Drawings of Scandinavian Plants 94–96

Chenopodium L.

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94. **Chenopodium berlandieri** MOQ. in DC. 1849

Annual, up to 1.5 m high, erect to ascending, usually much-branched, branches glabrous to farinose, usually with reddish spots at the nodes. Stem angular, striated. Leaves alternate, green, usually glabrous above, glabrous to farinose beneath. Lower leaves three-lobed, rhomboid, or ovate to lanceolate, 2—9 cm long, 1—6 cm broad, length 1—1 1/2 times the breadth, long-petiolate, petiole about equal in length to lamina. Margins entire to dentate, or with prominent lobes pointing forwards at about the middle of the leaf. Apex acute to apiculate. Upper leaves similar but smaller. Inflorescences mainly terminal, leafy, composed of many-flowered, rounded to oblong, distinct glomerules. Flowers perfect, usually farinose, 5-merous. Perianth lobes united below or to the middle, ovate, obtuse to acute, greenish to dark brown in the centre, light green to transparent in the outer parts, distinctly keeled on the back. The perianth almost entirely covers the seed. Pistil with a rather long style and two stigmas papillate to the base. Stamens 5. Seeds horizontal, black, orbicular, 0.9—1.3 mm in diameter, with rounded or somewhat narrowing margins, round in transection. Pericarp rather thin, yellowish to whitish, fairly firmly attached to the seed. Testa lustrous, with rounded to angled, deep, honeycomb-like pits, usually radially arranged. Radicula short and broad, closely attached to the seed. Embryo annular.

Flowering time: July to September.

Chromosome number: 2n=36.

Variation: Most vegetative characters are variable, particularly the shape and size of lower leaves (cf. Fig. 94). Four subspecies have been distinguished, mainly based on characters of leaves and inflorescences (for further information see AELLEN 1960). Most of the Scandinavian material belongs to ssp. *zschackei* (MURR.) ZOBEL.

Habitat and distribution: *C. berlandieri* is an occasional weed, usually found in the vicinity of harbours, mills and railway-yards, in fowl-runs and on waste ground. It is native to North America, but has been introduced into Europe as well as into other parts of the world. In Scandinavia most records are from the southern parts. In Denmark it has been recorded from most regions except the westernmost parts of Jylland, in Sweden northwards to Bohuslän—Uppland, in Norway from the provinces of Akershus, Vest-Agder, Hordaland and Sör-Tröndelag (cf. JÖRGENSEN 1973).

Comments: The taxonomic position of *C. berlandieri* is somewhat doubtful. On the one hand some forms of ssp. *berlandieri* show close affinity to *C. hircinum* and they are even presumed to hybridize (cf. AELLEN 1960). On the other hand,

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[1] ENGSTRAND is responsible for the drawings and GUSTAFSSON for the text.

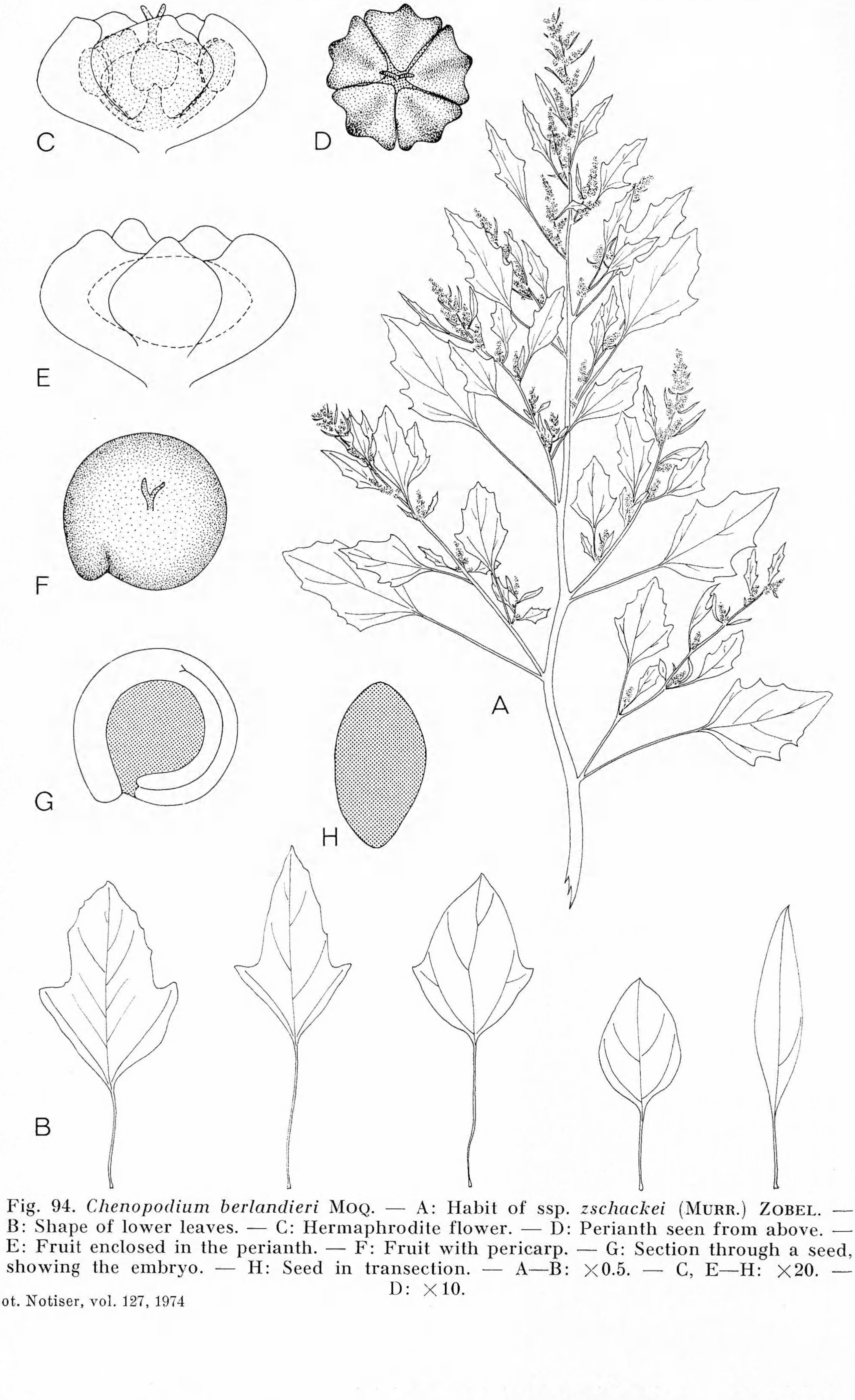

Fig. 94. *Chenopodium berlandieri* MOQ. — A: Habit of ssp. *zschackei* (MURR.) ZOBEL. — B: Shape of lower leaves. — C: Hermaphrodite flower. — D: Perianth seen from above. — E: Fruit enclosed in the perianth. — F: Fruit with pericarp. — G: Section through a seed, showing the embryo. — H: Seed in transection. — A—B: ×0.5. — C, E—H: ×20. — D: ×10.

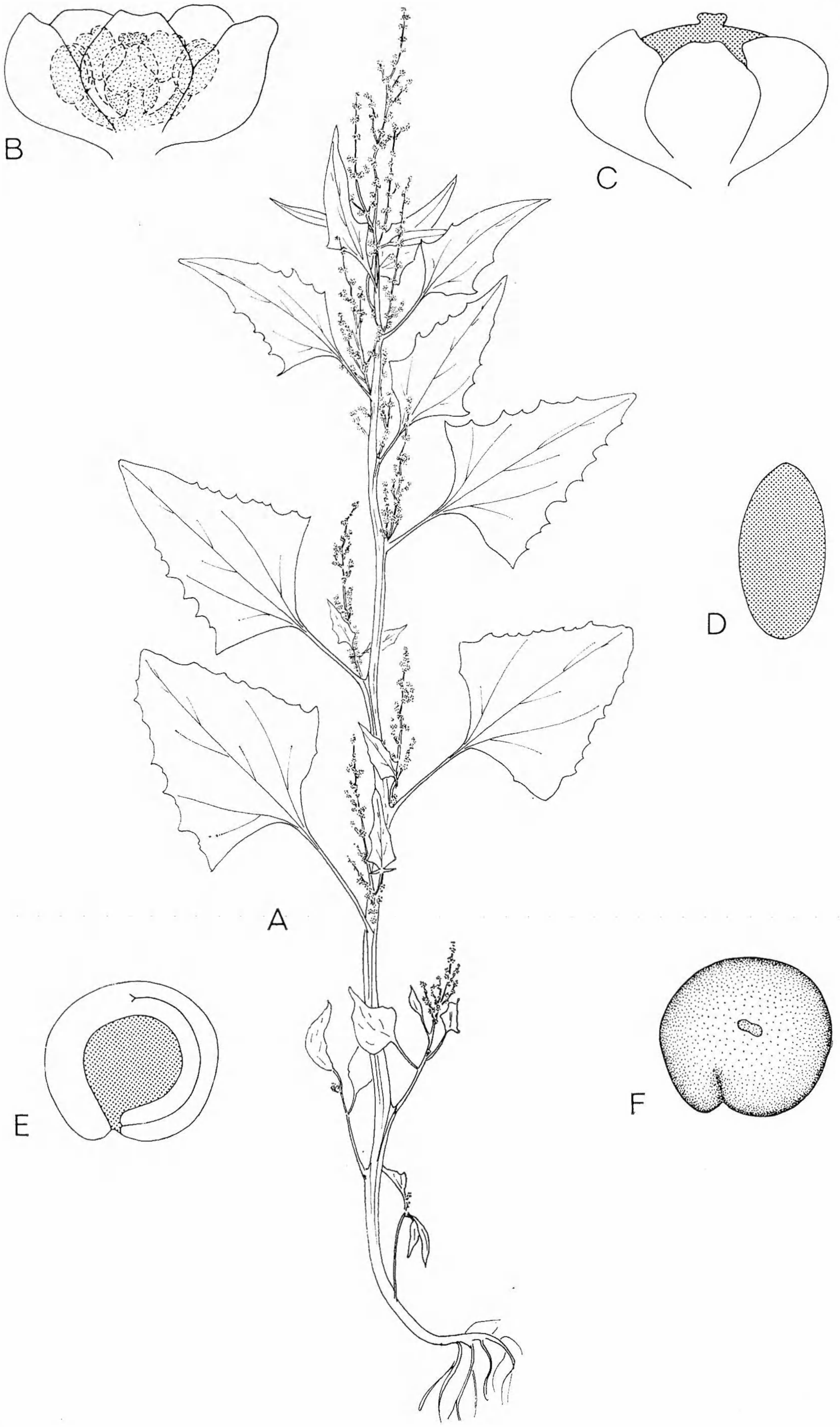

Fig. 95. *Chenopodium urbicum* L. — A: Habit. — B: Hermaphrodite flower. — C: Fruit enclosed in the perianth. — D: Seed in transection. — E: Section through a seed, showing the embryo. — F: Fruit with pericarp. — A: ×0.5. — B—F: ×20.

however, *C. berlandieri* has often been confused with *C. album* and according to AELLEN hybrids are regularly formed in habitats where they occur together. But, in Scandinavia *C. berlandieri* is readily distinguished from other species by the prominent, honeycomb-like, deep pits in the testa, which can even be observed through the pericarp.

95. **Chenopodium urbicum** L. 1753

Annual, up to 1 m high, erect, simple, rarely few-branched. Stem angular, striated. Leaves alternate except the lowermost opposite ones, bright greenish, glabrous or in young stages of development sometimes farinose, veins light-coloured, distinct. Lower leaves mostly triangular, base sometimes gradually tapering to the petiole, or truncate to hastate, 3—11 cm long, 3—10 cm broad, length 1—1 1/2 times the breadth, distinctly petiolate. Margins coarsely sinuate to dentate, rarely subentire, often with obtuse to acute, outward- to forward-pointing lobes at base. Apex obtuse to acute. Upper leaves triangular to lanceolate, with a truncate to cuneate base, petiolate, usually considerably longer than broad, entire to dentate, with or without basal lobes, obtuse to acute. Inflorescence a compact, rarely loose, rigid, erect, branched, in the most terminal parts leafless panicle, composed of many-flowered glomerules. Flowers small, perfect, glabrous, 5-merous. Perianth lobes united below only, broadly ovate to elliptic, green to dark brown and somewhat thickened in the centre, light green in the outer parts, mostly obtuse, rounded, rarely with a slight, broad keel on the back. The perianth only partly covers the seed. Pistil with an insignificant style and two short and rather thick stigmas papillate to the base. Stamens 5, the filaments united at the base. Seeds horizontal, black, orbicular, small, 0.6—1.0 mm in diameter, margins rounded or narrowing somewhat, usually appearing rounded or slightly keeled in transection. Pericarp rather thin, yellowish to whitish, papillose, rather loosely attached to the seed. Testa lustrous, faintly sculptured with small grooves and furrows. Radicula rather short, closely attached to the seed. Embryo annular.

Flowering time: July to September.

Chromosome number: 2n=18, 36 (cf. FEDOROV 1969).

Habitat and distribution: *C. urbicum* usually occurs close to human settlement such as along road-sides, in farmyards and on manure heaps. It is a Eurasian species, distributed throughout most parts of Europe, but rare and mainly occasional in the northernmost parts. In Scandinavia most records are from the southern parts. In Denmark scattered localities from the eastern part of Jylland to Sjælland, in Sweden from Skåne to Västergötland—Uppland, very rare north to Västerbotten, in Norway known from Östfold, Akershus and Hordaland, in Finland most records are from the Åland archipelago and along the coast from the region of Åbo to Karelia. Most Scandinavian records are old, *C. urbicum* probably being very rare nowadays.

96. **Chenopodium pratericola** RYDB. 1912
(Syn. *C. leptophyllum* auct.)

Annual, up to 1 m high, erect to ascending, usually branched at least in the upper parts. Stem angular, striated. Stem and branches glabrous to farinose, however in young stages of development conspicuously farinose. Leaves alternate, green and glabrous above, greyish and farinose beneath, the midvein and two lateral veins only distinct. Lower leaves narrowly elliptic to lanceolate, gradually tapering to the petiole, up to 6 cm long and 2 cm broad. Margins entire or with a tooth-like, forward-pointing, obtuse lobe on each side. Apex acute to apiculate. Upper leaves similar, but smaller. Inflorescence a branched, more or less leafy and compact panicle, composed of many-flowered, rounded to oblong glomerules.

