiastrum dichotomum* has one satellited chromosome pair and somewhat larger chromosomes than the tetraploid species. The basic number x=7 is not known in other genera of the *Montia* group.

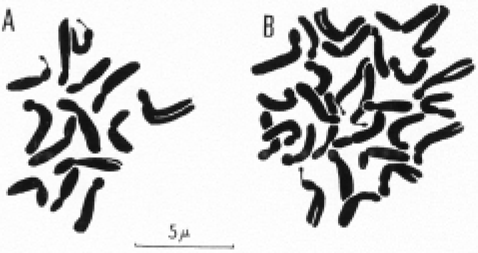


Fig. 11. Somatic metaphase plates in root tips. — A: *Montiastrum dichotomum* (2n=14; Canada, Vancouver Isl., M. C. Melbourn). — B: *M. lineare* (2n=28; U.S.A. Washington, Kittitas Co., P. Kern).

A few crossing experiments have been performed. Crossings between *M. lineare* (winter annual form, Mason 6192) and *M. dichotomum* (M. C. Melbourn) have been made in both directions (eight and four crossings, respectively). Seeds were only obtained in a single case, and then probably resulting from self-pollination.

Germination and pollen tube growth started a few minutes after pollination. The pollen tube usually penetrated into the stigmatic papilla cell but then stopped. Sometimes it failed to penetrate and then twisted among the papillae. The same phenomenon occurs among other taxa of the subfamily and will be discussed in detail in a later paper. No naturally occurring hybrids are known with certainty in the subfamily.

Crossings were made between individuals of different collections (Mason 6192 and Cronquist 7341) of the winter annual form of *M. lineare*, and between its summer annual (P. Kern) and winter annual (Mason 6192) forms (three crosses in both cases). In these cases full seed setting occurred. Crossings have also been made between individuals of the same collection (Mason 6192, five crossings) which also resulted in perfect seed setting.

The sparse results indicate a crossing barrier between *M. dichotomum* and *M. lineare*. This is supported by the fact that

Table 2. Characters of the winter and summer annual forms of *Montiastrum lineare*. Measurements have been made in herbarium specimens (25 of each form) which have been *a priori* classified to either of the two forms.

	Winter annual form	Summer annual form
Cotyledons persistent until flowering	—	+ (—)
Basal leaves withered at anthesis	+	— (+)
Stem height in cm	6—14	6—20
Number of short basal internodes	5—22	2—9
Number of basal lateral branches	6—21	0—7
Number of inflorescences	5—17	1—7
Length of common axis of inflorescence in cm	4—8	5—11
Number of flowers per inflorescence	3—8	6—12
Involucre length in mm (after anthesis)	2.7—4.9	4.2—6.3
Tepal length in mm	4.0—5.7	4.7—6.4
Seed length in mm	1.6—1.9	1.7—2.4

no true intermediates occur in the herbarium material examined, although the species are sometimes sympatric. In crossings between the two forms of *M. lineare* the progeny was morphologically similar to the winter annual in becoming rosulate, (p. 103) but its fertility was not tested because the plants failed to flower. The two forms sometimes occur together, but when collected simultaneously they are often in different stages of development (p. 117). Occasionally they flower at the same time, however. In the herbarium material many intermediates occur which may indicate that the two forms are not entirely isolated.

Winter and Summer Annual Forms of Montiastrum lineare

Within *Montiastrum lineare* two forms with different seasonal development, a winter annual and a summer annual, can be distinguished. The type specimen of *M. lineare* belongs to the summer annual form. Hooker (1847 p. 230) distinguished *Claytonia linearis* β *minus* which corresponds to the winter annual form (Geyer's Oregon collection no. 317, type in K). Later the two forms have been recognized only occasionally. The summer annual form constitutes about 65 % of the herbarium collections classified to either of the forms. In the cultivated material two collections belong to the summer annual form (P. Kern and Johnson 398) and the remainder to the winter annual form (p. 88). The two forms have the same chromosome number 2n=28.

The two forms may be distinguished by a combination of characters. Some of these seem to be correlated and reflect the different development of the forms. Table 2 shows that most characters overlap. About 35 percent of the herbarium material could not be classified with certainty in either of the forms. In uniform cultivation the differences tend to become exaggerated and the two forms are distinct. However, it is also possible that only the extremes are represented in the few cultivated collections.

THE WINTER ANNUAL FORM

In greenhouse cultivation the plants become rosulate and much branched. They remain in this stage for some months before flowering (sometimes flowering fails to appear entirely).

The rosulate plants can be forced to accelerate the flowering by a "frost" treatment. Some plants were placed outside the greenhouse for two weeks last winter (temperature +2° to —6°C). A few were killed but the remainder began to flower after two to four weeks when replaced in greenhouse. Plants sown at the same time but kept in the greenhouse as a control, did not begin flowering until one to two months later. In the open garden the plants hibernate in the rosulate stage and start flowering in early spring. Herbarium specimens are characterized by many ± withered basal leaves, and several lateral branches and inflorescences, and a diffuse main axis. Flowering plants have been gathered very early in the spring, even in January. In cultivation the seeds may germinate any time during the year, although there seems to be a periodic germination of dormant seeds (p. 114). The plants develop in a similar way regardless of the sowing season.

THE SUMMER ANNUAL FORM

This form is characterized by a rapid growth of the distinct main shoot which is terminated by an inflorescence. The development of lateral branches is suppressed, and usually they fail to develop until flowering. Herbarium specimens are characterized by a simple or poorly branched stem with a few short basal internodes. A basal rosette is lacking or consists of a few leaves only, representing a short strengthening stage. The cotyledons sometimes persist until flowering. Compared with the winter annual form the summer annual has a more rich-flowered inflorescence, large flowers and seeds. Dormant seeds germinate with the highest rates in spring (p. 114). The germination rate seems to increase after a pre-chilling treatment. When sown in autumn some seeds usually germinate and the plants develop normally, but their growth is much retarded (up to 70 days from germination till flowering, p. 114).

EVOLUTIONARY TRENDS IN THE TWO FORMS

The differences between the two forms are summarized in Tables 2 and 3, and in Fig. 10. One of the more conspicuous distinguishing characters is seed size. Similar differences between summer and winter annuals have been reported, e.g., in *Camelina* (review by STEBBINS 1950). The summer annual form has almost twice as heavy seeds as the winter annual.

Large seeds may be disadvantageous in dispersal but advantageous in establishment by producing vigorous seedlings with a greater chance for survival (cf. SALISBURY 1942). The differences in seed weight between the two forms of *M. lineare* probably evolved in response to the different life forms.

The summer annual is bound to develop rapidly from seed, and thus vigorous seedlings are obviously an essential quality. The winter annual on the other hand may accumulate organic matter in the rosette stage during the autumn and winter, and is thus less dependent on vigorous seedlings. Flowering may take place more or less simultaneously, although the winter annual starts earlier but has a prolonged total flowering time. To both it is essential that seed setting takes place before the summer drought.

Another factor which appears to be correlated to the life form is the ratio between seed weight and plant dry weight (Table 3). The summer annual form has a more "economic" seed production, which would probably be even more obvious if the energy content of the seeds were compared instead of their weight. Similar differences in seed production economy between closely related autogamous and allogamous annuals were found by STRID (1969 pp. 389—390).

In nature the plant dry weight of the winter annual form is somewhat smaller because its vegetative growth is arrested during the winter. The summer annual form has a low plant weight because of the suppression of lateral branches. It has been demonstrated in cultivated specimens that some lateral branches develop if the main shoot is injured. Such specimens often resemble poorly developed specimens of the winter annual form.

Table 3. Plant dry weight and seed weight of greenhouse cultivated *Montiastrum dichotomum* (M. C. MELBOURN), *M. lineare* summer annual form (P. KERN), and *M. lineare* winter annual form (MASON 6192). Five plants of each collection have been examined, the mean values are given. The results show the differences in plant dry weight, seed number, and seed weight. From these values the number of seeds per unit plant weight, and the seed weight in per cent of total plant weight are calculated. The results intend to illustrate the proportion between seed number and weight and plant weight with regard to the "economy" in production of vegetative organs and diaspores of the different taxa (further comments in the text).

	M. dichotomum	*M. lineare* summer annual	*M. lineare* winter annual
Plant dry weight in g	0.33	0.23	2.49
Number of flowers/plant	108	11	39
Number of seeds/plant	324	33	117
100-seed weight in g	0.013	0.25	0.13
Number of seeds/0.1 g plant weight	98.2	14.8	4.9
Seed weight in % of plant weight	12	35	7

The number of seeds per inflorescence is usually larger in the summer annual but the overall number of seeds per plant is much larger in the winter annual. This may indicate that hibernation with seeds is safer. Hibernating plants may be killed by early frost in the autumn or by frost drought in the spring. The larger number of seeds in the winter annual form may at least in part compensate for such elimination.

The two forms are thus distinguished by a number of biological and morphological characters which are more or less correlated to the life form. Intermediates are frequently found in nature, and the two forms do not seem distinct enough to merit taxonomic recognition.

The winter annual shows the greater similarity to the winter annual diploid *M. dichotomum* (Table 3). With regard to morphological characters the summer annual is more advanced and can be assumed to have evolved from the winter annual. Their differentiation seems rather recent.

Distributional Remarks

The disjunct distribution of *Montiastrum* has no parallel in the *Montia* group. Some points of agreement are found in *Claytonia* in which the perennials are chiefly mountainous and occur on both sides of the Bering Strait. The annual species occur in western North America, mainly south of the perennials and at lower altitudes.

The greater morphological resemblance in, e.g., branching habit, between the annual species and *M. vassilievii* is notable, although they are the most remote at present.

The two perennial species occur in small isolated areas which were not glaciated during the Quaternary Period (cf. HULTÉN 1937, 1968). The species seem to be relics in their present occurrences.

The two annual species center in the Columbia River System and are in part sympatric. They are similar with regard to plasticity, ecology, and reproduction, but *M. dichotomum* seems to be a rather rigid species, while *M. lineare* appears to be a complex, progressive species which may have evolved in direction for aggression partly through polyploidy and partly through selection for vigor, factors which may explain its wider distribution and more common occurrence. A similar expansion in *Claytonia perfoliata* is reported by STEBBINS (BAKER & STEBBINS 1965 pp. 173—190). It is possible that *Montiastrum lineare* originates from the present common area of the two species, and that it has become widespread rather recently because of its weedy tendency. There are indications from the herbarium material that *M. dichotomum* has steadily decreased since about 1920, whereas *M. lineare* has been stable or increased, and has often been gathered on outpost localities in recent years.

LITERATURE CITED

ABRAMS, L. 1964. Illustrated Flora of the Pacific States, Washington, Oregon, and California. II. — Stanford, Calif. 635 pp.

ALIOSHINA, L. A. 1963. Morphology of Pollen Grains in the Genus Claytonia Gronov. and Allied Genera. — Bot. Žurn. 48(8): 1191—1196.

ALMQUIST, S. 1884. Om blomdiagrammet hos Montia. — Bot. Notiser 1884: 156—161.

BAKER, W. H. 1956. Notes on the Flora of Idaho, 1. — Leafl. West. Bot. 8: 32—36.

— & STEBBINS, G. L. (eds.) 1965. The Genetics of Colonizing Species. — New York and London. 588 pp.

BOGLE, A. L. 1969. The Genera of Portulacaceae and Basellaceae in the Southeastern United States. — Journ. Arnold Arb. 50: 566—598.

BRANDEGEE, K. 1894. Studies in Portulacaceae. — Proc. Calif. Acad. Sci. Ser. 2, 4: 86—91.

DAVIES, R. J. 1952. Flora of Idaho. — Dubuque, Iowa. 828 pp.

— 1966. The North American Perennial Species of Claytonia. — Brittonia 18(4): 285—303.

EICHLER, A. W. 1878. Blüthendiagramme. 2. — Leipzig. 558 pp.

ERDTMAN, G. 1969. Handbook of Palynology. — Copenhagen. 486 pp.

FRANZ, E. 1908. Beiträge zur Kenntnis der Portulacaceen und Basellaceen. — Beibl. Bot. Jahrb. 97: 1—46.

GRAY, A. 1887. Contributions to American Botany. — Proc. Amer. Acad. Arts Sci. 14: 270—341.

GREENE, E. L. 1891. Flora Franciscana. 1—2: 177—180. — San Francisco.

HITCHCOCK, C. L. & CRONQUIST, A. 1964. Vascular Plants of the Pacific Northwest. 2. — Seattle, Wash. 597 pp.

HOLM, T. 1905. Claytonia Gronov. A Morphological and Anatomical Study. — Mem. Acad. Sci. Wash. 10: 25—37, 2 plates.

— 1913. Types of Claytonia Gronov. — In: Mindeskrift for JAPETUS STEENSTRUP, pp. 1—11, 3 plates. — København.

HOOKER, W. J. 1833. Flora Boreali-Americana, 1. — London. 480 pp.

— 1847. Catalogue of Mr. Geyer's Collection of Plants Gathered in the Upper Missouri, the Oregon Territory, and the Intervening Portion of the Rocky Mountains. — London Journ. Bot. 6: 206—256.

HOWELL, T. 1893. A Rearrangement of American Portulacaceae. — Erythea 1: 29—41.

HULTÉN, E. 1937. Outline of the History of Arctic and Boreal Biota during the Quarternary Period. — Stockholm. 165 pp.

— 1944. Flora of Alaska and Yukon, IV. — Lunds Univ. Årsskr. N.F. Avd. 2, 40(1): 571—795.

— 1968. Flora of Alaska and Neighboring Territories. A Manual of the Vascular Plants. — Stanford, Calif. 1008 pp.

KNOLL, F. 1930. Über Pollenkitt und Bestäubungsart. — Zeitschr. Bot. 23: 609—675.

KOMAROV, V. L. 1936. Flora SSSR. 6. — Leningrad and Moscow. 956 pp.

LEWIS, W. H. & SUDA, Y. 1968. Karyotypes in Relation to Classification and Phylogeny in Claytonia. — Ann. Missouri Bot. Gard. 55(1): 64—67.

NILSSON, Ö. 1966. Studies in Montia L. and Claytonia L. and Allied Genera. I. Two New Genera, Mona and Paxia. — Bot. Notiser 119(2): 265—285.

— 1966. Ditto. I. Correction and Additions. — Ibid. 119(3): 469.

— 1966. Ditto. II. Some Chromosome Numbers. — Ibid. 119(3): 464—468.

— 1967. Ditto. III. Pollen Morphology. — Grana Palynol. 7(2): 277—363.

— 1970. Ditto. IV. The Genus Crunocallis Rydb. — Bot. Notiser 123(1): 119—148.

PAX, F. & HOFFMANN, K. 1934. Portulacaceae. — In ENGLER & PRANTL, Die natürlichen Pflanzenfamilien (Ed. 2) 16 c: 234—262. — Leipzig.

PIPER, C. V. 1906. Flora of the State of Washington. — Contrib. U.S. Nat. Herb. 11: 1—637.

POELLNITZ, K. VON 1932. Claytonia Gronov. und Montia Mich. — Feddes Repert. 30: 279—325.

PORSILD, A. E. 1951. Botany of Southeastern Yukon Adjacent to the Canol Road. — Bull. Nat. Mus. Canada 121. 400 pp.

ROBINSON, B. L. 1897. Portulacaceae. — In A. GRAY, Synoptical Flora of North America 1(2): 262—279. — Cambridge, Mass.

RYDBERG, P. A. 1917. Flora of the Rocky Mountains and Adjacent Plains. Ed. 1. — New York. 1110 pp.

— 1932. Portulacaceae. — In: North American Flora 21(4): 279—336.

SALISBURY, E. J. 1942. The Reproductive Capacity of Plants. — London. 244 pp.

Stebbins, G. L. 1950. Variation and Evolution in Plants. — New York. 643 pp.

Strandmark, P. W. 1887. Förgreningen och bladställningen hos Montia särskildt med afseende på frågan om blommans orientering. — Bot. Notiser 1887: 164—174.

Strid, A. 1969. Evolutionary Trends in the Breeding System of Nigella (Ranunculaceae). — Bot. Notiser 122(3): 380—397.

Swanson, J. R. 1966. A Synopsis of Relationships in Montioideae (Portulacaceae). — Brittonia 13(3): 229—241.

Torrey, J. & Gray, A. 1838—40. A Flora of North America, 1. — New York. 711 pp.

Volkova, E. V. 1964. A Review of the Species of Claytonia in USSR. — Bot. Žurn. 49(12): 1760—1768.

Willis, J. C. 1892. The Distribution of the Seed in Claytonia. — Ann. Bot. 6: 382—383.

LIST OF MATERIAL EXAMINED

Montiastrum bostockii

CANADA, YUKON TERRITORY

Dawson Range, S of Selkirk W of Carmacha near headwaters of Klaza River, 4200 feet, 1933, Bostock 19 (CAN). — S of Burwash Landing, Kluane L., 1944, H. M. & L. G. Raup 12245 (S). — Mountain slopes E of the mouth of Slim's R., Kluane L., 4500—5300 feet, 1944, H. M. & L. G. Raup 12533 (C, S). — Headwaters of Bridge Creek, 1948, H. M. & K. A. Raup, W. H. Drury 13353 (S). — Upper Quill Creek Valley in the Tetamaqouche Pass, 4000—4600 feet, 1953, Freedman (F). — Alaska Hwy, Mile 1022, Mt. Decoele, 4100 feet, 1957, Schofield & Crum 8048 (S).

MANITOBA

Mile 349, Hudson Bay R.R., 1936, P. A. Taverner (CAN).

USA, ALASKA

Head of Ketchumstock Cr., 1921, O. J. Murie 190 (S).

Montiastrum dichotomum

CANADA, BRITISH COLUMBIA

Near Victoria, 1885, Fletcher 336 (BM). — Vicinity of Victoria, 1893, J. Macoun (K). — Vancouver Island, 1895, J. Macoun 238 (K). — Vancouver Island, vicinity of Victoria, 1908, J. Macoun 78821 and 78824 (F). — Vancouver Island, Gonzales, Victoria, 1916, C. F. Newcombe (V); 1916, W. R. Carter (V). — Vancouver Island, Wellington, 1917, W. R. Carter C. 585 (GH, UBC, V) and 1792 (V). — Victoria, Beacon Hill, 1925, G. A. Hardy 7535 (V). — Boston Bar, 1934, T. T. McCabe (UC). — 6 miles NW of and 500—1000 feet above Pritchard, 1935, T. T. McCabe 2070 (UC). — Ten Mile Point, Victoria, 1939, J. W. Eastham (UBC). — Vernon, 1943, V. C. Brink (UBC). — Vancouver Island, Lost Lake, 1948, G. A. Hardy 21358 (V). — White Lake near Oliver, 1955, T. M. C. Taylor 3207 (UBC). — Vancouver Island, Mt. Newton, 1959, M. C. Melbourn (LD).

USA, CALIFORNIA

Siskiyou Co., Yreka, 1876, E. L. Greene 691 (F, GH, NY). — Siskiyou Co., Oro Fino, 1909, G. D. Butler 677 (JEPS).

IDAHO

Moscow, about the College, 1897, L. F. Henderson 4582 (GH). — Coeur d'Alene Lake, 1905, M. E. Jones (UPS). — Santa, 1929, C. Epling (LA). — Kootenai Co., Post Falls, 1933, J. H. Christ 2124 (NY). — Bonner Co., La Clede, 1933, J. H. Christ 2140 (NY). — Latah Co., 3 miles N of Moscow, 1937, J. H. Christ & W. W. Ward 6913 (NY). — Adams Co., Fruitvale, 1938, J. H. Christ 9190 (NY). — Washington Co., W of Crane Creek Reservoir E of Midvale, 1938, J. H. Christ 9262 (NY). — Latah Co., 2 miles SE of Joel, 1940, J. H. Christ 10829 (NY). — Kootenai Co., 2 miles N of Worley, 1946, J. H. Christ 15083 (NY). — Latah Co., along the road to Moscow Mt., c. 4 miles NE of Moscow, 1949, W. H. Baker 5832 (NY). — Latah Co., NE of Moscow, 1949, W. H. Baker 5783 (NY, WTU). — Latah Co., S slope of Tomer's Butte, 4 miles SE of Moscow, 1951, W. H. Baker 7353 (WTU). — Kootenai Co., 6 miles W of Athol, 1951, W. H. Baker 7363 (WTU).

MONTANA

Lake Co., 1 miles S of Charlo, 1948, C. L. Hitchcock 17776 (WS, WTU).

OREGON

Columbia f. Wahlamet Plains (BM). — Wahlamet plains in wet places, Nuttall (NY). — Nuttall (GH, K). — Geyer 648 (BM, GH, K). — Wet Prairies, 188?, T. J. Howell (F); 1880 and 1886, T. J. Howell 3865 (NY); 1880, J. & T. J. Howell (WS). — Wasco Co., near The Dalles, 1882, T. Howell (GH, NY, ORE, OSC, WTU). — Salem, 1883, Drake & Dickson (F). — Washington Co., Forest Grove, 1884, L. F. Henderson 10335 (ORE). — Near Portland, 1886, T. J. Howell 617

(GH). — Washington Co., 1886, J. Howell (WS). — Salem, 1887, M. W. Gorman (WTU). — Marion Co., Salem, 1887, L. F. Henderson 138 (JEPS, OSC). — Gladstone, 1899, T. Howell (ORE). — Sherman Co., Deschutes River near Sherars Bridge, 1902, E. P. Sheldon S. 9083 (ORE). — Wasco Co., The Dalles, 1902, E. P. Sheldon 10102 (F, GH, NY, ORE, WS). — Umatilla Co., Meacham, 1923, W. Sherwood 28 (F). — Wasco Co., 1 mile SE of The Dalles, 1926, M. E. Peck 14583 (K). — Klamath Co., Klamath River, Mc Cullom's Mill, 1928, L. F. Henderson 9363 (ORE). — Marion Co., Battle Creek 8 miles S of Salem, 1932, M. E. Peck 17290 (OSC). — Jackson Co., near Pinehurst, 4000 feet, 1934, J. W. Thompson 10342 (LD, NY, WTU). — Jackson Co., Lower Table Rock, 2025 feet, 1942, L. E. Detling 5114 (ORE). — Lane Co., along the Willamette River, 1 mile W of Oakridge, 1948, W. H. Baker 5276 (OSC).

WASHINGTON

Goldendale, 1876, T. Howell (ORE). — Klickitat Co., White Salmon, 1878, W. N. Suksdorf (WS). — Klickitat Co., Bingen, 1880, W. N. Suksdorf 2224 (WS). — Klickitat Co., Falcon Valley, 1881, W. N. Suksdorf 30 (BM, F, K, NY, WS); 1882 (LD). — La Camas, 1884, L. F. Henderson 132 (OSC). — Spokane Co., 1889, W. N. Suksdorf 3320 (WS). — Clarke Co., Bachelors Island, 1894, W. N. Suksdorf 3527 (WS). — Klickitat Hills, 1895, T. Howell 89 (WS). — Grand Dalles, 1895, M. W. Gorman (WS). — Whitman Co., Pullman, 1897, A. D. E. Elmer 173 (K, NY, WS). — Klickitat Co., "Aphyllon rocks", Bingen, 1899, W. N. Suksdorf 3943 (WS). — Pullman, 1897, C. V. Piper 2667 (GH, NY, WS); 1899, A. D. E. Elmer 1506 (SMU). — Spokane, 1899, C. V. Piper (WS). — Klickitat Co., Bingen, 1907, W. N. Suksdorf 5937 (WS). — Klickitat Co., near Fulda, Falcon Valley, 1910, W. N. Suksdorf 6977 (WS). — Whitman Co., Kamiak Butte, 1921, H. St. John 6071 (WS). — Klickitat Co., Vila, near Bingen, 1922, W. N. Suksdorf 10772 (WS). — Okanogan Co., Omak, 1937, C. B. Fiker 2380 (WS). — Whatcom Co., Sandy Point, 1939, W. C. Muenscher 9782 (GH, WTU).

Montiastrum lineare

(A list of the collections from British Columbia, California, Idaho, Montana, Oregon and Washington is deposited in the Library of this institution; cf. Fig. 6 and pp. 101—102.)

CANADA, ALBERTA

Lonesome Lake, Waterton Lakes Park, 4200 feet, 1925, M. O. Malte & W. R. Watson (UC).

USA, NEVADA

Washoe Valley, 1865, Arelet 189 (NY). — Washoe Co., about Washoe Lake, 1570 m, 1902, C. F. Baker 1084 (F, GH, NY, UC, US). — Washoe Co., Franktown Creek, 1907, C. C. Brown (E). — Elko Co., 4 miles S of White Rock, 6000 feet, 1940, A. H. Holmgren 569 (WS).

UTAH

Weber Co., 3.3 miles W of Eden Chapel, 1947, A. O. Garrett & M. Melner 9481 (US).

LOCO INGN.

Ex Herb. W. M. C. Cusik (ORE). — America boreali-occidentalis, D. Douglas 1829 (GH, NY); — 1830 (BM). — Lewis Fork, Steven's Pacific Railroad Survey, 1858—60, Cooper (NY).

Montiastrum vassilievii

USSR, NE. SIBERIA

Basin of Anadyr, at Mt. Irgunej in the Raritkin mountain ridge, 1933, V. Vassiliev 1661 (LE).

Regional Studies in Alectoria (Lichenes) I

The Central and Southern African Species

By D. L. Hawksworth

Commonwealth Mycological Institute,
Kew, Surrey, England

ABSTRACT

Hawksworth, D. L. 1971. Regional studies in Alectoria (Lichenes) I. The central and southern African species. — Bot. Notiser 124: 122—128.

In central and southern Africa the lichen genus *Alectoria* Ach. is largely restricted to the highest mountains of Kenya, Tanzania and Uganda, where *A. angolensis* Dodge, *A.* cf. *chalybeiformis* (L.) Gray, *A. fuscescens* Gyeln. var. *nigrescentifusca* (Gyeln.) D. Hawksw. comb. nov., *A. motykae* D. Hawksw. sp. nov., *A. ruwenzoriensis* D. Hawksw. sp. nov. and *A. smithii* Dr. f. *esorediata* D. Hawksw. f. nov. occur. Reports of *A. bicolor* (Ehrh.) Nyl., *A. epichrysa* Stirt., *A. chalybeiformis* (L.) Gray f. *terrestris* Stizenb., *A. jubata* (L.) Ach., *A. jubata* (L.) Ach. var. *prolixa* Ach., *A. sulcata* (Lév.) Nyl. and *Parmelia lichinoidea* Nyl. ex Cromb. by earlier authors are also discussed.

INTRODUCTION

This is the first of a series of papers which will discuss the species of the lichen genus *Alectoria* Ach. present in different regions of the world. In the course of my studies it became clear that the central and southern African taxa were in particular need of revision and this paper presents such a revision and discusses the identities of taxa previously published as occurring in this area. Species known from northern Africa (including Algeria and Morocco) and islands off the Atlantic coast of Africa other than Cape Verde are not treated here.

In central and southern Africa the genus proves to be absent from South Africa and Rhodesia and almost entirely restricted to the alpine zones of the highest mountains of Kenya, Tanzania and Uganda (i.e. Mt. Elgon, Mt. Kenya, Mt. Kilimanjaro, Mt. Ruwenzori) where it appears to be rather rare. The endemism shown by this genus here appears to parallel that seen in *Usnea* P. Browne ex Adans. although many fewer species are represented.

KEY

1 a. Thallus yellowish-brown, grey-brown, pale grey, or dark brown to black; K+yellow or K+yellow changing to red 2
   b. Thallus dark brown to black; K− 3
2 a. Thallus K+yellow, KC+red (cf. barbatolic acid); lateral spinules present .... 5. *A. ruwenzoriensis* (p. 124).
   b. Thallus K+yellow changing to red, KC— (salazinic acid); lateral spinules absent .... 1. *A. angolensis* (p. 123).
3 a. Soralia present, PD+red; medulla PD— or PD+red 4
   b. Soralia absent; medulla PD− .... 6. *A. smithii* f. *esorediata* (p. 126).

4 a. Medulla PD+red 5
b. Medulla PD− . . . . 2. *A.* cf. *chalybeiformis* (p. 123).
5 a. Lateral spinules present; prostrate delicate plant; all soralia of the fissural type . . . . 4. *A. motykae* (p. 124).
b. Lateral spinules absent; pendent coarse plant; soralia fissural or tuberculate . . . . 3. *A. fuscescens* var. *nigrescentifusca* (p. 123).

1. **Alectoria angolensis** Dodge in Nova Hedwigia Beih. (in press)

SPECIMEN EXAMINED: ANGOLA: Amboim, Cuanza Sul, Capir, near the Carloaongo-Cuvo River, on rotting wood, III 1933, J. Gossweiler 9909 (VT).

This specimen (det. Prof. C. W. Dodge) is fragmentary but superficially shows some resemblance to *A. capillaris* (Ach.) Cromb. from which it may be distinguished by the fissural soralia and the presence of salazinic acid (demonstrated in G.A.*o*-T. and KK in this specimen). Salazinic acid has only otherwise been reported from this genus in '*A. cana*' by Solberg (1956), but, as later workers have not confirmed this, it seems possible that Solberg's material was contaminated with fragments of lichens belonging to other genera.

Although the cortical hyphae of Gossweiler's specimen are longitudinally orientated and rather conglutinate, I am not convinced that this specimen is really an *Alectoria*. It seems possible that it could be a member of the family Ramalinaceae Ag. in which case, from the structure of its cortex, it would be a member of *Desmaziera* Mont. sect. *Desmaziera* ser. *Cylindricae* Follm. & Hun. Little significance can be attributed to my failure to find usnic acid in Gossweiler's specimen since this acid often occurs in low concentrations and is difficult to demonstrate by microcrystal tests in several species of *Ramalina*. Salazinic acid is, however, unknown in *Desmaziera* Mont. (Follmann & Huneck 1969) although it occurs in many species of *Ramalina* Ach.

Further collections of *A. angolensis* are needed before its correct generic classification can be ascertained.

2. **Alectoria** cf. **chalybeiformis** (L.) Gray, Nat. Arr. Brit. Pl. 1: 408 (1821)

Lichen chalybeiformis L. Sp. Plant. 2: 1153 (1753). Type: sine loco, Herb. C. Linnaeus, sheet no. 1273.290 (LINN, lectotype).

AFRICAN SPECIMENS EXAMINED: TANZANIA: Kilimanjaro, valley below Johnsell Point (Grid Ref. CG 011 656), alt. 12,500 ft., hanging from rock in sheltered valley in alpine zone, 29 XII 1968, M. Bigger 2378 (BM). — UGANDA: Ruwenzori, Bujuku Hut, alt. 13,000 ft., on a vertical cliff, 19 VI 1968, S. B. Manum M 121 (Herb. Swinscow); — Ruwenzori, Bujuku Hut, alt. 13,000 ft., 19 VI 1968, S. B. Manum M 117 a (VT); — Mt. Elgon, Sasa Mountain Hut, (1°11′ N, 34°28′ E), alt. 3,200 m, 7 XII 1967, S. B. Manum (Herb. Swinscow).