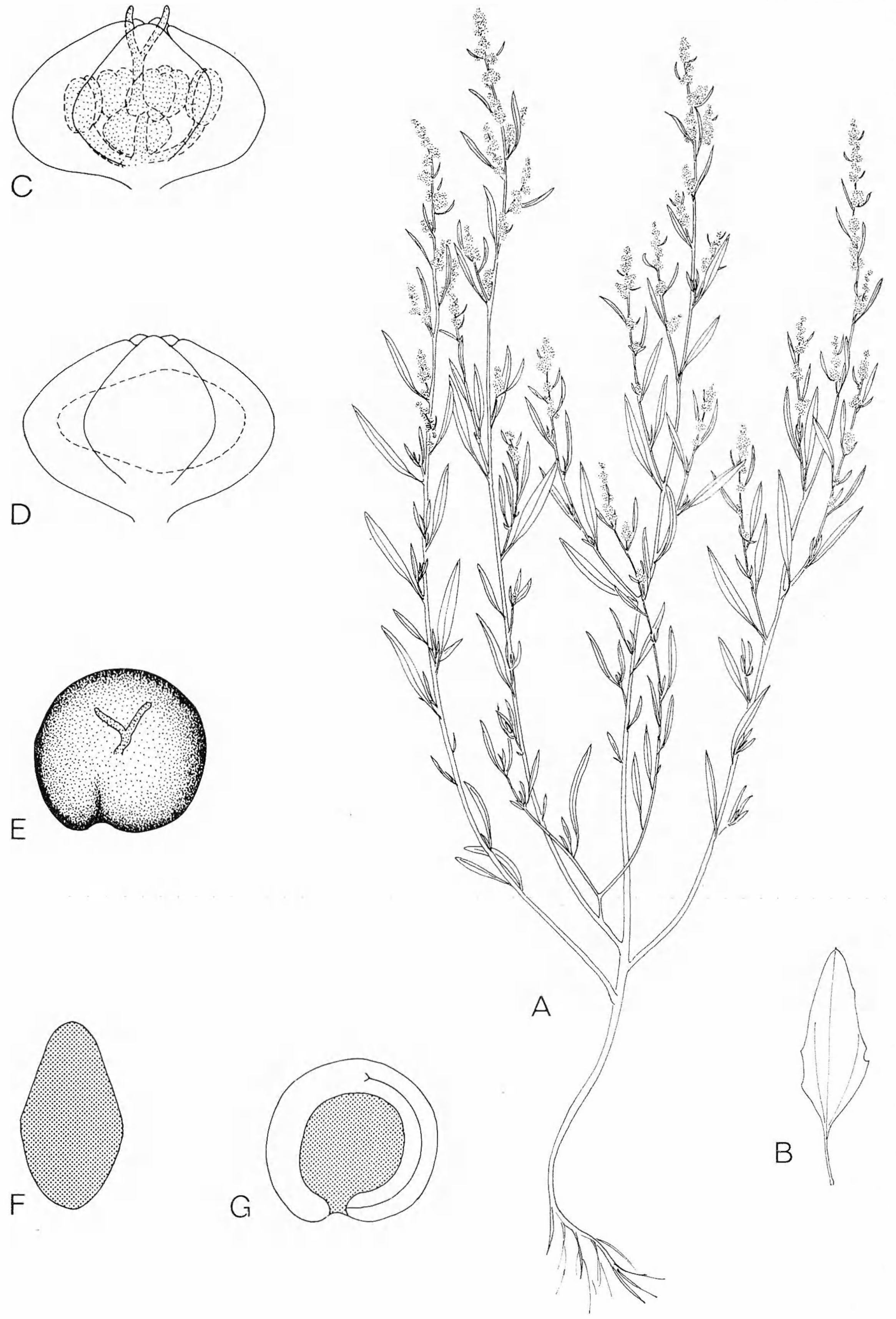

Fig. 96. *Chenopodium pratericola* Rydb. — A: Habit. — B: Shape of a diverging, lower leaf. — C: Hermaphrodite flower. — D: Fruit enclosed in the perianth. — E: Fruit with pericarp. — F: Seed in transection. — G: Section through a seed, showing the embryo. — A—B: ×0.5. — C—G: ×20.

Flowers perfect, farinose, 5-merous. Perianth lobes united up to the middle or nearly so, ovate to elliptic, obtuse to acute, dark-coloured in the centre, light green or membraneous in the outer parts, mostly keeled on the back. The perianth usually covers the seed. Pistil with a long style and two, long, filiform stigmas papillate to the base. Stamens 5. Seeds horizontal, black, orbicular, 0.8—1.2 mm in diameter, narrowing somewhat at the margins, rounded in transection. Pericarp rather thin, brownish, loosely attached to the seed. Testa lustrous, faintly sculptured by radial furrows and minute pits. Radicula rather short and broad, closely attached to the seed. Embryo annular.

Flowering time: July to August.

Chromosome number: 2n=18.

Habitat and distribution: *C. pratericola* occurs as a more or less occasional weed in the vicinity of harbours, mills, railway-yards and factories. Native to North America, but introduced into South America and Europe. In Scandinavia scattered localities, mainly in coastal regions. In Denmark recorded from the eastern parts of Jylland to Sjælland, in Sweden from Skåne to Norrbotten, in Norway from Östfold to Hordaland, Sör-Tröndelag and Buskerud, in Finland from Satakunta, Nyland and Karelia.

LITERATURE CITED

AELLEN, P. 1960. Chenopodium. — In HEGI, Illustrierte Flora von Mitteleuropa, 2. Aufl., III(2). — München.

FEDOROV, A. A. (Ed.) 1969. Chromosome numbers of flowering plants. — Leningrad.

JÖRGENSEN, P. M. 1973. The genus Chenopodium in Norway. — Norwegian Journ. Bot. 20: 303—319.

Révision Systématique du Genre Sonchus L. s.l.

V. Sous-genre 2. Dendrosonchus

Loutfy Boulos

BOULOS, L. 1974 03 29. Révision systématique du genre Sonchus L. s.l. V. Sous-genre 2. Dendrosonchus. — Bot. Notiser 127: 7—37. Lund. ISSN 0006-8195.

Nineteen species, one subspecies and one variety are discussed. For each taxon is given: nomenclature; vernacular names in different languages where known; uses where known; detailed description; distribution with localities; ecological and biological characters; chromosome numbers where known; palynological particulars, if any. For each taxon relationships with other taxa are discussed as well as any characteristics calling for special emphasis. 20 distribution maps and 21 illustrations are included. The distribution is almost entirely restricted to Macaronesia: fourteen species being endemic in the Canary Islands, three in Madeira, one on the Cape Verde Islands and one common to the western coast of Morocco and the eastern Canary Islands. Chromosome numbers of fifteen species are given, all 2n=18. Polyploids are not known.

This monographic study will be followed by one more part.

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22. **Sonchus congestus** WILLD.

WILLDENOW, Ges. Naturf. Fr. Berl. Mag. 1: 136, 1807. — Lectotype: Tenerife, BROUSSONET s.n., WILLDENOW No 11537 (B!).

Sonchus fruticosus JACQ. Coll 1: 13, 1786; non *S. fruticosus* L. f., 1781; non *S. fruticosus* Noronha, 1790; nom. nud.

S. jacquini DC. Cat. Hort. Monsp. 147, 1813.

S. macranthus POIR. Encycl. Suppl. 3: 289, 1813.

S. broussonetii DESF. Tab. (ed. 2) 101, 1815.

S. abbreviatus LINK, in BUCH, Phys. Canar. Ins. 149, 1825.

S. jacquini SPR. Syst. Veg. 3: 647, 1826; pro parte.

NOMS VERNACULAIRES. *En espagnol:* Cerrajón, Lechuna de pastór. — *En allemand:* Baum-Gänsedistel.

Plante vivace, 40—100 cm de hauteur, feuilles glabres, capitules glabres ou faiblement tomenteux à la base. *Racine* pivotante, ligneuse et ramifiée. *Collet* ligneux, 2—4 cm diam., ramifié. *Tige:* vieilles tiges ligneuses, cylindriques, pleines, dressées et portant des cicatrices foliares proéminentes; les jeunes molles, ailées, souvent couchées sur le sol à cause du nombre élevé des capitules qu'elles portent. *Feuilles du collet* 5—20×1—5 cm, non auriculées ou à très petites oreillettes; lobes ± opposés, marges finement denticulées. *Feuilles caulinaires* 15—45×3—12 cm, auriculées, les supérieures moins longues que les inférieures, mais munies d'oreillettes arrondies et larges; pennipartites à pinnatiséquées; lobes triangulaires, opposés ou subalternés, 0,5—5× 0,5—3 cm, marges denticulées, sommet aigu; nervure médiane 0,5—1,8 cm à la base, atténué vers le sommet; espaces interlobaires triangulaires-arrondis. *Pédoncule* 0,5—7 cm, souvent blanc-tomenteux. *Capitules* 2,5—3×3,5—6 cm lorsqu'ils sont ouverts. Nombre de fleurs 250—450 par capitule. *Écailles de l'involucre* 40—63; les externes 13—18, 7—13×4—9 mm, blanches-tomenteuses ou glabres,

Fig. 1. *Sonchus congestus*. ASPLUND 198 (S!).

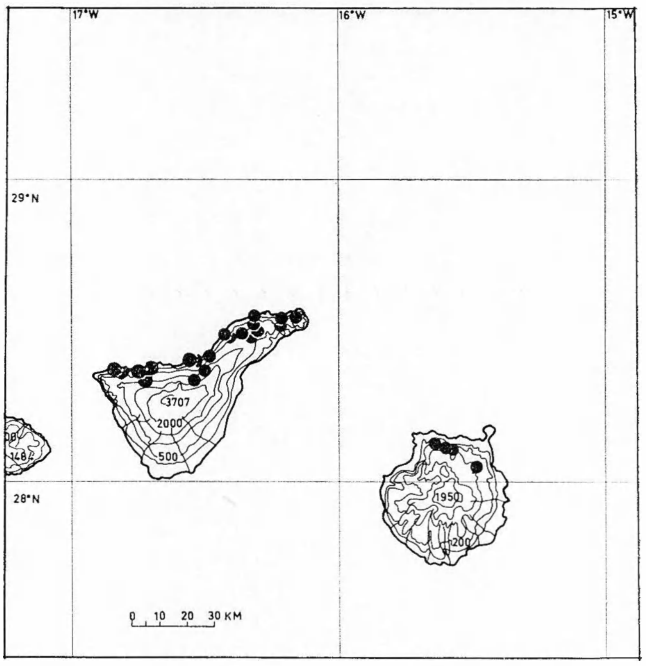

Fig. 2. *Sonchus congestus*. Distribution.

marges ondulées et irrégulièrement denticulées; les intermédiaires 11—20, 14—16 ×2,5—4 mm, marges ondulées et irrégulièrement denticulées; les internes 16—25, 14—17×1,5—2,5 mm, ondulées et denticulées dans la partie supérieure. *Corolle* vif jaune, 18—25 mm. *Ligule* 8—11×2—2,5 mm. *Tube de la corolle* 10—14 mm. *Anthères* 4—5×0,6—0,8 mm. *Akènes* 2,5—3×0,85—1,25 mm, ± elliptiques, comprimés à 2—3 côtes sur chaque face, noirâtres, faiblement à fortement rugueux transversalement. *Aigrette* 8—10 mm, caduque.

DISTRIBUTION. Tenerife et Gran Canaria, Îles Canaries; endémique.

Tenerife: Tacoronte, c. 600 m, ASPLUND 387 (S!); 500 m, PITARD 236 (G! L!); RØSTAD s.n. (O!) — Tegueste, BOURGEAU 1377 (C! CGE! G! K! MA! P! UPS! W!); BOURGEAU 559 (BM! CGE! G! K! P! W!); BOULOS s.n. (CAI!) — Don Pedro Alvarez, 575 m, E Tegueste, LID s.n. (O!) — Puerto de la Cruz, ERIK WALL 794 (S!); JØRSTAD s.n. (O!) — Orotava, La Mocana, 450 m, BURCHARD 68 (CGE! G! S!) — Malpair, près de Orotava, PRIOR s.n. (K!) — Puerto Orotava, PRIOR s.n. (K!); BURCHARD 99 (O! ZT!) — Orotava, BORNMÜLLER 895 (LD!); LEMANN s.n. (CGE!); RODRIGUEZ s.n. (MA!); COOL 184 (L!) — Entre Puerto de la Cruz et le Jardin Botanique, BOULOS s.n. (CAI!) — c. 10 km S Orotava, BOULOS s.n. (CAI!) — Bco Hoya, S Hidalgo, 300 et 350 m, LID s.n. (O!) — Hoya de Meleque, DAHLSTEDT s.n. (UPS!) — Bco Los Silos, 150, 400 et 500 m, LID s.n. (O!) — Tinca Garcia Docte, 4 km S Tejina, 300 m, LID s.n. (O!) — Las Mercedes, Cruz El Carmen, 1020 m, LID s.n. (O!) — Icod, BOULOS s.n. (B! CAI! G! K! MPU!); (écrit Ikod), TRETTEWY 154 (K!) — Entre Icod et El Tanque, BOULOS s.n. (B! BM! CAI!) — Caldera de Rula, S Icod, 600 m, LID s.n. (O!) — Buen Paso, NE Icod, 200 m, LID s.n. (O!) — Bco del Drago, 550 m, LID s.n. (O!) — Entre Agua Garcia et Laguna, MURRAY s.n. (G! K!) — Agua Garcia, LOWE 105 bis (K!) — Agua Garcia Tacoronte, ASPLUND 647 (S!) — Laguna, DE LA PARRANDIÈRE s.n. (G! K! MPU! P!) — Buenavista, BOULOS s.n. (BM! CAI!) — Santa Ursula, PEREZ s.n. (K!); c. 200 m, ASPLUND 198 (G! S!); MASFERRER s.n. (BC!) — La Mina, 800 m, PITARD s.n. (P!) — Roque Icoso, Anaga peninsula, 750 m, LEMS 2699 (L!) — Bajamar, 200 m, BORNMÜLLER 2543 (LD! P!) — Entre Taganana et San Andres, 600 m, BORNMÜLLER 2543 (G! P! W!) — Bco de la Florida, BOURGEAU s.n. (G!) — Taganana, 500 et 800 m, PITARD s.n. (P!) — Vueltas de Taganana, 600 m, PITARD s.n. (P!) — Calle del Vina, RØSTAD s.n. (O!) — Forêt N Ténérife, DE LA PARRANDIÈRE s.n. (P!) — s. loc., BROUSSONET s.n. (lectotype Willdenow Herbarium No 11537 B!, isolectotypes G-DC! MPU!); SCHULTZ BIPONTINUS s.n. (P!); COURANT s.n. (MPU!).

Gran Canaria: Moya, ASPLUND 84 (G! S!) — Entre Las Palmas et Agaete, près de Guia, BOULOS s.n. (CAI!) — W Atalaya, 580 m, LID s.n. (O!) — Bco Calabozo, 350 m, LID s.n. (O!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus congestus* est une espèce commune dans l'île de Tenerife et rare dans Gran Canaria. Elle croît dans les stations rocheuses assez humides des champs cultivés et les terrains négligés entre 100 et 1000 m d'altitude. Floraison et fructification principalement de février à juillet.

CARACTÈRES CARYOLOGIQUES. 2n =18 (LARSEN 1960; ROUX et BOULOS 1972.

DISCUSSION. *Sonchus congestus* représente l'une des espèces la plus commune et, au même temps, la plus polymorphe de sa section et même du sous-genre *Dendrosonchus*. Elle existe sous deux formes: l'une possède des feuilles profondément séquées, qui a été décrite comme une espèce (*S. abbreviatus*) et l'autre avec des feuilles moins séquées. Nous avons considéré *S. abbreviatus* comme synonyme de *S. congestus* car nous avons observé dans une même station, et même, sur la même souche, ces deux formes des feuilles.

L'espèce la plus voisine de *S. congestus* est *S. acaulis*. Il est facile de les distinguer, l'une de l'autre, grâce aux caractères suivants, rapides à examiner:

Espèce	tige	feuilles	capitules
S. acaulis	très courte, rarement ramifiée	pubescentes	densément tomenteux
S. congestus	longue, ramifiée	glabres	légèrement tomenteux

23. **Sonchus acaulis** DUM.-COURS.

DUMONT DE COURSET, Bot. Cult. (ed. 2) 4: 12, 1811. — Lectotype: Île de Tenerife (P!).

Sonchus jacquini SPR. Syst. Veg. 3: 647, 1826; pro parte.

S. jacquini DC. Cat. Hort. Monsp. 147, 1813, β *congestus* DC. Prodr. 7: 188, 1838; exc. syn.

S. chuquitensis MEYEN ex WALP. in Nov. Act. Nat. Cur. 19, Suppl. 1: 294, 1843.

S. altissimus VAHL ex SCH. BIP. in WEBB et BERTH. Phyt. Canar. 2: 431, 1849—1850.

S. polyodon WEBB et BERTH. Phyt. Canar. 2: 431, 1849—1850.

NOM VERNACULAIRE. *En espagnol:* Cerrajón.

Plante vivace, 50—80 cm de hauteur, feuilles pubescentes, groupées en rosette à la base, capitules densement blanc-tomenteux. *Racine* pivotante, ligneuse, ramifiée. *Collet* ligneux, 1—4 cm diam., non ramifié. *Tige* très courte, ligneuse, rarement ramifiée. *Feuilles du collet* 5—15×2—3 cm, pennipartites à pinnatiséquées, lobes ± triangulaires, 1—2×0,8—1,5 cm, marges finement denticulées. *Feuilles caulinaires* 10—45×6—18 cm, pinnatifides à pennipartites, rarement pinnatiséquées; tomenteuses à l'état juvénile et devenant légèrement pubescentes plus tard; nervure médiane 1—3 cm diam. à la base, atténuée vers le sommet; lobes ± triangulaires, souvent réfléchis, 1—7×1—3 cm, sommet aigu, marges irrégulièrement séquées et finement denticulées; feuilles devenant de plus en plus petites vers l'inflorescence. *Pédoncule* 0,5—10 cm, tomenteux, specialement à la base et au-dessous du capitule, à une bractée. *Capitules* 1,5—2,5×4—5 cm lorsqu'ils sont ouverts, densement tomenteux. Nombre de fleurs 350—450 par capitule. *Écailles de l'involucre* 52—64; les externes 17—20, 6—18×2,5—6 mm, densément blanches-tomenteuses à la base, sommet acuminé, marges entières; les intermédiaires 10—14, 16—19×2,5—4 mm, moins blanches-tomenteuses que les externes; les internes 22—30, 12—14×1,5—2 mm, glabres. *Corolle* jaune, 20—32 mm. *Ligule* 10—16 ×1,5—2 mm. *Tube de la corolle* 10—16

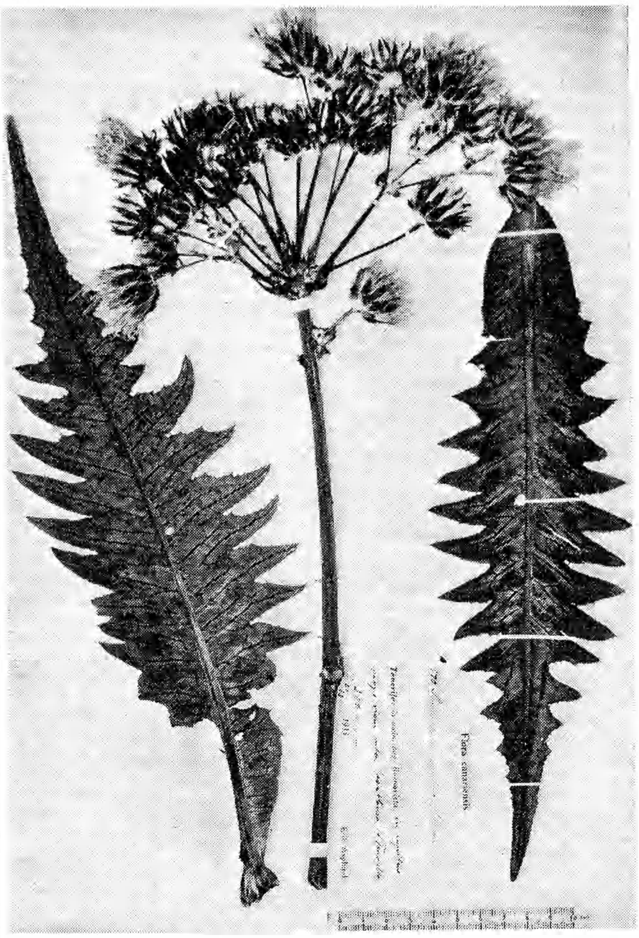

Fig. 3. *Sonchus acaulis*. Asplund 590 (S!).

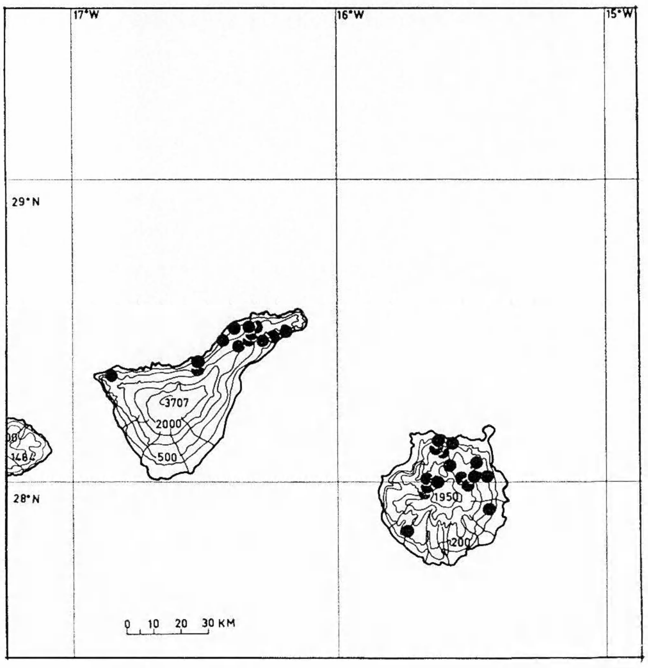

Fig. 4. *Sonchus acaulis*. Distribution.

mm. *Anthères* 4—5×0,6 mm. *Akènes* 3—3,5×1—1,5 mm, ± elliptiques, comprimés, à 1—3 côtes sur chaque face; couleur variée: jaune, jaune-verdâtre, jaune-brunâtre, brun, ardoise, noirâtre; fortement rugueux transversalement. *Aigrette* 8—10 mm, caduque.

DISTRIBUTION. Tenerife et Gran Canaria, Îles Canaries; endémique.

Tenerife: La Laguna, Bourgeau 198 (BM! CGE! G! LE! P! W!); Schultz Bipontinus s.n. (P!); Pitard 602 (G! L!); Bourgeau 1378 (C! CGE! G! K! MA! MPU! P! UPS! W!); Murray s.n. (K!); Boulos s.n. (CAI!); Cool 544 a (L!) — Près de La Laguna, Masferrar s.n. (BC!) — S La Laguna, Murray s.n. (K!) — Entre La Laguna et Santa Cruz, Boulos s.n. (CAI!) — Tegueste, 650 m, Pitard s.n. (P!) — Don Pedro Alvarez, 575 m, E Tegueste, Lid s.n. (O!) — Bco San Antonio, Valle de Orotava, c. 800 m, Asplund 619 (G! K! UPS!) — Agua Marrsa, Orotava, Bunner s.n. (W!) — Tacaronte, 600 m, Pitard s.n. (P!); Bco San Juan, Tacaronte, 450 m, Lid s.n. (O!) — Bco San Andres, 50 m, Lid s.n. (O!) — Bco Moya, 500 m, Lid s.n. (O!) — La Esperanza, 925 m, Lid s.n. (O!) — Las Canteras, 680 m, Lid s.n. (O!) — Montaña de la Crinita, Aguamansa, 1240 m, Lid s.n. (O!) — Aguamansa, Mt. Joco, 1300 m, Lid s.n. (O!) — Cueva Negra, Bco Los Silos, 400 et 500 m, Lid s.n. (O!) — Tinca Garcia Docte, 300 m, 4 km SW Tejina, Lid s.n. (O!) — Valle Jimenez, Røstad s.n. (O!) — Near Buenavista, Asplund 590 (S!) — Las Mesas, NW Santa Cruz, 570 et 590 m, Lid s.n. (O!) — Hoya de Meleque, Dahlstedt s.n. (UPS!) — s. loc., Ventenant s.n. (G!).

Gran Canaria: Caldera de Bandama, Murray s.n. (K!) — Cuesta de Silva, Murray s.n. (K!) — Bco Angostura, Murray s.n. (G!) — Santa Brigida, Boulos s.n. (CAI!) — Valleseco, Boulos s.n. (CAI! MPU! O!) — Entre San Mateo et Tenteniguada, Boulos s.n. (CAI!) — Bco Tejeda, 880 m, Lid s.n. (O!) — Hill above Tejeda, 1250 m, Lid s.n. (O!) — Vista Tejeda, N Mt. Constantino, 1660 m, Lid s.n. (O!) — Cruz Tejeda, Boulos s.n. (B! BM! CAI!); 1500 m, Kunkel 9934 (M!) — La Fuente, 1 km S Cruz Tejeda, Colla de las Palomas, 1600 m, Lid s.n. (O!) — La Culata, 2 km S Cruz Tejeda, 1650 m, Lid s.n. (O!) — Mt. Montañon, SE San Mateo, 1050—1150 m, Sunding s.n. (O!) — Los Chorros, près de San Mateo, 800 m, Burchard 229 (CGE! G!) — Rocky slopes S Pagador, 110—130 m, Sunding 242 et 247

(O!) — Mt. Lentiscal, 370—500 m, SUNDING 435 (O!) — Bco Calabozo, in rocks, 350 m, LID s.n. (O!) — Las Lagunetas, 1400 m, LID s.n. (O!) — Above Las Lagunetas, against Cruz Tejeda, 1450 m, LID s.n. (O!) — Entre Tejeda et Lagunetas, BOULOS s.n. (CAI!) — Mt. Sierra, Bco Guayadeque, 550 m, LID s.n. (O!) — Bco Guiniguada at Tafira Alta, 300 m, LID s.n. (O!); 400 m, BORNMÜLLER 2539 (G! LD! LE! O! P! W!); SUNDING s.n. (O!) — Bco Moya, below Hotel Pilar, 500 m, LID s.n. (O!) — Tinca Garcia Docte, 4 km SW Tejina, 300 m, LID s.n. (O!) — Montaña Cruz at Atalaya, 650 m, LID s.n. (O!) — Bco del Dragonal, GELERT s.n. (C!) — Mogán, S Gran Canaria, ELSIE HULTÉN s.n. (S!) — Hautes montagnes, DESPRÉAUX s.n. (G!) — s. loc. SCHULTZ BIPONTINUS s.n. (P!); DESPRÉAUX s.n. (K!); DESPRÉAUX 191 (G!); HUMBERT s.n. (P!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus acaulis* est une espèce vivace, poussant sur les murs, les rochers escarpées, à l'état isolé ou en mélange avec d'autres plantes herbacées, dans les vallées, à une altitude de 200 à 1700 m, plus répandue entre 800 et 1200 m. Floraison janvier à mai (principalement mars) et fructification mars à mai.

CARACTÈRES CARYOLOGIQUES. 2n =18 (HENIN; ROUX et BOULOS 1972).

DISCUSSION. *Sonchus acaulis* est caractérisé par des capitules à grand nombre de fleurs (340—450) et d'écailles d'involucre nombreuses (52—64). Les écailles externes sont exceptionnellement longues et larges (6—18×2,5—6 mm) possédant un tomentum blanc et très dense, facile à détacher.

Nous avons observé que les individus qui croissent dans l'île de Tenerife sont plus longs et possèdent des tiges florifères plus ramifiées, des capitules plus nombreux, et couverts d'un tomentum moins dense, des fleurs plus longues, des feuilles plus longues, plus larges et plus profondément séquées que ceux de Gran Canaria.

SCHULTZ BIPONTINUS (1849—1850) a distingué trois variétés dans cette espèce: var. *abbreviatus* SCH. BIP., var. *elongata* SCH. BIP. et var. *palmensis* SCH. BIP. Nous avons rencontré les types de ces variétés (P!), et il nous semble que les plantes de Gran Canaria représentent la variété *abbreviatus*, celles de Tenerife la variété *elongata*; alors que la variété *palmensis* représente une espèce distincte: *Sonchus hierrensis*. Cette dernière avait déjà attiré l'attention de SCHULTZ BIPONTINUS (1849—1850) qui a écrit dans sa description «Nam species propria?».

24. **Sonchus hierrensis** (PITARD) BOULOS

BOULOS in Nytt Mag. Bot. 14: 11, 1967. — Lectotype: Hierro, Riscos de Jinama, in silvis, 800 m, PITARD 603 (P!); isolectotypes (G! ZT!).

Sonchus jacquini DC. var. *hierrensis* PITARD, in PITARD et PROUST, Iles Canar. Fl. Archipel, 258, 1908.

S. congestus WILLD. var. *palmensis* SCH. BIP. in WEBB et BERTH. Phyt. Canar. 2: 432, 1849—1850; non *S. palmensis* (SCH. BIP.) BOULOS, 1967.

S. ortunoi SVENT. Addit. Fl. Canar. 1: 81, T. 33, 1960.

NOMS VERNACULAIRES. *En espagnol:* Angoja, Serrajón.

USAGES. A Vallehormoso, île de Gomera, les jeunes feuilles de la plante sont mangées par les oies.

Plante vivace, ligneuse, robuste, ramifiée, 60—220 cm de hauteur, feuilles caulinaires groupées en touffes au sommet des tiges végétatives ou à la base des tiges florifières. *Racine* pivotante, ligneuse, ramifiée. *Collet* ligneux, 3—15 cm diam., généralement non ramifié. *Tige:* vieilles tiges robustes, ramifiées, ligneuses, cylindriques, 4—10 cm diam., à écorce parfois caduque, portant des bases des feuilles; jeunes tiges tendres, lisses et portant les capitules. *Feuilles caulinaires* 10—45×2—8 cm, les juvéniles blanches-tomenteuses, les plus âgées légèrement pubescentes ou glabres; pennipartites à pinnatiséquées; lobes 10—15 paires (peu nombreux chez les supérieures), ± triangulaires, ± opposés, 1—3,5×0,5—2 cm, à marges entières ou irrégulierement denticulées, sommet aigu; nervure médiane proéminente, 6—15 mm

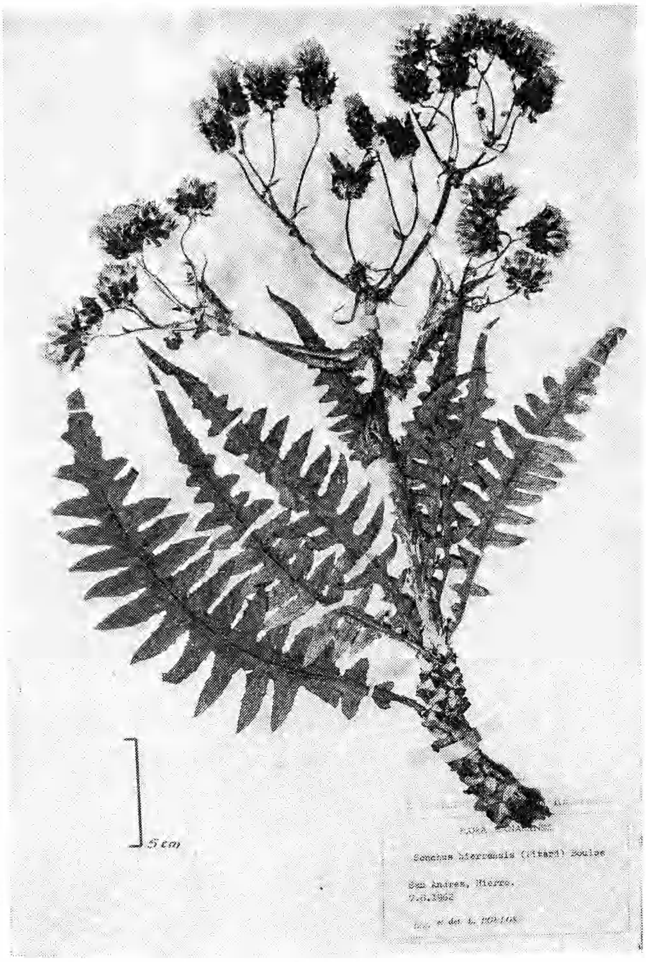

Fig. 5. *Sonchus hierrensis*. Boulos s.n. (CAI!).