Bigger's specimen is 20 cm long, pendent, dark olivaceous, nitidous, slightly paler basally, with main branches to 0.5 mm diam., with abundant irregular isotomic-dichotomic branching, and both fissural and tuberculate types of soralia. As the cortex and medulla react PD− and the soralia react PD+ bright red (fumarprotocetraric acid) this material is closest to *A. chalybeiformis* (L.) Gray. As its colour and pendent habit differ from the usual morphotypes of this species in Europe, North America, and Antarctica, it may merit some infraspecific rank. In the absence of more material, however, I am disinclined to describe it as new. All Manum's collections are fragmentary and consequently do not help in the elucidation of this problem.

3. **Alectoria fuscescens** Gyeln. var. **nigrescentifusca** (Gyeln.) D. Hawksw., comb. nov.

Bryopogon nigrescens f. *nigrescentifuscus* Gyeln. in Acta Geobot. Hung. 2: 163 (1937). Type: U.S.S.R., Sibiria, Krasnojarsk Distr., Ewenkijsk, Jambukan River, (64°51′ N, 68° 49′ E), 8 VIII 1935, N. Grachow (BP no. 33.973, holotype).

AFRICAN SPECIMEN EXAMINED: TANZANIA: Kilimanjaro, nr. Peters Hut in the *Philippia* region, on a bird stone, alt. 3,870 m, 27 VI 1948, O. Hedberg 1401 (UPS).

This variety superficially resembles some forms of *A. lanestris* (Ach.) Gyeln. but is distinguished from it by the positive reactions of the medulla with PD, the paler basal parts of the thallus, abundant soralia, and its more rigid habit. It is distinguished from other varieties of *A. fuscescens* by the darker colour (dark brown) and rather slender habit.

4. **Alectoria motykae** D. Hawksw., sp. nov.

TYPE: KENYA: Mt. Kenya, Teleki Valley, alpine regions, on vertical surfaces of boulders in the upper part of the valley (overgrowing *Andraea rupestris* Hedw.), alt. 4,200 m, 28 VII 1948, O. Hedberg 1720 b (UPS, holotype).

Thallus fruticosus, mollis, decumbens, usque ad 5—8 cm longus, atrofuscescens vel nigrescens, non nitidus, basi et apicibus plerumque concoloribus. Rami principales repetite iso-dichotomiter ramosi, ad 0.3 mm crassi. Rami laterales spiniformes, plerumque frequentes, interdum rarissimi, breves, ad 2—3 mm longi, arcuate ad ramos principales curvati. Pseudocyphellae desunt. Soralia frequentia in ramis medialibus et apicalibus sita, alba, fissuriformia, concava, usque ad c. 1 mm longa, lateriora quam rami. Soredia plerumque frequentia. Structura anatomica ut in omni specie *Alectoriae*. Apothecia et pycnidia ignota.

Cortex K, C, KC et PD non coloratur; medulla similiter sed PD rubescens; soralia K, C, KC non colorantur sed PD celeriter rubescentia. Thallus acidum fumarprotocetraricum continens.

OTHER SPECIMEN EXAMINED: UGANDA: Mt. Elgon, crater Up, on tree heaths, alt. 13,000 ft., I 1918, R. A. Dummer 3774 (BM ex K).

Thallus fruticose, flaccid, prostrate, usually 5—8 cm long, dark fuscous brown to blackish, not shining, base and apices usually concolourous. Main branches isotomic-dichotomically branched, to 0.3 mm broad. Lateral spinules present, usually frequent but occasionally rare, short, to 2—3 mm long, arcuately curved towards the main stem. Pseudocyphellae absent. Soralia frequent on median and apical branches, usually to about 1 mm long, lateral, oval, fissural, concave. Soredia usually frequent. Anatomical structure as in other species of *Alectoria*. Apothecia and pycnidia unknown.

Cortex K —, C —, KC —, PD —; medulla K —, C —, KC —, PD + red; soralia K —, C —, KC —, PD + rapidly red. Contains fumarprotocetratic acid.

A. motykae resembles *A. nidulifera* Norrl. ex Nyl. in some characters but in *A. nidulifera* the thallus is cervine brown, the soralia are invariably narrower than the branches on which they arise and also usually isidiate and spinulate, and the whole plant has a caespitose habit. *A. simplicior* (Vain.) Lynge has similar soralia to those of *A. motykae* but they are generally greenish-brown in colour and consistently PD —; the thallus of *A. simplicior* is also darker than that of *A. motykae*.

This new species is named in recognition of the valuable contributions made by Prof. Dr. J. Motyka (Lublin, Poland) to our knowledge of this genus.

5. **Alectoria ruwenzoriensis** D. Hawksw., sp. nov.

TYPE: UGANDA: Ruwenzori, Mijusi Valley, epiphytic on stems of *Helichrysum stuhlmannii*-shrubs, alt. 3,900 m, 27 III 1948, O. Hedberg 521 f (UPS, holotype).

Thallus fruticosus, rigidiusculus, pendulus vel prostratus, nigrescens, non nitidus sed opacus, apicibus vel concoloribus vel cervino-brunneis. Rami principales aniso-dichotomiter ramosi, verisimiliter submonopodiales ad apicem, plerumque in obtusos angulos divergentes; rami principales ad 0.4 mm crassi, morientes e baso. Rami laterales frequentes, plerumque pallidiores quam rami principales, divergentes ad 90° ad ramos principales, arcuati, ad 1 cm longi. Pseudocyphellae desunt. Soralia rarissima vel nulla, minutissima, fissuriformia, numquam lateriora quam rami,

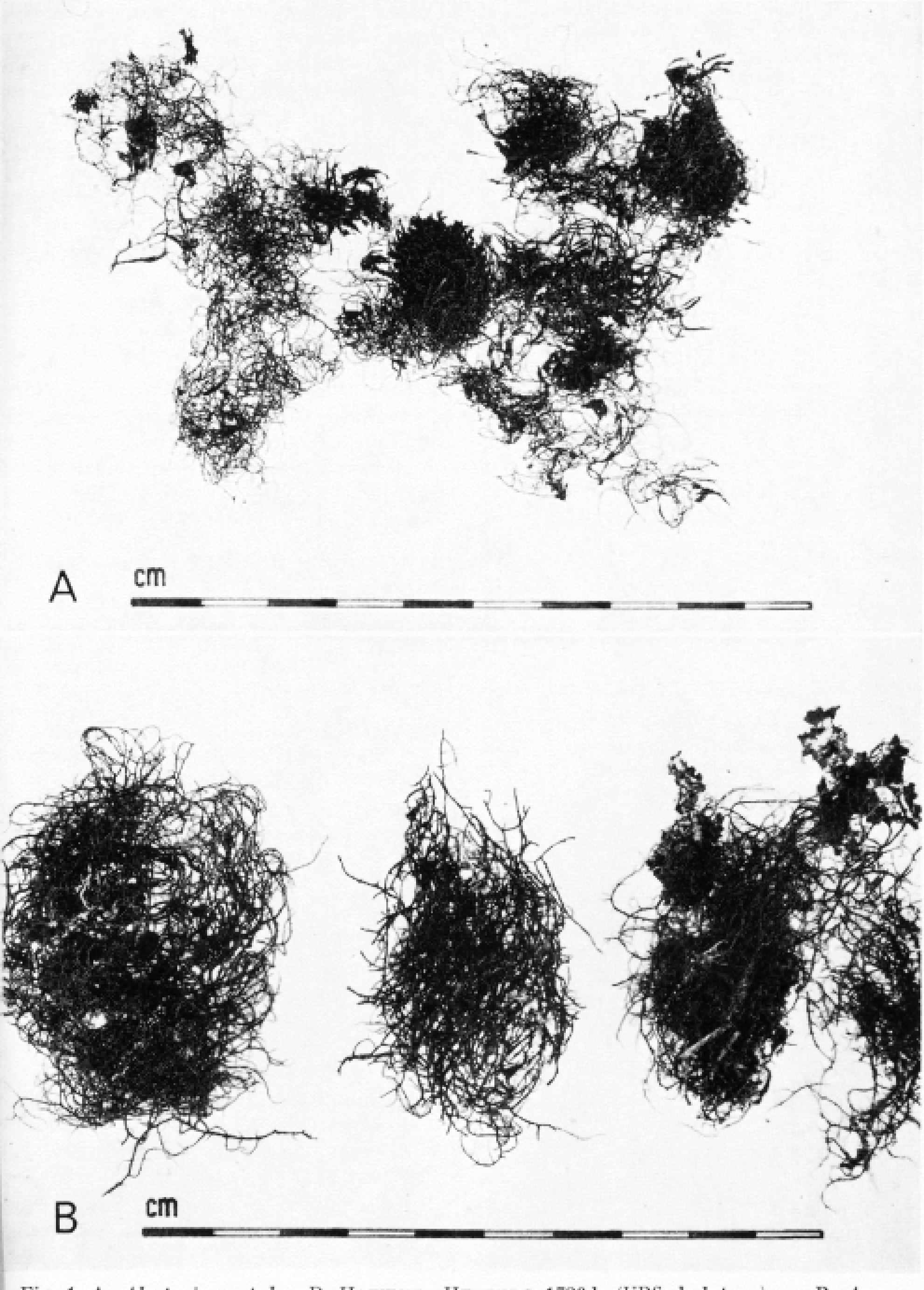


Fig. 1. A: *Alectoria motykae* D. Hawksw., Hedberg 1720 b (UPS, holotype). — B: *A. ruwenzoriensis* D. Hawksw., Hedberg 521 f (UPS, holotype). — Photographs by D. W. Fry.

ad 0.3 mm longa. Structura anatomica ut in omni specie *Alectoriae*. Apothecia et pycnidia ignota.

Cortex et medulla in pallidis partibus K flavescentes, C—, KC rubescentes, PD aurantiaci colorantur, quod demonstrare nonnumquam difficile est. Thallus acidum cf. barbatolicum continens.

OTHER SPECIMENS EXAMINED: TANZANIA: Kilimanjaro, near Peters Hut in the *Philippia* region, on the ground in the "*Philippia* scrub", alt. 3,800 m, 16 VI 1948, O. Hedberg 1217 e (UPS); — Kilimanjaro, above Marangu in the *Philippia* region, in the bottom layer among *Philippia* shrubs below Peters Hut, alt. 3,700 m, 21 VI 1948, O. Hedberg (UPS). — UGANDA: Ruwenzori, Bukurunga Valley, western slopes of Central Portal Peaks, on steep rock, alt. 4,250 m, 3 IV 1948, O. Hedberg 663 c (UPS); — Ruwenzori, Bukurunga Valley, in the side-valley on the SE slope of Mt. Gessi, epiphytic on *Helichrysum* shrubs, alt. 3,900 m, 4 IV 1948, O. Hedberg 669 (UPS).

Thallus fruticose, rigid, pendent or prostrate, black, matt, apices concolourous or cervine brown. Branching of the main stems anisotomic-dichotomic, appearing submonopodial near the apices, branches usually diverging at obtuse angles, main branches to 0.4 mm wide, dying from the base. Lateral branches frequent, usually paler than the main branches, arising at 90°, arcuate, to 1 cm long. Pseudocyphellae absent. Soralia rare or absent. If present minute, fissural, never broader than the branches on which they arise, to 0.3 mm long. Anatomical structure as in other species of *Alectoria*. Apothecia and pycnidia unknown.

Cortex and medulla in the paler areas K+yellow, C−, KC+red, PD+orange red. In some specimens the reactions are difficult to demonstrate. Probably contains barbatolic acid.

The habit of *A. ruwenzoriensis* is very similar to that of the Himalayan *A. poeltii* Bystrek from which it differs principally in the chemical constituents and type of soralia. *A ruwenzoriensis* is, however, most closely related to *A. nadvornikiana* Gyeln. (and more particularly to the var. *spinulosa* [Ahln. ex Räs.] Mot.) but is distinguished from it by the much coarser habit, the darker colour of the apical branches, the soralia, and in that the thallus dies upwards from the base. This new species has not been treated as a subspecies in view of its geographical isolation from *A. nadvornikiana* (a circum-boreal species in the Northern Hemisphere) and the absence of any evidence for intergradation between the two. Some plants of *A. smithii* f. *esorediata* may superficially resemble *A. ruwenzoriensis* but are readily distinguished from it by microchemical tests.

The reactions of *A. ruwenzoriensis* are not always easy to demonstrate on the basal parts of the thallus and consequently should be made on the paler, more apical parts.

6. **Alectoria smithii** DR. f. **esorediata** D. Hawksw., f. nov.

TYPE: UGANDA: Ruwenzori, Mijusi Hut, tallus slopes on the western side of Mt. Gessi, on a boulder, alt. 4,300 m, 28 III 1948, O. Hedberg 548 a (UPS, holotype).

Planta ut in *Alectoria smithii* f. *smithii* sed differt thallo compactiore, soraliis nullis et apice obscuro-atrobrunneo vel nigrescenti-fusco, non olivaceo.

Plant as in *Alectoria smithii* f. *smithii* but differing in the more compact thallus, the absence of soralia, and the dull dark brown to blackish fuscous and not olivaceous apices.

This specimen is clearly conspecific with *A. smithii* Du Rietz, a species with a rather wide distribution in oceanic western and central Alpine areas of Europe, which is also well known in Himalaya, the mountains of western China and New Guinea, but which appears to be absent from North and South America and Japan. Hedberg's specimen has the narrow fissures typical of f. *smithii*, but they do not form the sprouts of spinules and soredia normally found in f. *smithii*. This species does not appear to produce any lichen acids.

EXCLUDED RECORDS

1. **Alectoria bicolor** (EHRH.) NYL.

Reported by JATTA (1909 p. 538) from "Ruwenzori, Bujongolo nella valle de Mobuku (m 3800); tr." whose record was cited by ZAHLBRUCKNER and HAUMAN (1936 p. 24). The material on which this record is based has not been traced but it seems probable that it is an error for *A. motykae, A. ruwenzoriensis* or *A. smithii.*

2. **Alectoria epichrysa** STIRT. in Journ. Linn. Soc. London (Bot.) 14: 367 (1875)

TYPE: CAPE VERDE: H. N. MOSELEY (BM, holotype).

This specimen was redetermined as *Teloschistes flavicans* (SW.) NORM. (sub '*Physcia flavicans*') by CROMBIE (1878 p. 212) and the type proved to be its rather dull form, f. *cinerascens* (STEIN) MÜLL. ARG. *A. epichrysa* should therefore be treated as a synonym of *T. flavicans.* There is no authentic specimen of *A. epichrysa* in GLAM.

3. **Alectoria chalybeiformis** (L.) GRAY f. **terrestris** STIZENB. in Ber. Thätigk. St. Gall. Nat. Ges. 1888—1889: 149 (1890)

TYPE: SOUTH AFRICA: O.F.S., Smithfield, II 1870, C. S. ORPEN (SAM no. 46939, lectotype).
Alectoria prolixa var. *chalybeiformis* f. *terrestris* (STIZENB.) STIZENB. in Ann. Naturhist. Hofmus. (Wien) 7: 129 (1892).

This record is also cited by DOIDGE (1950 p. 327). KEISSLER (1959 p. 129) examined the type in ZT and considered it to be an alga. This specimen has been mislaid and a duplicate in SAM is designated here as a lectotype. The lectotype has been determined by Dr. D. J. HIBBERD as *Nostoc commune* (VAUCH.) BORN. & FLAH. var. *flagelliforme* (BERK. & CURT.) BORN. & FLAH. Slides made from the lectotype specimen are deposited in BM and IMI (no. 145817).

4. **Alectoria jubata** (L.) ACH.

Reported by DOIDGE (1950 p. 327) on the basis of a collection from South Africa "ad terram, prope Smithfield, O. F. State, C. S. ORPEN" (SAM no. 46938). This specimen is the alga *Nostoc commune* (VAUCH.) BORN. & FLAH. var. *flagelliforme* (BERK. & CURT.) BORN. & FLAH.

5. **Alectoria jubata** (L.) ACH. var. **prolixa** ACH., nom. rejic.

ZAHLBRUCKNER and HAUMAN (1936 p. 23) recorded this taxon from Ruwenzori "4000 m, abondant sur vielles branches de *Philippia:* HAUMAN 946 et 915 b" and FREY (1967 p. 223) reported it from "Muhavura, 3950 m. ü. M., saxicol an NW-exponierter Felswand", in the alpine belt, 1953—1954, H. U. STAUFFER. HAUMAN's specimens, formerly in BRLU, were unfortunately destroyed in World War II (DUVIGNEAUD *in litt.*), but from their habitat it seems probable that they were *A. ruwenzoriensis.* It seems probable that STAUFFER's collection, as it was determined by MOTYKA, and as it occurred on rock, belongs to *A.* cf. *chalybeiformis.* STAUFFER's collection has not been seen by me. The reasons for the rejection of the name '*A. jubata* ACH. var. *prolixa*' are discussed by HAWKSWORTH (1970 p. 239).

6. **Alectoria sulcata** (LÉV.) NYL.

Reported from Cape Verde by STIRTON (1875 p. 367) on the basis of a specimen collected by H. N. MOSELEY. CROMBIE (1878 p. 212) redetermined MOSELEY's specimen as *Anaptychia leucomelaena* (L.) MASSAL. (sub '*Physcia leucomela*') and, although this specimen now appears to be absent from both BM and GLAM, there seems no reason to doubt CROMBIE's view. *A. sulcata* appears to be confined to Himalaya, Japan, western China, and Formosa.

7. **Parmelia lichinoidea** Nyl. ex Cromb. in Journ. Bot. (London) 14: 19 (1876)

TYPE: SOUTH AFRICA: Cape of Good Hope, summit of Table Mountain, IX 1874, A. E. Eaton (BM, lectotype).

This species is mentioned here as Crombie (1876 a), Vainio (1903 p. 14) and Hue (1890 p. 291) all considered it to be very closely related to *A. pubescens* (L.) R. H. Howe (sub '*P. lanata*'). The type specimen is, however, strongly dorsiventrally compressed, and the hyphae in its cortex are randomly orientated. It is therefore clear that it belongs to the genus *Parmelia* Ach. nom. cons. and not to *Alectoria*. The thallus and medulla were negative to K, C, KC and PD, a slight residue remained after extraction on a slide with acetone, but determinable crystals were not obtained in either G.E. or G.A.W. *P. lichinoidea* appears to be related to *P. stygia* (L.) Ach. from which it differs in size and in its chemistry; and to *P. almquistii* Vain. which resembles it in size but not in its chemical reactions.

The name *Parmelia lichinoidea* appeared in two publications of Crombie in 1876, and there has been some confusion in the literature as to which appeared first. Crombie (1876 a) was published in January 1876, however, whilst Crombie (1876 b) did not appear until 11 July 1876.

ACKNOWLEDGEMENTS

I am indebted to the directors and curators of the herbaria cited in the text for permission to study specimens in their care; and particularly to Dr. R. Santesson for the loan of Hedberg's important collections. I am also grateful to Dr. O. Almborn, Prof. C. W. Dodge, Prof. P. Duvigneaud, Dr. D. J. Hibberd, Dr. T. D. V. Swinscow and Mr. E. C. Wallace for help in various ways.

LITERATURE CITED

Crombie, J. M. 1876 a. New lichens from the Cape of Good Hope. — Journ. Bot. (London) 14: 18—21.

— 1876 b. Lichenes capenses: — An enumeration of the lichens collected at the Cape of Good Hope by the Rev. A. E. Eaton during the Venus-Transit Expedition in 1874. — Journ. Linn. Soc. London (Bot.) 15: 165—180.

— 1878. The lichens of the 'Challenger' Expedition (with a revision of those enumerated by Dr. J. Stirton in Linn. Journ. Bot. XIV. pp. 366—375). — Ibid. 16: 211—231.

Doidge, E. M. 1950. The South African fungi and lichens to the end of 1945. — Bothalia 5: 1—1094.

Follmann, G. & Huneck, S. 1969. Mitteilungen über Flechteninhaltsstoffe LXI. Zur Chemotaxonomie der Flechtenfamilie Ramalinaceae. — Willdenowia 5: 181—216.

Frey, E. 1967. Die Lichenologischen Ergebnisse der Forschungreisen des Dr. Hans Ulrich Stauffer in Zentralafrika (Virunga-Vulkane 1954/1955) und Südafrika-Australien-Ozeanien-USA 1963/1964. — Bot. Jahrb. 86: 209—255.

Hawksworth, D. L. 1970. Chemical and nomenclatural notes on Alectoria (Lichenes) II. — Taxon 19: 237—243.

Hue, A. M. 1890. Lichenes exoticos a Professore W. Nylander descriptos vel recognitos et in Herbario Musei Parisiensis pro maxima parte asservatos in ordine systematico disposuit. — Nouv. Arch. Mus. Hist. Nat. Paris. Sér. 3. 2: 209—322.

Jatta, A. 1909. Lichenes. — In L. A. G. M. F. Francesco (ed.), Il Ruwenzori. Parte scientifica. 1: 537—547. — Milan.

Keissler, K. 1958—1960. Usneaceae. — In Rabenhorst, Kryptogamen-Flora 9, 5(4): 1—755. — Leipzig.

Solberg, Y. J. 1956. Dyeing of wool with lichens and lichen substances. — Acta Chem. Scand. 10: 1116—1123.

Stirton, J. 1875. Enumeration of the lichens collected by H. N. Moseley, M. A., Naturalist to H. M. S. 'Challenger', in the islands of the Atlantic Ocean. — Journ. Linn. Soc. London (Bot.) 14: 366—375.

Stizenberger, E. 1890. Lichenaea africana. — Ber. Thätigk. St. Gall. Naturw. Ges. 1888—1889: 105—149.

Vainio, E. A. 1903. Botanique. Lichens. — In: Expédition antarctique Belge. Résultats du voyage du S. Y. Belgica en 1897—1898—1899, pp. 1—46. — Anvers.

Zahlbruckner, A. & Hauman, L. 1936. Les lichens des hautes altitudes au Ruwenzori. — Mém. Inst. Roy. Col. Belge, Sect. Sci. Nat. Med. 8° coll. 5: 1—31.

Variation and Taxonomy of Hierochloë (Gramineae) in the Northern Hemisphere

By Gunnar Weimarck

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

WEIMARCK, G. 1971. Variation and taxonomy of Hierochloë (Gramineae) in the Northern Hemisphere. — Bot. Notiser 124: 129—175.*

The taxonomy of *Hierochloë australis,* the *H. odorata* complex, and the *H. alpina* complex is treated on the basis of evidence from morphology, cytology, chemistry, reproduction, and distribution. Taxa dealt with are *H. australis* (SCHRADER) ROEMER & SCHULTES, *H. odorata* (L.) WAHLENB. ssp. *odorata, H. odorata* (L.) WAHLENB. ssp. *baltica* G. WEIM. ssp. nov., *H. hirta* (SCHRANK) BORBÁS ssp. *hirta, H. hirta* (SCHRANK) BORBÁS ssp. *arctica* (PRESL) G. WEIM. comb. nov., *H. repens* (HOST) SIMONKAI, *H. alpina* (WILLD.) ROEMER & SCHULTES ssp. *alpina,* and *H. alpina* (WILLD.) ROEMER & SCHULTES ssp. *orthantha* (SØRENSEN) G. WEIM. comb. nov.

INTRODUCTION

This paper treats the variation and taxonomy of some taxa of *Hierochloë*. It presents part of an investigation on the genus in the Northern Hemisphere. Other parts of the investigation that have been published are WEIMARCK 1963, 1967 a, b, and 1970 a, b, and c.

North-west and Central Europe, South Greenland, and North-east North America form two regions of more intensive investigation. Taxa occurring within these regions were also studied in other parts of the Northern Hemisphere, but more extensively. Taxa not occurring in the two main regions could not for practical reasons be included in the investigation.

The taxa treated can be divided into three groups, viz.:

1) *Hierochloë australis* (SCHRADER) ROEMER & SCHULTES
2) the *H. odorata* complex, consisting of
   H. odorata (L.) WAHLENB.
      ssp. *odorata*
      ssp. *baltica* G. WEIM. ssp. nov.
   H. hirta (SCHRANK) BORBÁS
      ssp. *hirta*
      ssp. *arctica* (PRESL) G. WEIM. comb. nov.
   H. repens (HOST) SIMONKAI
3) the *H. alpina* complex, consisting of
   H. alpina (WILLD.) ROEMER & SCHULTES
      ssp. *alpina*
      ssp. *orthantha* (SØRENSEN) G. WEIM. comb. nov.

All eight taxa investigated have more or less reduced sexual reproduction because of facultative or obligate apomixis. Due to apomixis and polyploidy the taxa are separated by strong reproductive barriers. The genetic interchange between individuals of the same taxon is greatly restricted for the same reasons.

The variation pattern of such completely or partly apomictic groups does not always make them fit very well into the rigid

---

* Preprint distributed on March 30, 1971.

hierarchical system. In this treatment of *Hierochloë* morphological discontinuities present in the material were used in such a way that units distinguishable in almost all cases (except for young and incomplete specimens) were given specific rank, whilst the distinction of taxa given subspecific rank can be problematic in some regions.

The morphological criteria used for distinguishing between taxa have been tested in the experimental material. They were confirmed by cytological, chemical, and other evidence.

In regions from which little or no experimental material was available the determination of herbarium material was made from the same morphological criteria. It must be kept in mind that the determinations may be somewhat preliminary in those regions because the risk of misinterpreting natural units in a critical genus such as *Hierochloë* is higher in the absence of experimental data. However I find the method used to be the only reasonable one.

What has been treated as "*Hierochloë odorata*" in my earlier papers (Weimarck 1963, 1967 a, b, and 1970 b, and c) corresponds to what was above termed the *H. odorata* complex. "*H. odorata* 2n=28" should be referred to *H. odorata* ssp. *odorata* with the exception of the collection B C C in Weimarck (1970 b Table 8, p. 253), which belongs to *H. repens*.

"*Hierochloë odorata* 2n=42" corresponds mainly to *H. odorata* ssp. *baltica*. Exceptions are some collections which on morphological grounds are placed with ssp. *odorata* together with the tetraploids (cf. pp. 145—146). Hexaploid collections of ssp. *odorata* dealt with earlier are A T F, A H F, and A O D (Weimarck 1970 b Table 9, p. 254). A hexaploid collection of ssp. *odorata* is also A H E treated in Weimarck (1967 a p. 224). The rest of the hexaploids in earlier papers belong to ssp. *baltica*.

"*Hierochloë odorata* 2n=56" corresponds to *H. hirta* with ssp. *hirta* and ssp. *arctica*. The collections A R B, A N N, A N M, A L H, A L F, A L E, A G O, A G N, A G M, A L D, A G S, A L A, A K U, A H M, and B A C in Weimarck (1970 b pp. 246, 256—257) belong to ssp. *hirta*, and the other octoploids dealt with earlier to ssp. *arctica*.

"*Hierochloë alpina*" and "*H. monticola*" treated in earlier papers (Weimarck 1967 b; 1970 a, b, and c) correspond to *H. alpina* ssp. *alpina* and ssp. *orthantha*, respectively.

Hierochloë occidentalis Buckl. and *H. pauciflora* R. Br. dealt with in Weimarck (1970 b) are not included in the present study. Closely allied to the *odorata* complex but also left out are the Central and East Asiatic *H. glabra* Trin. and *H. bungeana* Trin. Other members of the genus in Asia, New Zealand, and South America seem to have less strong affinities to the taxa treated.

MATERIAL AND METHODS

The study is based partly on herbarium material, partly on living plants cultivated for the purpose in the Botanical Gardens, Lund. Almost all plants kept in culture originate from rhizomes collected in the field. Thus they represent biotypes actually established in nature. A minor proportion were grown from caryopses received from other collectors. The plants, usually six from each locality, were grown under approximately uniform conditions in a mixture of sand, peat, and compost 1 : 1 : 1 and placed in the open in partial shade.

Each locality is designated by three capital letters, and each individual plant in a collection by an arabic numeral. Voucher specimens are preserved at the Botanical Museum, Lund (LD).

Descriptions and measurements have been made from herbarium material on loan and from voucher specimens of cultivated plants originally collected in the field. The data given can therefore be expected to cover the range of modification met with in nature with the exception of mere malformations. Supplementary morphological studies have also been made of the cultivated material.

The variation in height of flowering shoots and in number of spikelets per panicle found under natural conditions was generally greater than that displayed in the same material after transplantation to the relatively uniform conditions in culture. This was in most taxa true especially for those plants whose voucher specimens had lower culms and fewer spikelets than is normal. Still in *Hierochloë hirta* ssp. *hirta* the maximum variation was diminished rather than the minimum variation. Modification is likely to cause only part of the total variation found under natural conditions.

Certain values given in brackets denote extremes, values without brackets denote the range of "normal" variation.

Chromosome counts were made partly from sections and partly from squash preparations of root tips.

Root tips for sectioning were fixed according to Müntzing's modification of Navashin-Karpechenko's method (MÜNTZING 1933 p. 131). This was done in the morning, the whole plant having been kept overnight in a refrigerator at a temperature of 0—+4°C. The tips were sectioned in paraffin (14—16 µ). The slides were left in 1 % gentian violet overnight.

Root tips for squashing were pretreated overnight in dilute colchicine/8-hydroxyquinoline solution (usually 0.1 % colchicine and 0.03 % 8-hydroxyquinoline in distilled water) at ±0°C. After being fixed in absolute alcohol and glacial acetic acid 3:1 the meristems were stained in Feulgen and prepared by ÖSTERGREN and HENEEN's method (1962). Several other techniques were tried out, including pretreatment with α-monobromnaphtalene which has been found to be very satisfactory for *Anthoxanthum* (I. HEDBERG 1970 p. 154). These all gave inferior results in the present material.

The photomicrographs were made with a Nikon Microflex camera on a Leitz microscope.

The methods for studying the development of the embryo-sac and the germinating capacity of the caryopses have been described by WEIMARCK (1967 a p. 210). In addition it should be mentioned that the tests of germination capacity were completed after a few months. Caryopses not germinated by then were assumed to be non-functional due to obvious decomposition.

The chromatographical and numerical methods used for studying population structures and diagnostic patterns of taxa were described by WEIMARCK (1970 b pp. 233—235).

The herbarium material studied is presented in Figs. 2, 5, 6, 10, 13, 15, 16, 19, 22, and 25. Each dot represents a locality from where specimens have been studied in this investigation. In many cases the localities were so close together that they could not each be represented by a dot. Some collections have also been omitted because the localities were too inexactly defined or could not be identified at all. No difference was made between old records and more recent ones. I do not consider the material to be sufficient for forming a judgment about a possible increase or decrease of frequency or area of distribution.