à la base, atténuée vers le sommet; feuilles supérieures munies d'oreillettes larges et arrondies, devenant plus petites chez les inférieures. *Pédoncule* 0,5—8 cm, blanc tomenteux, spécialement au-dessous des capitules. *Capitules* 2—3×4—5 cm lorsqu'ils sont ouverts. Nombre de fleurs 200—375 par capitule. *Écailles de l'involucre* 40—57, sommet obtus et cilié; les externes 11—20, 7—13×4—8 mm, ovales à triangulaires; les intermédiaires 10—14, 12—14×3—5 mm; les internes 19—23, 12—14×1,2—2,5 mm. *Corolle* jaune, 22—30 mm. *Ligule* 11—15 mm. *Tube de la corolle* 11—15 mm. *Anthères* 4,5—5 mm. *Akènes* 3,25—3,75×1,25—1,5 mm, jaune-bruns à brunâtres, elliptiques, comprimés, à 2—3 côtes sur chaque face, fortement rugueux transversalement. *Aigrette* 8—12 mm, caduque.

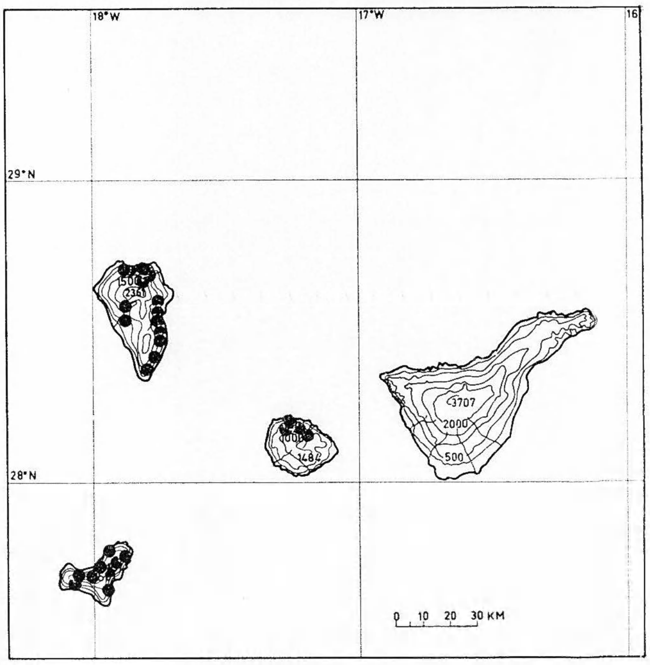

Fig. 6. *Sonchus hierrensis*. Distribution.

DISTRIBUTION. Hierro, La Palma et Gomera, Îles Canaries; endémique.

Hierro: Sabinosa, Boulos s.n. (B! BM! CAI! G! K! MPU! O!) — Bco Sabinosa, 300 m, Lid s.n. (O!) — Los Llanillos, El Golfo, 200—300 m, Bornmüller 2546 (G! LE! P! W!); Boulos s.n. (CAI! K!) — Las Lapas, Boulos s.n. (CAI! K!) — Frontera, Boulos s.n. (BM! CAI! G!) — W Frontera, 200 m, Lid s.n. (O!) — 2 km SW San Andres, Boulos s.n. (CAI!) — San Andres, Boulos s.n. (B! BM! CAI! G! K!) — 1,5 km NE San Andres, Boulos s.n. (CAI!) — La Caldera, 770 et 780 m, Lid s.n. (O!) — SW Caldera, 2 km S Valverde, 700 m, Lid s.n. (O!) — Bco Santiago, 350 m, Lid s.n. (O!) — Taibique, Boulos s.n. (CAI! MPU! O!) — El Pinar, 2 km W Taibique, 950 m, Lid s.n. (O!) — Erese, Boulos s.n. (BR! CAI! LD! S!) — Guarazoca, Boulos s.n. (CAI! G! K!) — Jarales, Boulos s.n. (B! CAI! G! MPU!) — Risco de Jinama, 800 m, Pitard 603 (Type P!, isotype G!) — Vuelta de Xinamar, Murray s.n. (K!) — Roque Tiguirote, 450 m, Lid s.n. (O!) — La Dehesa, slope facing west, 900 m, Lid s.n. (O!).

La Palma: Caldera El Capaderos, Sprague et Hutchinson 448 (K!) — Bco Las Angustias, 1000 m, Pitard s.n. (P!); 700 m, Lid s.n. (O!) — El Paso, Boulos s.n. (B! BM! CAI!) — Fuencaliente, Boulos s.n. (CAI! G! K!) — Entre Sabina et Tiguerorte, Boulos s.n. (CAI!) — Mazo, Boulos s.n. (B! BM! CAI! K!) — San Pedro, c. 9 km S Santa Cruz, Boulos s.n. (B! BM! CAI! K!

MPU!) — Breña Alta, BOULOS s.n. (B! BM! CAI! G! K! MPU!) — La Cuesta, SW Santa Cruz, BOULOS s.n. (BR! CAI! G! P!) — Las Nieves, BOULOS s.n. (CAI!) — Bco del Rio, 2 km N Las Nieves, BOULOS s.n. (CAI! G!); 600 et 800 m, PITARD s.n. (P!) — Bco del Agua, 400 m, Los Sauces, LID s.n. (O!) — Bco del Agua, Santa Lucia, 220 m, LID s.n. (O!) — Barlovento, 600 m, LID s.n. (O!) — 4—5 km W Barlovento, BOULOS s.n. (CAI!) — Gallegos, c. 9 km W Barlovento, BOULOS s.n. (CAI!) — Bco Madera, MURRAY s.n. (K!). Gomera: Vallehermoso, BOULOS s.n. (B! BM! BR! CAI! G! K! MPU! O! S!) — Près de Roque de Vallehermoso, BOULOS s.n. (BR! CAI! P! S!) — Rosa de Las Piedras, 2 km SE Vallehermoso, BOULOS s.n. (CAI! G! K! S!) — El Cedro, S Hermigua, BOULOS s.n. (BM! CAI! MPU! O!) — c. 8 km NE Alajero, S Hermigua, BOULOS s.n. (CAI!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus hierrensis* croît dans les stations rocheuses fraiches et ombragées de la région forestière et sur les bords rocheux des champs, entre 200 et 1000 m d'altitude. Floraison et fructification de mars à août.

CARACTÈRES CARYOLOGIQUES. 2n =18 (ROUX et BOULOS 1972).

PARTICULARITÉES PALYNOLOGIQUES. *Sonchus hierrensis* présente un épaississement polaire caractéristique. Le nombre d'épines polaires atteint 26 et les lacunes porales sont très développées.

DISCUSSION. *Sonchus hierrensis* est une espèce mal connue, qui a été décrite par SCHULTZ BIPONTINUS (1849—1850) comme une variété de *S. congestus* WILLD., et par PITARD (1908) comme une variété de *S. jacquini* DC.

En effet, cette épithète mérite le rang d'une espèce pour les caractères très particuliers de ces pollens et de sa macromorphologie. La hauteur de la plante est extraordinaire (jusqu'à 2,2 m), avec des tiges ligneuses, ayant jusqu'à 10 cm de diamètre et portant une écorce qui tombe par plaques, en particulier chez les vieilles plantes.

Il nous semble aussi, que cette espèce, ayant une répartition géographique limitée aux trois îles occidentales de l'archipel des îles Canaries: Hierro, La Palma et Gomera, est isolée génétiquement, c.-à-d. que les barrières génétiques sont bien développées chez elle.

25. **Sonchus daltonii** WEBB

WEBB in HOOK. Niger Fl. 144, 1849. — Lectotype: Cape Verdes, Niger Expedition, HOOKER s.n. (K!).

NOMS VERNACULAIRES. *En portugais:* Coroa de rei, Tortoinho.

Plante vivace, 25—70 cm de hauteur, tige courte et ligneuse, feuilles en rosette à la base. *Collet* ligneux, épais. *Tige* épaisse, courte, portant les bases des feuilles après leur chute. *Feuilles du collet* en rosette, 5—25×2—5 cm, pinnatifides à pennipartites; lobes triangulaires à arrondis, souvent imbriqués, marges légèrement denticulées, sommet pointu. *Feuilles caulinaires* 10—30×3—10 cm, glabres, pennipartites à pinnatiséquées; lobes 6—10 paires, opposés ou irrégulièrement disposés, triangulaires à arrondis, marges légèrement serrées, sommet pointu; nervure médiane proéminente, épaisse et triangulaire à la base, 1—1,4 cm; feuilles deviennent de plus en plus petites vers le sommet, avec des oreillettes arrondies et larges et des lobes petits et peu nombreux. *Pédoncule* 0,5—7 cm. *Capitules* nombreux, 2—2,5×3—4 cm pendant l'anthèse. Nombre de fleurs 290—470 par capitule. *Écailles de l'involucre* 57—70, marges ciliées et sommet obtus; les externes 20—22, 8—13×5—8,5 mm; les intermédiaires 18—22, 14—16×3—5 mm; les internes 19—26, 15—17×1—2 mm. *Corolle* jaune, 13,5—19 mm. *Ligule* 5,5—8×1,5—2 mm. *Tube de la corolle* 8—11 mm. *Anthères* 3,5—4 mm. *Akènes* 2,5—3×1—1,2 mm, comprimés, atténués aux deux bouts, jaune-brunâtres ou bruns, à 1—3 côtes sur chaque face, transversalement rugueux. *Aigrette* 10—12 mm, ± caduque.

Fig. 7. *Sonchus daltonii.* LOWE s.n. (K!).

DISTRIBUTION. Îles de Cap Vert, endémique.

Fogo: Near Fernão Gomes, 1750 m, SUNDING 2817 b (O!); 15 km NE St. Filipe, 1000 m, CHEVALIER 45198 (P!) — St. Antão: Cova, CHEVALIER 45514, 45587 (P!); s. loc. SCHMIDT s.n. (P!) — St. Nicolau: Caminho da Caldeira, LOWE s.n. (BM! K!); Ribeira Brava, CARDOSO s.n. (in litt.) — St. Vicente: Sommet de Monte Verde, LOWE s.n. (K!); VOGEL (in litt.); s. loc. LOWE s.n. (BM!) — St. Thiago: 500 m, HOOKER s.n. (in litt.) — s. loc., CARDOSO 184 (K!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus daltonii* est une plante vivace croissant dans les stations rocheuses à une altitude de 500 à 1750 m et dans les vallées. Floraison de février à mars, fructification mars à avril.

DISCUSSION. *Sonchus daltonii* est la seule espèce endémique du genre *Sonchus* dans l'archipel des îles du Cap Vert.

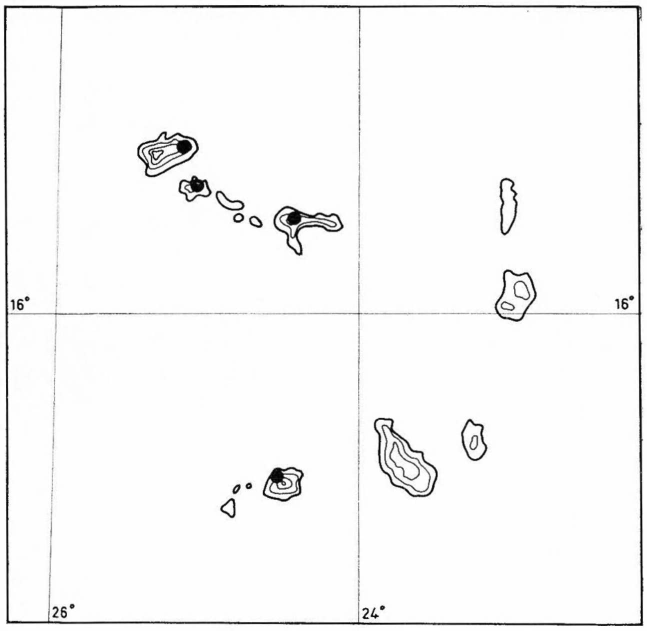

Fig. 8. *Sonchus daltonii.* Distribution.

La presence de *S. daltonii,* espèce endémique du sous-genre *Dendrosonchus,* dans ces îles est intéressante du point de vue paléogéographique. Elle confirme la théorie de l'existence probable de l'île Atlantique comprenant les quatre archipels actuels: Cap Vert, Canaries, Madère et Açores, sur l'emplacement desquels devaient se trouver trois chaînes des montagnes (les Canaries et Madère d'une même chaîne).

L'absence d'espèces endémiques dans l'archipel des Açores est due probablement à sa situation septentrionale, hors de la limite climatique actuelle du sousgenre *Dendrosonchus.*

26. **Sonchus bornmuelleri** PITARD

PITARD in PITARD et PROUST, Iles Canar. Fl. Archipel 259, 1908. — Holotype: Canaries: Palma, Cumplida, prope Barlovento, ad rupes maritimos, PITARD s.n. (P!); isotype (G!).