The data from which the maps were prepared are preserved at the Department of Plant Taxonomy, Lund, in the form of a card index. The herbaria from which material has been studied are listed for each taxon. From some of the herbaria only part of the material was on loan. Abbreviations are made in accordance with LANJOUW and STAFLEU (1964). In all, c. 6275 sheets were investigated. Countries are enumerated in approximate order from north and west towards south and east, beginning in North Europe. Regional subdivision and territories are in accordance with HYLANDER (1953, map towards p. 392), and TUTIN et al. (1964, map towards p. 464).

Although the maps are not in themselves distribution maps, they still serve the purpose of showing the approximate distribution of the taxa.

Hierochloë R. BR., nom. cons.

[*Hierochloë* GMELIN (1747 p. 100)]; *Holcus* LINNAEUS (1753 p. 1048) pro parte; *Savastana* SCHRANK (1789 a p. 337; 1789 b p. 100); *Torresia* RUIZ & PAVON (1794 p. 125); *Disarrenum* LABILLARDIÈRE (1806 p. 82); *Hierochloë* BROWN (1810 p. 208); *Dimesia* RAFINESQUE (1818 p. 175; nom. nud.).

The generic name *Hierochloë* was conserved by the International Botanical Congress in Vienna 1905 (WETTSTEIN & al. 1906 p. 234).

Type species: *Hierochloë odorata* (L.) WAHLENB. (LANJOUW & al. 1966 p. 260).

The genus is placed in the tribe Phalarideae and has according to current opinion close affinities to *Anthoxanthum*. Although displaying several specialized features, such as peculiar spikelet morphology, it appears to have certain characters less advanced than *Anthoxanthum*. Thus, it shows less floral reduction, a less elaborate karyotype (cf. I. HEDBERG 1970), and a higher basic chromosome number (cf. also AVDULOV 1931 pp. 368—370).

GENERAL DESCRIPTION OF TAXA TREATED

Perennial grasses forming dense to loose tufts or large patches; the whole plant giving off an aroma of coumarin. *Vegetative shoots*: basal sheaths brownish to reddish or purple, without laminae; a few assimilating leaves. *Flowering shoots* erect, normally flowering early in the vegetative period, before the vegetative shoots develop fully; basal sheaths brownish to red-

Table 1. Observed cases of modification in connexion with late flowering 1962—67 in collections acquired 1962—64 from Norway, Sweden, and Finland.

Taxon	Country	Year of acquisition	Number of collections	Number of modified late-flowering collections					
				1962	1963	1964	1965	1966	1967
H. odorata ssp. *odorata* (4x)	Sweden	1962	23	1	3	1	0	2	0
		1963	20	—	1	0	0	10	3
		1964	2	—	—	0	0	0	0
	Norway	1964	52	—	—	0	1	30	1
H. odorata ssp. *baltica*	Sweden	1962	31	0	22	0	2	20	2
		1963	13	—	0	0	0	2	0
	Finland	1962	1	0	1	0	0	1	0
		1964	5	—	—	0	0	1	1
H. hirta ssp. *hirta*	Sweden	1962	6	0	0	0	1	0	0
		1963	10	—	0	0	0	0	0
	Norway, Finland	1964	6	—	—	0	0	0	0
H. hirta ssp. *arctica*	Sweden	1962	2	0	0	0	0	1	0
		1963	20	—	0	0	1	5	0
		1964	1	—	—	0	0	0	0
	Norway	1964	6	—	—	0	0	3	0
	Finland	1962	2	0	0	0	0	1	0
		1964	22	—	—	0	0	3	0

dish or purple, without laminae; above them 1—2(—4) assimilating leaves with very short laminae; sheaths of these leaves long, green, surrounding culm, glabrous or almost glabrous. *Panicle* spreading when flowering, contracted during pre- and postfloral stages. *Spikelets* with 3 florets; the lower 2 florets male, with 3 stamens; the upper floret bisexual, with 2 stamens and a pistil with 2 plumose stigmas; all 3 florets at almost the same height, with simple, unicellular hairs at base. *Glumes* ovate, 3-nerved at base, thin, more or less membranous, usually glabrous, of about the same length as the florets, first green at base, often with a purplish shading in the form of an inverted V. *Lemma of male florets* ovate, usually faintly 5-nerved, roughish with short projections or hairs on back, with unicellular hairs towards apex and on margins; hyaline at apex, sometimes with an awn. *Palea of male florets* narrowly ovate, somewhat shorter than lemma, bifid at apex, faintly 2-nerved, roughish on back, with 0.05—0.25 (—0.5) mm long unicellular hairs on nerves towards apex. *Lemma of bisexual floret* ovate, faintly 5-nerved, becoming hardened, with unicellular hairs towards apex, sometimes with an awn. *Palea of bisexual floret* narrowly ovate, somewhat shorter than lemma, very faintly 1- or 2-nerved, with 0.05—0.25(—0.5) mm long unicellular hairs on nerves towards apex. *Caryopsis*, if well-developed and mature, ellipsoid, up to 3.0 mm long and 1.2 mm broad; very often abortive. *Pollen grains* 1-ulcerate, spheroidal, spread at the 3-nucleate stage, sometimes irregular or abortive. *Basic chromosome number* $x=7$; all chromosomes approximately metacentric; satellites very small, only sporadically observed with the technique used.

A conspicuous morphological variation is connected with the fact that a second flowering may occur during summer or early autumn. Such late-flowering culms sometimes look normal, but usually they deviate in a characteristic way (Fig. 9 p. 144). The culm-leaves have very long laminae as in vegetative shoots, and the panicle is very loose and has very fine, long branches with few spikelets. The panicle sometimes gets stuck in the uppermost sheath, causing the culm to grow in a U-shape. Morphologically deviating, late-flowering culms were developed in the material studied during the present investigation, both in nature and during cultivation. It is without doubt a question of mere modification in connexion with second flowering. I have observed it in all taxa dealt with here with the exception of *Hierochloë australis* and *H. repens.*

Specimens displaying the characteristic morphological modifications in connexion with late flowering at the time of collection were found in *Hierochloë odorata* ssp. *odorata* from Löten parish, Hedmark, Norway (A R C, 23.6. 1964; Fig. 9 *A*), *H. hirta* ssp. *hirta* from Nilsiä parish, Savonia borealis, Finland (A X D, 3.8. 1964; Fig. 9 *C*), and *H. hirta* ssp. *arctica* from Attmar parish, Medelpad, Sweden (A N O, 12.7. 1963; Fig. 9 *D*). A corresponding case in *H. odorata* ssp. *baltica* from Trosa, Södermanland, Sweden is illustrated from cultivation (A H N, 15.9. 1963; Fig. 9 *B*).

Observed cases of modified late-flowering specimens during cultivation are given in Table 1. Modification in connexion with late flowering obviously occurs in different degrees in different collections and during different years. Conditions during cultivation presumably cause late flowering more frequently than in nature.

Key to Taxa Treated

1\. Spikelets with long awns (at least one exceeding 1.0 mm); plant densely or loosely tufted 2

1\. Spikelets with short awns (up to 1.0 mm) or without awns; plant with creeping rhizomes 4

2\. Pedicels with 0.1—0.3 mm long hairs immediately below spikelets; longest awn up to 3.0 mm .... *H. australis* (p. 134)

2\. Pedicels glabrous or with up to 0.1 mm long, sparse hairs; longest awn more than 4.5 mm (*H. alpina*) 3

3\. Awn on lemma of upper male floret inserted up to 2.3 mm above base of lemma; awn usually twisted at base, geniculate .... *H. alpina* ssp. *alpina* (p. 156)

3\. Awn on lemma of upper male floret inserted more than 2.3 mm above base of lemma; awn usually not twisted, straight .... *H. alpina* ssp. *orthantha* (p. 161)

4\. Panicle compact, usually with more than 120 spikelets in dense clusters; pedicels often with 0.1—0.3 mm long hairs immediately below spikelets; leaves caesious .... *H. repens* (p. 154)

4\. Panicle loose, usually with less than 100 spikelets not densely clustered; pedicels glabrous or with up to 0.1 mm long, sparse hairs; leaves green, more rarely slightly caesious 5

5\. Lemma of bisexual floret with appressed or only slightly spreading hairs; lemma of male florets awnless, mucronate, or with a very thin awn, and with sparse marginal hairs (*H. odorata*) 6

5\. Lemma of bisexual floret with distinctly spreading hairs; lemma of male florets with a coarse awn, rarely mucronate, and with dense marginal hairs (*H. hirta*) 7

6\. Middle nerve of lemma of male florets reaching apex or base of apical incision if present; lemna almost always awned or mucronate .. *H. odorata* ssp. *odorata* (p. 136)

6\. Middle nerve of lemma of male florets ending below apex or base of apical incision if present; lemma unawned, rarely with a very short awn *H. odorata* ssp. *baltica* (p. 141)

7\. Awn on lemma of male florets gently bent outwards; panicle usually with 9 nodes or more, dark purplish brown in the mature condition; lower main branches of panicle usually pendulous .... *H. hirta* ssp. *hirta* (p. 146)

7\. Awn on lemma of male florets straight or slightly bent inwards, or rarely developed as a mucro; panicle usually with up to 8 nodes, golden brown in the mature condition; lower main branches of panicle usually not pendulous *H. hirta* ssp. *arctica* (p. 150)

Fig. 1. *Hierochloë australis*, collection B B A (Italy). — *A:* Habit. — *B:* Glumes. — *C:* Florets. — *A* ×0.5; *B, C* ×5.

Hierochloë australis (Schrader) Roemer & Schultes

Holcus australis Schrader (1806 pp. 253—254). — *Hierochloa australis* (Schrader) Roemer & Schultes (1817 p. 514). Type collection: "Holcus odoratus Linn. — Exemplaria die 11. Apr. prope Ratisbonam legi: in den Schwabelweisbergen." Hoppe (M; lectotype). The sheet belongs to an exsiccate cited by Schrader.

Holcus odoratus Linnaeus (1753 p. 1048) pro parte excl. typo; excl. syn. ?Bauhin (1620, 1623), Loeselius (1703), Linnaeus (1737, 1745), Gmelin (1747).

Hierochloë aristata Wulfen (Fenzl & Graf 1858 p. 82). Type collection: "Hierochloë aristata. — Aprili in Rupibus Castelli Cusano sive Purgesimo prope Cividale Wulfen" (W; lectotype). The locality is given by Wulfen, and the sheet is from his herbarium.

Hierochloë hirta (Schrank) Borbás (1900 p. 315) sensu Borbás, non sensu orig., excl. typo; cf. p. 146.

DESCRIPTION (cf. Fig. 1)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with up to 10 mm long internodes, covered with sheaths; plant densely to loosely tufted. *Vegetative shoots:* basal sheaths brownish or reddish; leaf laminae linear or narrowly elliptic, with serrulate margins, (1.5—)3.0—5.5(—9.0) mm broad, often somewhat caesious on adaxial surface, glabrous on both surfaces or pilose on adaxial surface; hairs long, simple, unicellular; nerves on both surfaces with sparse prickles; ligule 1.0—3.0 mm long, obtuse to acute. *Flowering shoots* inclusive of panicle 30—60(—80) cm high in the mature condition, with nodes up to about half the length; basal sheaths brownish or reddish; sheaths of assimilating leaves often somewhat widened upwards; lamina of uppermost leaf (0—)1.0—3.0(—15.0) mm long, (0.5—)1.0—3.5 mm broad; ligule of uppermost leaf (1.0—)1.5—3.0(—4.0) mm long, obtuse or acute, often incised. *Panicle* (25—)35—70 mm long; nodes 6—8; main lateral branches long, slightly tortuous, 1—2 at lower nodes, 1 at each of upper 3—5 nodes; pedicels immediately below base of glumes with simple, unicellular hairs 0.1—0.3 mm long; spikelets

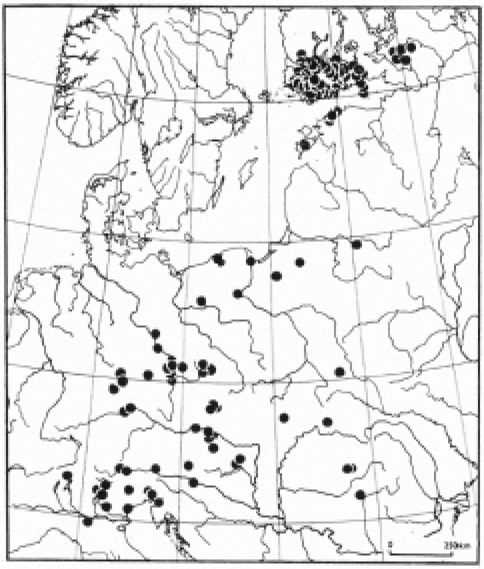


Fig. 2. *Hierochloë australis.* Localities of herbarium material.

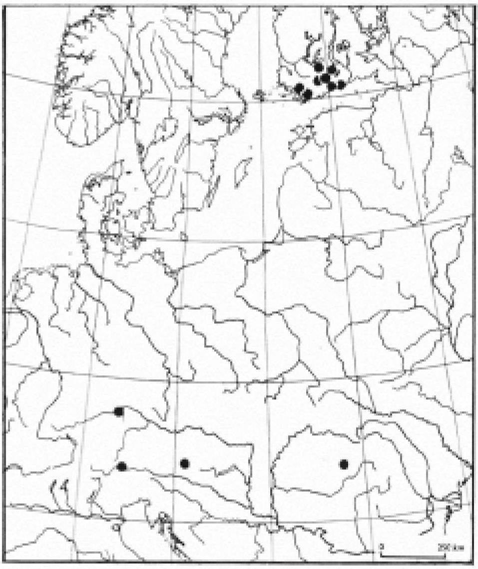


Fig. 3. *Hierochloë australis.* Localities of cultivated material, $2n=14$.

(11—)20—35(—70) in number. *Glumes* (3.0—)3.5—5.5(—6.0) mm long, glabrous or roughish and with sparse hairs on back, silvery-glittering in the mature condition; hairs at base of florets 0.15—0.3 mm long. *Lemma of male florets* 3.0—4.5 mm long, more or less deeply bifid at apex, 3- or faintly 5-nerved, towards apex with up to 0.4 mm long hairs; margins sparsely ciliate with simple, somewhat curly, 0.3—0.6 mm long hairs; middle nerve reaching base of apical incision; awn on lemma of lower male floret 0.1—0.5(—3.0) mm long, scaberulous, inserted at base of apical incision 0.1—0.3 mm below apex; awn on lemma of upper male floret 1.0—3.0 mm long, scaberulous towards apex, twisted at base, geniculate, inserted at base of apical incision 1.0—2.0 mm below apex. *Anthers of male florets* 2.0—3.0 mm long. *Lemma of bisexual floret* 3.0—4.0 mm long; awn absent (—0.5 mm long); hairs towards apex of lemma 0.05—0.2 mm long, appressed. *Anthers of bisexual floret* 1.3—2.6 mm long.

DISTRIBUTION AND HABITAT

Hierochloë australis has a fairly small area of distribution limited to Europe. It occurs in South Finland, the western and south-western parts of European Russia, Poland, Germany, Switzerland, Austria, Northern Italy, Northern Yugoslavia, and Romania. It was placed by HULTÉN (1950 pp. 74*, 107*) in his phytogeographical group "East-European continental plants connecting with Scandinavia by way of the Baltic countries".

Fig. 2 shows where the herbarium material studied was collected (BM, C, DAO, H, K, LD, LE, LINN, M, MT, PRC, S, TRH, TUR, UPS, W; c. 1100 sheets).

Hierochloë australis usually grows in rather dry, moderately shady forests and skirts of forests. In the northern part of the area it occurs in pine or spruce forests with or without deciduous trees, towards the south also in deciduous forests such as beech forests. It can also occur in secondary localities such as clearings.

CHROMOSOME NUMBER

Diploid collections (2n = 14) were found in Finland, Germany, Austria, Italy, and Romania. VAARAMA (in TISCHLER 1950 p. 209) reported the same number. *Hierochloë australis* is the only diploid member of the genus known to me.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 3 and listed on p. 168. Fig 27 *A* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

Reduced embryo-sacs of the Polygonum type could be formed, but also unreduced ones of the Hieracium type and possibly of the Antennaria type (WEIMARCK 1967 a pp. 212—218; cf. MAHESHWARI 1950 p. 87; BATTAGLIA 1963 pp. 246—248). Female meiosis was sometimes abnormal. Male meiosis was usually normal, but disturbances and abortion occurred.

Germinating capacity was low, being 0 % in the collection A H T (Hollola, Tavastia australis, Finland), and 3 % in the collection A E K (Weltenburg, Bayern, Germany).

Results from a chromatographic study indicated that sexual reproduction could actually occur (WEIMARCK 1970 b p. 263). They confirmed the assumption based on embryological evidence that apomixis is at most facultative. The actual functioning also of unreduced embryo-sacs is likely but could not be absolutely proved.

VARIATION

Morphological variation in *Hierochloë australis* was found to be moderate (cf. pp. 134—135). A regional pattern in chromatographically obtained characters, such as described in *Lathyrus sphaericus* by BRUNSBERG (1965 pp. 388—389), was not found. Local variation within populations caused practically all variation found in the material (WEIMARCK 1970 b p. 237).

The species is well-defined and gives the impression of being morphologically uniform throughout its area of distribution.

Hierochloë odorata (L.) WAHLENB.

Hierochloë odorata (L.) WAHLENB. ssp. **odorata**

Holcus odoratus LINNAEUS (1753 p. 1048) pro parte incl. typo; excl. syn. SCHEUCHZER 1719; non sensu SCHRANK (1789 b pp. 643—644) nec sensu HOST (1801 p. 4). — *Hierochloa odorata* (L.) WAHLENBERG (1820 p. 32). Type collection: LINNAEUS' sheet 1212: 14, second specimen from the left (LINN; lectotype). The sheet bears LINNAEUS' own hand-writing "odoratus 5", the numeral referring to the numbering within the genus *Holcus* (1753 p. 1048). Two other members of the *odorata* complex on the sheet cannot with certainty be referred to taxon. Two specimens are *H. australis*.

Holcus borealis SCHRADER (1806 pp. 252, 253); superfluous epithet. — *Hierochloa borealis* (SCHRADER) ROEMER & SCHULTES (1817 p. 513) pro parte; excl. syn. ?QUENSEL 1804, HOST 1805, PERSOON 1805, SCHRANK 1789 a.

Holcus fragrans WILLDENOW (1806 p. 936) non sensu LÖVE & LÖVE (1965 p. 11). — *Hierochloa fragrans* (WILLD.) ROEMER & SCHULTES (1817 p. 514). *Hierochloë odorata* var. *fragrans* (WILLD.) RICHTER (1890 p. 31). Type collection not seen. Description and distribution confirm the synonymy.

Savastana Nashii BICKNELL (1898 pp. 104—105). — *Hierochloë Nashii* (BICKNELL) KACZMAREK (1914 p. 198). Type collection not seen; cf. p. 141.

PALISOT DE BEAUVOIS (1812 p. 62) cited *Holcus odoratus* L. under the generic name *Hierochloa* without explicitly making the combination. The publication is therefore not valid. However, PALISOT DE BEAUVOIS has been incorrectly cited by several authors as the auctor of the combination when used for *Hierochloë odorata* s.l. Moreover, what he intended was what is correctly named *H. australis* (SCHRADER) ROEMER & SCHULTES.

DESCRIPTION (cf. Fig. 4 *A*—*C*)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with (5—)10—30(—40) mm long internodes, with 7—12 mm long, not persistent, light- to dark-coloured scales at nodes; rhizome system loosely matted.

Fig. 4. *A—C: Hierochloë odorata* ssp. *odorata*, collection A H C (Sweden, Västergötland). — *A:* Habit. — *B:* Glumes. — *C:* Florets. — *D—F: Hierochloë odorata* ssp. *baltica*, collection A F R (Sweden, Uppland). — *D:* Habit. — *E:* Glumes. — *F:* Florets. — *A, D* ×0.5; *B, C, E, F* ×5.

Vegetative shoots: basal sheaths brownish or reddish; leaf laminae linear or narrowly elliptic, with serrulate margins, (2.0—) 3.0—6.0(—8.0) mm broad, glabrous and shiny on abaxial surface, pilose and sometimes slightly caesious on adaxial surface; hairs long, simple, unicellular; nerves on both surfaces with sparse prickles; ligule (0.3—)0.5—2.5(—8.0) mm long, truncate, obtuse or acute. *Flowering shoots* inclusive of panicle (10—)25—60(—90) cm high in the mature condition, with nodes only at base; basal sheaths brownish or reddish; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf (3.0—)5.0—15.0(—45.0) mm long, (1.5—)2.0—4.0(—6.5) mm broad; ligule of uppermost leaf (0.3—)1.5—2.5 (—8.0) mm long, obtuse or acute, often incised. *Panicle* (25—)35—90(—125) mm long; nodes (4—)6—9(—11); main lateral branches long, often slightly tortuous, 2 at lower nodes, 1 at 1—4(—5) upper nodes; branches and pedicels glabrous or with few, simple, unicellular hairs up to 0.1 mm long; spikelets (8—)25—60(—100) in number. *Glumes* (2.5—)3.5—5.5(—7.5) mm long, glabrous, gold-glittering in the mature condition; hairs at base of florets 0.25—0.9 mm long. *Lemma of male florets* (2.5—)3.0—4.5(—5.5) mm long, acute, mucronate or slightly emarginate or bifid at apex, 5-nerved, towards apex with up to 0.3 mm long hairs; hyaline part at apex usually 0.1—0.3 mm broad; margins sparsely ciliate with simple and (less frequently) bifurcate, straight or somewhat curly, 0.3—0.6(—0.8) mm long hairs; middle nerve reaching apex or base of apical incision if present, more rarely ending below it (cf. p. 146); awn, if present, on lemma of lower male floret 0.1—0.5 mm long, faintly scaberulous, inserted at apex as a mucro or at base of apical incision if present 0.1—0.2 mm below apex; awn, if present, on lemma of upper male floret 0.1—0.2(—0.8) mm long, faintly scaberulous, inserted at apex as a mucro or at base of apical incision if present 0.1—0.2 mm below apex. *Anthers of male florets* 1.6—2.3 mm long. *Lemma of bisexual floret* 2.5—3.8(—4.2) mm long; awn absent (—0.5 mm long); hairs towards apex of lemma (0.05—)0.1—0.6 mm long, appressed or slightly spreading. *Anthers of bisexual floret* 1.2—1.6 mm long.

DISTRIBUTION AND HABITAT

Hierochloë odorata ssp. *odorata* is found mainly in north-western Europe and north-eastern North America. It occurs in Iceland, Norway, Sweden, Denmark, North-west European Russia, Holland, Germany, Poland, Czechoslovakia, Switzerland, South-east France, Britain, Ireland, Quebec, Labrador, Newfoundland, Nova Scotia, New Brunswick, Maine, New Hampshire, Rhode Island, Connecticut, New York, and New Jersey. Thus it belongs to the group of amphi-Atlantic taxa treated by HULTÉN (1958). It seems to fit best within the phytogeographical group including among others *Rhynchospora fusca, Carex flava,* and *Potamogeton obtusifolius* (HULTÉN 1958 p. 17).

Figs. 5 and 6 show where the herbarium material studied was collected (BM, C, CAN, DAO, GH, GRO, H, K, LD, LINN, M, MT, O, PRC, S, TRH, TUR, UPS, W; c. 1125 sheets).

Hierochloë odorata ssp. *odorata* occurs in moist meadows and fens, often at the edge of forests or adjacent to the margins of lakes and streams, even close to brackish or salt water. Its frequency has been noticeably reduced in cultivated regions, presumably due to recent draining, cultivation, and the expansion of towns.

CHROMOSOME NUMBERS

Tetraploid collections (2n=28) were found in Norway, on the mountain ridge in Central and North Sweden, in South-west Sweden, Denmark, the Netherlands, Ireland, and Quebec. Tetraploid collections, in all likelihood referable to *Hierochloë odorata* ssp. *odorata* but of which I have not seen voucher specimens were re-

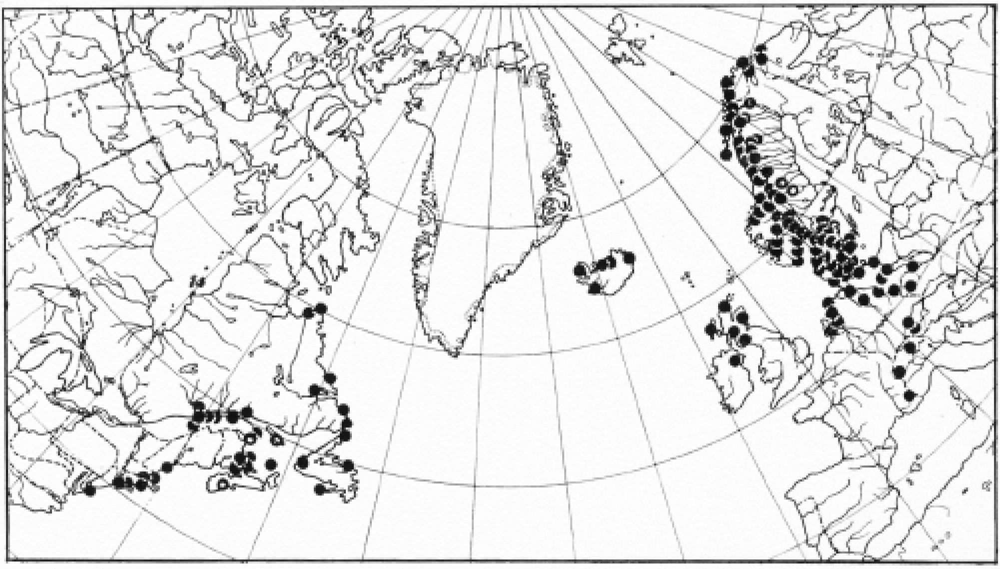


Fig. 5. *Hierochloë odorata* ssp. *odorata*. Localities of herbarium material (total). Circles: specimens not determinable with certainty.

ported from Iceland (Löve & Löve 1956 pp. 83, 93), and from Connecticut (Reeder & Norstog 1961 p. 82), both as being *H. odorata*.

Hexaploid collections (2n=42) were found in a restricted area in West Sweden, in North Norway, in Germany, and in Switzerland.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 7 (European localities only) and listed on p. 168. Fig. 27 *B* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

Tetraploid samples investigated formed reduced embryo-sacs of the Polygonum type (Weimarck 1967 a pp. 218—221). Female meiosis was usually fairly normal, but degenerative traces were found. Male meiosis was usually only slightly disturbed in the collections A E F (Kågeröd, Skåne, Sweden) and A M O (Tärna, Lycksele Lappmark, Sweden). It could break down totally in the collection A H B (Stala, Bohuslän, Sweden).

The hexaploid collection A H E (Källvene, Västergötland, Sweden) formed unreduced embryo-sacs of the Hieracium type (Weimarck 1967 a p. 224). Few cases only of female meiosis were observed, one of them abnormal. Male meiosis was frequently disturbed.

Germinating capacity was varied in three collections studied in this respect, being 36 % in A E F, 6 % in A H B, and 27 % in A H E (Weimarck 1967 a p. 229). The tetraploid samples, which are not agamospermous, may also be regarded as apomicts, although facultative ones, seen in the light of information on reproduction and chromatographically demonstrated variation (Weimarck 1967 a p. 230; 1970 b p. 263). Their vegetative reproduction obviously dominates spreading at least in shorter distances, and their amphimictic seed-setting is reduced in effectivity.

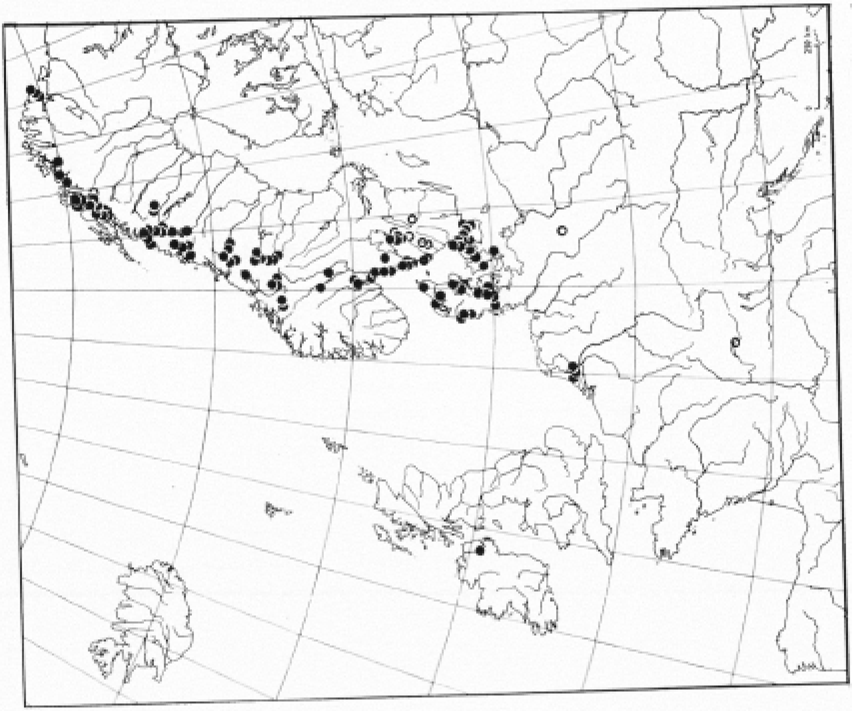


Fig. 7. *Hierochloë odorata* ssp. *odorata*. Localities of cultivated material (from Europe only). Dots: 2n=28. Circles: 2n=42.

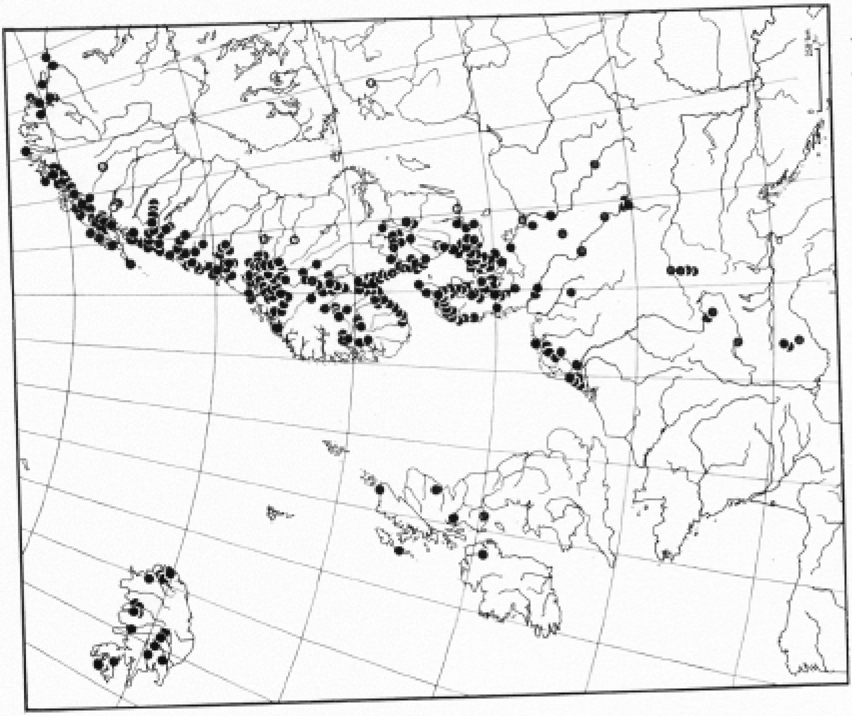


Fig. 6. *Hierochloë odorata* ssp. *odorata*. Localities of herbarium material (detail). Circles: specimens not determinable with certainty.