Plante vivace, 50—80 cm de hauteur, feuilles groupées en rosette à la base, ramifications florifères presque nues, capitules peu nombreux. *Collet* ligneux, court. *Tige* ligneuse, courte, portant les bases des feuilles après leur chute. *Feuilles*

Fig. 9. *Sonchus bornmuelleri*. Holotype, PITARD s.n. (P!).

caulinaires 7—20×1—7 cm, plus foncées sur la face supérieure, légèrement pubescentes vers la base; pennipartites à pinnatiséquées; lobes ± rectangulaires à semicirculaires ou ± triangulaires, 0,5—3× 0,5—1 cm, marges irrégulièrement spinellées, sommet arrondi; nervure médiane proéminente, 6—8 mm à la base, atténuée vers le sommet. *Pédoncule* 3—25 mm, tomenteux. *Capitules* 1,5—1,8×2,5—3 cm lorsqu'ils sont ouverts, tomenteux à la base. Nombre de fleurs ± 200 par capitule. *Écailles de l'involucre* ± 56; les externes 16, 4—9×2—4 mm, tomenteuses à la base, marges ciliées, irrégulièrement serrées dans la partie supérieure, sommet acuminé, bilobé ou obtus; les intermediaires 14, 8—9×1,5—3 mm, moins

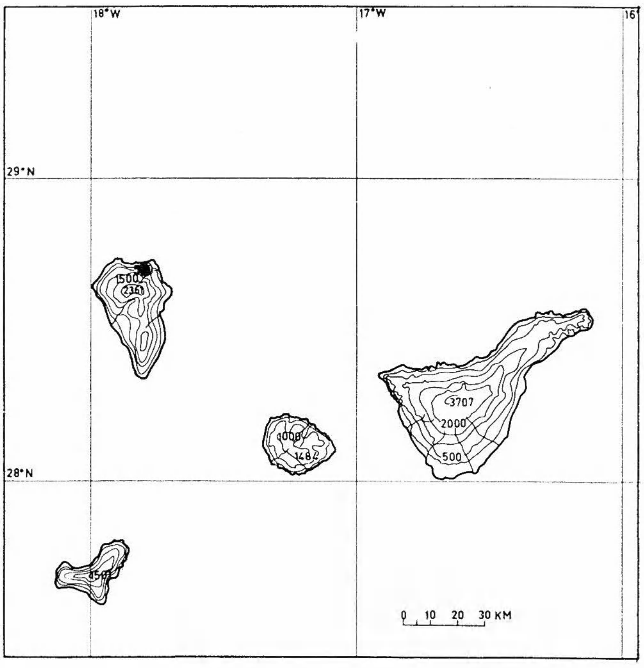

Fig. 10. *Sonchus bornmuelleri*. Distribution.

tomenteuses à la base que les externes, marges densément ciliées dans la partie supérieure, sommet obtus ou bilobé; les internes 26, 8—9×0,8—1,2 mm, légèrement ciliées vers un sommet obtus. *Corolle* jaune, 13—17 mm. *Ligule* 6,5—8,5 mm. *Tube de la corolle* 6,5—8,5 mm. *Anthères* 4×0,5 mm. *Akènes* 2—2,5×1 mm, noirâtres, ± elliptiques, à 2—3 côtes sur chaque face, fortement rugueux transversalement. *Aigrette* 8 mm, caduque.

DISTRIBUTION. La Palma, Îles Canaries; endémique.

La Palma: Cumplida, prope Barlovento, PITARD s.n. (Holotype P!; isotype G!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus bornmuelleri* est une plante vivace poussant sur les rochers maritimes dans la partie septentrionale de l'île de La Palma. Floraison et fructification de mars à mai.

DISCUSSION. *Sonchus bornmuelleri* est une espèce très rare, connue seulement de la collection du type, endémique de l'île de La Palma, archipel des îles

Canaries. Elle est caractérisée par une tige courte, portant des feuilles en rosette et une inflorescence presque nue. Les capitules sont tomenteux à la base. Les marges des feuilles portent des épines acérées.

27. **Sonchus radicatus** Ait.

Aiton, Hort. Kew. (ed. 1) 3: 116, 1789. — Lectotype: Île de Tenerife, Mason s.n. (G-DC!).

Sonchus radicatus Link, Enum. Hort. Berol. 2: 279, 1822.

NOMS VERNACULAIRES. *En anglais:* Long-rooted Sow-thistle — *En allemand:* Bewurzelte Gänsedistel.

Plante vivace, 20—80 cm de hauteur, tige courte, non ou peu ramifiée, feuilles glabres, en rosette. *Racine* pivotante, longue, ramifiée, renflée, résistante à l'érosion. *Collet* 1 cm diam. *Tige* non ou peu ramifiée, ligneuse, cylindrique, 1—5 cm, rarement plus longue, portant les bases des feuilles tombées; la ramification florifère porte très peu de feuilles courtes, largement espacées et pourvues de ± 3 paires des lobes inégaux et obtus. *Feuilles du collet* présentes sur les jeunes individus seulement, 3—10×1—3,5 cm, typiquement lyrées; lobes triangulaires, le terminal cordé, rarement triangulaire, marges entières ou légèrement denticulées, sommet faiblement pointu; nervure médiane 3—4 mm diam. à la base. *Feuilles caulinaires* en rosette dense vers la base, 10—30× 3—8 cm, blanchâtres en-dessous, lyrées, à 3—7 paires de lobes, irrégulièrement disposées, ± triangulaires, à marges entières ou légèrement denticulées, sommet pointu; espaces interlobaires arrondis; nervure médiane proéminente, triangulaire à la base, atteignant 3—8 mm diam. *Pédoncule* 1—5 cm, à l'aisselle d'une bractée et pourvu de 1—3 bractées immédiatement au-dessous de l'involucre. *Capitules* généralement peu nombreux, 1,5 ×3 cm pendant l'anthèse. Nombre de fleurs 200—420 par capitule. *Écailles de l'involucre* 41—58, ciliées vers un sommet obtus; les externes 15—18, 3—6×2—3 mm; les intermédiaires 10—19, 7—9×2—2,5 mm; les internes 16—21, 9—12×1,2—2,2 mm. *Corolle* jaune, 11—17 mm. *Ligule* 5,5—8,5×2—2,5 mm. *Tube de la corolle* 5,5—8,5 mm. *Anthères* 3,5—4 mm. *Akènes* 2—2,5×0,6—0,8 mm, brunâtres ou brun-foncés, atténués aux deux extrémités, comprimés, à 1—3 côtes principales et plusieurs côtes fines sur chaque face, ± lisses. *Aigrette* 4,5—6 mm, caduque.

DISTRIBUTION. Tenerife, Îles Canaries; endémique.

Tenerife: Taganana, Lowe 288 (K!); Bornmüller 893 (G! P! W!); Bornmüller 2536 (LD! LE!) — Below Roque Animas, 100 m, Lid s.n. (O!); W Taganana, Hamilton s.n. (E!) — Entre Taganana et Taborno, Asplund 1318 (G!) — Orotava, Parrandière s.n. (K!) — El Balaya, Valle de Las Yeguas, 110 m, Lid s.n. (O!) — Laguna, Parrandière s.n. (G!) — Las Canteras, N La Laguna, Boulos s.n. (B! BR! CAI! G! K! MPU!); 680 m, Lid s.n. (O!) — Bajamar, Asplund 1153 s.n. (G! K!); Bourgeau 875 (CGE! E! G! P!); Murray s.n. (BM!); Baxamar (=Bajamar), Bourgeau 1380 (C! E! G! K! MA! P! UPS! W!) — Près de Buenavista, prope El Fraile, Boulos s.n. (CAI!); Asplund 1019 (G! UPS!); Lems 2631 a (L!) — Bco Hoya, S Holidago, 150 m, Lid s.n. (O!); Boulos (B! CAI! MPU!) — Santa Ursula, Perez 8 (K!) — Bco Los Silos, 150 m et 300 m, Lid s.n. (O!) — Cuevas Negras (Bco Los Silos), 500 m, Lid s.n. (O!) — s. loc., Mason s.n. (Lectotype G-DC!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus radicatus* croît dans les stations rocheuses, sur les pentes, sur les murs, etc. Elle résiste à l'érosion grace à sa racine longue et bien développée. Floraison et fructification de mars à septembre, mais principalement de mai à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18 (Larsen 1960; Roux et Boulos 1972).

DISCUSSION. De Candolle (1838) et Schultz Bipontinus (1849—1850) ont signalé la présence de *Sonchus radicatus* dans l'île de Madère et dans la région de

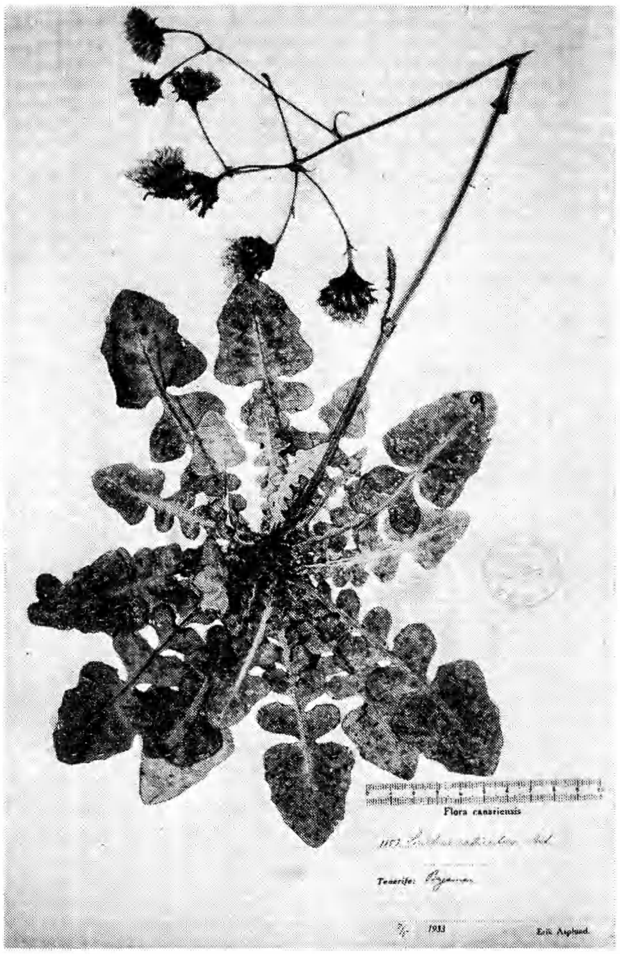

Fig. 11. *Sonchus radicatus*. ASPLUND 1153 (K!).

Mogador, Maroc, d'après des échantillons récoltés par BROUSSONET.

PITARD et PROUST (1908) l'ont signalé dans l'île de Gomera de l'archipel des îles Canaries.

Nous croyons que la plante de Madère représente *S. ustulatus,* et que la plante de Gomera représente *S. gomerensis*. La présence de *S. radicatus* au Maroc est douteuse, car les récoltes faites par BROUSSONET au Maroc étaient souvent mélangées avec celles de îles Canaries.

Nous considérons donc, *Sonchus radicatus* comme espèce endémique de l'île de Tenerife de l'archipel des îles Canaries.

28. **Sonchus gomerensis** BOULOS

BOULOS, in Nytt Mag. Bot. 14: 11, 1967. — Holotype: Vailehermoso, Île de Gomera, BOULOS s.n. (CAI!); isotypes (B! BM! BR! CAI! G! K! MPU! O! P!).

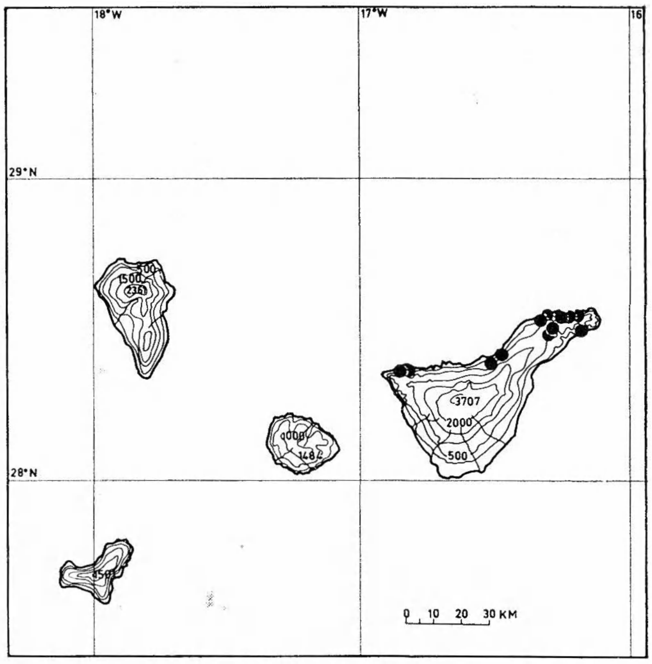

Fig. 12. *Sonchus radicatus*. Distribution.

Sonchus gonzalezpadroni SVENT. Addit. Fl. Canar. 1: 79, t. 32, 1960; nom. illegit.

NOM VERNACULAIRE. *En espagnol:* Serrajón.

USAGES. La plante est consommée par les oies dans la région de Vallehormoso, Île de Gomera, Îles Canaries.

Plante vivace, 30—80 cm de hauteur, ramifiée à la base, feuilles en rosette, capitules nombreux. *Racine* pivotante, richement ramifiée. *Collet* ligneux, 1—2 cm diam., généralement ramifié. *Tige* très courte, ligneuse, avec des feuilles en rosette et portant une ramification florifère cylindrique et creuse. *Feuilles du collet* en rosette, 8—40×3—8 cm, blanchâtres en-dessous, légèrement pubescentes grâce au tomentum blanc qui est plus dense chez les feuilles juvéniles; pinnatiséquées; lobes ± triangulaires, ± ovales ou irréguliers, 5—30×5—25 mm, marges denticulées, sommet aigu; nervure médiane proéminente, 7—10 mm à la base, atténuée vers l'apex. *Feuilles caulinaires* peu nombreuses et moins développées que du collet, 3—5×0,5—1,5 cm, pennipartites à pinnatiséquées, auriculées, oreillettes bien developpées; lobes ± triangulaires, marges

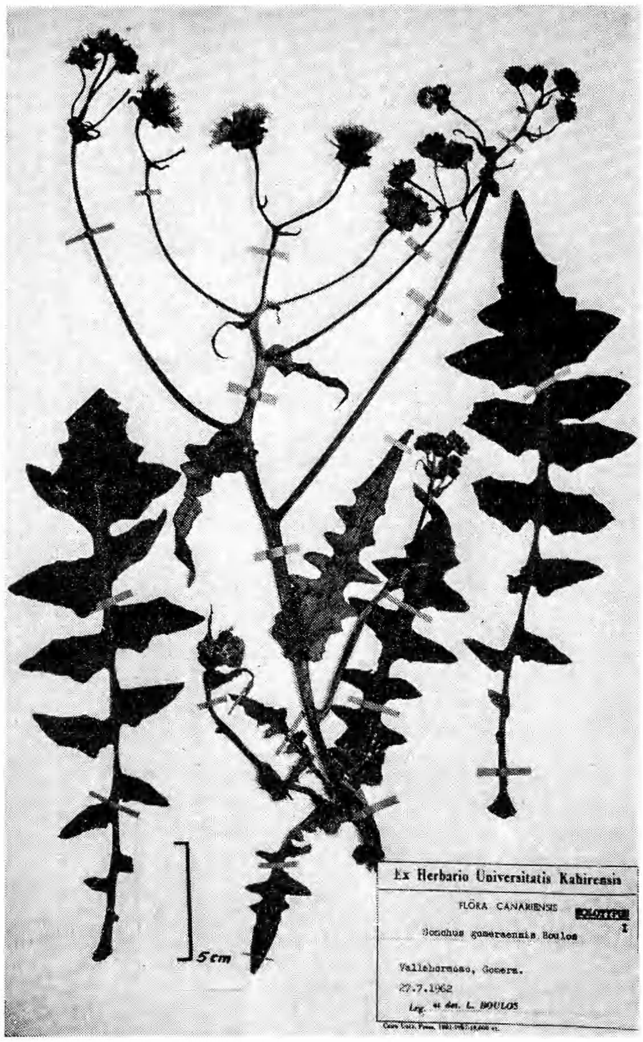

Fig. 13. *Sonchus gomerensis*. Holotype, BOULOS s.n. (CAI!).

légèrement denticulées, sommet aigu. *Pédoncule* 1—7 cm, glabre, à l'aisselle d'une bractée. *Capitules* nombreux, 1,5—2×2,5—3,5 cm lorsqu'ils sont ouverts. Nombre de fleurs 265—480 par capitule. *Écailles de l'involucre* ± 44, sommet cilié; les externes 18, 6—10×2,5—4 mm; les intermédiaires 12, 10—13×2—3 mm; les internes 14, 10—13×1,2—2 mm. *Corolle* jaune, ± 18 mm. *Ligule* 10 mm. *Tube de la corolle* 8 mm. *Anthères* 4 mm. *Akènes* 2,8—3,2×1—1,2 mm, brunâtres, elliptique-ovoïdes, atténués et souvent courbés vers la base, à 2—3 côtes sur chaque face, rugueux transversalement. *Aigrette* 9—11 mm, caduque.

DISTRIBUTION. Gomera, Îles Canaries; endémique.

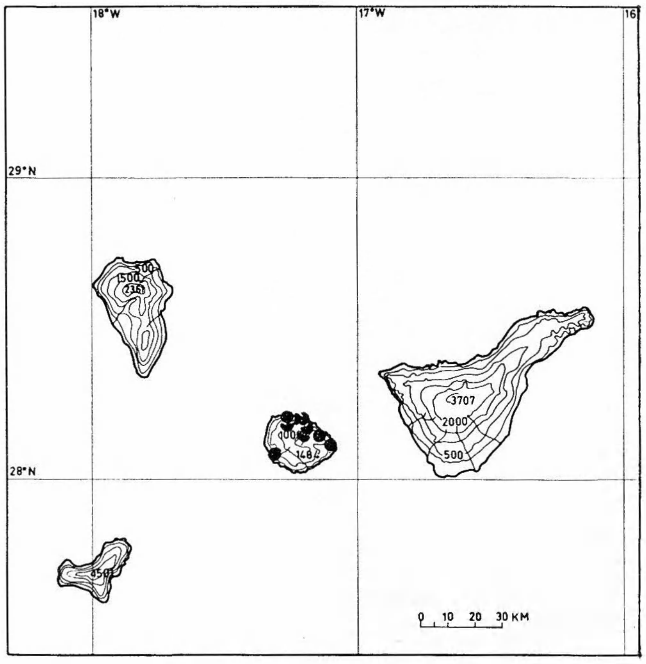

Fig. 14. *Sonchus gomerensis*. Distribution.

Gomera: Valle Gran Rey, BOULOS s.n. (B! CAI! K! MPU!) — Bco Ancones, 600 m, Valle Gran Rey, SVENTENIUS s.n. (in litt.) — Valle Marandón, 600—800 m, SVENTENIUS s.n. (in litt.) — Agulo, 400 m, PITARD s.n. (P!); BOULOS s.n. (CAI! G! K!) — Vallehermoso, BOULOS s.n. (Type, B! BM! BR! CAI! G! K! MPU! O! P!) — Plage de Vallehermoso, près de Punta de Los Organos, BOULOS s.n. (CAI!) — La Laja, 6 km E Vallehermosos, BOULOS s.n. (CAI! G! K!) — Hermigua, Bco Liria, 320 m, LID s.n. (O!) — 2 km S El Cedro (c. 9 km S Hermigua), BOULOS s.n. (CAI!) — El Cedro, S Hermigua, BOULOS s.n. (BR! CAI! LD! O! P! S!) — 3 km N El Cedro, sur la route d'Hermigua, BOULOS s.n. (CAI! K! O!) — Aguajilva, BOULOS s.n. (BM! CAI! MPU!) — 9—11 km de San Sebastian, sur la route principale du nord de l'île, BOULOS s.n. (B! BM! CAI! G! K! LD! MPU! O! P! S!) — Entre Hermigua et Agulo, BURCHARD 370 (E!) — Entre San Sebastian et Aguajilva, BOULOS s.n. (B! BM! CAI! G!) — San Sebastian, MURRAY s.n. (K!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus gomerensis* croît dans des stations humides, sur les bordures des champs cultivés, dans les forêts d'*Erica arborea* L., *Juniperus cedrus* WEBB et BERTH. de l'île de Gomera. Il se trouve également sur des pentes rocheuses, assez sèches dans la région NE de la même île. Dans ces dernières stations, les plantes présentent une forme différente de celles qui croîssent en forêts ou dans les stations humides. En général, cette espèce se rencontre à une altitude de 300 à 800 m. Floraison et fructification d'avril à octobre.

CARACTÈRES CARYOLOGIQUES. 2n =18 (Roux et Boulos 1972).

DISCUSSION. *Sonchus gomerensis* est une espèce polymorphe, endémique de l'île de Gomera des îles Canaries. Elle fut toujours confondue avec *S. radicatus,* une espèce endémique de l'île de Tenerife. Les différences entre ces deux espèces sont nettes. Les akènes chez *S. gomerensis* sont rugueux, 2,8—3,2×1—1,2 mm, alors que chez *S. radicatus* ils sont ± lisses, 2—2,5 ×0,6—0,8 mm. Les feuilles et les tiges sont différentes chez les deux espèces dans leurs détails.

Nous croyons que les individus de *S. gomerensis* qui croîssent dans les milieux secs, représentent un écotype particulier qui pourrait être considéré comme une sous-espèce. Une étude plus détaillée est nécessaire afin de mieux définir et préciser cette épithète infraspécifique.

29. **Sonchus gummifer** Link

Link in Buch, Beschr. Canar. Ins. 146, 1825. — Type: Île de Tenerife, Link, non vide.

NOM VERNACULAIRE. *En espagnol:* Serrajón.

Plante vivace, 20—80 cm de hauteur, peu ou non ramifiée, tige 5—20 cm, portant les bases des feuilles après leur chute, feuilles groupées à la base. *Racine* pivotante, ligneuse. *Collet* ligneux, plein, solide, non ramifié, 1—2 cm diam. *Tige* ligneuse, pleine, brunâtre, courte, portant les bases des feuilles mortes. *Feuilles du collet* en rosette chez les sujets jeunes, 5—15×1—3 cm, glabres, pinnatiséquées, tombant avec l'âge, nervure médiane proéminente; lobes opposés, alternés ou subalternés, ovales ou ± triangulaires, lobe terminal plus grand et large que les lateraux, reserrés à la base, sommet aigu, marges entières ou pourvues de quelques dents écartées. *Feuilles caulinaires* groupées vers la base, 10—25×2—5 cm, pinnatiséquées, les lobes les plus longs au milieu, quelquefois imbriqués; feuilles devenant plus petites et très écartées vers l'inflorescence, à plusieures lobes, petits et égaux, donnant une forme caractéristique à la plante. *Pédoncule* 0,5—7,5 cm, la partie la plus large au-dessous du capitule, glabre, à 1—2 bractées. *Capitules* 1—1,5×2,5 cm pendant l'anthèse, glabres ou très légèrement tomenteux. Nombre de fleurs ± 160 par capitule. *Écailles de l'involucre* ± 55, sommet obtus et cilié; les externes 15, brunâtres, 2—4×2,5 mm; les intermédiaires 14, brunâtres sur leur nervure médiane, 6—9×2 mm; les internes 26, 9×1,5 mm. *Corolle* jaunâtre, ± 11 mm. *Ligule* 6,5 mm. *Tube de la corolle* 4,5 mm. *Anthères* 3 mm. *Akènes* 2,5×1 mm, lancéolés à elliptiques, ± lisses, pourvus d'une côte principale et 2—3 côtes moins importantes sur chaque face. *Aigrette* 7 mm, caduque.

DISTRIBUTION. Île de Tenerife, Îles Canaries; endémique.

Tenerife: Güimar, Bco Badajoz, Bornmüller 2533 (LD!); Boulos s.n. (B! BM! BR! CAI! G! K! LD! MPU! O! P! S!) — Igueste de Candilaria, Bco Martin, 480 m, Lid s.n. (O!) — Bco Balajo, 1 km W Igueste de Anaga, 100 m, Lid s.n. (O!) — Bco Hondo, 560 m, 15 km S Santa Cruz, Lid s.n. (O!) — Santa Cruz, 150—200 m, Burchard 302 (CGE! G! S!); Bornmüller 2535 (G! L! P!); 100 m, Bornmüller 896 (P! W!); Bourgeau 502 (C!) — Valle Seco, N Santa Cruz, Vahl s.n. (C!) — Bco Bufadero, N Santa Cruz, Pitard 234 (G! L! P!); Pitard s.n. (LD!); Bourgeau 1379 (C! G! P! UPS! W!); Murray s.n. (G!) — E Mercedes (N La Laguna), Knoche 95 (MPU!) — Bajamar, Bourgeau 649 (CGE! G! K! P! W!) — El Balaya, 110 m, Valle Las Yeguas, Lid s.n. (O!) — Bco Goteras, 550 m, Lid s.n. (O!) — Bco Herques, 500 et 600 m, Lid s.n. (O!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus gummifer* croît dans les fentes des roches et pentes,

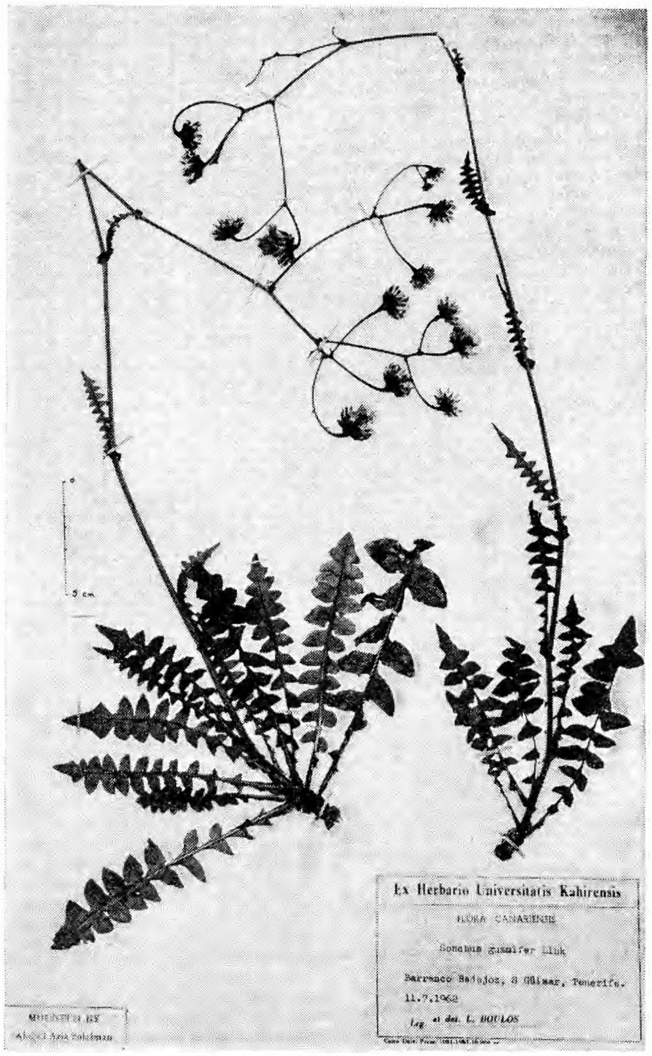

Fig. 15. *Sonchus gummifer*. BOULOS s.n. (CAI!).

relativement fraiches, de la zone maritime, entre 0 et 650 m d'altitude. Floraison et fructification d'avril à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18 (ROUX et BOULOS 1972).

DISCUSSION. *Sonchus gummifer* est une espèce voisine de *S. radicatus*; les deux espèces sont connues de la même île, Tenerife.

Il est facile de distinguer ces deux espèces par les différences macromorphologiques suivants: la tige chez *S. gummifer* est 5—20 cm (rarement plus courte chez les jeunes plantes), ligneuse, solide. Les ramifications florifères sont fragiles, portant des petites feuilles, pourvues de ± 10 paires de lobes égaux et aigus. En outre, la tige chez *S. radicatus* est moins ligneuse, moins longue (1—5 cm) et les ramifications florifères portent des petites feuilles pourvues de ± 3 paires de lobes inégaux et obtus.

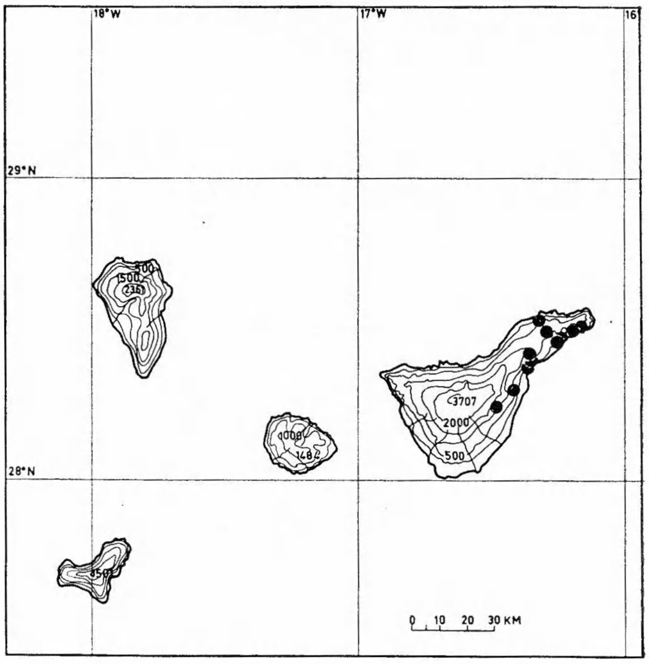

Fig. 16. *Sonchus gummifer*. Distribution.

30. **Sonchus ustulatus** LOWE

LOWE in Trans. Camb. Phil. Soc. 4: 22, 1831. — Type: Île de Madère, non vide; types des variétés (G!).

Sonchus dentatus BANKS ex LOWE, in Trans. Camb. Phil. Soc. 4: 23, 1831; non *S. dentatus* LEDEB., 1829.

Plante vivace, 20—80 cm de hauteur, ligneuse à la base, feuilles en rosette, bases des feuilles persistantes sur les tiges. *Racine* pivotante, ligneuse vers le collet. *Collet* court, ligneux, ± 3 cm diam., non ou peu ramifié. *Tige* ligneuse, pleine, cylindrique, 1—3 cm diam., portant les bases persistantes des feuilles. *Feuilles du collet* polymorphes, 10—45×3—10 cm, groupées en rosette, pennipartites à pinnatiséquées, glabres, à nervure médiane large à la base (8—14 mm), atténuée vers le sommet; lobes 6—12 paires, ± opposés, souvent imbriqués, 1,5—3,5×1—2,5 cm,

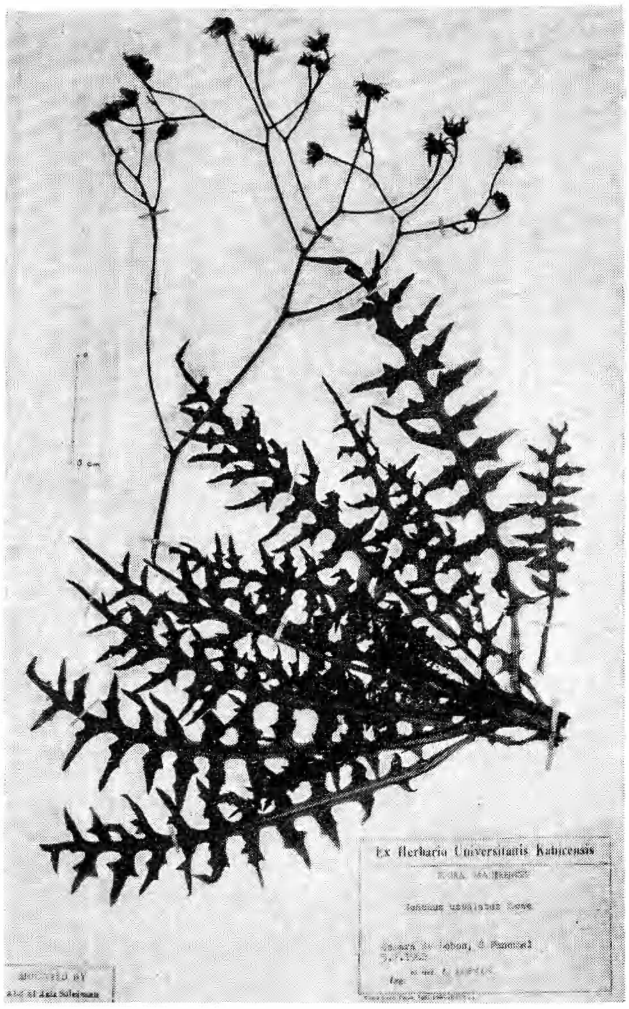

Fig. 17. *Sonchus ustulatus*. BOULOS s.n. (CAI!).