VARIATION

The number of nodes and spikelets per panicle varied considerably within the material under natural conditions (Fig. 8 *A*).

"*Hierochloa borealis* RS β *microstachya*" HARTMAN (1849 p. 308) is likely to correspond to specimens of *Hierochloë odorata* ssp. *odorata* having very small spikelets.

Occasional spikelets with four florets were found in herbarium specimens from Hamburg. This type of aberration was described from Iceland by NORSTOG (1960 a).

Morphologically deviating late-flowering specimens, most probably of *Hierochloë odorata* ssp. *odorata*, were given the name var. *uechtritzii* by ASCHERSON and GRAEBNER (1898 p. 30), who considered them to be examples of seasonal dimorphism (cf. pp. 132—133).

A similar phenomenon was described by BICKNELL (1898 pp. 104—105) as *Savastana nashii* [=*Hierochloa nashii* (BICKNELL) KACZMAREK (1914 p. 198)], and by FERNALD (1917 p. 152) as *Hierochloa odorata* (L.) WAHLENB. var. *fragrans* (WILLD.) RICHTER f. *camesii*. REEDER and NORSTOG (1961) found scattered culms with the characteristic features later on in the summer, at least up to the end of June, among otherwise normal-looking tetraploid *H. odorata* in Connecticut. Referring to the recent discovery that the tetraploids of Connecticut set seed sexually in contrast to the octoploids from Ohio and Michigan studied by NORSTOG (1960 b, 1963) they believed that the deviating flowering shoots represented extreme variant specimens of highly variable amphimictic populations, a matter which I do not find convincingly proved.

LÖVE and LÖVE (1965 p. 12) propose the name *Hierochloë nashii* for sexual tetraploids in general in eastern North America. Their interpretation of REEDER and NORSTOG's results is, however, hardly plausible.

With respect to chromatographically obtained patterns the absence of the spot group 27—28 in some Scandinavian and in the two Canadian collections is the most conspicuous deviation (WEIMARCK 1970 b pp. 252—253). It is, however, not accompanied by any morphological characteristics as far as is known. The removal of the Romanian collection B C C, which belongs to *Hierochloë repens*, decreases the overall variation to a certain extent.

Hierochloë odorata ssp. *odorata* as defined here is somewhat heterogeneous in Europe. It usually has an awn or a mucro on the lemma of male florets, although this is lacking in some cases. Its area of distribution only slightly overlaps that of *H. odorata* ssp. *baltica*, and it is usually tetraploid but occasionally hexaploid.

I do not at present feel justified in treating North American plants as a separate taxon. Although some specimens admittedly deviate somewhat from the habit normally found in European *Hierochloë odorata* ssp. *odorata*, the variation falls within or is close to that of European material.

Hierochloë odorata (L.) WAHLENB. ssp. **baltica** G. WEIM., ssp. nov.

?"*Hierochloa borealis* RÖM. β *fragrans*" HARTMAN (1838 p. 20); non sensu orig.

Diagnosis: Gramen perenne rhizomatosum simile *Hierochloae odoratae* ssp. *odoratae*, sed flosculis masculis non aristatis vel mucronatis, lemmatibus flosculorum masculorum apice late membranaceis.

Type collection: Plantae Suecicae exsiccatae 121. "Hierochloë odorata (L.) P. BEAUV. — Prov. Södermanland, Paroecia Ornö, in prato litorali uliginoso prope templum. 17 jun. 1927. Leg. Erik Asplund." (LD; holotype). The specimen to the right on the sheet was chosen as type. The collection has not been cytologically investigated but is morphologically characteristic. The locality is fairly central to the area of distribution, and there are isotypes in many herbaria.

DESCRIPTION (cf. Fig. 4 *D*—*F* p. 137)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with 10—30(—40) mm long internodes, with 7—12 mm long, not per-

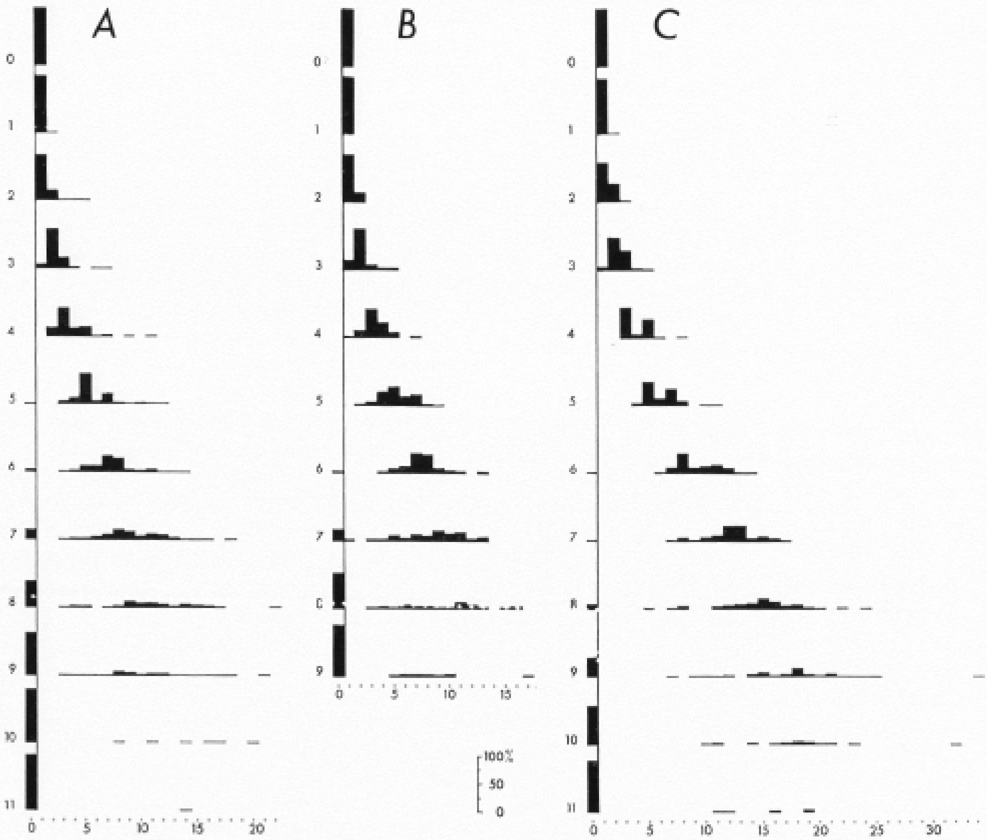


Fig. 8. Panicle diagrams. Vertical axis: numbering of nodes. The terminal spikelet is denoted by 0. Horizontal axis: number of spikelets at each node. The height of each column gives the percentage (cf. scale) of specimens having a particular number of spikelets at that node. — *A: Hierochloë odorata* ssp. *odorata* 2n=28, 153 specimens from 23 collections (Norway, Sweden). — *B: H. odorata* ssp. *baltica*, 96 specimens from 12 collections (Sweden). — *C: H. hirta* ssp. *hirta*, 62 specimens from 10 collections (Norway, Sweden). — *D: H. hirta* ssp. *arctica*, 235 specimens from 40 collections (Norway, Sweden, Finland). — *E: H. repens*, 14 specimens from 5 collections (Czechoslovakia, Hungary, Romania). — *A—D:* voucher specimens of cytologically investigated collections from the field. *E:* herbarium specimens (PRH). — Since the number of specimens studied is not the same in all collections, a statistical analysis of the diagrams should be avoided. They are intended to illustrate the actual variation found in the material studied.

sistent, light- to dark-coloured scales at nodes; rhizome system loosely matted. *Vegetative shoots*: basal sheaths brownish or reddish; leaf laminae linear or narrowly elliptic, with serrulate margins, (2.2—)4.0—5.5(—6.5) mm broad, glabrous and shiny on abaxial surface, pilose and sometimes slightly caesious on adaxial surface; hairs long, simple, unicellular; nerves on both surfaces with sparse prickles; ligule (0.5—)1.5—3.5 mm long, truncate, obtuse or acute. *Flowering shoots* inclusive of panicle 25—60(—85) cm high in the mature condition, with nodes only at base: basal sheaths brownish or reddish; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf 4.0—20.0(—45.0) mm long, (1.5—)2.0—

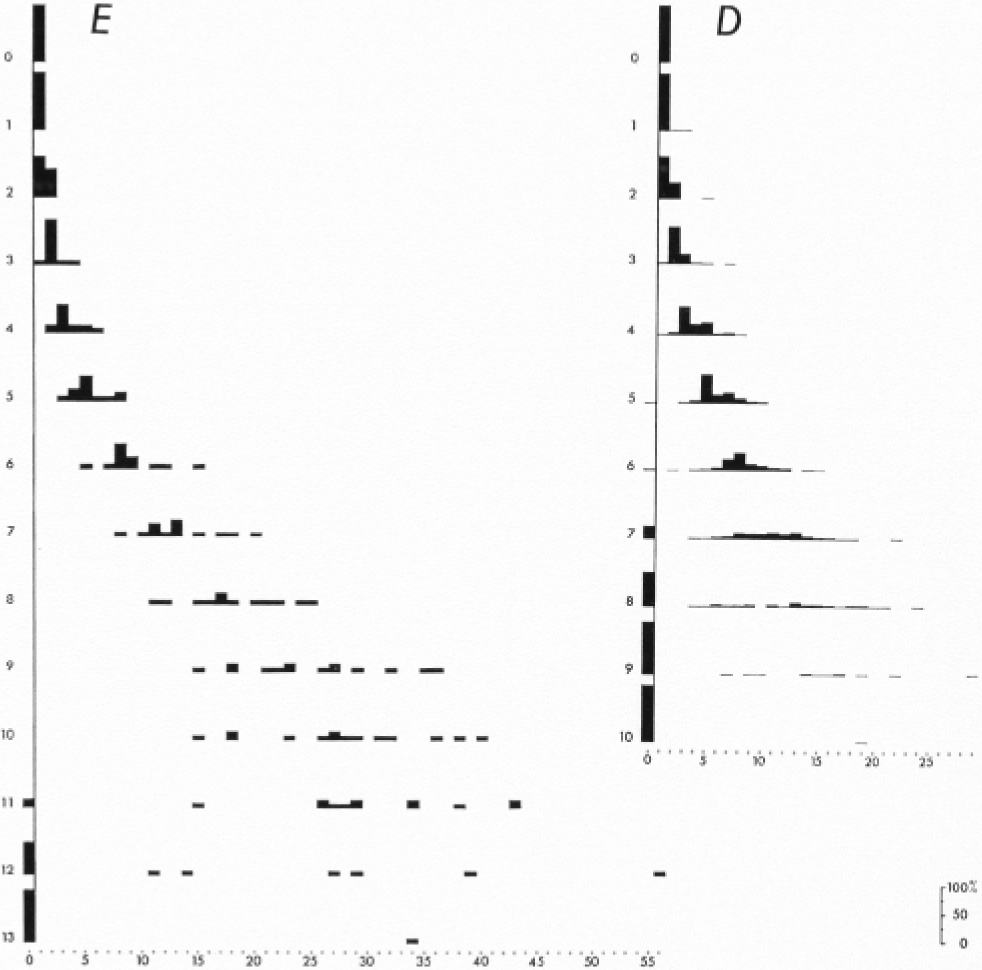


Fig. 8.

4.0(—6.5) mm broad; ligule of uppermost leaf 1.5—4.5 mm long, obtuse or acute, often incised. *Panicle* (30—)40—75(—100) mm long; nodes (5—)6—8(—9); main lateral branches long, often slightly tortuous, 2 at lower nodes, 1 at 1—4 upper nodes; branches and pedicels glabrous or with few, simple, unicellular hairs up to 0.1 mm long; spikelets (14—)20—50(—85) in number. *Glumes* (4.0—)4.5—6.0(—8.0) mm long, glabrous, gold-glittering in the mature condition; hairs at base of florets 0.5—0.9 mm long. *Lemma of male florets* (3.2—)3.7—5.2(—6.0) mm long, slightly emarginate or bifid at apex, 5-nerved, towards apex with up to 0.3 mm long hairs; hyaline part at apex usually 0.3—0.5 mm broad; margins sparsely ciliate with simple or sometimes bifurcate, straight, 0.5—0.8 mm long hairs; middle nerve ending below apical incision or more rarely reaching it; awn on lemma of both male florets absent (—0.1 mm long). *Anthers of male florets* 1.3—1.9 mm long. *Lemma of bisexual floret* 2.5—4.5 mm long; awn absent; hairs towards apex of lemma 0.15—0.25 mm

Fig. 9. Examples of morphologically modified late-flowering shoots. — *A: Hierochloë odorata* ssp. *odorata* (A R C 7, 23.6. 1964; from the field). — *B: H. odorata* ssp. *baltica* (A H N 3, 15.9. 1963; cultivated). — *C: H. hirta* ssp. *hirta* (A X D 3, 3.8. 1964; from the field). — *D: H. hirta* ssp. *arctica* (A N O 4, 12.7. 1963; from the field). — ×0.25.

long, appressed or slightly spreading. *Anthers of bisexual floret* 1.0—1.8 mm long.

DISTRIBUTION AND HABITAT

Hierochloë odorata ssp. *baltica* has a restricted area of distribution in North Europe. It occurs in different parts of Central and East Sweden, South-west and West Finland, and the westernmost parts of European Russia. It is obviously endemic in the region. Neo-endemism is strongly indicated (cf. p. 146). It fits into Hultén's phytogeographical group "Endemic plants" of a boreal or boreal-montane type (1950 pp. 83*, 108*).

Fig. 10 shows where the herbarium material studied was collected (BM, C, H, LD, LE, MT, O, S, TRH, TUR, UPS; c. 450 sheets).

Hierochloë odorata ssp. *baltica* occurs in about the same types of localities as ssp. *odorata* (cf. p. 138). It seems, however, to be far more capable of colonizing secondary localities, roadsides, ditches, etc. Obviously it can thus apophytically escape eradication even if wiped out on the original site.

CHROMOSOME NUMBER

Hexaploid collections (2n=42) were found in Sweden and Finland. Collections in all likelihood referable to *Hierochloë odorata* ssp. *baltica* but of which I have seen no voucher specimens were reported from Finland to be hexaploid (Vaarama in Löve & Löve 1948 p. 23; Sorsa 1962 p. 9, as n=21; 1963 p. 10, ditto), all as being *Hierochloë odorata.*

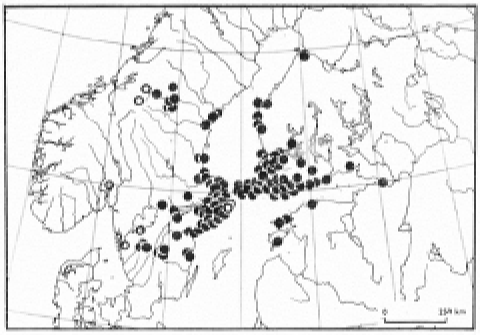


Fig. 10. *Hierochloë odorata* ssp. *baltica.* Localities of herbarium material. Circles: specimens not determinable with certainty.

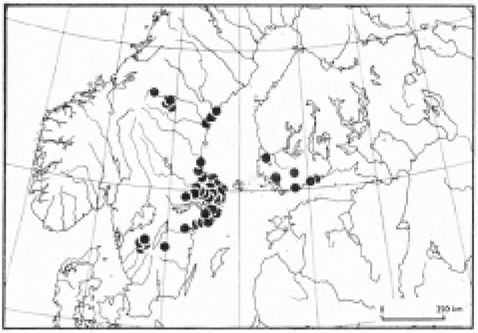


Fig. 11. *Hierochloë odorata* ssp. *baltica.* Localities of cultivated material, 2n=42.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 11 and listed on p. 170. Fig. 27 *C* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

In the collection A F P (Uppsala Näs, Uppland, Sweden) all or at least almost all embryo-sacs were unreduced and of the Hieracium type (WEIMARCK 1967 a pp. 221—224). One possible case only of a reduced embryo-sac of the Polygonum type was recorded. Female meiosis was apparently rare. Male meiosis was frequently disturbed.

Germinating capacity was low, 3 % in the test made. Chromatographically obtained evidence indicated clonal propagation in the localities investigated (WEIMARCK 1970 b p. 263).

VARIATION

Variation in number of nodes and spikelets per panicle under natural conditions fell within that of *Hierochloë odorata* ssp. *odorata,* but lacked the extreme values (Fig. 8 *B* p. 142).

Variation in chromatographically obtained patterns is not very great (WEIMARCK 1970 b p. 254). No variation occurs in the spot group 27—28. The elimination of the collections A T F, A H F, and A O D, which are to be referred to *Hierochloë odorata* ssp. *odorata* (see below), concerns three of the four highest values of deviation from the mean in Table 9 (loc. cit.), and should cause some further decrease of the overall values.

The most substantial characteristics of *Hierochloë odorata* ssp. *baltica* are the absence of an awn or a mucro on the lemma of its male florets, its restricted area of distribution, and (in cytologically investigated material) its invariably hexaploid chromosome number.

My conception of the taxonomy in *Hierochloë odorata* is based on a combination of phyletical and phenetical considerations. I regard *H. odorata* ssp. *odorata* as a system of morphologically somewhat variable, partly amphimictic biotypes. Hexaploids have obviously been formed from the tetraploids more than once as a result of, for example, the union of one reduced and one unreduced gamete. Meiosis in tetraploids is sometimes disturbed (see p. 139), giving good theoretical facilities for hexaploids to be formed in that way. Hexaploids having an awn or a mucro on the lemma of male florets are in this treatment grouped together with the tetraploids in *H. odorata* ssp. *odorata.* The reason is that these two cytotypes seem to be indistinguishable from one another morphologically. The length of stomata, which has been of value in several other cases when discerning members of a polyploid series, is of no use here due to considerable overlapping. The cytotypes of *H. odorata* ssp. *odorata* have probably a very similar gene content, although the chromosome number is different and a gene transport between existing individuals of the cytotypes can be estimated to be very rare or quite impossible.

The origin of *Hierochloë odorata* ssp. *baltica* is in all likelihood to be found within tetraploid *H. odorata* ssp. *odorata*, most probably in biotypes lacking an awn or a mucro. Only those hexaploids which had acquired the characteristic floral morphological features and occur within the restricted area are regarded as belonging to *H. odorata* ssp. *baltica*. As defined here the subspecies forms a natural unit and is most probably monophyletic. It gives the impression of being very uniform. One hypothesis is that the taxon consists of closely confined biotypes, made permanent by obligate or almost obligate apomixis. Its origin is likely to be fairly recent. Perhaps it was formed after the last ice age.

In the overlapping areas of distribution of *Hierochloë odorata* ssp. *odorata* and ssp. *baltica*, i.e. in South-west and North-west Sweden, and in the Baltic provinces, arises the problem of the correct determination of specimens not investigated cytologically but having the morphological characteristics of *H. odorata* ssp. *baltica*, because a small number of tetraploids there have been found to show some similarity to *H. odorata* ssp. *baltica* in these respects. The circles in Fig. 10 and some of them in Figs. 5 and 6 reflect this uncertainty.

Hierochloë hirta (SCHRANK) BORBÁS

Hierochloë hirta (SCHRANK) BORBÁS ssp. **hirta**

Savastana hirta SCHRANK (1789 a pp. 337—338). — *Hierochloë hirta* (SCHRANK) BORBÁS (1900 p. 315) non sensu BORBÁS. Type collection: "Hierochloe odorata (L.) P. B. — Oberbayern, München. Isarauen bei Föhring nördlich von München. Anfang Mai 1906." WOLLMANN (M; neotype). The locality was chosen to be in the vicinity of SCHRANK's original locality ". . . auf einer Isarinsel unweit Harlaching . . .". A specimen seen by SCHRANK was not available.

Hierochloa odorata (L.) WAHLENB. var. *firma* NYLANDER (1844 pp. 1—2). Type collection: "Hierochloa borealis (Schrad.) R & S. v. firma m. — Sordavala junio 1843. Nylander." (H; lectotype). Locality and date correspond to information given by NYLANDER. The hand-writing is most likely NYLANDER's own (I. KUKKONEN, pers. comm.).

DESCRIPTION (cf. Fig. 12 *A—C*)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with (15—)20—45(—60) mm long internodes, with 7—12 mm long, not persistent, light- to dark-coloured scales at nodes; rhizome system loosely matted. *Vegetative shoots*: basal sheaths brownish or reddish; leaf laminae linear or narrowly elliptic, with serrulate margins, (2.5—) 3.0—4.5(—5.5) mm broad, glabrous and shiny on abaxial surface, pilose and sometimes slightly caesious on adaxial surface; hairs long, simple, unicellular; nerves on both surfaces with sparse prickles; ligule 0.5—2.5 mm long, truncate, obtuse or acute. *Flowering shoots* inclusive of panicle 40—85(—110) cm high in the mature condition, with nodes only at base; basal sheaths brownish or reddish; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf 10—45(—60) mm long, 3.0—4.5 mm broad; ligule of uppermost leaf 2.5—5.5

Fig. 12. *A—C: Hierochloë hirta* ssp. *hirta*, collection A R B (Norway, Hedmark). — *A:* Habit. — *B:* Glumes. — *C:* Florets. — *D—F: H. hirta* ssp. *arctica*, collection A L L (Sweden, Dalarna). — *D:* Habit. — *E:* Glumes. — *F:* Florets. — *A, D* ×0.5; *B, C, E, F* ×5.

Fig. 12.

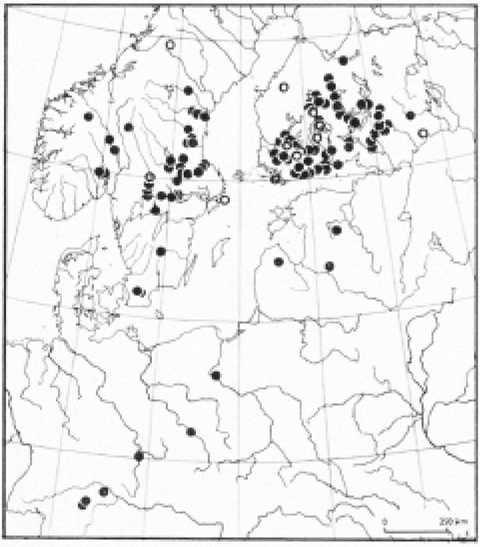


Fig. 13. *Hierochloë hirta* ssp. *hirta*. Localities of herbarium material. Circles: specimens not determinable with certainty.

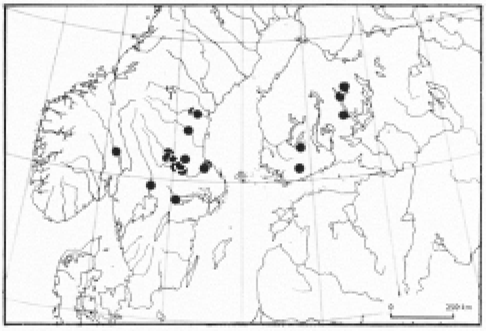


Fig. 14. *Hierochloë hirta* ssp. *hirta*. Localities of cultivated material. 2n=56.

mm long, obtuse or acute, often incised. *Panicle* (50—)75—150 mm long; nodes (5—)9—10(—12); main lateral branches long, often slightly tortuous, the lower ones often somewhat pendulous, 2 at lower nodes, 1 at (0—)2—3 upper nodes; branches and pedicels glabrous or with few, simple, unicellular hairs up to 0.1 mm long; spikelets (19—)50—100(—140) in number. *Glumes* 4.0—5.6(—6.3) mm long, glabrous, gold- to brown-glittering in the mature condition, almost always distinctly purplish; hairs at base of florets 0.5—0.9 mm long. *Lemma of male florets* 3.0—5.0 mm long, acute or slightly emarginate or bifid at apex, 5-nerved, towards apex with up to 0.5 mm long hairs; margins densely ciliate with simple and bifurcate, straight hairs 0.5—1.0 mm long; middle nerve reaching apex or base of apical incision if present; awn on lemma of lower male floret 0.2—0.8 mm long, scaberulous, inserted at apex or at base of apical incision if present 0.1—0.5 mm below apex; awn on lemma of upper male floret (0.0—)0.2—1.0 mm long, scaberulous, inserted at apex or at base of apical incision if present 0.1—0.5 mm below apex; both awns tapering towards end, gently but distinctly bent outwards. *Anthers of male florets* 1.6—2.1 mm long. *Lemma of bisexual floret* 2.9—3.5 mm long; awn absent; hairs towards apex of lemma 0.4—0.8 mm long, distinctly spreading. *Anthers of bisexual floret* 1.2—1.3 mm long.

DISTRIBUTION AND HABITAT

Hierochloë hirta ssp. *hirta* has an area of distribution of about the same size as that of *H. australis* (see p. 135) and partly coinciding with it. It occurs in South Norway, Central and South Sweden, South and East Finland, the western parts of European Russia, Poland, Czechoslovakia, and South Germany. It should be placed in the phytogeographical group where HULTÉN placed *H. australis* (see p. 135).

Fig. 13 shows where the herbarium material studied was collected (C, GH, H, LD, LE, M, MT, O, PRC, S, TRH, TUR, UPS, W; c. 350 sheets).

Hierochloë hirta ssp. *hirta* grows in light, sandy or gravelly soil, often on margins of lakes and streams. It can occur in meadows, but I have not seen it in fens. The localities are often secondary.

Table 2. Chromatographically separated chemical leaf constituents. Spots are numbered as in Weimarck 1970 b. Division into spot groups is indicated by short horizontal lines. Spot intensity, stated as not visible, less clearly visible, and more clearly visible, is represented by the symbols ·, – and +, respectively. For technique see Weimarck 1970 b. — A: *Hierochloë hirta* ssp. *hirta;* neotype (M). — B: *H. hirta* ssp. *hirta;* Sweden. Skåne. Stehag. Shore of Lake Ringsjön 2.6. 1947 H. Rufelt (LD). — C: *H. hirta* ssp. *hirta;* Sweden. Skåne. Klinta. 6. 1893 L. Fr. Rosengren (LD). — D: *H. repens;* isotype of *H. odorata* ssp. *pannonica* (C). — E: *H. stepporum;* European Russia. Voronezk, Novochopersk. Near Varvarin 9.6. 1963 A. K. Skvortsov (M).

	A	B	C	D	E	
1	·	·	·	·	·	1
2	·	+	·	–	+	2
3	+	–	+	·	·	3
4	+	–	+	+	·	4
5	·	–	+	+	+	5
6	+	+	+	+	+	6
7	+	+	+	+	–	7
8	–	·	+	–	·	8
9	+	–	–	·	·	9
10	·	·	·	·	·	10
11	–	–	–	+	·	11
12	–	–	–	·	·	12
13	+	–	–	·	·	13
14	+	+	+	+	–	14
15	·	·	·	·	·	15
16	–	–	·	·	·	16
17	·	·	·	+	·	17
18	–	–	+	+	–	18
19	·	·	·	·	·	19
20	·	–	·	+	·	20
21	·	–	–	+	·	21
22	+	–	–	·	·	22
23	·	·	·	·	·	23
24	–	–	–	–	·	24
25	·	·	·	·	·	25
26	·	·	·	·	·	26
27	+	+	+	·	–	27
28	+	+	+	·	+	28
29	+	+	+	·	+	29
30	+	–	–	·	–	30
31	·	–	·	·	·	31
32	·	–	·	·	·	32
33	·	–	+	·	·	33
34	·	–	+	·	+	34
35	·	·	·	·	·	35
36	·	·	·	·	·	36
37	·	·	·	·	·	37
38	+	–	–	·	·	38
39	+	–	–	·	·	39
40	+	–	+	·	·	40
41	+	+	+	·	·	41

CHROMOSOME NUMBER

Octoploid collections (2n=56) were found in Norway, Sweden, and Finland. The localities where the samples were collected for cultivation in this investigation are shown in Fig. 14 and listed on p. 170. Fig. 27 *D* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

Embryo-sac development and meiosis have not yet been studied. Germinating capacity was very low in the collection A G M (Gustafs, Dalarna, Sweden), where 1 out of 145 caryopses sown germinated.

Chromatographically obtained evidence (Weimarck 1970 b p. 263) indicated vegetative propagation in the localities studied.

VARIATION

The variation range of the number of nodes and spikelets per panicle under natural conditions (Fig. 8 *C* p. 142) was about as great as that in *Hierochloë odorata* ssp. *odorata,* but the values were generally higher.

Variation in chromatographic pattern (Weimarck 1970 b pp. 256—257) mainly involved the spot group 29—34. This group was found to be characteristic for the taxon, although only the spot 29 was invariably represented in the material. Members of the group occur also in *H. australis,* which, however, lacks the group 38—41.

The neotype (see p. 146) was checked chromatographically before the choice (Table 2). It turned out to have the spots 29 and 30 of the diagnostic group. The specimens studied earlier, although geographically distant from the type locality, did thus coincide well with the type specimen also chromatographically.

Chromatographically obtained spot patterns of two herbarium collections from Skåne, Sweden, are also presented in Table 2. No *Hierochloë hirta* ssp. *hirta* from southernmost Sweden was included in Weimarck 1970 b. The patterns of the collections from Skåne agree well with those in the *H. hirta* ssp. *hirta* collections studied before.

Hierochloë hirta ssp. *hirta* has usually a very characteristic general habit and is easy to distinguish from all other members of the *H. odorata* complex. Important characteristics are the length of the panicle with its often pendulous lower main branches and usually dark brown and purplish colour, and the slightly protruding short awn on the lemma of male florets. Difficulties in distinguishing it from *H. hirta* ssp. *arctica* occur almost only in some very young specimens which are not yet fully-coloured and with the florets still immature and hidden within the glumes. They can be mistaken for extreme variants of *H. hirta* ssp. *arctica*. The circles in Fig. 13 denote such cases.

Hierochloë hirta (Schrank) Borbás ssp. **arctica** (Presl) G. Weim., comb. nov.

Hierochloë arctica Presl (1830 p. 252). Type collection: "Hierochloë arctica J. S. Presl nov. sp." (PR 25243; lectotype). The sheet is marked "Mus. Boh. coll. Hänke".