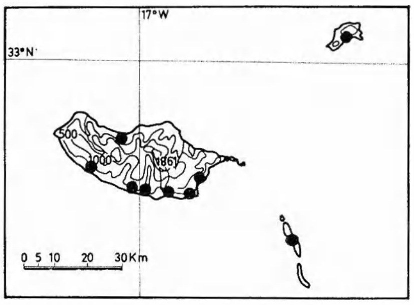

Fig. 18. *Sonchus ustulatus*. Distribution.

triangulaires, oblongs, ovales, elliptiques ou arrondis, marges entières ou irrégulièrement denticulées, sommet aigu, espaces interlobaires arrondis. *Feuilles caulinaires* peu nombreuses, courtes, écartées, pourvues d'un petit nombre de lobes. *Pédoncule* 0,5—8 cm, la partie la plus large au-dessous du capitule, à une bractée. *Capitules* 1,5—1,8×4—4,5 cm pendant l'anthèse. Nombre de fleurs ± 100 par capitule. *Écailles de l'involucre* 30—35, à sommet obtus et cilié; les externes 9—12, 2,5—5×1,5—2 mm; les intermediaires 6—7, 8—10×2 mm; les internes 15—18, 8—10×1,5 mm. *Corolle* jaune, 16—22 mm. *Ligule* 10—15×2—2,5 mm. *Tube de la corolle* 6—7 mm. *Anthères* 4—4,5 mm. *Akènes* 2,75—3×1—1,25 mm, jaune-brunâtres, oblong-elliptiques, comprimés, à 2—3 côtes sur chaque face, ± lisses ou faiblement rugueux. *Aigrette* 6—7 mm, caduque.

DISTRIBUTION. Îles de Madère, Porto Santo et Desertas, archipel de Madère; endémique.

Madère: Funchal, MANDON 163 (C! G! K! LE!); HEER s.n. (G!); LEMANN s.n. (CGE!); BOULOS s.n. (B! BM! CAI! G! K! MPU!) — Caniço, LEMANN s.n. (CGE!) — Porto Novo, BOULOS s.n. (B! CAI! K!) — Ponta Cruz, FAVRAT 85 (G!) — Paraia Formoso, CARTER s.n. (CGE!) — Camara de Lobos, BOULOS s.n. (BM! CAI! G! K!) — Arco, VAHL s.n. (C!) — São Vicente, BOULOS s.n. (B! BM! CAI! G! K!) — Cabo Garajau, PICKERING s.n. (BM!) — s. loc., MASON 249 (CGE! G!); LOWE 197 (G-DC!).

Porto Santo: Rocha das Cenouras, steep volcanic rock facing south, 100 ft, PICKERING 324 (K!).

Desertas: MASON 249 A (P!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus ustulatus* est une espèce assez abondante sur les falaises et roches maritimes près de la mer à l'île de Madère et les îles voisines de Porto Santo et Desertas. Floraison et fructification de juin à janvier.

DISCUSSION. *Sonchus ustulatus* est endémique de l'archipel de Madère. C'est une espèce caractérisée par ses feuilles en rosette, ses tiges courtes et portant les bases persistantes des feuilles après leur chute. Les nervures médianes des feuilles sont très larges à leurs bases (8—14 mm); les fleurs sont longues (16—22 mm). La longueur de la ligule est double celle du tube de la corolle. La ramification florifère porte des capitules lâches et peu nombreux.

LOWE (1868) a distingué trois variétés dans cette espèce: var. *angustifolia* LOWE, var. *imbricata* LOWE, et var. *latifolia* LOWE. Ces variétés ont été décrite d'après les différentes formes des feuilles, caractères peu importants. Nous les considérons, donc, comme synonymes de l'espèce-type.

31. **Sonchus fauces-orci** KNOCHE

KNOCHE, Vagandi Mos, Reiseskizzen, Kanar. Ins. 244, t. 24, 1923. — Lectotype: Bco del Infierno, Adeje, Tenerife, KNOCHE 882 (MPU!).

Plante vivace, 30—50 cm de hauteur, ramifiée à la base, tiges très rugueuses vers un collet volumineux, pédoncule renflé et pourvue de ± 12 bractées dans la partie supérieure. *Collet* volumineux, ± 4 cm diam., ligneux, plein, ramifié. *Tige* rarement ramifiée, ligneuse, tordue, à écorce rugueuse et grisâtre. *Feuilles caulinaires* groupées à la base de l'inflorescence ou au sommet des tiges végétatives, glabres, lyrées, 5—18×3—8 cm, lobes irrégulièrement séquées, marges mucronées. *Pédoncule* 1—6 cm, 0,5 mm diam. dans la partie inférieure qui porte ± 3 bractées; partie supérieure 2,5 mm diam., à ± 12 bractées triangulaires, 1—3×1 mm. *Capitules* 3—12 sur chaque tige florifère, 1—1,5×3 cm pendant l'anthèse. Nombre de fleurs ± 80 par capitule. *Écailles de l'involucre* ± 37; les externes 14, triangulaires à oblancéolées ou elliptiques, 3,5—8×1,5—3 mm; les intermediaires 8, typiquement oblancéolées, 10—13×3—4 mm; les internes 15, oblancéolées, rarement oblongues, 12—14×2—4 mm. *Corolle* jaune, 14—18 mm. *Ligule* 9—12×2—2,5 mm. *Tube de la corolle* 5—6 mm. *Anthères* 5 mm. *Akènes* 3,25—3,5×0,75 mm, brunâtres, oblong-elliptiques, souvent courbés, à ± 3 côtes sur chaque face, ± lisses. *Aigrette* ± 6 mm, caduque.

DISTRIBUTION. SW Tenerife, Îles Canaries; endémique.

Tenerife: Bco del Infierno, Adeje, KNOCHE 882 (Lectotype MPU!) — El Guelgue, Masca, SVENTENIUS s.n. (CAI!); Masca, 600 m, SVENTENIUS 97 (RAB!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus fauces-orci* croît dans les fissures humides entre les rochers à l'ombre, à une altitude de 600—1000 m. Floraison et fructification de février à mai.

DISCUSSION. *Sonchus fauces-orci* est une espèce voisine de *S. pinnatifidus*. Il est facile de distinguer l'une de l'autre par les caractères suivants:

Espèce	nombre de bractées sur la partie supérieure du pédoncule	relation entre la longueur de la ligule et du tube de la corolle
S. fauces-orci	±12	4 : 5 environ
S. pinnatifidus	± 6	2 : 1 environ

32. **Sonchus pinnatifidus** CAV.

CAVANILLES in Anal. Cienc. Nat. 4: 78, 1801; non *S. pinnatifidus* LAG. ex DC., 1838. — Type: Non vide.

Sonchus acidus SCHOUSB. ex WILLD. Sp. Pl. 3: 1511, 1803.

S. glaucus THUNB. in Ges. Naturf. Fr. Berl. Mag. 1: 135, 1807.

S. runcinatus VENT. ex SCH. BIP. in WEBB et BERTH. Hist. Nat. Iles Canar. 3(2): 434, 1849—1850; non *S. runcinatus* (FIORI) ZENARI, 1924.

NOMS VERNACULAIRES. *En espagnol:* Cerrajón — *En allemand:* Sanere Gänsedistel.

Plante vivace, 50—150 cm de hauteur, tiges ligneuses, richement ramifiées surtout à la base, feuilles glabres. *Racine* ligneuse, pivotante. *Collet* ligneux, richement ramifié. *Tige* ramifiée vers le sommet, ligneuse, cylindrique, pleine, 4—15 mm diam. (plus épaisse vers la base), blanchâtre, crème-jaunâtre ou grisâtre, pourvue des traces des feuilles; ramifications florifères lisses, à feuilles courtes et possédant un petit nombre des lobes. *Feuilles caulinaires* 5—30×2—4 cm,

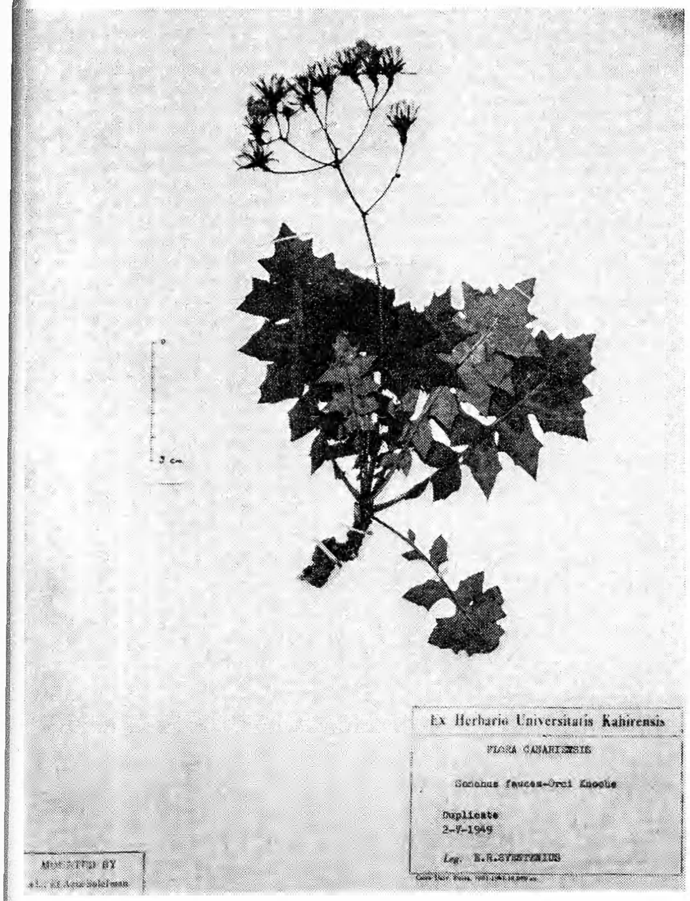

Fig. 19. *Sonchus fauces-orci*. SVENTENIUS s.n. (CAI!).

groupées sur le sommet des tiges végétatives ou à la base des tiges florifères, pinnatiséquées, lobes triangulaires, rarement ± elliptiques, 1—7×0,2—3,5 cm, marges entières, rarement légèrement denticulées, sommet acuminé; nervure médiane proéminente blanchâtre ou crème-jaunâtre, 3 mm diam. à la base. *Pédoncule* 1—8 cm, partie la plus large au-dessous du capitule à ± 6 bractées triangulaires donnant une forme caractéristique à la plante. *Capitules* 1—1,5×3 cm pendant l'anthèse. Nombre de fleurs ± 130 par capitule. *Écailles de l'involucre* ± 40; les externes 15, 4—9×2 mm; les intermediaires 12, 10—14×2—3 mm; les internes 13, 12—15×1,5—2 mm. *Corolle* jaune, 14—20 mm. *Ligule* 6—9×1,5 mm. *Tube de la corolle* 8—11 mm. *Anthères* 4 mm. *Akènes* ± 2,75×1 mm, brunâtres ou ardoises, oblancéolés, comprimés, à 1—2 côtes principales sur chaque face, rugueux. *Aigrette* 7—10 mm, ± caduque.

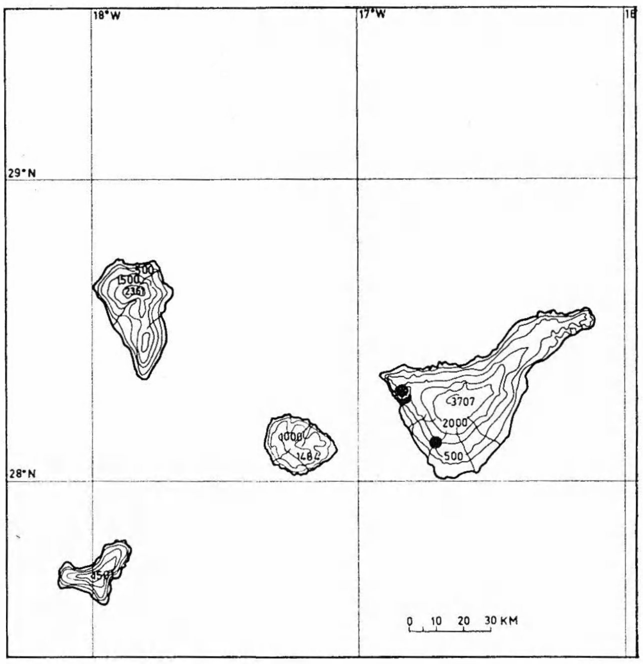

Fig. 20. *Sonchus fauces-orci*. Distribution.

DISTRIBUTION. Fuerteventura et Lanzarote, Îles Canaries, et Maroc.

Fuerteventura: Mña Cardon, 600 m, BURCHARD 295 (CGE! G!); Chilegua, Mña Cardon, BURCHARD 375 (W!).

Lanzarote: Mña Los Helechos, steep rocks facing west, 520 m, LID s.n. (O!); Summit La Mesa, 600 m, LID s.n. (O!) — Famara, 600 m, SVENTENIUS (CAI!) — Teguise, BOURGEAU (in litt.).

Maroc: Mogador, WALL s.n. (S!); BALL s.n. (K!); WALL 794 (S!); IBRAHIM s.n. (G!) — Oued Ksseb, près Mogador, BALANSA s.n. (G! P!) — Dj. Hadid, près Mogador, BALANSA s.n. (P!) — Safi, Sidi Bou Zid (Cap Safi), JAHANDIEZ 72 (G! LD!); LID s.n. (O!); GATTEFOSSÉ s.n. (K! O! P! S!); GATTEFOSSÉ 1381 G! K! MPU! O!); WILCZEK, DUTOIT et PAULSEN s.n. (O!); BOULOS s.n. (B! BM! CAI! G! K! MPU! O!); WILCZEK DUTOIT et GIRARDET 73 (G!); LINDBERG 1896 (K! LD!) — Gaha, Dj. Amsitten, 850 m, JAHANDIEZ 40 (G!) — Agadir, PAILLER 258 (RAB!) — Kheneg El Hammam, SAUVAGE 3779 (RAB!) — Mt. Et Tleta, N Agadir, IBRAHIM 6 (P!) — Ouled Aissa, IBRAHIM s.n. (P!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Au Maroc, *Sonchus pinnatifidus* croît sur les falaises calcaires maritimes à une altitude de 100 m environ. JAHANDIEZ l'a récolté sur des rochers calcaires à Dj. Amsitten à une

Fig. 21. *Sonchus pinnatifidus*. UGGLA s.n. (S!).