Hierochloë odorata (L.) Wahlenb. var. *annulata* Petrov (1930 pp. 131—132; incidentally also as *H. annulata*). Type collection: "Jakutsk. obl. Kolymsk. okr. 28.7. 1905 I. Šulga no. 387." (LE; lectotype).

DESCRIPTION (cf. Fig. 12 *D—F* p. 147)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with (10—)20—40(—50) mm long internodes, with 7—12 mm long, not persistent, light- to dark-coloured scales at nodes; rhizome system loosely matted. *Vegetative shoots*: basal sheaths brownish or reddish; leaf laminae linear or narrowly elliptic, with serrulate margins, (2.5—)3.0—5.0(—6.5) mm broad, glabrous and shiny on abaxial surface, pilose and sometimes slightly caesious on adaxial surface; hairs long, simple, unicellular; nerves on both surfaces with sparse prickles; ligule 1.0—2.5 mm long, truncate, obtuse or acute. *Flowering shoots* inclusive of panicle (20—)30—75 cm high in the mature condition, with nodes only at base; basal sheaths brownish or reddish; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf 5—20(—40) mm long, 1.5—5.0 mm broad; ligule of uppermost leaf 1.0—4.0 mm long, obtuse or acute, often incised. *Panicle* (30—)45—85 mm long; nodes (4—)7—8(—10); main lateral branches long, often slightly tortuous, 2 at lower nodes, 1 at upper 1—2 nodes; branches and pedicels glabrous or with few, simple, unicellular hairs up to 0.1 mm long; spikelets (15—)20—70(—85) in number. *Glumes* (4.0—)4.5—6.0(—6.3) mm long, glabrous, gold-glittering in the mature condition; hairs at base of florets 0.5—1.0 mm long. *Lemma of male florets* 3.5—5.5 mm long, acute or slightly emarginate or bifid at apex, 5-nerved, towards apex with hairs up to 0.8 mm long; margins densely ciliate with simple and bifurcate, straight or somewhat curly hairs 0.6—1.0 mm long; middle nerve reaching apex or base of apical incision if present; awn on lemma of both male florets (rarely absent but then developed as a mucro) 0.2—0.7 mm long, scaberulous, straight or less frequently somewhat bent in- or outwards, of approximately uniform thickness. *Anthers of male florets* 1.3—2.0 mm long. *Lemma of bisexual floret* 2.8—3.5 mm long; awn absent; hairs towards apex of lemma 0.4—0.7 mm long, simple and bifurcate, distinctly spreading. *Anthers of bisexual floret* 1.1—1.9 mm long.

DISTRIBUTION AND HABITAT

Hierochloë hirta ssp. *arctica* has an area of distribution which is boreal circumpolar and has a continental tendency. It occurs in Norway, Sweden, Finland, North, West, and Central European Russia, Poland, Germany, Czechoslovakia, ?North Italy, Asiatic Russia, China, the Aleutian Islands, Alaska, Yukon, the Mackenzie District, British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, ?New

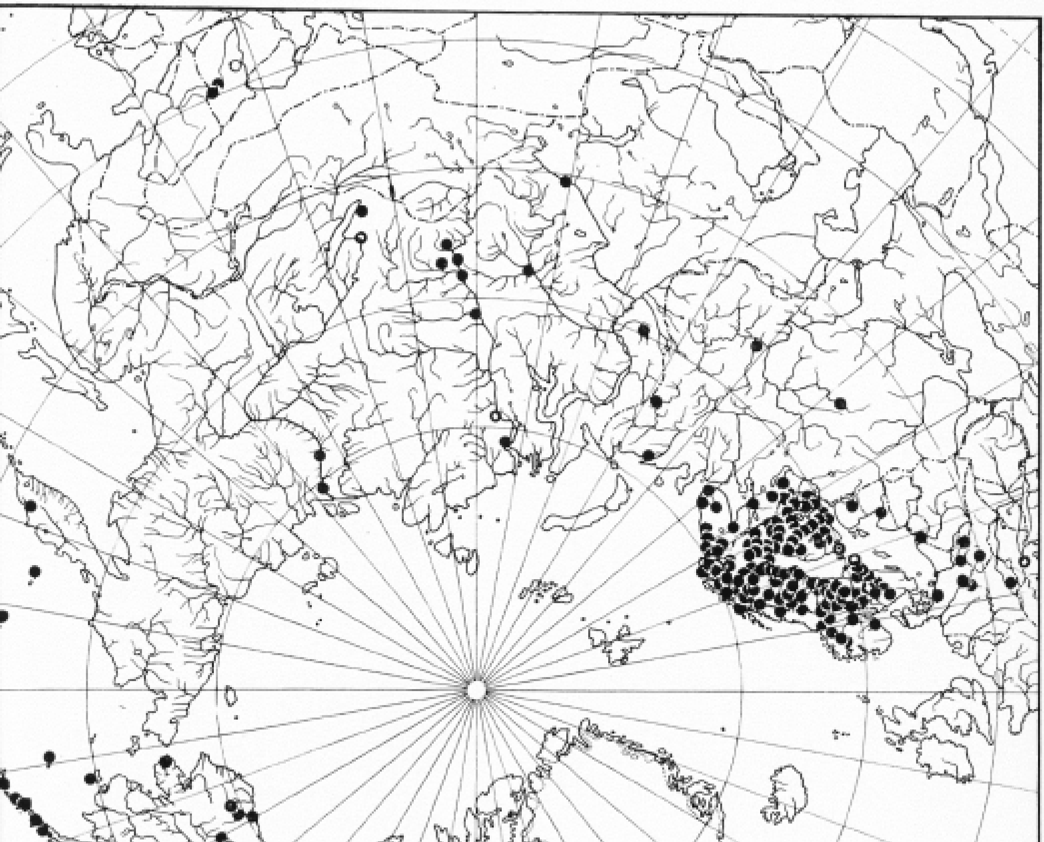


Fig. 15. *Hierochloë hirta* ssp. *arctica*. Localities of herbarium material (total). Circles: specimens not determinable with certainty.

Brunswick, New Hampshire, Vermont, Massachusetts, New York, New Jersey, Ohio, Michigan, Indiana, Wisconsin, Illinois, ?Iowa, Minnesota, North Dakota, South Dakota, Montana, Wyoming, Colorado, and Washington. It fits into the group characterized by HULTÉN (1962 pp. 6—7) as taxa indigenous to the whole circumpolar area, being boreal, as far as is known lacking north and south of arctic-montane ranges, and as far as is known lacking east-western races in their circumpolar range. HULTÉN placed *H. odorata* in his wider definition in this group.

Figs. 15 and 16 show where the herbarium material studied was collected (BM, C, CAN, GH, GRO, H, K, LD, LE, M, MT, O, PR, PRC, S, TRH, TUR, UPS, W; c. 1025 sheets).

Hierochloë hirta ssp. *arctica* occurs in approximately the same types of habitat as *H. odorata* ssp. *odorata* (p. 138) but also in somewhat drier meadows and poorer bog- or heath-like biotopes. I have not seen it close to salt or brackish water. Its apophytic tendency is obviously stronger than that of *H. odorata* ssp. *odorata* but perhaps not as strong as that of *H. hirta* ssp. *hirta*. NORSTOG (1960 b pp. 362—363) reported all the seven localitites in Ohio where he found the taxon to be railroad rights-of-way, and road-sides.

CHROMOSOME NUMBERS

Octoploid collections (2n=56) were found in Norway, Sweden, Finland, Ontario, New Hampshire, and Minnesota. A collection from Graham Island, British Columbia, which was reported to be octoploid by TAYLOR and MULLIGAN (1968 p. 31; as *Hierochloë odorata*) could be referred to *H. hirta* ssp. *arctica* after an examination of a voucher specimen (M). The same is true of an octoploid collection from Cabin Creek, the Mackenzie District (BOWDEN 1960 p. 551: W. J. CODY & R. L. GUTTERIDGE no. 7942, as *H. odorata*; vouchers from MT, W).

Octoploid collections, in all likelihood referable to *Hierochloë hirta* ssp. *arctica* but of which I have not seen voucher specimens, were reported from Ontario and Saskatchewan (BOWDEN 1960 p. 551), New Hampshire (LÖVE & LÖVE in LÖVE & SOLBRIG 1964 p. 201; LÖVE & LÖVE 1966 p. 18), and Ohio and Michigan (NORSTOG 1960 b p. 361; REEDER & NORSTOG 1961 p. 82), all as being *H. odorata*.

One collection from Quebec (later cultivated in Lund; A D B) was found to be decaploid (2n=70) by O. HEDBERG (1967 p. 311, no. 3411). Whether this decaploid really represents a biotype permanently established in nature is not known. It may, however, very well be an ephemeral aberrant that has originated from lower polyploid ancestors. Morphologically, it falls within the normal variation range of *Hierochloë hirta* ssp. *arctica* (voucher in UPS).

Among the offspring of an octoploid plant received as a rhizome from Minnesota (A K K) I have found one dodecaploid plant (2n=c. 84), in all likelihood the result of the union of one reduced and one unreduced gamete. In this case the high-polyploid plant was only an aberrant one but illustrates very well the possibility that new cytotypes can be created suddenly due to the reproductive unbalance present.

The record of a tetraploid (2n=28) from Manitoba (LÖVE & LÖVE 1956 p. 247; 1965 p. 12) should be referred to *Hierochloë hirta* ssp. *arctica* judging from what is known of its area of distribution. However, I have not examined the voucher specimen and so could not check the record.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 17 (European localities only) and listed on p. 171. Fig. 27 *E* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

The collections A N C (Kvikkjokk, Lule Lappmark, Sweden) and A G P (Norrbärke, Dalarna, Sweden) formed unreduced em-

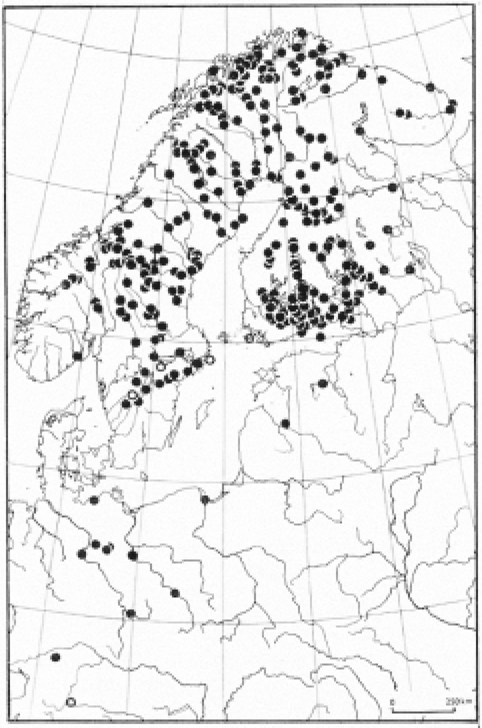


Fig. 16. *Hierochloë hirta* ssp. *arctica*. Localities of herbarium material (detail). Circles: specimens not determinable with certainty.

bryo-sacs of the Hieracium type. In addition, the collection A N C appeared to form occasional unreduced embryo-sacs of the Antennaria type and the collection A G P reduced embryo-sacs of the Polygonum type (Weimarck 1967 a pp. 224—227). Female meiosis was rare. Male meiosis was badly disturbed.

Germinating capacity was 9 % in both collections studied (Weimarck 1967 a p. 229).

VARIATION

The variation range of the number of nodes and spikelets per panicle under natural conditions (Fig. 8 *D* p. 143) was intermediary between that in *Hierochloë hirta* ssp. *hirta* and *H. odorata* ssp. *baltica*.

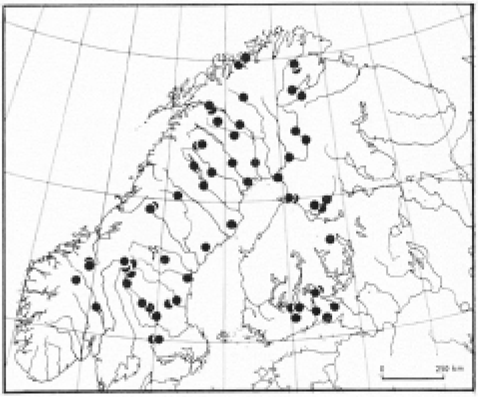


Fig. 17. *Hierochloë hirta* ssp. *arctica*. Localities of cultivated material (from Europe only), 2n=56.

All European collections studied chromatographically lacked the spot group 29—34 regarded as diagnostic for *Hierochloë hirta* ssp. *hirta* when combined with the group 38—41. Spots 33 and 34 were found in the collection A K E (Mount Washington, New Hampshire, USA). No member of the spot group 38—41, considered to be more or less diagnostic for both subspecies of *H. hirta*, was found in the collections A X K (Valkeala, Savonia australis, Finland) and A D F (Carleton, Ontario, Canada).

The distinct awn and dense marginal hairs on the lemma of male florets, the spreading hairs on the lemma of bisexual florets, and the spot group 38—41 almost always found in material chromatographically studied, are common to *Hierochloë hirta* ssp. *hirta* and ssp. *arctica*. The general habit of ssp. *arctica* is, on the contrary, more similar to that of *H. odorata*. Circles in Figs. 15 and 16 denote specimens not determinable with certainty, mostly not fully developed ones and therefore resembling *H. odorata*.

Although with some hesitation, I have here treated *arctica* as a subspecies under *Hierochloë hirta* with reference to their common characteristics, in spite of the fact that they seem to be far more distant from each other than is *H. odorata* ssp. *baltica* from ssp. *odorata*.

Neither morphological nor chromatographical evidence favours a further subdivision of *Hierochloë hirta* ssp. *arctica*.

Hierochloë repens (Host) Simonkai

Holcus repens Host (1805 pp. 3—4). — *Hierochloa repens* (Host) Simonkai 1886 p. 560). Type collection: "Holcus repens" Host (W, Herb. Host no. 2386; lectotype). The text on the sheet is in Host's own handwriting (G.-H. Leute, pers. comm.).

Hierochloa orientalis Fries & Heuffel (Heuffel 1858 a p. 29; 1858 b p. 224). Type collection not seen. Description and distribution confirm the synonymy.

Hierochloa vinealis Schur (1859 p. 12). Type collection not seen. Description and distribution confirm the synonymy.

Hierochloë odorata (L.) Beauv. ssp. *pannonica* Chrtek & Jirásek (1964 pp. 247—250). Type collection: "Hierochloë odorata (L.) Wahlb. — Transsilvania: Torda, in vineis et inter segetes." G. et J. Wolff (PRC; holotype).

DESCRIPTION (cf. Fig. 18)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with 10—25(—40) mm long internodes, with 7—12 mm long, not persistent, light- to dark-coloured scales at nodes; rhizome system loosely matted. *Vegetative shoots*: basal sheaths greyish to brownish; leaf laminae linear or narrowly elliptic, with crenulate or serrulate margins, (5.0—)7.0—9.0(—11.0) mm broad,

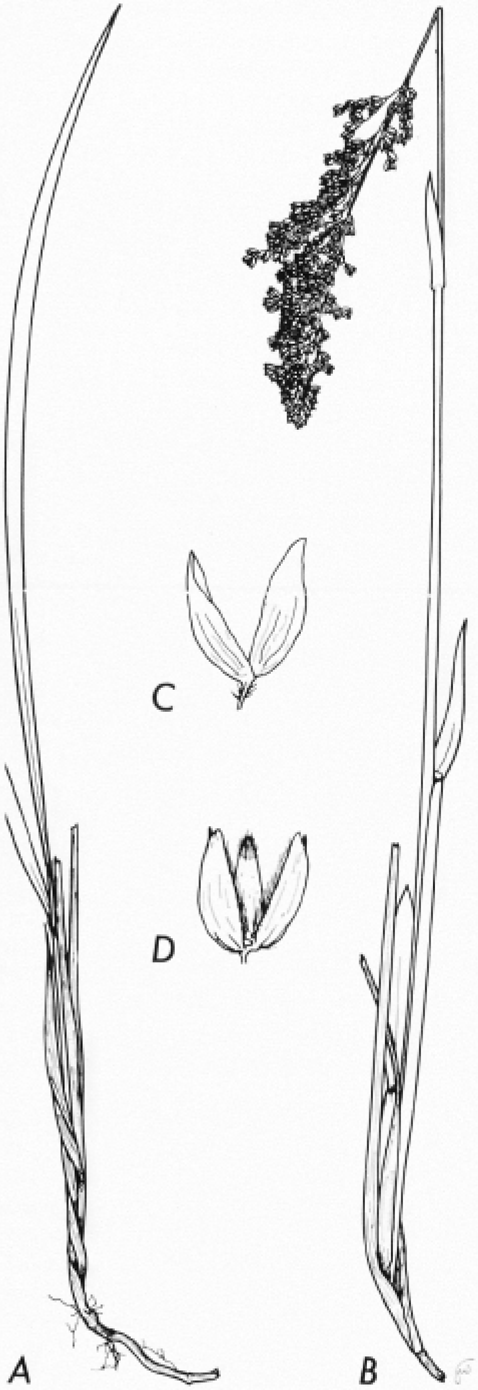


Fig. 18.

Fig. 18. *Hierochloë repens*, combined specimens from the lectotype collection. — *A, B:* Habit. — *C:* Glumes. — *D:* Florets. — *A, B* ×0.5; *C, D* ×5.

glabrous and caesious on both surfaces; nerves on both surfaces usually without prickles; ligule 0.5—1.5 mm long, truncate. *Flowering shoots* inclusive of panicle (30—)45—70(—90) cm high in the mature condition, with nodes only at base; basal sheaths greyish or brownish; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf (12—)20—35(—60) mm long, 4.0—7.5 (—9.0) mm broad; ligule of uppermost leaf 2.0—3.5 mm long, obtuse or truncate, often incised. *Panicle* (50—)65—100 (—140) mm long; nodes (10—)11—12 (—13); main lateral branches long, often slightly tortuous, 2 at lower nodes, 1 at 1(—2) upper nodes; branches and pedicels glabrous or pedicels immediately below base of glumes with simple, unicellular, 0.1—0.3 mm long hairs; spikelets (80—)120—160(—300) in number. *Glumes* (3.0—)3.4—4.2(—4.6) mm long, glabrous, gold- or silvery-glittering in the mature condition; hairs at base of florets 0.3—0.6 mm long. *Lemma of male florets* (3.1—) 3.3—3.8(—4.3) mm long, acute, 5-nerved, towards apex with up to 0.3 mm long hairs; margins densely ciliate with simple, straight or slightly curly hairs 0.3—0.6 mm long; middle nerve reaching apex or ending immediately below it; awn on lemma of both male florets (0.1—)0.2—0.5 (—0.8) mm long, smooth or very faintly scaberulous, inserted at apex or on back of lemma immediately below apex. *Anthers of male florets* 1.9—2.7 mm long. *Lemma of bisexual floret* 2.5—3.5 mm long; awn absent; hairs towards apex of lemma 0.3—0.6 mm long, appressed or spreading. *Anthers of bisexual floret* 1.6—2.2 mm long.

DISTRIBUTION AND HABITAT

Hierochloë repens is found in South-east Europe and adjacent South-west Asia. It occurs in Czechoslovakia, Austria, Hungary, Romania, Bulgaria, South European Russia, and South-west Asiatic Russia. The area of distribution can be characterized as eupontic, coinciding quite well with, for example, that of *Linum flavum* (see WALTER 1954 p. 182).

Fig. 19 shows where the herbarium material studied was collected (BM, C, K, LD, LE, M, PRC, S, UPS, W; c. 80 sheets).

Hierochloë repens occurs in dry, sandy or gravelly biotopes, in steppes and pine forests but also as a weed in cultivated fields and vineyards.

CHROMOSOME NUMBER

Tetraploid collections ($2n=28$) have been found in Czechoslovakia and Romania. The collection from Czechoslovakia (B C D) has in addition 2 B-chromosomes. B-chromosomes were not found in other taxa within this investigation.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 20 and listed on p. 172. Fig. 27 *F* (p. 165) shows a mitotic metaphase plate.

REPRODUCTION

The results of an investigation on the development of the embryo-sac in the collection B C C (Iași, Romania) have not been published before due to shortage of material. It can be postulated preliminarily that most young nucelli (25 out of 29; 86 %) contained an embryo-sac mother cell or a derivative thereof. Tetrad formation was apparently normal. In one case only were a few embryo-sac initials present. A few nucelli were degenerative. Reduced embryo-sacs of the Polygonum type were formed. No stage later than the organized eight-nucleate embryo-sac was found in the material. Male meiosis was somewhat disturbed. *Hierochloë repens* thus is in these respects strongly suggestive of tetraploid *H. odorata* ssp. *odorata* (cf. WEIMARCK 1967 a).

Germinating capacity was not tested. The vegetative reproduction by rhizomes is reported to be very aggressive. Nothing is, however, known of the type of reproduction prevailing in nature.

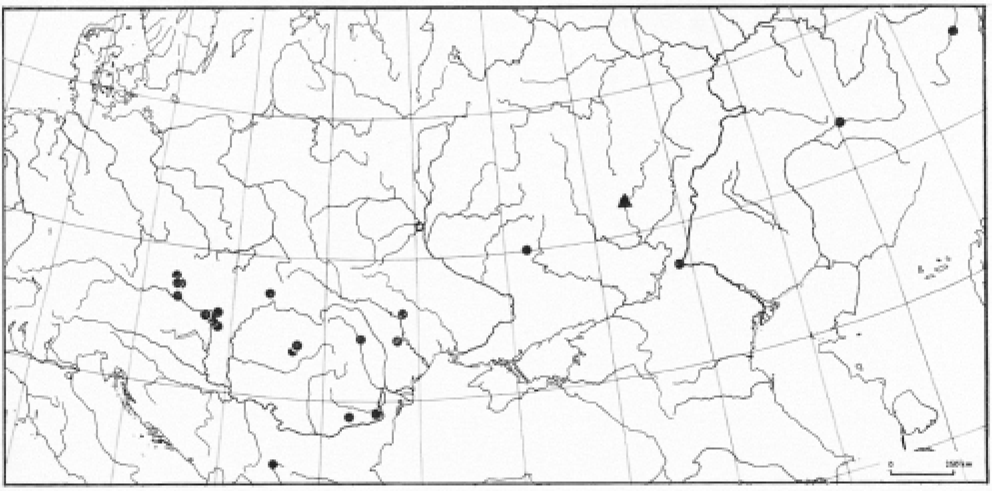


Fig. 19. *Hierochloë repens.* Localities of herbarium material. Circle: specimen not determinable with certainty. Triangular symbol: *H. stepporum.*

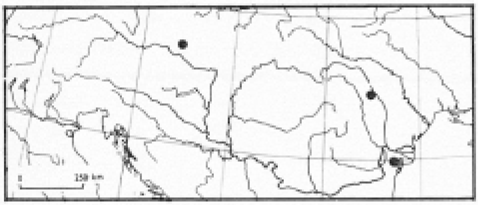


Fig. 20. *Hierochloë repens.* Localities of cultivated material, 2n=28 and (north-western collection) 2n=28+2B.

VARIATION

The variation of the number of nodes and spikelets per panicle in herbarium specimens (Fig. 8 *E* p. 143) may not be quite representative on account of the relatively few specimens studied. Flowering in cultivated specimens was sparse.

The collection B C C studied embryologically displayed a remarkable variation in spikelet structure. In 61 spikelets studied, both upper florets were hermaphrodite in 25 cases (41 %), and all three were hermaphrodite in 5 (8 %). One case of a spikelet with four hermaphrodite florets was also found.

Hierochloë stepporum Smirnov (1958 p. 81) shows a close affinity to *H. repens.* The taxonomic status of *stepporum* relative to *repens* could not at the time be clarified, since the material available was too scanty. One collection of *H. stepporum* is marked on Fig. 19 by a triangular symbol. This collection has a longer awn on the lemma of male florets than is usual in *H. repens,* and hairs more spreading on the lemma of bisexual florets. It was tested chromatographically (Table 2 p. 149). In comparison with the collection B C C (Weimarck 1970 b p. 253) and an isotype of *H. odorata* ssp. *pannonica* (Table 2), the *H. stepporum* sample exhibits certain differences. The spots 29 and 30 are common to both the *H. stepporum* sample and to most *H. hirta* ssp. *hirta* specimens studied. The two collections of *H. repens* both have similar patterns consisting of very few spots.

Another specimen studied of *Hierochloë stepporum* (Teplen' 16.3. 1938 P. A. Smirnov; LE) has shorter awns and looser panicle.

Hierochloë alpina (Willd.) Roemer & Schultes

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **alpina**

Holcus alpinus Swartz ex Willdenow (1806 p. 937). — *Hierochloa alpina* (Willd.)

Roemer & Schultes (1817 p. 515). Type collection: "Herb. Swartzii. 1. Från fjället Kärpile i Torneå Lappmark. Liljeblad." (S; lectotype). The specimen in Swartz' herbarium was collected by Liljeblad. Mount Kärpile was claimed by Wahlenberg (1812 p. 32) to be the original locality of *Aira alpina* Liljeblad (1792 p. 49; see below), a name commented upon by Swartz (1807 p. 45). — *Aira alpina* Liljeblad was not cited in Willdenow (1806).

Aira alpina Liljeblad (1792 p. 49) non Linnaeus (1753 p. 65). Type collection: as above (S; lectotype).

Hierochloë monstruosa (Koidzumi) Honda (1926 p. 319). — "*Hierochloe alpina* Roem. & Schlz. var? *monstruosus*" Koidzumi (1918 p. 63). Type collection not seen.

DESCRIPTION (cf. Fig. 21 *A*—*C*)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with up to 10 mm long internodes, covered with sheaths; plant densely tufted. *Vegetative shoots*: basal sheaths brown to deep purple; leaf laminae linear, generally folded together, with densely serrulate margins, 1.5—3.0 mm broad, glabrous and shiny on abaxial surface, pilose on adaxial surface; hairs short, simple, unicellular; nerves on adaxial surface with sparse prickles; ligule 0.3—1.0 mm long, truncate. *Flowering shoots* inclusive of panicle (5—)20—35(—55) cm high in the mature condition, with nodes only at base; basal sheaths deep purple; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf (2.5—) 3.5—8.0(—35.0) mm long, (0.5—)1.0—3.0 (—5.0) mm broad; ligule of uppermost leaf 0.4—1.5 mm long, truncate or obtuse. *Panicle* (12—)20—50(—60) mm long; nodes 4—7(—8); main lateral branches short, usually not tortuous, (1—)2 at lower nodes, 1 at (0—)1—3(—4) upper nodes; branches and pedicels glabrous or with few, simple, unicellular hairs up to 0.1 mm long; spikelets (3—)10—20(—35) in number. *Glumes* (4.0—)4.5—6.9(—7.5) mm long, glabrous or roughish, gold-glittering in the mature condition; hairs at base of florets 0.25—0.5 mm long. *Lemma of male florets* (3.9—)4.5—6.0(—6.5) mm long, deeply or very deeply bifid at apex, 5-nerved, towards apex with up to 1.25 mm long hairs; margins moderately ciliate with simple, straight or somewhat curly, 0.6—1.0 mm long hairs; middle nerve reaching base of apical incision; awn on lemma of lower male floret 0.6—3.5 mm long, scaberulous, inserted at base of apical incision 0.5—2.5 mm below apex; awn on lemma of upper male floret 5.5—9.0 (—10.5) mm long, scaberulous except at the base, almost always twisted at the base, almost always distinctly geniculate, inserted at base of apical incision (2.0—) 3.0—4.5 mm below apex and (0.9—)1.3—2.1(—2.5) mm above base of lemma. *Anthers of male florets* 1.6—2.2 mm long. *Lemma of bisexual floret* 3.5—5.2 mm long; awn (0.0—)0.1—1.5 mm long, scaberulous, inserted at base of apical incision 0.1—0.2 mm below apex; hairs towards apex of lemma 0.25—0.8 mm long, appressed or spreading. *Anthers of bisexual floret* 1.3—1.7 mm long.

DISTRIBUTION AND HABITAT

Hierochloë alpina ssp. *alpina* has an arctic circumpolar area of distribution. It occurs in Spitsbergen, in the northernmost parts of Norway, Sweden, Finland, European Russia, and Asiatic Russia, in part of South Asiatic Russia, in Japan, the Aleutian Islands, Alaska, Yukon, the Mackenzie, Keewatin, and Franklin Districts, British Columbia, Quebec, Labrador, and Greenland. It was placed by Hultén (1962 p. 6) in the phytogeographical group of taxa indigenous to the entire circumpolar area, being arctic-montane and occurring also on isolated southern mountains but not south of the central Asiatic desert belt. The herbarium material studied (BM, C, CAN, DAO, GH, GRO, H, K, LD, M, MT, O, PRC, S, TI, TRH, TUR, UPS, W; c. 1775 sheets) is shown in Fig. 29.

Hierochloë alpina ssp. *alpina* occurs as a rule above or north of the tree line, more

Fig. 21. *A—C: Hierochloë alpina* ssp. *alpina*, collection B G G (Greenland). — *A:* Habit. — *B:* Glumes. — *C:* Florets. — *D—F: H. alpina* ssp. *orthantha*, collection B F R (Greenland). — *D:* Habit. — *E:* Glumes. — *F:* Florets. — *A, D* ×0.5; *B, C, E, F* ×5.

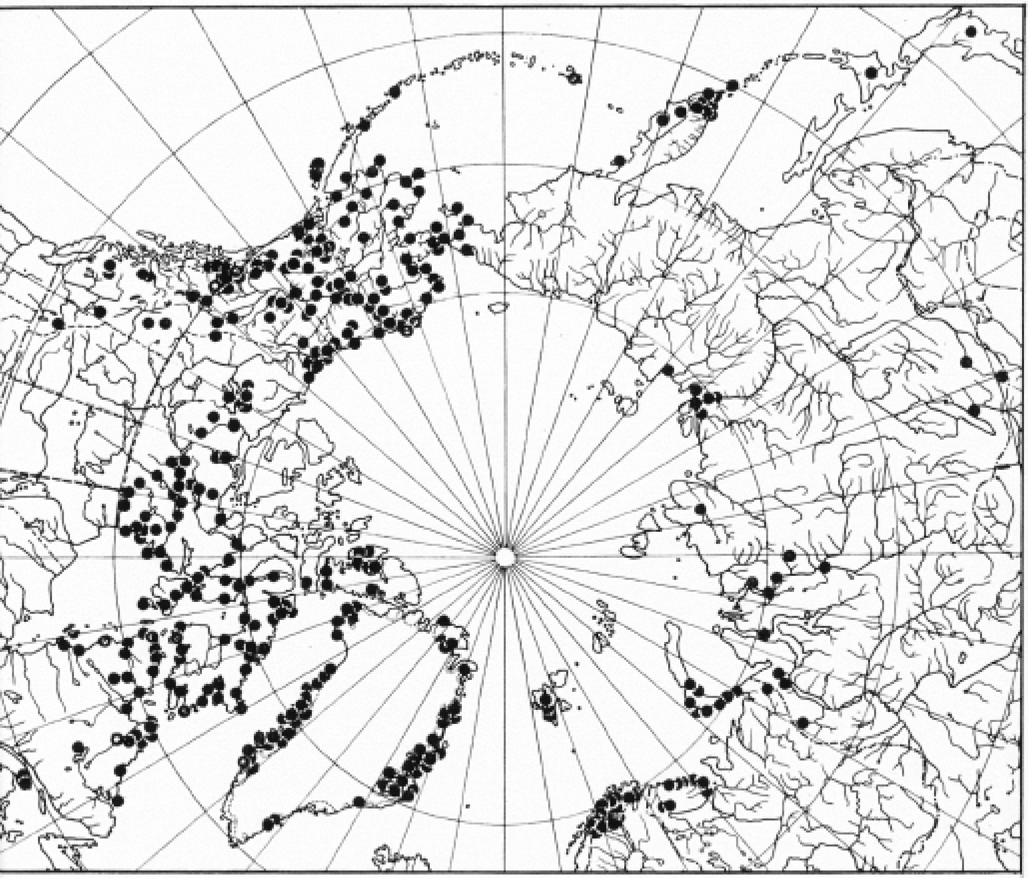


Fig. 22. *Hierochloë alpina* ssp. *alpina*. Localities of herbarium material. Circles: specimens not determinable with certainty.

exceptionally in open forests. It grows usually in places strongly exposed to wind and with little snow-cover during the winter, where the vegetative cover is not closed.

Cultivation was impossible in the open in Lund but could be managed in the Arktisk Hus in Copenhagen.

CHROMOSOME NUMBERS

Specimens collected in Greenland and grown from caryopses from Asiatic Russia have been found to be octoploid ($2n=56$). Voucher specimens of collections reported to be octoploid were checked. These were from Southampton Island, the Keewatin District (BOWDEN 1960 p. 551, DAO 44130), Frobisher Bay, the Franklin District (BOWDEN 1960 p. 551, DAO 44112; O. HEDBERG 1967 p. 310 no. 3137, UPS), and Charcot's Land, Greenland (HOLMEN & LÆGAARD in sched., C, UPS). All specimens were reported as being *Hierochloë alpina*.

Octoploid collections, in all likelihood referable to *Hierochloë alpina* ssp. *alpina* but of which I have not seen voucher specimens, were reported from Spitsbergen

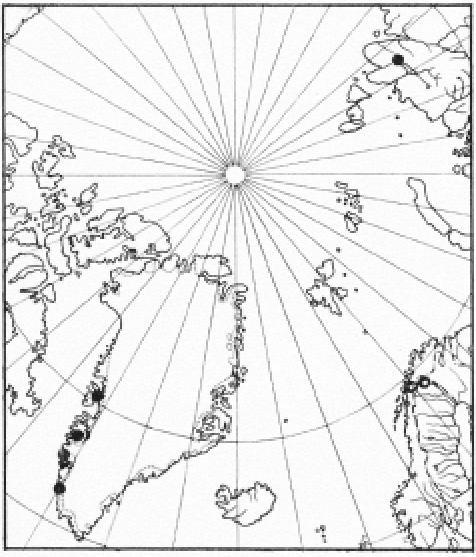


Fig. 23. *Hierochloë alpina* ssp. *alpina*. Localities of cultivated material. Dots: 2n=56. Circles: deviating numbers.

(Flovik 1938 p. 301), Norway (Knaben & Engelskjön 1967 p. 15), Asiatic Russia (Sokolovskaja 1960 p. 44; 1963 p. 49; Sokolovskaja & Strelkova 1960 p. 373; Zhukova 1964 p. 984), Japan (Tateoka 1954 p. 46), Alaska (Johnson & Packer 1968 p. 414), the Keewatin District (Löve & Ritchie 1966 p. 432), and Greenland (Sørensen 1954 p. 6; Jørgensen, Sørensen & Westergaard 1958 p. 12).

Aneuploid collections were found in Norway (2n=72) and Finland (2n=66; Weimarck 1970 a). There was no evidence that these specimens deviated morphologically from the other material studied. A possible explanation of the cytological variation is that aneuploid gametes might have functioned in cases of sporadical amphimixis. Plants with deviating numbers can obviously be established under natural conditions. Aneuploid specimens of *Hierochloë odorata* and *H. hirta* were remarkably enough not found.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 23 and listed on p. 172. Fig. 27 *G* (p. 165) shows a mitotic metaphase plate; see also Weimarck 1970 a.

REPRODUCTION

The collection B D R, 2n=66 (Enontekiö, Lapponia enontekensis, Finland), the collections B G D, B G F, B G H, B G K, and B G M, 2n=56 (Søndre Strømfjord, Greenland), and the collection B G A, 2n==56 (Godthåb, Greenland) all developed unreduced embryo-sacs of the Hieracium type (Weimarck 1970 c). In addition, unreduced embryo-sacs of the Antennaria type and reduced ones of the Polygonum type appeared to occur though rarely. Female meiosis was rare and could be abnormal. Male meiosis was badly disturbed or wholly abortive. Germinating capacity was not tested.

Embryological and chromatographical evidence in combination indicated that the apomixis was facultative in the collection B D R (Weimarck 1970 b p. 263).

VARIATION

The number of nodes and spikelets per panicle in nature is shown in Fig. 24 *A*.

Occasional spikelets with four florets were found in some herbarium specimens from Alaska. Proliferous panicles with green and strongly elongated lemmata were found in a number of specimens from North-east Siberia, Alaska, Yukon, and the Mackenzie District. Such abnormalities were not found in other parts of the area of distribution. The epithet *monstruosa* applied to different ranks (cf. p. 157) refers to such proliferous specimens.

A few cases of late-flowering specimens slightly modified in the same ways as described for the *Hierochloë odorata* complex were found in the herbarium material.

The chromatographic study of *Hierochloë alpina* ssp. *alpina* did not permit of any conclusions as to regional or local spot pattern variation.

The awn on the lemma of upper male florets varies considerably. Although usually twisted and geniculate, either or both of these characteristics can be lacking. The most reliable characteristic for distinguishing between *Hierochloë alpina* ssp. *alpina* and ssp. *orthantha* is the point of insertion of the awn on lemma of upper male florets. It can be expressed either as an absolute measure or as a relative index. Both gave roughly the same precision in classification when tested on material previously determined by means of a combination of awn insertion, awn twisting, awn bending, spikelet size, and internodal length of rhizome. In most *H. alpina* ssp. *alpina* plants the point of insertion is about 1.5—2.0 mm above the base of the lemma, and the relation between the distance from the point of insertion to the base of the lemma and the total length of the lemma expressed as a quotient is about 0.23—0.38. The values 2.3 mm and quotient 0.40 were found to denote the discontinuity between *H. alpina* ssp. *alpina* and ssp. *orthantha*. Few specimens raised doubts or were classified contrary to the above-mentioned previous determination based on a greater number of characters.

SØRENSEN (1954 p. 8) stressed the fact that some Alaskan specimens of *Hierochloë alpina* were morphologically deviating. Specimens labelled by him as aberrants do not, however, belong with those having the characteristics of *H. alpina* ssp. *orthantha* cited below (p. 164). Nor did SØRENSEN refer them to his *H. orthantha*, but said they perhaps represented another distinct unit not possible to elucidate further from his material. In my opinion these specimens fall within the accepted range of variation in *H. alpina* ssp. *alpina* although on its periphery.

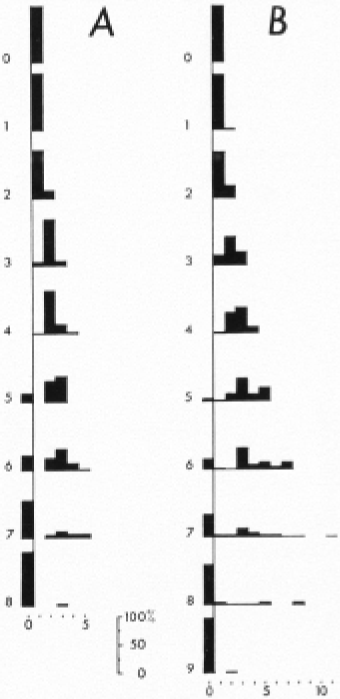


Fig. 24. Panicle diagrams. — *A: Hierochloë alpina* ssp. *alpina*. 52 specimens from 18 collections (Norway, Finland, Greenland). — *B: H. alpina* ssp. *orthantha*. 32 specimens from 13 collections (USA, Greenland). — Voucher specimens of cytologically investigated collections from the field. See also Fig. 8.

Hierochloë alpina (WILLD.) ROEMER & SCHULTES ssp. **orthantha** (SØRENSEN) G. WEIM., comb. nov.

Hierochloë orthantha SØRENSEN (1954 pp. 3—11). Type collection: "Hierochloë orthantha Th. S. — S. Grønl.: Tunugdliarfik Fjord. B. W. I. (Kiagtût.). Elyna-Hede, Löss. 8.7. 1947 Thorv. Sørensen No. 124." (C; holotype).

Holcus alpinus SWARTZ ex WILLDENOW (1806 p. 937) pro parte excl. typo.

Holcus monticola BIGELOW (1816 p. 334). — *Hierochloë monticola* (BIGELOW) LÖVE & LÖVE (in LÖVE & SOLBRIG 1964 p. 201) non MEZ (1921 pp. 291—292). Type collection not seen.

DESCRIPTION (cf. Fig. 28 *D—F* p. 158)

The following specifications are to be added to the general description of taxa treated (pp. 131—132):

Rhizome with up to 20 mm long internodes, covered with sheaths; plant mode-

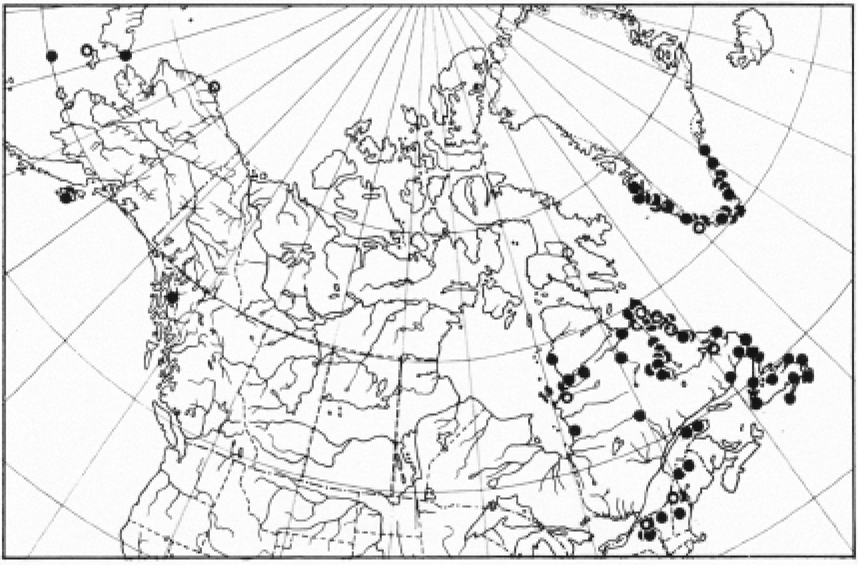


Fig. 25. *Hierochloë alpina* ssp. *orthantha*. Localities of herbarium material. Circles: specimens not determinable with certainty. For localities in the western part of the map, see text p. 164.

rately tufted. *Vegetative shoots*: basal sheaths brown to deep purple; leaf laminae linear, often folded, with sparsely serrulate margins, 2.0—5.0 mm broad, glabrous and shiny on abaxial surface, pilose on adaxial surface; hairs short, simple, unicellular; nerves on adaxial surface with sparse prickles; ligule 0.3—1.0 mm long, truncate. *Flowering shoots* inclusive of panicle (20—)35—60(—75) cm high in the mature condition, with nodes only at base; basal sheaths deep purple; sheaths of assimilating leaves usually tightly surrounding culm; lamina of uppermost leaf (8.0—) 12.0—25.0(—48.0) mm long, 2.0—5.0 mm broad; ligule of uppermost leaf 0.4—1.5 mm long, truncate or obtuse. *Panicle* (25—)35—70 mm long; nodes (5—)6—8(—9); main lateral branches short, usually not tortuous, 1 at each node or 2 at lower or middle nodes, 1 at 1—2 upper nodes and at lowermost node; branches and pedicels glabrous or with sparse, simple, unicellular hairs up to 0.1 mm long; spikelets (8—)15—30(—35) in number. *Glumes* 6.0—8.0 mm long, glabrous, gold-glittering in the mature condition; hairs at base of florets 0.3—0.8 mm long. *Lemma of male florets* 5.6—7.3 mm long, deeply bifid at apex, 5-nerved, towards apex with hairs up to 0.8 mm long; margins moderately ciliate with simple and (few) bifurcate, straight or slightly curly hairs 0.6—1.25 mm long; middle nerve reaching base of apical incision; awn on lemma of lower male florets 1.8—4.5(—6.5) mm long, scaberulous, inserted at base of apical incision 0.6—2.0 mm below apex; awn on lemma of upper male floret 4.5—7.0 mm long, scaberulous except in the basal part, not twisted or slightly twisted at base, straight or slightly geniculate, inserted at base of apical incision 1.5—3.0 mm below apex and (2.2—)2.6—4.0(—4.5) mm above base of lemma. *Anthers of male florets* 1.6—2.6 mm long. *Lemma of bisexual floret* 4.0—5.0 mm long; awn (0.0—)0.1—1.5 mm long, scaberulous, inserted at base of apical incision 0.1—0.2 mm below apex; hairs towards apex 0.25—0.8 mm long, appressed or spreading. *Anthers of bisexual floret* 1.6—1.9 mm long.

DISTRIBUTION AND HABITAT

Hierochloë alpina ssp. *orthantha* is found in South Greenland and adjacent parts of North America. A few records in Alaska and the Bering Strait region will be commented on below (p. 164). It occurs in ?easternmost Asiatic Russia, ?Alaska, Quebec, Labrador, Newfoundland, Maine, Vermont, New Hampshire, New York, and South Greenland.

Fig. 25 shows where the herbarium material studied was collected (C, CAN, DAO, GH, LD, M, MT, S, TUR, UPS, W; c. 375 sheets).

Hierochloë alpina ssp. *orthantha* can occur in biotopes of about the same character as for *H. alpina* ssp. *alpina* but also, and more typically, in wetter places less exposed to wind and with a more closed vegetative cover.

Most material was cultivated in the Arktisk Hus in Copenhagen, but specimens from New Hampshire also thrived in the open in Lund.

CHROMOSOME NUMBERS

Enneaploid collections ($2n=63$) were found in Greenland and New Hampshire. SØRENSEN gives the number $2n=63$ in his original description of *Hierochloë orthantha* (1954 p. 7); cf. also JØRGENSEN, SØRENSEN & WESTERGAARD 1958 p. 12). Collections likely to be referable to *H. alpina* ssp. *orthantha* but of which I have not seen voucher specimens were reported to be enneaploid from New Hampshire (LÖVE & LÖVE in LÖVE & SOLBRIG 1964 p. 201; LÖVE & LÖVE 1966 p. 18), all as being *H. monticola.*

An octoploid collection ($2n=56$) was reported under the name *Hierochloë alpina* from New York by BOWDEN (1960 p. 551; Whiteface Mountain, W. G. DORE s.n. near DORE 14270 17.6. 1953, DAO 44315). Morphologically the specimens are typical *H. alpina* ssp. *orthantha.* A re-count would be highly desirable, but cannot be made from the original slide because of cytotechnical difficulties (R. J. MOORE in sched.).

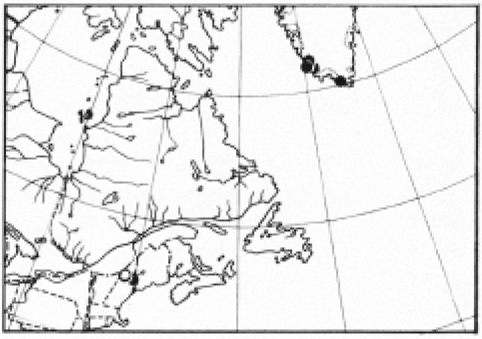


Fig. 26. *Hierochloë alpina* ssp. *orthantha.* Localities of cultivated material. Dots: $2n=63$. Circle: deviating number.

One collection of morphologically typical *Hierochloë alpina* ssp. *orthantha* grown from caryopses from Mount Washington, New Hampshire (A K F) has $2n=58$. Whether this chromosome number is actually found in plants growing under natural conditions or represents a mere aberration is not known.

The localities where the samples were collected for cultivation in this investigation are shown in Fig. 26 and listed on p. 173. Fig. 28 *A* and *B* (p. 167) shows mitotic metaphase plates.

REPRODUCTION

The enneaploid collections A K D, B F B, B F D, B F F, B F M, B F N, B F O, B F P, and B F R all formed unreduced embryo-sacs of the Hieracium type (WEIMARCK 1967 b, 1970 c p. 501). Unreduced embryo-sacs of the Antennaria type and reduced embryo-sacs of the Polygonum type possibly occurred in some cases. Female meiosis was rare and irregular. Male meiosis was badly disturbed or wholly abortive. Germination capacity was not tested.

Population structure was not studied chromatographically.

VARIATION

The variation range of the number of nodes and spikelets per panicle under natural conditions (Fig. 24 *B* p. 161) is greater than that in *Hierochloë alpina* ssp. *alpina*. The values are generally somewhat higher.

Spikelets with four florets or with a tendency to proliferation were not seen. A few cases of late flowering were observed in the cultivated material but these were not accompanied by quite as typical morphological modifications as seen in other taxa treated.

Morphological variation in the herbarium material studied from North-east North America is considerable with regard to characteristics used for distinguishing between the subspecies. Several specimens are almost intermediate. The morphological and cytological variation found here together indicate that the reproductive barriers between *Hierochloë alpina* ssp. *alpina* and ssp. *orthantha* may not be quite absolute. The stable chromosome number 2n=63 in all other collections recorded indicates on the other hand that *H. alpina* ssp. *orthantha* should be obligately apomictic.

The herbarium collections from Alaska and the Bering Strait region present a severe problem. All available morphological information supports the inclusion of some of them in *Hierochloë alpina* ssp. *orthantha* (An der Beringsstrasse: Luetke-Hafen 7—10.8. 1881 A. & A. Krause no. 187, UPS; Alaska: St. Mathew Island 26.7. 1944 F. L. Beals no. 274, DAO 44164; Alaska: Kodiak Island 28.6. 1939 E. H. & H. B. Looff no. 1013, DAO 44166; Alaska: Kodiak Island 30.6. 1962 E. Hultén, S; Alaska: Juneau 7.9. 1932 E. Hultén, S; Alaska, Mount Roberts 26.7. 1925 J. P. Anderson no. 225, S). Others are intermediate between *H. alpina* ssp. *alpina* and ssp. *orthantha* (Alaska: St. Lawrence Island .8. 1933 O. W. Geist, CAN 253104; Alaska: Point Barrow 20.7. 1950 J. H. Thomas no. 2063, GH). A grouping of this material together with the North-east American *H. alpina* ssp. *orthantha* yields a geographical pattern difficult to explain and, as far as I know, unparalleled (Hultén 1968 and pers. comm.). A mistake as to the labelling of the specimens seems extremely improbable, and the subspecies is with almost absolute certainty not either introduced, the type of localities taken into consideration. Another possibility is that there is in Alaska and adjacent territories another line of variation in *Hierochloë alpina* parallel to the line of variation represented by ssp. *orthantha*. Unfortunately, there are no cytological or other complementary data for such specimens. A special investigation of the variation in the region is badly needed. In the absence of more detailed information, I have found it necessary to include at the time the plants with straight, untwisted awn, more elongated rhizome internodes, etc., provisionally in *H. alpina* ssp. *orthantha*. This subspecies is thereby possibly somewhat heterogeneous from a phyletic point of view.

An origin of *Hierochloë alpina ssp. orthantha*, as it is defined here, within or close to *H. alpina* ssp. *alpina* seems highly plausible. *H. alpina* can thus to a certain extent be regarded as a parallel to *H. odorata* as to its taxonomic structure. The variation pattern in Alaska and the Bering Strait region, which lies outside the area

Fig. 27. Mitotic metaphase plates. — *A: Hierochloë australis*, collection A K B (Finland, Regio aboënsis), 2n=14. — *B: H. odorata* ssp. *odorata*, collection A O A (The Netherlands), 2n=28. — *C: H. odorata* ssp. *baltica*, collection A E U (Sweden, Västergötland), 2n=42. — *D: H. hirta* ssp. *hirta*, collection A G O (Sweden, Dalarna), 2n=56. — *E: H. hirta* ssp. *arctica*, collection A T O (Sweden, Torne Lappmark), 2n=56. — *F: H. repens*, collection B C D (Czechoslovakia), 2n=28+2 B (indicated by arrows). — *G: H. alpina* ssp. *alpina*, collection B F U (Greenland), 2n=56. — Squash preparation. ×1500.

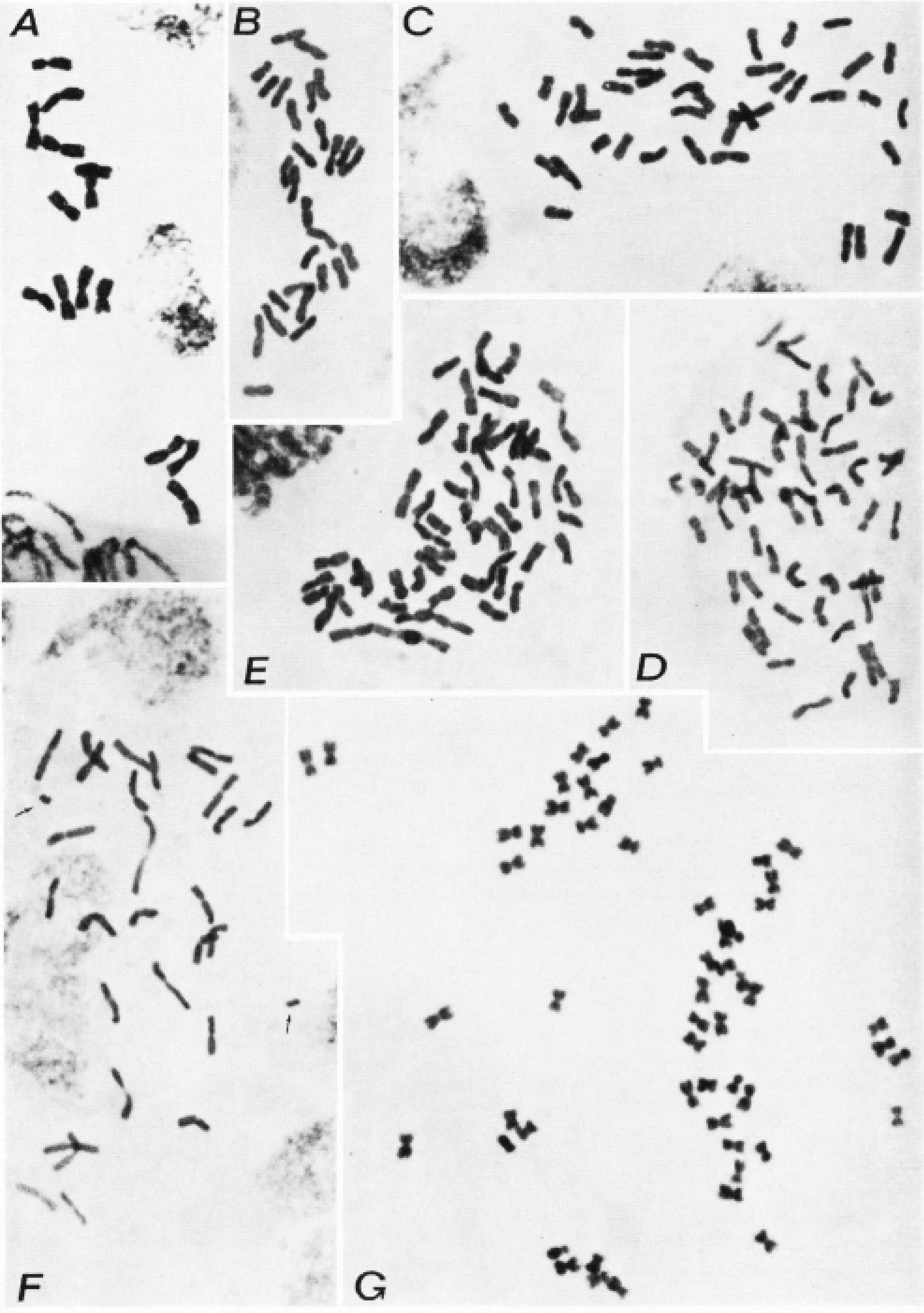


Fig. 27.

of the more intensive investigation, is still very incompletely known.

The two members of the *Hierochloë alpina* complex, although usually easily distinguishable, are in certain regions linked together. Geographically they are not completely isolated, perhaps not reproductively either. Thus it is reasonable to treat them as subspecies.

SUMMARY AND DISCUSSION

The taxa treated form three distinct groups. The most complicated of these is the *Hierochloë odorata* complex, whose members show closer affinities among themselves than they do to *H. australis* and the *H. alpina* complex. Evolutionary trends are often difficult or impossible to interpret. *H. odorata* ssp. *baltica* has, however, probably originated from certain ssp. *odorata* types. It is also reasonable to assume that *H. alpina* ssp. *orthantha* has been differentiated from ssp. *alpina*. In some characteristics such as panicle density and bristle form *H. repens,* which occupies a fairly peripheral position in the *H. odorata* complex, seems to connect other members of the *odorata* complex discussed with the Asiatic species *H. glabra* not dealt with here. *H. hirta* ssp. *hirta* and ssp. *arctica* are grouped together more for practical and phenetic reasons than out of phyletic considerations. They are perhaps but indirectly related to each other.

The pattern of differentiation is complicated by the facultative or (at least almost) obligate apomixis found in most taxa studied. The apomictic potentiality has caused an upset of reproductive balance. The low germinating capacity of caryopses found is in all likelihood a consequence thereof. All taxa are perennials, and especially the members of the *Hierochloë odorata* complex are likely to form long-lived clones by rhizomes, a matter which should be seen in connexion with the disturbed generative reproduction.

The occurrence of a long polyploid series and some additional aneuploids within the groups should also be related to apomixis and the perennial habit. One almost certain example of a sudden raise of polyploid level due to reproductive unbalance was recorded in the cultivated material, and such spontaneous polyploidization in the past, combined with hybridization or not, is most likely to have initiated much of the variation met with to-day.

Gene combinations can thus have been completely or partly fixed in certain biotypes. However, the genetic system operating in *Hierochloë* has obviously not resulted in such a polymorphism as that recorded in certain apomictic *Taraxacum, Hieracium, Rubus, Ranunculus,* and *Poa,* for example. On the contrary, it has given rise to a relatively small number of taxa which are sufficiently closely connected to form distinct groups. The taxa are separated by small but usually reliable diagnostic characteristics and have areas of distribution comparable with such ones of normal amphimictic plants.

ACKNOWLEDGEMENTS

Much advice and valuable criticism has been given by the head of the Institute, Prof. H. RUNEMARK, by Dr R. DAHLGREN, and by other teachers and colleagues. The Directors and Keepers of the Herbaria sending material on loan, have also given much valuable information and advice on request. The Directors of the Herbaria in Copenhagen, Lund, and Munich have kindly permitted me to take leaf fragments for chromatography. I am also very grateful for the valuable help given by all those who have collected material for cultivation, and those who have participated in the field work. In the latter respect by far the most indispensable assistance was given by my wife, who has also in many other ways facilitated my work. Of the technical staff I want to mention especially Mrs I. LARSSON and Miss W. PIEKARSKA. Mrs M. PETERSSON checked the manuscript.

The work was made possible by grants from Knut and Alice Wallenbergs Stiftelse, Kungl. Fysiografiska Sällskapet i Lund, Kungl. Vetenskapsakademien, and Lunds Universitet.

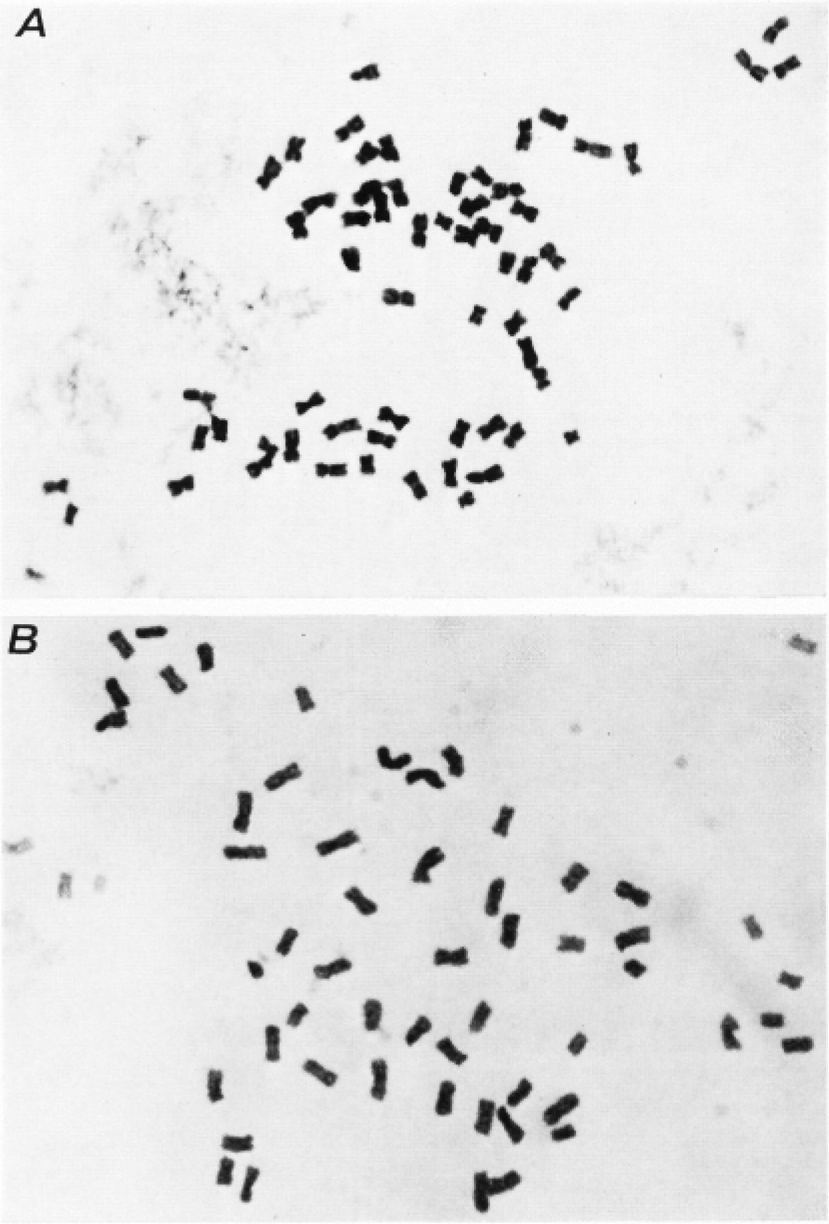


Fig. 28. Mitotic metaphase plates. — *A: Hierochloë alpina* ssp. *orthantha,* collection A K D (USA, New Hampshire), $2n=63$. — *B: H. alpina* ssp. *orthantha,* collection A K F (USA, New Hampshire), $2n=58$. — Squash preparation. ×1500.

Appendix. Localities of cultivated material

Collections by the author unless otherwise stated.

Hierochloë australis (Schrader) Roemer & Schultes, 2n = 14

FINLAND. Regio aboënsis. Karjalohja. Karkalinniemi, dryish esker slope (P. Siltanen): A D G. — Paimio. Hääsvuori, dry morain soil on slope (I. Kukkonen): A K B. — Vihti. Irjala, Varesmäki (J. Jalas): A P R. — Hyvinkää. The lake, Kytäjärvi, c. 2000 m N, in coniferous forest: B A B. — Tavastia australis. Hollola. Hahmajärvi, Rautakorpi, southerly slope in dry forest (J. Puro): A H T. — Hollola. Isosaari, in pine and birch forest: A X L. — Tyrväntö. Lepaa Puutarhaopisto c. 500 m SE, dry esker slope in mixed forest: B A D. — Nylandia. Sibbo. Östersundom, mixed forest opposite Katriholmen, among boulders: A X S. — Esbo. Along W side of Kyrkvägen, mixed forest: A X T.

AUSTRIA. Steiermark. Grazer Bergland. Gsoller Kogel, c. 600 m s m, limestone (F. Widder): A D D.

GERMANY. Bayern. Weltenburg. Donaudurchbruch (H. Merxmüller): A E K.

ITALY. Höhlensteintal. Landro, steep easterly slope, c. 1420 m s m: B B A.

ROMANIA. Cluj. Aghires (K. Brunsberg): B B C.

Hierochloë odorata (L.) Wahlenb. ssp. **odorata,** 2n = 28

NORWAY. Finnmark. Vardö. Bussesund, near Svartnes ferry, sand: A U F. — Vardö. Komagvær, on the north bank of Komagelven: A U E. — Nord-Varanger. Skallelven, the bridge c. 1600 m NE, meadow: A U D. — Alta. Rafsbotn, close to the shore, among bushes: A U C. — Talvik. Jansnes, on the shore: A U S. — Troms. Nordreisa. Oksfjorden, Lerbugt, meadow with bushes near road: A T X. — Tromsö. Between Sandvika and Ramfjordnes, shore meadow: A T K. — Tromsö. Tromsdalen, slope on the south bank of Tromsdalselva: A T I. — Tromsö. Near north limit of built-up area, fen: A T H. — Balsfjord. Nederli, near south-west part of Sagelvvand: A T G. — Målselv. North-west slope of Alap, fen: A T E. — Målselv. Between Myre and Lundnes, near the brook, Maukbekken, wet slope: A T C. — Målselv. Berg, slope near the river, Målselven: A T B. — Salangen. Between Höglund and Bekkebotn, near the lakes, Småvatna, fen: A T A. — Salangen. Close to A T A, fen and road-side: A S X. — Salangen. Löksebotn, shore of Löksefjord: A S U. — Salangen. Lavangseidet farm c. 1000 m SW, road-side: A S T. — Lavangen. Spansdalen, fen near road: A S S. — Lavangen. Sölvfjeldet c. 4000 m S, along brook from Höitind: A S R. — Nordland. Ankenes. Gratangseidet, the boundary of Troms c. 500 m SW, wet slope: A S P. — Fauske. Vargåsmyren, fen near road: A S O. — Bodin. The church c. 200 m SSW, meadow close to brook: A S N. — Fauske: Valnesfjord, by brook near bridge: A S M. — Fauske. Finneid, gravelly slope near road: A S L. — Saltdal. Rognan, near south part of the lake, Fiskvågvand, fen: A S K. — Saltdal. Junkerdal, Stornesmoen c. 600 m E, open pine wood: A S I. — Saltdal. Junkerdalen, Gamfossbrua c. 1000 m ESE, road-side and fen: A S H. — Saltdal. Junkerdalen, meadow near brook Solvågbekk: A S G. — Nord-Rana. Mouth of the river, Gubbeltåen c. 1000 m SW, meadow near road: A S F. — Nord-Rana. Mouth of brook from Laplien in the river, Rana elv, sandy hill: A S E. — Korgen. Kongsdalen, Lillemoen c. 1000 m NW, wet forest: A S D. — Hattfjelldal. Kongsdalen, by brook from north slope of Jörentind, fen: A S C. — Korgen. Kongsdalen, Svartvasmoen c. 1100 m ENE, by brook from Mount Jörentind, fen: A S B. — Vefsn. Angermoen, road-side near brook from Blåfjeldet: A S A. — Nord-Tröndelag. Namsskogan. The road to Björnstad station c. 2000 m SW, on the north-west bank of Namsen: A R X. — Grong. Formo, south limit of built-up area c. 1500 m S, fen: A R U. — Nordli. Eidet, between the lakes Sandsjöen and Laksjöen, edge of field: A R T. — Nordli. Storeng c. 1500 m ESE, slope of Spjetfjeldet, among recently planted spruce: A R S. — Snåsa. Jörstad, between station and Finsås, fen: A R R. — Stiklestad. Verdal, Myren c. 800 m NNW, along railway: A R P. — Sör-Tröndelag. Stören. Skjerli, near road to Snöan station, road-side: A R O. — Budal. Storrödseter c. 150 m W, fen: A R N. — Soknedal. Garli, near the mouth of the river, Garåen, gravelly slope: A R M. — Oppdal. Lönset, Gravaune c. 250 m W, in slope among boulders: A R L. — Möre og Romsdal. Sunndal. Grödalen, Vangene c. 1500 m SE, wet slope: A R K. — Oppland. Fåberg. Bleken seter c. 1000 m SSE, close to north-west part of Lake Lonka, fen: A R E. — Fåberg, near A R E, fen: A R D. — Hedmark. Löten. Kvernhuslökka c. 2400 m NW, near the Nordby-Olseter cross-roads, among bushes: A R C. — Oslo. Bygdöy, on the shore of Frognerkilen near Seterhytten: A R A. — Akershus. Asker, Hval, near Hvalstrand, stony shore: A P X. — Östfold. Råde. Tom c. 1000 m ESE, among bushes along track: A P U. — Borge. On the shore of Hunnebunden, in bank of seaweed: A P T.

SWEDEN. Lule Lappmark. Kvikkjokk. On the shore of the lake, Tarraure, near Tarrekaise mountain hut, in Salix thickets:

A N A. — Kvikkjokk. Between Kvikkjokk and Tarrekaise mountain hut, Passeuksa c. 1500 m SSE, open birch forest: A N B. — Kvikkjokk. Between Kvikkjokk and Tarrekaise mountain hut, Bäcken c. 1000 m ESE, margins of spruce and birch forest: A N D. — Kvikkjokk. The chapel c. 500 m SSW, in margins of Salix thickets: A N E. — Lycksele Lappmark. Tärna. Above tree-line, slope near the brook, Västra Syterbäcken: A M O. — Tärna. Near A M O, in Salix thickets: A M P. — Tärna. Near A M O, tree-line, along brook: A M R. — Jämtland. Åre. Mount Åreskutan, Blåsten c. 1500 m NE, among Salix along brook: A M E. — Åre. Mount Åreskutan, Totthummeln c. 1200 m N, gravelly slope: A M H. — Enafors. On the bank of Enan near bridge, in Salix thickets: A M I. — Storlien. The station c. 800 m NNW, in open birch forest: A M K. — Storlien. Skurdalshöjden, Bånggården c. 900 m SE, among Salix and Betula shrubs: A M L. — Härjedalen. Ljungdalen. Mount Jelgatsåive, slope towards Mount Helags (O. Hedberg): A D A. — Ljungdalen. Kesudalen tourist station c. 1000 m E, wet slope: A L S. — Ljungdalen. Kesudalen tourist station c. 1000 m S, mountain heath land: A L T. — Ljungdalen. Kesudalen tourist station c. 1500 m W, wet slope, tree-line: A L U. — Ljungdalen. Kesudalen huts c. 200 m S, along brook: A L X. — Tännäs. Along brook from the lakes, Ösjöarna, wet slope: A L N. — Tännäs. Ramundberget tourist station c. 400 m NE, on the bank of Ljusnan: A L O. — Dalsland. Bäcke. Hjulsrud c. 500 m S, close to the river, Teåkersälven: A G T. — Bohuslän. Skee. Stene schoolhouse c. 500 m NW, fen in forest margin: A G U. — Tanum. Mjölkeröd c. 1200 m S, fen: A G X. — Stala. Tjuvekilen c. 800 m NNE, in scrub margin: A H B. — Röra. Dandal c. 1000 m SW, road ditch: A H A. — Torsby. The island, Stora Trälen, north shore, meadow: A E R. — Ytterby. Old church c. 400 m NE, fen: A E P. — Ytterby, Near Marstrand-Rollsbo cross-roads, fen (H. Andersson): A O C. — Kungälv. Fridhem c. 700 m NE, fen with bushes: A E O. — Säve. Grimås, fen on landward side of Ragnhildsholmen: A E N. — Västergötland. Medelplana. Axvall c. 400 m W, wet forest: A H K. — Gökhem. Marka church c. 1600 m W, moist meadow: A H C. — Luttra. Sköttning 600 m NW, wet meadow: A H D. — Åsle. Fårdala 600 m WSW, fen: A H G. — Friggeråker. Marjarp, Bäckebo c. 1500 m S, wet meadow with Salix shrubs: A H H. — Nödinge. The station c. 500 m NNW, in Phragmites: A E S. — Halland. Vallda. Sandön, Keholmen, shore: A E M. — Ölmevalla. Vindö Island, northern part, fen: A E L. — Skåne. Hov. Between Norrviken and Kattvik, road-side: A F G. — Källna. Källna farm c. 100 m W, small wood near brook: B C B. — Kropp. St. Ljungberg c. 500 m SSE, fen: A F F. — V. Sönnarslöv. Wet slope near the brook, Längstebäcken: A A T. — Kågeröd. The church c. 400 m NW, fen: A A S. — Kågeröd. Knutstorp castle c. 700 m ENE, fen: A E F. — Kågeröd. The station c. 600 m NW, moist meadow: A E G. — Kågeröd. Simmelsberga c. 600 m ENE, road-side: A E H. — Torrlösa. Trolleholm castle c. 1000 m N, fen: A E E. — Bosjökloster. The cemetery c. 900 m N, forest margin along ditch: A P S. — Hällestad. Skrivaremöllan c. 500 m ENE, along brook: B B D. — N. Nöbbelöv. The church c. 700 m WSW, moist meadow: A K P. — Östraby. Bromölla c. 300 m E, along brook (G. Mattiasson): B A G. — N. Åsum. Skönabäck c. 300 m NNW, edge of fen in shrubs: B D O. — Kivik. The built-up area c. 800 m S, between boulders on shore: B D P.

DENMARK. Sjælland. København. Raadvad knivefabrik c. 400 m NW, meadow: B D L. — Roskilde. Between parts of St. Hans' Hospital, near brook: B D K. — Slots Bjærgby. Vårby farm c. 400 m NE, meadow: B D H. — Møn. Damsholte. Askeby farm c. 1500 m NW, along ditch in margin of the former lake, Røddinge Sø: B D I. — Fyn. Hårby. Løgismose castle c. 1500 m S, shore meadow at the edge of forest: B D G. — Jylland. Astrup. Enggården c. 500 m W, in ditch along railway: B C T. — Nibe. Sebbersund, along ditch in shore meadow: B C S. — Gimming. Tjærby, edge of pasture: B C R. — Braband. Gellerup c. 1000 m W, on shore of the lake, Braband Sø: B C O. — Beder. Fløjstrup Strand, sandy shore: B C P. — Tømmerby. The church c. 700 m E, meadow: B C U. — He. East part of bridge Agersbæk—Hindø c. 500 m S, meadow: B C X. — Velling. The church c. 200 m N, shore meadow: B D A. — Tarm. Sønderbro c. 500 m S, meadow: B D B. — Vejle. Munkebjærg station c. 500 m NE, sandy shore: B D F. — Løjt. The church c. 4500 m NNE, sandy shore of Genner Bugt: B D E. — Tønder. Højer 2 km E, near river (B. Nordenstam): B B B. — Højer. The built-up area c. 1500 m E, near river: B D C. — Gråsten (S. Lægaard): B C N. — Gråsten. The castle c. 700 m WSW, isthmus between lakes: B D D.

THE NETHERLANDS. Molenpolder, bo.; (E. Kliphuis): A D C. — Kamerbeekse Nessen (E. E. van der Voo): A K L, A O B. — Hoogmade (J. H. Kern & C. G. G. J. van Steenis): A O A.

IRELAND. Lough Neagh; cult. in Leicester (T. G. Tutin): A H P.

CANADA. Quebec. Kamouraska. Ste Anne-de-la-Pocatière, brackish tidal marsh; cult.

in Ottawa (W. G. Dore & al. 17294): A D E. — Shore of River Ouelle, pasture (M. Raymond & al.): A D I. — Montreal (cult?): A K G.

Hierochloë odorata (L.) Wahlenb. ssp. **odorata,** 2n=42

SWEDEN. Västergötland. Kälvene. The church c. 1200 m NW, swampy meadow: A H E. — Skörstorp. Skarpås c. 700 m ESE, meadow and edges of forests: A H F. — Hössna. Oset, fen: A E T. — Tranemo. Limmared station c. 1100 m SSW, road-side: A F D. — Tranemo. Former Uddebo station c. 800 m SW, moist meadow: A F E. — Småland. Norra Ljunga. The fen Bruusekärret (S. Gustafsson): B G R. — Nässjö. North-west part of lake, Gisshultsjön c. 200 m NW, pasture with bushes: B E A.

GERMANY. Brandenburg. Berlin. Lieper Bucht c. 1000 m S, bank of Havel (G. Wagenitz): B E X.

SCHWEIZ. Valais. Lake Tanay, pasture, 1410 m s m (C. Favarger): A O D.

NORWAY. Troms. Överbygd. Skjold cross-roads c. 1000 m SW, wet depression: A T F.

Hierochloë odorata (L.) Wahlenb. ssp. **baltica** G. Weim., 2n=42

SWEDEN. Ångermanland. Anundsjö. The church c. 300 m E, along ditch near track: B D X. — Nordingrå. Shore of sound opposite the island Långsön: A N I. — Härnösand. Island Härnön, Specksta c. 200 m NE, along ditches in fields: A N K. — Medelpad. Alnö. Stornäset, wet forest near shore: A N L. — Jämtland. Åre, Mount Åreskutan, Blåsten c. 2000 m SE, among Salix thickets: A M G. — Åre. Blåsten c. 2000 m ENE, snow-bed: A M F. — Frösö. Along brook to north part of the lake, Ändsjön, wet forest: A M C. — Sunne. Vällviken, birch forest: A M D. — Berg. Shore of the lake, Storsjön at the foot of Hoverberget, among Salix shrubs: A M A. — Gästrikland. Hamrånge. Axmarshamn c. 100 m SW, shore meadow: A N U. — Gävle. Tolvfors estate c. 1400 m NNW, at the brook, Tolvforsbäcken: A L B. — Västmanland. Haraker. Svanå station c. 400 m WNW, along ditch in field: A G L. — Uppland. Älvkarleby. The church c. 2500 m WSW, near floating-way: A K X. — Tärnsjö. At Ingbo well (O. Hedberg): A K T. — Östhammar. Boda c. 400 m NNW, shore meadow: A G F. — Öregrund. Ängsholmen c. 1100 m NNW, wet meadow close to small lake: A G G. — Bälinge. Fallet 100 m W, road-side: A F O. — Funbo. East side of the lake, Gorrsjön, fen: A F R. — Almunge. North-east part of the lake, Lötsjön c. 100 m E, fen: A F S. — Fasterna. Ålderskogen c. 1300 m SSE, wet meadow and edges of forest: A F T. — Rimbo. West shore of the lake, Långsjön, in Phragmites: A F U. — Frötuna. The lake Månsjön c. 200 m S, road-side: A F X. — Länna. Hysingsvik pier c. 200 m NW, shore meadow: A G A. — Söderby-Karl. At north part of Rådasjön, pasture: A G B. — Väddö. Flottskär, Brevik c. 300 m E, shore: A G C. — Väddö. Wet meadow (O. Hedberg): B A X. — Dannemora. The station c. 900 m SW, moist birch forest: A G D. — Film. The river between lakes Filmsjön and Gruvsjön c. 200 m S, meadow near road: A G E. — Börstil. Near north-west part of Granfjärden, fen: A G H. — Vittinge. The brick works c. 200 m SSE, fen, along brook: A G I. — Västerlöfsta. On north-east shore of the lake, Vansjön: A G K. — Uppsala-Näs. Sätrasjön; cult. in Uppsala: A D H. — Uppsala-Näs. Björnarbo c. 400 m S, along ditch in edge of forest near the lake, Sätrasjön: A F P. — Stockholm. Near Fiskartorpsvägen, moist slope close to Phragmites: A F H. — Södermanland. Nacka. St. Nyckelviken, fen: A F M. — Dalarö. Sandemar c. 1500 m NE, fen: A F K. — Södertälje. Between Vasa and ihe lake, Måsnaren, fen: A F N. — Torö. Storudden, the church c. 1800 m NW, along ditch: A F L. — Trosa. The church c. 600 m SSW, shore meadow: A H N. — Svärta. Nystugan c. 150 m SE, drained peat: A H O. — Östergötland. Kvillinge. Loddby factory, shore meadow (G. Tyler): A P P. — Västergötland. Hällstad. Between Väby and the lake, Bredsjön, along ditch and on shore: A F A. — Dalum. Silarp, c. 800 m S, along brook near road: A F B. — Kölaby. The church c. 1000 m SSE, moist slope near brook: A F C. — Brunn. The church c. 400 m SSW, wet slope: A E U. — S. Ving. Säby c. 1000 m WNW, sandy shore of Lake Mogden: A E X. — Småland. Frinnaryd. North shore of Lake Söljen, gravel: B B E.

FINLAND. Satakunta. Eura. By east part of the lake, Turajärvi, along river near watermill: B A F. — Regio aboënsis. Piikiö. The island, Jauhosaari, shore meadow (N. Tarén): A H S. — Nylandia. Helsinki. Herttuniemi, ruderal shore meadow: A X P. — Sibbo. Östersundom, opposite Björnö, shore meadow: A X R. — Ingå. The church c. 400 m SE, ruderal shore meadow in Phragmites: A X U. — Pyhäjärvi. Haavisto, by east part of the lake, Pursilanjärvi, shore meadow: B A A.

Hierochloë hirta (Schrank) Borbás ssp. **hirta,** 2n=56

NORWAY. Hedmark. Nes. Nedre Gjestvang c. 1200 m WSW, sandy shore of Lake Mjösa: A R B.

SWEDEN. Medelpad. Stöde. The church c. 50 m S, near the river, Ljungan: ANM. — Torp. Near Getterån station, on bank of Ljungan: ANN. — Hälsingland. Ljusdal. North shore of the lake, Borrsjön, gravel: ANP. — Dalarna. Mora. Mora Noret, gravelly shore of Lake Siljan: ALH. — Leksand. Åkerö c. 600 m SSW, shore of Lake Siljan, at edge of pine forest: ALF. — Borlänge. Mjälga, edge of pond: ALD. — Gagnef. Bäsna. Near northern shore of the lake, Hemtjärn, meadow: AGO. — Gagnef. Close to AGO: ALE. — Torsång. Tylla, bank of Dalälven near bridge: AGN. — Gustafs. Boberg, bank of Dalälven: AGM. — Svärdsjö. Borgärdet, meadow near northern shore of the lake, Säckan: ALC. — Värmland. Övre Ullerud. The church c. 1000 m W, sandy hill near the river, Klarälven: AGS. — Uppland. Älvkarleby. The church c. 1000 m W, sandy bank of Dalälven: AKU. — Älvkarleby. Skutskär chapel c. 1300 m E, dry slope near track: ALA. — Närke. Ringkarleby. Myrö c. 250 m SSE, along ditch between field and forest: AHL. — Lillkyrka. Sjölunda c. 500 m SW, along ditch: AHM.

FINLAND. Savonia borealis. Nilsiä. Tiirinlahti, road-side: AXD. — Kuopio. Between Pitkälahti and Lamperila, road-side: AXE. — Joroinen. Järvikylä c. 300 m SE, gravelly slope near road: AXF. — Regio aboënsis. Vihti. Koikkala c. 150 m S, sandy shore of the lake, Hidenvesi: AXX. — Tavastia australis. Tyrväntö. Lepaa Puutarhaopisto c. 500 m NNW, shore meadow: BAC.

Hierochloë hirta (Schrank) Borbás ssp. **arctica** (Presl) G. Weim., $2n=56$

NORWAY. Troms. Kvænangen. Mount Riddovarre c. 4000 m SE, edge of fen: AUA. — Nordreisa. S. Sandnes c. 1000 m S, northwest slope of mount Fatavarre, by brook: ATU. — Sör-Tröndelag. Oppdal. Stölan station c. 300 m NE, among bushes in sandy island in river Driva: ARI. — Oppdal. Vårstigen, Skåkbäcken c. 100 m S, close to track: ARH. — Oppland. Vågå. Sendnes c. 500 m ESE, near the lake, Vågåvatn, sandy point: ARG. — Fåberg. Jörstadmoen, Kastrud cross-roads c. 200 m E, edge of field below slope: ARF.

SWEDEN. Torne Lappmark. Jukkasjärvi. Låktatjåkka station c. 500 m S, mountain slope: AAH. — Jukkasjärvi. Kärkevagge: AAR. — Jukkasjärvi. Kärkevagge, near Slåttatjåkko (H. Weimarck): ACG. — Jukkasjärvi. Låktatjåkko near Kopparåsen station (O. Hedberg): ACT. — Jukkasjärvi. Låktavagge (O. Hedberg): ACU. — Jukkasjärvi. Katterjåkk station c. 1000 m SE, edges of fen, and snow-beds (M. Sonesson): ACO. — Jukkasjärvi. Holmajärvi. Along brook in fen: BBF. — Vittangi. Saarikoski, moist bank of Vittangiälven: ABF. — Vittangi. Close to ABF: ATP. — Vittangi. The church c. 300 m E, shore of the lake, Julkathenjärvi: ABC. — Vittangi. The church c. 700 m E, shore of the lake, Julkathenjärvi: ATO. — Lule Lappmark. Gällivare. By rapids near the lake, Moskojärvi (O. Hedberg): AKS. — Kvikkjokk. Near Pårek mountain hut, moist slope (O. Hedberg): AKR. — Kvikkjokk. Njunjes farms c. 2000 m W, open birch forest: ANC. — Pite Lappmark. Arvidsjaur. Trollforsen station c. 3000 m NNE, sandy bank of Piteälven: AMX. — Arjeplog. Aspnäs c. 300 m SE, along brook: AMU. — Arvidsjaur. Sotträskliden c. 1000 m S, peaty mire near lake: AMT. — Lycksele Lappmark. Sorsele. Råstrand, bank of Vindelälven: AMS. — Norrbotten. Överkalix. Near bridge to Hedensbyn, bank of Kalix älv, among bushes: ATR. — Edefors. Övre Svartlå, bank of Flarkån: ANF. — Nederluleå. S. Sunderbyn, Näset, road-side and meadow: ANG. — Västerbotten. Bygdeå. Robertsfors c. 5000 m NW, shore meadow near the river, Rickleån: ANH. — Jämtland. Frostviken. Brattlidfjället c. 4000 m SE, road-side: AMN. — Frostviken. Vågen, road-side: AMM. — Revsund. Stavre, shore of the lake, Revsundssjön: AMB. — Härjedalen. Tännäs. Flon c. 2000 m NW, small sandy island in the river, Ljusnan: ALP. — Funäsdalen. Northerly slope of Vättafjället (O. Hedberg): ACX. — Funäsdalen. Southerly slope of Hamrafjället (O. Hedberg): ACS. — Högvålen c. 6000 m S, along brook (O. Hedberg): ACR. — Ångermanland. Gottne. Gottne huts, edge of mire near road (M. Sonesson): ACP. — Medelpad. Attmar. The church c. 600 m NNE, shore meadow at lake Marmen: ANO. — Hälsingland. Arbrå. Forneby, the school-house c. 1000 m W, along brook: ANS. — Alfta. Bank of Voxnan: ANT. — Dalarna. Särna. Near Gammelgården, sandy slope by the lake, Särnasjön: ALL. — Särna. The railway yard: ALM. — Älvdalen. The station c. 200 m S, near ditch: ALK. — Orsa. Bäcka c. 600 m SSW, sandy shore of the lake, Orsasjön: ALI. — Rättvik. Hedslund c. 900 m ESE, sandy hill near the river, Enån: ALG. — Ludvika. Håksberg station c. 1100 m SSE, shore of Lake Övre Hillen: AGR. — Norrbärke. Near the sound between Lilla Snöån and Sundet, among bushes: AGP.

FINLAND. Lapponia enontekensis. Enontekiö. Ala Saarikoski, close to River

Könkämä, meadow in birch forest: A A U. — Enontekiö. Near A A U; A T N. — Lapponia inarensis. Utsjoki. Kevo Subarctic Research Station c. 700 m WSW, meadow on gravelly hill; A U G. — Utsjoki. Along the brook, Tshieskutjoki east of road, birch forest: A U I. — Utsjoki. Along the brook, Iivvanashjoki, east of road, meadow: A U H. — Inari. South part of the lake, Solojärvi, along brook and in fen: A U K. — Ivalo. The hospital c. 200 m SW, among bushes on bank: A U L. — Lapponia kemensis. Sodankylä. Rovala c. 1000 m E, on the north-east shore of the lake, Orajärvi, peat-bog: A U M. — Pelkosenniemi. The cross-roads Kemijärvi—Savukoski c. 1000 m N, close to bridge near the river, Kemijoki, in Salix thickets; A U N. — Rovaniemi. The church c. 1500 m SSW, sandy bank of the river, Kemijoki: A U O. — Ostrobottnia borealis. Kemi. The Kemijoki bridge c. 100 m SW, in gravel among bushes: A U P. — Oulu. Toppila, cross-roads, along ditch: A U R. — Oulujoki. Pikkarala ferry c. 700 m SW, road-side: A U S. — Ostrobottnia kajanensis. Puolanka. Lehto c. 1300 m W, wet meadow along path: A U T. — Ristijärvi. The church c. 1500 m ESE, along ditch in peat: A U X. — Hyrynsalmi. The church c. 2000 m NE, shore of the bay, Haukilahti; A X A. — Hyrynsalmi. On north shore of the lake, Mikitänjärvi, pasture: A X B. — Karelia borealis. Rautavaara. Nikinmäki, road-side; A X C. — Karelia australis. Miehikkälä. Purho, near north part of the former lake, Mustajärvi, edge of field: A X I. — Savonia australis. Hirvensalmi. Mäntyniemi, moist meadow along road-side (A. Vaarama): A H R. — Mikkeli. Northern shore of Lake Hietanen, sand: A X G. — Valkeala. Harju station c. 1500 m NNE, on railway bank and bank of river near bridge: A X K. — Lappeenranta. The town c. 2000 m E, road-side: A X H. — Tavastia australis. Tyrväntö. Lepaa Puutarhaopisto c. 400 m SE, along ditch near track; B A E. — Hollola. Kukkila, bridge to Isosaari c. 300 m E, edge of field: A X M. — Lammi: A D K. — Nylandia. Mäntsälä. Hirvihaara, Lainela c. 300 m SW, in peat along ditch: A X N. — Mäntsälä. The church c. 800 m S, along brook and in edge of field: A X O.

CANADA. Ontario. Carleton, gravelly flood-bank of Rideau River above Billings Bridge (W. G. Dore, DAO 14218): A D F.

USA. Minnesota. Kittson, Halma c. 5000 m N, wet meadow (J. W. Moore): A K A. — New Hampshire. Mount Washington, Tuckerman's Ravine (E. Kjellqvist): A K E.

Hierochloë hirta (Schrank) Borbás ssp. **arctica** (Presl) G. Weim., 2n=c. 84.

USA. Minnesota. Grown from caryopses of A K A; 1 specimen: A K K (3 specimens 2n=56).

Hierochloë hirta (Schrank) Borbás ssp. **arctica** (Presl) G. Weim., 2n=70.

CANADA. Quebec. Fort Chimo, sandy bank of river (O. Hedberg): A D B.

Hierochloë repens (Host) Simonkai, 2n=28.

ROMANIA. Iaşi, Valea lui David (C. Burduja): B C C. — Dobrudja, Babadag, Poiana "Calul Mort" (C. Burduja); B D S.

Hierochloë repens (Host) Simonkai, 2n=28 +2B.

CZECHOSLOVAKIA. Senica, near Borský Mikuláš along road to Šáštín, in sand (J. Vicherek); B C D.

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **alpina,** 2n=56.

ASIATIC RUSSIA. Taimyr: B E K.

GREENLAND. Nugssuaq peninsula, Sarqaq valley (G. Bengtsson): B H H. — Søndre Strømfjord. Air-base c. 1500 m NE, mountain slope; B G B. — Søndre Strømfjord. Air-base c. 2000 m NE, on ridge near small lake: B G C. — Søndre Strømfjord. △ 434 c. 1000 m NE, low ridge; B G D. — Søndre Strømfjord. △ 434 c. 3000 m NE, ridge near lake: B G E. — Søndre Strømfjord. Ridge between · 520 and △ 513: B G F. — Søndre Strømfjord. Ridge between △ 513 and △ 475: B G G. — Søndre Strømfjord. Ridge between the lakes, Store and Lille Saltsø: B G H. — Søndre Strømfjord. Ridge between △ 330 and the lake, Store Saltsø: B G I. — Søndre Strømfjord. Ridge between Ravneklippen and the lake, Store Saltsø near road: B G K. — Søndre Strømfjord. Near river from the lake, Aujuitsup tasia in front of glacier tongue in the valley, Sandflugtsdalen, in sand: B G L. — Søndre Strømfjord. The glacier tongue in the valley, Sandflugtsdalen, c. 2000 m W, on ridge: B G M. — Søndre Strømfjord. Ridge between Sandflugtsdalen and the lake, Aujuitsup tasia: B G N. — Tovqussaq (T. W. Böcher); B G S. — Godthåb. South-west slope of Mount Lille Malene, on rocks: B F U. — Godthåb, Ridge near heliport, on rocks: B F X. — Godthåb. Close to B F X, in peat; B G A. — Frederikshåb, NE of Qingua (L. Bolt-Clausen, S. Frederiksen); B G O.

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **alpina,** 2n=66.

FINLAND. Lapponia enontekensis. Enontekiö. Markkina, old cemetery c. 50 m E, near path: A T S. — Enontekiö. Close to A T S: B D R. — Enontekiö. Markkina, old cemetery c. 100 m NE: B H G.

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **alpina,** 2n=72.

NORWAY. Troms. Storfjord. North-east slope of Mannfjell, tree-line: B H D.

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **orthantha** (Sørensen) G. Weim., 2n=63

USA. New Hampshire. Mount Washington, Alpine Garden (E. Kjellqvist): A K D.

GREENLAND. Frederikshåb. Avangnardleq fiord, Kangigdlivik, near brook: B F H. — Frederikshåb, near B F H, close to the sea: B F L. — Frederikshåb. Avangnardleq fiord, Kangigdlivik c. 3000 m NE, mountain slope: B F N. — Frederikshåb. Nerutussoq fiord, Akugdleq bay c. 1000 m SE, gravelly terrace: B F O. — Frederikshåb. Nerutussoq fiord, near Akugdleq fiord: B F P. — Frederikshåb. Lake Navdlûngûp tasia c. 1000 m W, in rock crevices: B F R. — Frederikshåb. Head of Nigerdleq fiord c. 3000 m S, mountain heath land: B F C. — Frederikshåb. Head of Nigerdleq fiord c. 4000 m SW, ridge near lake: B F D. — Frederikshåb. Head of Nigerdleq fiord c. 2000 m ENE, mountain heath land: B F F. — Frederikshåb. The town c. 1000 m NE, rocky hill slope: B F T. — Narssarssuaq. The air-base c. 1000 m SSW, mountain slope: B F B.

Hierochloë alpina (Willd.) Roemer & Schultes ssp. **orthantha** (Sørensen) G. Weim., 2n =58

USA. New Hampshire. Mount Washington, near A K D: A K F.

LITERATURE CITED

Ascherson, P. & Graebner, P. 1898—1902. Synopsis der mitteleuropäischen Flora 2(1). — Leipzig. V+795 pp.

Avdulov, N. P. 1931. Kario-sistematičeskoe issledovanie semeistva zlakov. (Mit deutscher Zusammenfassung.) — Trudy prikl. Bot. Genet. Selek. Suppl. 44. 428 pp.

Battaglia, E. 1963. Apomixis. — In Maheshwari, P. (ed.). Recent advances in the embryology of Angiosperms. pp. 221—264. — Delhi. X+467 pp.

Bauhin, C. 1620. Prodromos theatri botanici. — Francofurti ad Moenum. 160 pp.

— 1623. Pinax theatri botanici. — Basileae. 522 pp.

Bicknell, E. P. 1898. Two new grasses from Van Cortlandt Park, New York City. — Bull. Torrey bot. Club 25: 104—107.

Bigelow, J. 1816. Some account of the White Mountains of New Hampshire. — New Engl. J. Med. Surg. 5: 321—338.

Borbás, V. von 1900. A balaton flórájá. — Budapest. 431 pp.

Bowden, W. M. 1960. Chromosome numbers and taxonomic notes on northern grasses III. Twenty-five genera. — Can. J. Bot. 38: 541—557.

Brown, R. 1810. Prodromus florae Novae Hollandiae et insulae Van-Diemen. — Londini. VII+pp. 145—592.

Brunsberg, K. 1965. The usefulness of thin-layer chromatographic analysis of phenolic compounds in European Lathyrus L. — Bot. Notiser 118: 377—402.

Chrtek, J. & Jirásek, V. 1964. Beitrag zur Kenntnis der Veränderlichkeit von Hierochloë odorata (L.) Pal.-Beauv. in der Tschechoslowakei. — Preslia 36: 245—250.

Fenzl, E. & Graf, P. R. (eds.) 1858. Wulfen's Flora norica phanerogama. — Wien. XIV +816 pp.

Fernald, M. L. 1917. Some new or critical plants of Eastern North America. — Rhodora 19: 152—155.

Flovik, K. 1938. Cytological studies of arctic grasses. — Hereditas 24: 265—376.

Gmelin, J. G. 1747. Flora sibirica sive historia plantarum Sibiriae I. — Petropoli. CXXX +221 pp.

Hartman, C. J. 1838. Handbok i Skandinaviens flora 2. Ed. 3. — Stockholm. XXXII +350 pp.

— 1849. Handbok i Skandinaviens flora. Ed. 5. — Stockholm. XXIV+CXX+503 pp.

Hedberg, I. 1970. Cytotaxonomic studies on Anthoxanthum odoratum L. s. lat. IV. Karyotypes, meiosis and the origin of tetraploid A. odoratum. — Hereditas 64: 153—175.

Hedberg, O. 1967. Chromosome numbers of vascular plants from arctic and sub-arctic North America. — Ark. Bot. Ser. 2. 6(6): 309—326.

Heuffel, J. 1858 a. Diagnosen neuer, oder verwechselter Pflanzen-Arten aus dem Banate. — Öst. bot. Z. 8: 25—29.

— 1858 b. Enumeratio plantarum in Banatu Temesiensi sponte crescentium et frequentius cultarum. — Verh. zool.-bot. Ges. Wien 8: 39—240.

Honda, M. 1926. Revisio graminum Japoniae X. — Bot. Mag., Tokyo 40: 317—329.

Host, N. Th. 1801. Icones et descriptiones graminum austriacorum I. — Vindobonae. 74 pp.

— 1805. Icones et descriptiones graminum austriacorum III. — Vindobonae. 66 pp.

Hultén, E. 1950. Atlas över växternas utbredning i Norden. — Stockholm. 119*+512 pp.

— 1958. The amphi-atlantic plants and their phytogeographical connections. — K. svenska Vetensk-Akad. Handl. Ser. 4. 7(1). 340 pp.

— 1962. The circumpolar plants. I. — Ibid. 8(5). 275 pp.

— 1968. Flora of Alaska and neighboring territories. — Stanford. XXII+1008 pp.

Hylander, N. 1953. Nordisk kärlväxtflora I. — Stockholm. XV+392 pp.

Johnson, A. W. & Packer, J. G. 1968. Chromosome numbers in the flora of Ogotoruk Creek, N. W. Alaska. — Bot. Notiser 121: 403—456.

Jørgensen, C. A., Sørensen, Th. & Westergaard, M. 1958. The flowering plants of Greenland. — Biol. Skr. 9(4). 172 pp.

Kaczmarek, R. M. 1914. Priority of Hierochloa. — Amer. Midl. Nat. 3: 198.

Knaben, G. & Engelskjön, T. 1967. Chromosome numbers of Scandinavian arctic-alpine plant species II. — Acta Boreal. A. Scientia 21. 57 pp.

Koidzumi, G. 1918. Contributiones ad floram Asiae interioris. — Bot. Mag., Tokyo 32: 53—63.

Labillardière, J.-J. 1806. Novae Hollandiae plantarum specimen II. — Parisiis. 130 pp.

Lanjouw, J. & al. (eds.) 1966. International code of botanical nomenclature. — Regnum veg. 46. 402 pp.

Lanjouw, J. & Stafleu, F. A. 1964. Index herbariorum. I. The herbaria of the world. Ed. 5. — Regnum veg. 31. 251 pp.

Liljeblad, S. 1792. Utkast til en svensk flora. — Upsala. 358 pp.

Linnaeus, C. 1737. Flora lapponica. — Amstelaedami. 372 pp.

— 1745. Flora svecica. — Stockholmiae. XII +419 pp.

— 1753. Species plantarum — Holmiae. 1200 pp.

Loeselius, J. 1703. Flora prussica. — Regiomonti. 294 pp.

Löve, Á. & Löve, D. 1948. Chromosome numbers of northern plant species. — Reykjavík. 131 pp.

— — 1956. Cytotaxonomical conspectus of the Icelandic flora. — Acta Horti gothoburg. 20: 65—291.

— — 1965. Taxonomic remarks on some American alpine plants. — Univ. Colo. Stud. Ser. Biol. 17. 43 pp.

— — 1966. Cytotaxonomy of the alpine vascular plants of Mount Washington. — Ibid. 24. 74 pp.

— & Ritchie, J. C. 1966. Chromosome numbers from central Northern Canada. — Can. J. Bot. 44: 429—439.

— & Solbrig, O. T. 1964. IOPB chromosome number reports II. — Taxon 13: 201—209.

Maheshwari, P. 1950. An introduction to the embryology of Angiosperms. — New York, Toronto, London. X+453 pp.

Mez, C. 1921. Gramineae novae vel minus cognitae IV. — Reprium nov. Spec. Regni veg. 17: 291—303.

Müntzing, A. 1933. Apomictic and sexual seed formation in Poa. — Hereditas 17: 131—154.

Norstog, K. J. 1960 a. Some observations on the spikelet of Hierochloë odorata. — Bull. Torrey bot. Club 87: 95—98.

— 1960 b. The occurrence and distribution of Hierochloë odorata in Ohio. — Ohio J. Sci. 60: 358—365.

— 1963. Apomixis and polyembryony in Hierochloë odorata. — Am. J. Bot. 50: 815—821.

Nylander, F. 1844. Spicilegium plantarum fennicarum. — Helsingforsiae. 31 pp.

Östergren, G. & Heneen, W. K. 1962. A squash technique for chromosome morphological studies. — Hereditas 48: 332—341.

Palisot de Beauvois, A.-M.-F.-J. 1812. Essai d'une nouvelle agrostographie. — Paris. LXXIV+182 pp.

Persoon, C. H. 1805. Synopsis plantarum I. — Parisiis Lutetiorum. XII+546 pp.

Petrov, V. A. 1930. Flora Jakutii. I. — Leningrad. XII+221 pp.

Presl, K. B. (ed.) 1830. Reliquiae Haenkeanae 1(4—5). pp. 207—356. — Pragae.

Quensel, C. 1804—1805. — In Palmstruch, J. W. (ed.). Svensk botanik 3. — Stockholm.

Rafinesque, C. S. 1818. Flora Americae Septentrionalis (review). — Am. mon. Mag. 2: 170—176.

Reeder, J. R. & Norstog, K. J. 1961. The status of Hierochloë Nashii and its relationship to H. odorata. — Bull. Torrey bot. Club 88: 77—84.

Richter, K. 1890. Plantae Europeae I. — Leipzig. VII+378 pp.

Roemer, J. J. & Schultes, J. A. 1817. Systema vegetabilium II (II), pp. 481—958. — Stuttgardtiae.

Ruiz, H. & Pavon, J. 1794. Florae peruvianae, et chilensis prodromus. — Madrid. XXII+153 pp.

Scheuchzer, J. 1719. Agrostographia. — Tiguri. 512 pp.

Schrader, H. A. 1806. Flora Germanica I. — Gottingae. 432 pp.

Schrank, F. von Paula 1789 a. Baiersche Flora I. — München. 753 pp.

— 1789 b. Baiersche Flora II. — München. 670 pp.

Schur, F. 1859. Beobachtungen in der Flora von Siebenbürgen, nebst Beschreibung neuer Pflanzenarten und Varieteten I. — Öst. bot. Z. 9: 9—16.

Simonkai, L. 1886. Erdély Edényes Flórájának. — Budapest. XLIX+678 pp.

Smirnov, P. A. 1958. O Hierochloa odorata avtorov srednerusskoi flory. (Mit deutscher Zusammenfassung.) — Byull. mosk. Obshch. Ispyt. Prir. Div. biol. 63(5): 77—82.

Sokolovskaja, A. P. 1960. Geografičeskoe rasprostranenie poliploidnych vidov rastenij (issledovanie flory o. Sachalina). (With English summary.) — Vest. leningr. gos. Univ. Ser. Biol. 21(4): 42—58.

— 1963. Geografičeskoe rasprostranenie poliploidnych vidov rastenij (issledovanie flory poluostrova Kamčatki). (With English summary.) — Ibid. 15(3): 38—52.

— & Strelkova, O. S. 1960. Geografičeskoe rasprostranenie poliploidnych vidov rastenij v Evraziatskoj Arktike. (With English summary.) — Bot. Zh. SSSR 45: 369—381.

Sørensen, Th. 1954. New species of Hierochloë, Calamagrostis, and Braya. — Meddr Grønland 136(8). 24 pp.

Sorsa, V, 1962. Chromosomenzahlen finnischer Kormophyten I. — Suomal. Tiedeakat. Toim. Ser. A. IV. Biologica 58. 14 pp.

— 1963. Chromosomenzahlen finnischer Kormophyten II. — Ibid. 68. 14 pp.

Swartz, O. 1807. Ueber die Gattung Holcus. — In Schrader, H. A. (ed.). Neues Journal für die Botanik 2(2), pp. 39—49. — Erfurt. 376 pp.

Tateoka, T. 1954. Karyotaxonomic studies in Poaceae I. — Rep. natn. Inst. Genet., Misima 4: 45—47.

Taylor, R. L. & Mulligan, G. A. 1968. Flora of the Queen Charlotte Islands 2. — Ottawa. IX+148 pp.

Tischler, G. 1950. Die Chromosomenzahlen der Gefässpflanzen Mitteleuropas. — 's Gravenhage. 263 pp.

Tutin, T. G., Heywood, V. H., Burges, N. A., Valentine, D. H., Walters, S. M., & Webb, D. A. 1964. Flora Europaea I. — Cambridge. XXXII+464 pp.

Wahlenberg, G. 1812. Flora lapponica. — Berolini. LXVI+550 pp.

— 1820. Flora upsaliensis. — Upsaliae. VIII +495 pp.

Walter, H. Einführung in die Phytologie III. Grundlagen der Pflanzenverbreitung II. Arealkunde. — Stuttgart. 245 pp.

Weimarck, G. 1963. Kromosomtal hos Hierochloë odorata i Skandinavien. — Bot. Notiser 116: 172—176.

— 1967 a. Apomixis and sexuality in Hierochloë australis and in Swedish H. odorata on different polyploid levels. — Ibid. 120: 209—235.

— 1967 b. Apomixis in Hierochloë monticola (Gramineae). — Ibid. 120: 448—455.

— 1970 a. Hierochloë alpina (Gramineae) 2n=66 in Northern Finland. — Ibid. 123: 201—202.

— 1970 b. Spontaneous and induced variation in some chemical leaf constituents in Hierochloë (Gramineae). — Ibid. 123: 231—268.

— 1970 c. Apomixis and sexuality in Hierochloë alpina (Gramineae) from Finland and Greenland and in H. monticola from Greenland. — Ibid. 123: 495—504.

Wettstein, R. von, Wiesner, J. & Zahlbruckner, A. (eds.) 1906. Verhandlungen des internationalen botanischen Kongresses in Wien 1905. — Jena.

Willdenow, C. L. 1806. Caroli a Linné Species plantarum. Ed. 4. IV(II). — Berolini. Pp. 633—1157.

Zhukova, P. G. 1967. Čisla chromosom u nektorych vidov rastenij krajnego severovostoka SSSR. — Bot. Zh. SSSR 52: 983—987.

Botanical Literature

Tétényi, P.: Infraspecific chemical taxa of medicinal plants. — Akadémiai Kiadó, Budapest 1970. 225 pp. Price U.S. $ 7.20 bound.

The possible causes of infraspecific differentiation and the classification and nomenclature of infraspecific chemical taxa are discussed in a general part. The main chapters, almost two-thirds of the book, review the occurrence of organic compounds like terpenes, phenolics and alkaloids.

In the introduction the author stresses that "the detection of the existence of chemically differentiated infraspecific taxa may promote the determination of the interrelations of the species and its varieties."

The taxonomical value of the occurrence of substances is dependent on the type of evolution — parallel or convergent phylogeny. Thus Tétényi refers to examples of analogous and homologous appearance of compounds of certain taxa. He rightly emphasizes that not a single substance but rather the fundamental tendencies of metabolism are of the greatest significance for a taxonomical judgment. His unchallenged opinion, however, that the ontogeny of chemical processes in plants is the reflection of phylogeny, deserves outside criticism. Certainly Haeckel's biogenetical law has been successfully applied to many phylogenetical problems. In the special case of intrinsic changes of metabolism during ontogeny, however, it must be an impossible task to decide whether the stepwise changes of a synthesis chain do reflect true phylogenetical evolution or not. The formation of compounds often occurs in different ways due to reaction to different environmental stimuli. Further, the principle of convergence and the possibility of the disappearance of earlier precursors or enzymes are factors which can miscredit a general application of Haeckel's law to chemical metabolism.

The author presents an interesting discussion about form and function in chemical taxa. The chemical characteristics are said to be functional ones and thus of more conservative nature than the morphological ones. The reader must agree with his opinion that this statement can only be accepted in the case of certain morphological characteristics. Tétényi also refers to statements that chemical information is more fundamental due to the primary nature of functional changes, which do not always correspond to the form retained at certain earlier stages of evolution. From this he concludes that it is advisable to begin a taxonomical work with the investigation of chemical characteristics followed by the morphological ones of the taxa.

This work by Péter Tétényi is a critical, basic review of our knowledge on infraspecific chemical taxa. The author has succeeded in his ambition to write a comprehensive survey in this field with an interesting presentation and analysis of problems of uncontestable importance.

Ulf Olsson

Schuster, Rudolf M.: The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. I. XX +802 pp. 84 figures. Oct. 24, 1966. — Vol. II. XII+1062 pp. 301 figures. "1969" (in fact published on July 30, 1970). — Columbia University Press, New York. Price $20 each (cloth).

Professor R. Schuster (Dept. of Botany, Amherst, Mass., U.S.A.) is known as one of the leading authorities on the liverworts. He has made extensive travels in order to gain a solid knowledge of their variation and ecology. His field experience covers such remote areas as Greenland. Tierra del Fuego, New Guinea, New Zealand and Tasmania. He has also been a frequent guest in many herbaria, not least in Europe, where important type collections are preserved. He has published revisions of several groups of Hepaticae especially from exotic districts. The present treatise which is the fruit of more than twenty-five years of research can be characterized as a unique event in the history of Hepaticology.

This work is much more than a flora of North American liverworts. In fact, it is a treasure of information in all fields of this topic. Dr. SCHUSTER is least of all a mere compilator. The large variety of information is presented and evaluated critically. The text is elucidated by an exceedingly rich illustrative material. The author is an excellent artist. His drawings show in a scholarly way as well the habitus of the whole plant as detailed analyses of essential characters, especially in difficult species.

Vol. I begins, somewhat unconventionally, with an extensive bibliography (more than 2500 titles), which covers the literature to the end of 1962. Later titles will be mentioned in a supplement in Vol. III. Next chapter presents a broad historical outline from "ancient Greeks" to the present. Modern hepaticology begins with MICHELI (Nova genera, 1729) and DILLENIUS (Historia muscorum, 1741). In many respects, they had more elaborate ideas of the taxonomy of liverwort than LINNAEUS (Species plantarum, 1753), the starting point of binary nomenclature. It could be added that the herbaria of MICHELI (at Firenze) and DILLENIUS (at Oxford) are still retained. Through LINNAEUS's references their specimens may be used for lectotypification in cases where the material in the Linnaean herbarium is lacking or probably not seen by him in 1753. STEPHANI, the black sheep of the hepaticologists, is also duly mentioned. He managed to describe, usually with meaningless diagnoses, over 3000 new "species" often in the wrong genus. This jungle of superfluous names, which can be cleansed only gradually, is a lasting burden to hepaticology of the present century.

Further important headings in the general treatment in Vol. I. are Morphology, cytology and biology, Evolution of the Hepaticae, Methodology, collectors and literature, and Phylogeny and classification. Special chapters are devoted to Morphology of vegetative organs, Ontogeny of sexual organs and Development of the sporophyte. SCHUSTER's views of the evolution indicate a possible diphyletic origin of the Hepaticae. It is evident, however, that these problems, as well as "the origin of a land flora" in general, involve much speculation and few exact data.

The system of Hepaticae proposed by SCHUSTER comprises 61 families in 7 orders. This is a noteworthy splitting compared to another recent classification (K. MÜLLER, Die Lebermoose Europas, 1951), in which 40 families in 3 orders were recognised.

Vol. I ends with a systematic treatment of Orders Calobryales and Jungermanniales (Suborders Herbertinae and Ptilidiinae). Vol. II treats the major part of Jungermanniales. The remainder of this suborder will be revised in a forthcoming vol. III together with Orders Metzgeriales to Marchantiales. It should be noted that SCHUSTER treats the Anthocerotales, otherwise regarded as an order of Hepaticae, as a proper class, Anthocerotae, at the same level as Hepaticae. By an unfortunate misprint (p. 386) this group has happened to be placed as Order 8 under Hepaticae.

SCHUSTER's descriptions of species, genera and higher taxa are very detailed, but a skilful use of italics for essential characters has made them easy to survey. Much attention has been paid to subspecific variation. Under each species there is a discussion on "Ecology" and "Differentiation". No doubt the author's rich experience from the field has enabled him to develop reasonable ideas when judging what may be environmental variation and what may be due to genetic factors. As we know too little about the processes behind the differentiation, it is certainly difficult, in many cases, to come to an objective decision. Keys to families, genera, species and subspecific variation seem to be logic and easy to follow, as far as the reviewer can judge. In the Jungermanniales there are two main keys to genera, one to "asexually reproducing plants" and one to "plants without sexual reproduction". SCHUSTER has a critical attitude towards nomenclature. It is evident that he sometimes prefers to retain well-established but somewhat obscure (or even incorrect names) instead of digging up an unknown substitute or creating a *nomen novum*. Orthodox experts of nomenclature will probably raise objections to some of his names. SCHUSTER's thorough revisions have resulted in a considerable amount of new taxa and recombinations.

The diagnoses have sometimes been compiled without the aid of a Latin grammar. Some epithets have also got the wrong ending especially when the taxon has been transferred from one genus to another. Some examples: *Anastrophyllum saxicolus* (recte *-cola* (noun) or *-colum*), *Solenostoma crenuliformis* (recte *-forme*), *S. ontariensis* (recte *-ense*), and *S. sphaerocarpum* var. *nana* (recte *nanum*). *Solenostoma* subg. *Luridae* should better be *Lurida*.

These remarks are trifles and cannot obscure the fact that this treatise is not only a flora, not only a textbook, but an encyclopaedia which for many years will remain the standard work in this field of botany.

OVE ALMBORN

OPERA BOTANICA

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

Vol. 2. H. Runemark: Studies in Rhizocarpon. I. Taxonomy of the Yellow Species in Europe. 1956. 152 pp. — H. Runemark: Studies in Rhizocarpon. II. Distribution and Ecology of the Yellow Species in Europe. 1956. 150 pp. — G. Knaben: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. A. Cytotaxonomical Aspects. 1959. 76 pp. — Price Sw. Kr. 30 (15).

Vol. 3. A. Gustavsson: Studies in Nordic Peronosporas. I. Taxonomic Revision. 1959. 271 pp. — A. Gustavsson: Studies in Nordic Peronosporas. II. General Account. 1959. 61 pp. — G. Knaben: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. B. Experimental Studies. 1959. 96 pp. — Price Sw. Kr. 30 (15).

Vol. 4. R. Dahlgren: Revision of the Genus Aspalathus. I. The Species with Flat Leaflets. 1960. 393 pp. — Price Sw. Kr. 30 (15).

Vol. 5. Á. Löve and D. Löve: Chromosome Numbers of Central and Northwest European Plant Species. 1961. 581 pp. — Price Sw. Kr. 40 (20), bound Sw. Kr. 48 (28).

Vol. 6. Å. Persson: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. I. Description of the Vegetation. 1961. 187 pp. — R. Dahlgren: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 1—2. 1961. 120 p. — Å. Persson: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. II. Habitat Conditions. 1962. 100 pp. — Price Sw. Kr. 40 (20).

Vol. 7. N. Malmer: Studies on Mire Vegetation in the Archaean Area of Southwestern Götaland (South Sweden). I. Vegetation and Habitat Conditions on the Åkhult Mire. 1962. 322 pp. — II. Distribution and Seasonal Variation in Elementary Constituents on Some Mire Sites. 1962. 67 pp. — Price Sw. Kr. 40 (20).

Vol. 8. R. Dahlgren: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 3. 1963. 183 pp. — N. Sylvén: Det skandinaviska floraområdets Carices Distigmaticae. (The Carices Distigmaticae of the Scandinavian Flora District.) 1963. 161 pp. — C. Bliding: A. Critical Survey of European Taxa in Ulvales. I. Capsosiphon, Percursaria, Blidingia, Enteromorpha. 1963. 160 pp. — Price Sw. Kr. 40 (20).

Vol. 9. R. Dahlgren: Studies on Aspalathus and Some Related Genera in South Africa. 1963. 301 pp. — S. O. Strandhede: Chromosome Studies in Eleocharis, subser. Palustres. III. Observations on Western European Taxa. 1965. 86 pp. — Price Sw. Kr. 40 (20).

Vol. 10. R. Dahlgren: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 4. 1965. 231 pp. — S. O. Strandhede: Morphologic Variation and Taxonomy in European Eleocharis, subser. Palustres. 1966. 187 pp. — Price Sw. Kr. 40 (20).

Vol. 11. R. Dahlgren: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 5. 1966. 266 pp. — G. Nordborg: Sanguisorba L., Sarcopoterium Spach and Bencomia Webb et Berth. Delimination and Subdivision of the Genera. 1966. 103 pp. — Price Sw. Kr. 50 (30).

Vol. 12. B. E. Berglund: Late-Quaternary Vegetation in Eastern Blekinge, Southeastern Sweden. I. Late-Glacial Time. 1966. 180 pp. — II. Post-Glacial Time. 1966. 190 pp. — Price Sw. Kr. 70 (42).

No. 13. S. Snogerup: Studies in the Aegean Flora VIII. Erysimum Sect. Cheiranthus. A. Taxonomy. 1967. 70 pp. — Price Sw. Kr. 15 (9).

No. 14. S. Snogerup: Studies in the Aegean Flora IX. Erysimum Sect. Cheiranthus. B. Variation and Evolution in the Small-Population System. 1967. 85 pp. — Price Sw. Kr. 16 (9.40).

No. 15. R. Dahlgren: Studies on Penaeaceae I. Systematics and Gross Morphology of the Genus Stylapterus A. Juss. 1967. 40 pp. — Price Sw. Kr. 8 (4.80).

No. 16. G. Nordborg: The Genus Sanguisorba Section Poterium. Experimental Studies and Taxonomy. 1967. 166 pp. — Price Sw. Kr. 27 (16.20).

No. 17. I. Björkqvist: Studies in Alisma L. I. Distribution, Variation and Germination. 1967. 128 pp. — Price Sw. Kr. 25 (15).

No. 18. R. Dahlgren: Studies on Penaeaceae II. The Genera Brachysiphon, Sonderothamnus and Saltera. 1968. 72 pp. — Price Sw. Kr. 13 (7.80).

No. 19. I. Björkqvist: Studies in Alisma L. II. Chromosome Studies, Crossing Experiments and Taxonomy. 1968. 138 pp. — Price Sw. Kr. 25 (15).

No. 20. B. Nordenstam: The Genus Euryops. I. Taxonomy. 1968. 409 pp. — Price Sw. Kr. 55 (33).

No. 21. R. Dahlgren: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 6. 1968. 309 pp. — Price Sw. Kr. 75 (45).

No. 22. R. Dahlgren: Revision of the Genus Aspalathus. III. The Species with Flat and Simple Leaves. 1968. 126 pp. — Price Sw. Kr. 30 (18).

No. 23. B. Nordenstam: Phytogeography of the Genus Euryops (Compositae). A Contribution of the Phytogeography of Southern Africa. 1969. 77 pp. — Price Sw. Kr. 20 (12).

No. 24. T. Mörnsjö: Studies on Vegetation and Development of a Peatland in Scania, South Sweden. 1969. 187 pp. — Price Sw. Kr. 50 (30).

No. 25. G. Tyler: Studies in the Ecology of Baltic Sea-Shore Meadows. II. Flora and Vegetation. 1969. 101 pp. — Price Sw. Kr. 25 (15).

No. 26. M. Sonesson: Studies on Mire Vegetation in the Torneträsk Area, Northern Sweden. III. Communities of the Poor Mires. 1970. 120 pp. — Price Sw. Kr. 30 (18).

No. 27. F. Andersson: Ecological Studies in a Scanian Woodland and Meadow Area, Southern Sweden. I. Vegetational and Environmental structure. 1970. 190 pp. — Price Sw. Kr. 50 (30).

No. 28. A. Strid: Studies in the Aegean Flora. XVI. Biosystematics of the Nigella arvensis Complex. With Special Reference to the Problem of Non-adaptive Radiation. 1970. 169 pp. — Price Sw. Kr. 50 (30).

BOTANISKA NOTISER SUPPLEMENT

Vol. 1. S. Waldheim: Kleinmoosgesellschaften und Bodenverhältnisse in Schonen. 1947. 203 pp. — O. Almborn: Distribution and Ecology of some South Scandinavian Lichens. 1948. 252 pp. — Price Sw. Kr. 15 (10).

Vol. 2. H. Hjelmqvist: Studies on the Floral Morphology and Phylogeny of the Amentiferae. 1948. 171 pp. — O. Andersson: Larger Fungi on Sandy Grass Heaths and Sand Dunes in Scandinavia. 1950. 89 pp. — A. Almestrand and A. Lundh: Studies on the Vegetation and Hydrochemistry of Scanian Lakes I—II. 1951. 174 pp. — Price Sw. Kr. 15 (10).

Vol. 3. A. Lundh: Studies on the Vegetation and Hydrochemistry of Scanian Lakes III. 1951. 138 pp. — O. Hedberg, O. Mårtensson, and S. Rudberg: Botanical Investigations in the Pältsa Region of Northernmost Sweden. 1952. 209 pp. — K. H. Rechinger fil.: Monograph of the Genus Rumex in Africa. 1954. 114 pp. — Price Sw. Kr. 15 (10).

Opera Botanica is edited by the Lund Botanical Society in cooperation with the Department of Plant Taxonomy, University of Lund. It consists of larger treatises issued at indefinite times.

All parts of Opera Botanica and its predecessor Botaniska Notiser Supplement are still available.

Members of the Lund Botanical Society receive both series at the reduced price indicated in parentheses and should apply directly to Opera Botanica, Botanical Museum, Ö. Vallgatan 18, S-223 61 Lund, Sweden. Booksellers and nonmembers should apply to C. W. K. Gleerup Bokförlag, Öresundsvägen 1, S-222 38 Lund, Sweden.

OTHER PUBLICATIONS

Generalregister till Botaniska Notiser 1839—1938. General Index to Botaniska Notiser 1839—1938. — Price Sw. Kr. 15 (10).

Förteckning över Nordens växter. 1. Kärlväxter. List of the Plants of N. W. Europe (Sweden, Norway, Denmark, East Fennoscandia, Iceland and the Faeroes). 1. Vascular Plants. Ed. 4. By N. Hylander. Lund 1955. — Price Sw. Kr. 15 (10).