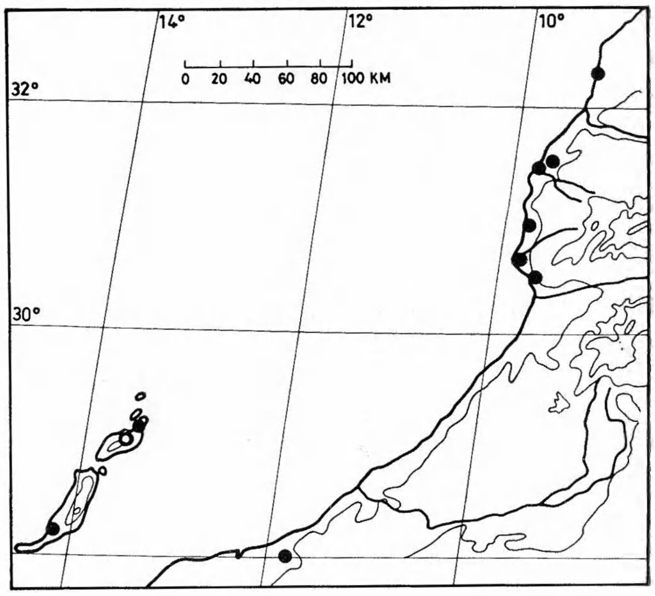

Fig. 22. *Sonchus pinnatifidus*. Distribution.

altitude de 850 m. Aux îles Canaries la plante croît à une altitude de 600 m environ dans des stations rocheuses sèches et montagneuses. Floraison et fructification de février à mai.

CARACTÈRES CARYOLOGIQUES. 2n =18 (ROUX et BOULOS 1972).

DISCUSSION. *Sonchus pinnatifidus* est la seule espèce connue du sous-genre *Dendrosonchus* qui existe hors des trois archipels atlantiques: Cap Vert, Canaries et Madère. Aux îles Canaries elle est connue des îles orientales de l'archipel, Lanzarote et Fuerteventura et en Afrique sur la côte atlantique marocaine à Essauira (Mogador) et Safi.

Cette espèce est caractérisée par ses pédoncules portant ± 6 bractées sur une partie rénflée, au-dessous du capitule. Ce caractère est plus net chez *S. fauces-orci,* espèce endémique de l'île de Tenerife, où le nombre de ces bractées est ± 12.

33. **Sonchus brachylobus** WEBB et BERTH.

WEBB et BERTHELOT, Hist. Nat. Iles Canar. 3(2): 438, 1849—1850. — Lectotype: Cuesta de Silva, Gran Canaria, DESPRÉAUX s.n. (P!).

NOM VERNACULAIRE. *En espagnol:* Cerrajón.

Plante vivace, 20—70 cm de hauteur, rhizomateuse, ligneuse, ramifiée surtout à la base; feuilles totalement glabres, coriaces, lyrées; capitules peu nombreux. *Rhizome* long, ± 1 cm diam., ligneux, à un grand nombre de noeuds, portant des racines fibreuses et très fines. *Collet* ligneux, ramifié. *Tige* ligneuse, ± cylindrique, pleine; vieilles tiges grisâtres, 5—15 mm diam.; les jeunes lisses, crème-jaunâtres. *Feuilles du collet* glabres, 5—8 ×3—4 cm, lyrées, lobe terminal 3—4 cm, presque orbiculaire, lobes lateraux mal développés (une paire, ± 1 cm), souvent manquent donnant une feuille à pétiole long. *Feuilles caulinaires* glabres, lyrées, 6—15×3—7,5 cm; lobe terminal large, deltoïde à ± orbiculaire, 3—8×3—7,5 cm; lobes lateraux 3—4 paires, triangulaires à arrondis, 1—2×1,5 cm, marges légèrement dentées; feuilles supérieures non séquées, ± rhomboïdes, embrassant la tige par 2 oreillettes arrondies. *Pédon-*

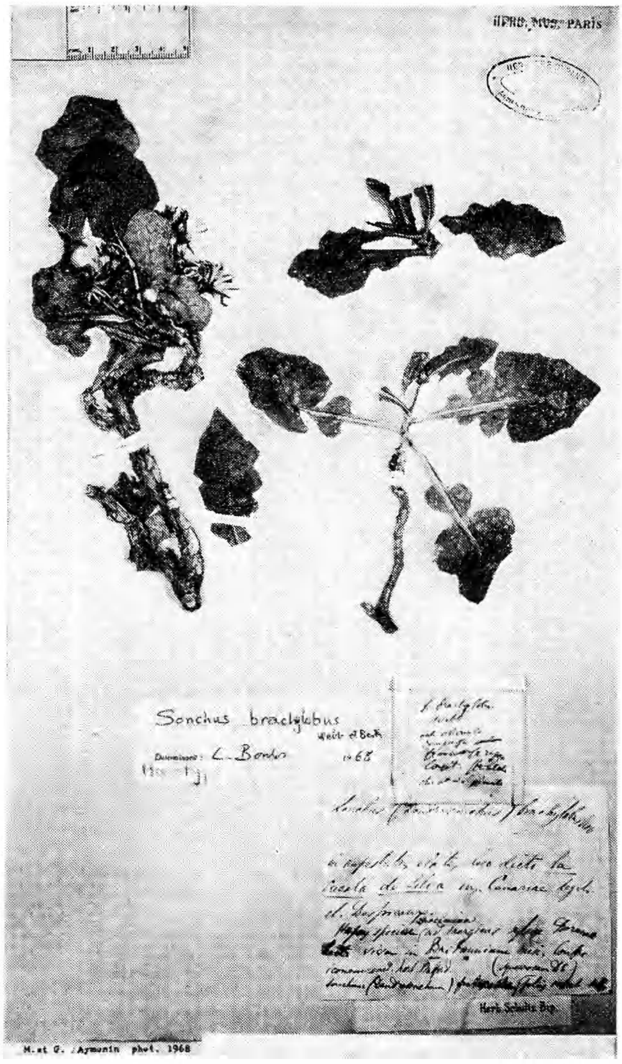

Fig. 23. *Sonchus brachylobus.* Lectotype, DESPRÉAUX s.n. (P!).

cule 1—2,5 cm, à ± 3 bractées triangulaires, 1—2×1 mm. *Capitules* peu nombreux, ± 1,5×2 cm pendant l'anthèse. Nombre de fleurs ± 60 par capitule. *Écailles de l'involucre* ± 27; les externes 10, 2—9×2 mm; les intermediaires 9, 11—14×2 mm; les internes 8, 12—14×2 mm. *Corolle* jaune, 11—13 mm. *Ligule* 7—8×2,5 mm. *Tube de la corolle* 4—5 mm. *Anthères* 4 mm. *Akènes* 2,4—3×0,8—1 mm, brunâtres, étroitement obovales à ± elliptiques, courbés ou étroits, lisses ou rugueux, à 3 côtes sur chaque face. *Aigrette* ± 6 mm, partiellement caduque.

DISTRIBUTION. Gran Canaria, Îles Canaries; endémique.

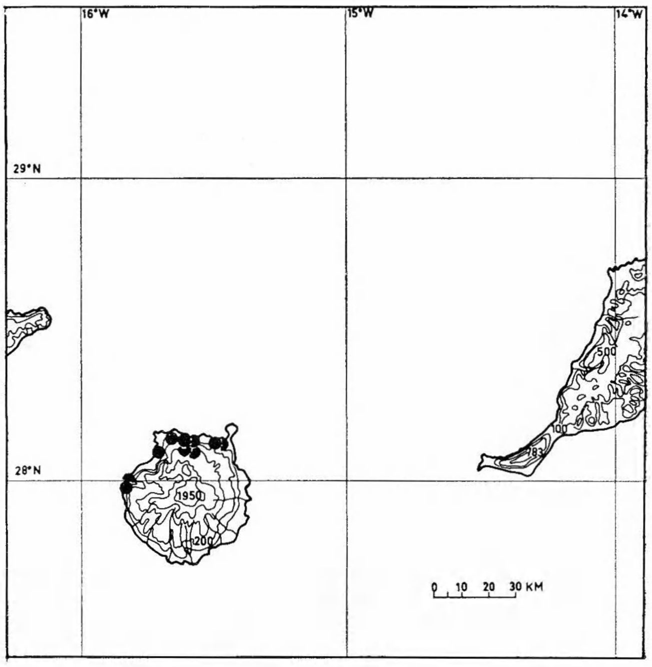

Fig. 24. *Sonchus brachylobus.* Distribution.

Gran Canaria: Roque Marciega, 20 m, Playa San Nicolás, LID s.n. (O!) — Uda del Peñon Bermejo, SW San Nicolás, SUNDING 1834 (O!) — Agaete, Roque Nieves, 70 et 80 m, LID s.n. (O!) — Cuesta de Silva, DESPRÉAUX s.n. (Lectotype P!); MURRAY s.n. (K!); 300 m, BURCHARD 248 (G!) — Entre Guia et El Pagador, BOULOS s.n. (BM! CAI! MPU!) — Près Guia, BOULOS s.n. (B! CAI!); Bco San Felipe, près Guia, PITARD s.n. (P!); above San Felipe, 120 m, SUNDING 1652 (O!); lower part of Bco Moya, SE San Felipe, SUNDING 159 (O!); slopes above San Felipe, facing Bco Calabozo, 120—150 m, SUNDING 270 (O!) — Along the road across Bco Calabozo, 250 m, SUNDING 1704 (O!); Bco Calabozo, 330 m, LID s.n. (O!) — Calbeza del Morro, near Bahia Confital, 50 m, LID s.n. (O!); Bco Cordero, Bahia Confital, 125 m, LID s.n. (O!); Rock at Bahia Confital, LID s.n. (O!) — Hormiguero, 200 m, KUNKEL 10101 (M!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus brachylobus* croît dans la zone maritime, dans les fissures des rochers, à une altitude de 20 à 330 m, N et NW de l'île de Gran Canaria. La période de floraison et de fructification est très courte (3 à 4 semaines), de février à avril.

CARACTÈRES CARYOLOGIQUES. 2n = 18 (ROUX et BOULOS 1972).

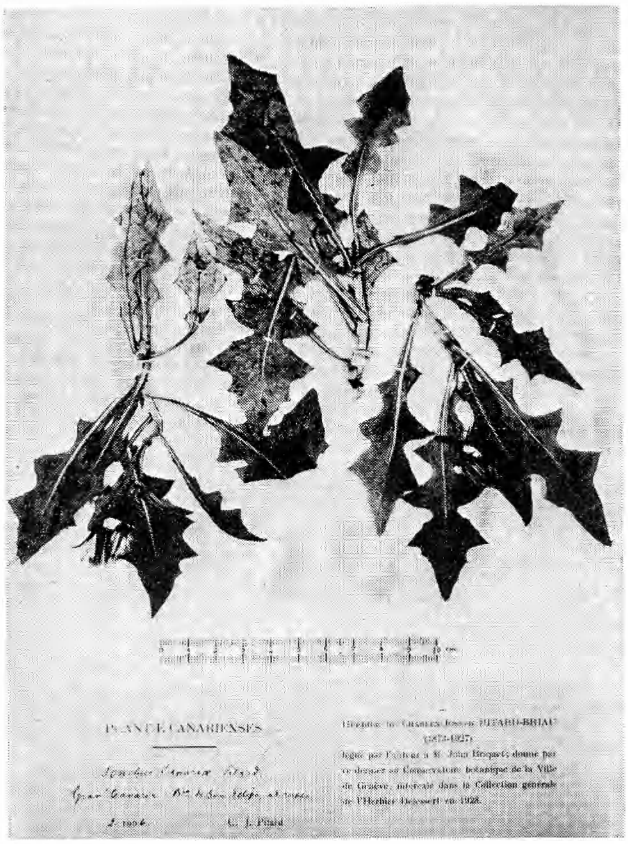

Fig. 25. *Sonchus brachylobus* var. *canariae*. Lectotype, BOULOS s.n. (G!).

DISCUSSION. *Sonchus brachylobus* est caractérisé par ses feuilles totalement glabres, coriaces, lyrées, à un grand lobe terminal. Les capitules sont peu nombreux, à un nombre assez faible de fleurs (± 60) et des écailles (± 27). La ligule est plus longue que le tube de la corolle.

33 a. **Sonchus brachylobus** WEBB et BERTH. var. **canariae** (PITARD) BOULOS

BOULOS in Nytt Mag. Bot. 14: 13, fig. 7, 1967. — Lectotype: Bco San Felipe, 150 m, près Guia, PITARD s.n. (G!).
Sonchus canariae PITARD, in PITARD et PROUST, Iles Canaries Fl. Archipel 261, 1908.

DISTRIBUTION. Gran Canaria, Îles Canaries; endémique.

Gran Canaria: Bco San Felipe, 150 m, près Guia, PITARD s.n. (Lectotype G!, isolectotype P!); slopes above San Felipe, facing Bco Calabozo, 150—200 m, SUNDING 271 (O!); above San Felipe, c. 120 m, SUNDING 1637 (O!) — Roque Marciega, 20, 25 et 30 m, Playa San Nicolás, LID s.n. (O!); La Marciega, W Aldea de San Nicolás, SUNDING s.n. (O!) — Uda del Peñon Bermejo, SW San Nicolás, SUNDING 1833 (O!) — Along the road across Bco Calabozo, 250 m, SUNDING 1703 (O!) — Roque Nieves, near Agaete, 80 m, LID s.n. (O!).

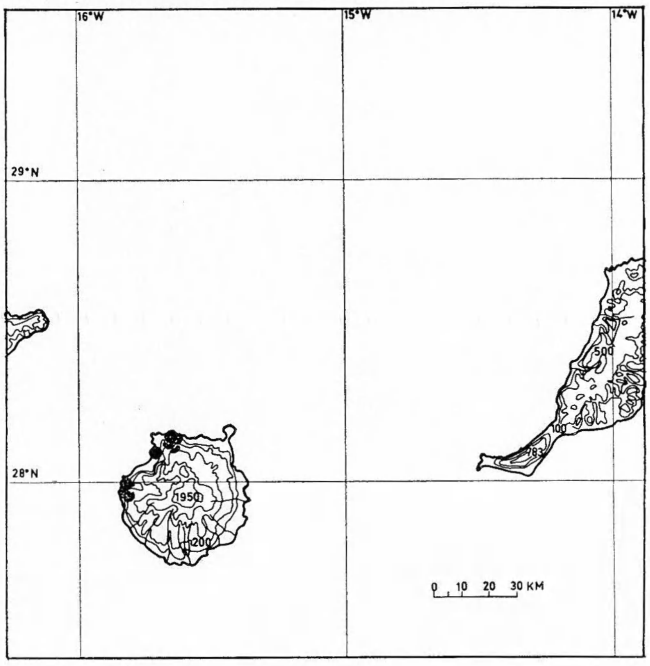

Fig. 26. *Sonchus brachylobus* var. *canariae*. Distribution.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus brachylobus* var. *canariae* croît mélangée avec l'espèce-type. Floraison et fructification de février à avril.

DISCUSSION. La variété *canariae* du *Sonchus brachylobus* est facile à distinguer de l'espèce-type par son port plus court et moins ramifié, ses feuilles moins longues, à lobe terminal ± triangulaire et lobes latéraux plus développés que chez l'espèce-type. Les akènes sont souvent noirâtres, plus rugeux que chez l'espèce-type. Des formes intermédiaires entre les deux taxons ont été observées.

34. **Sonchus pinnatus** AIT.

AITON in Hort. Kew. (ed. 1) 3: 116, 1789. — Lectotype: Madère, MASON s.n. (BM!).
Sonchus hyoseridifolius HORNEM., Hort. Hafn. 2: 752, 1813—1815.
S. pinnatus AIT. 1789 var. *latiloba* LOWE, Man. Fl. Mad. 1: 551, 1868.

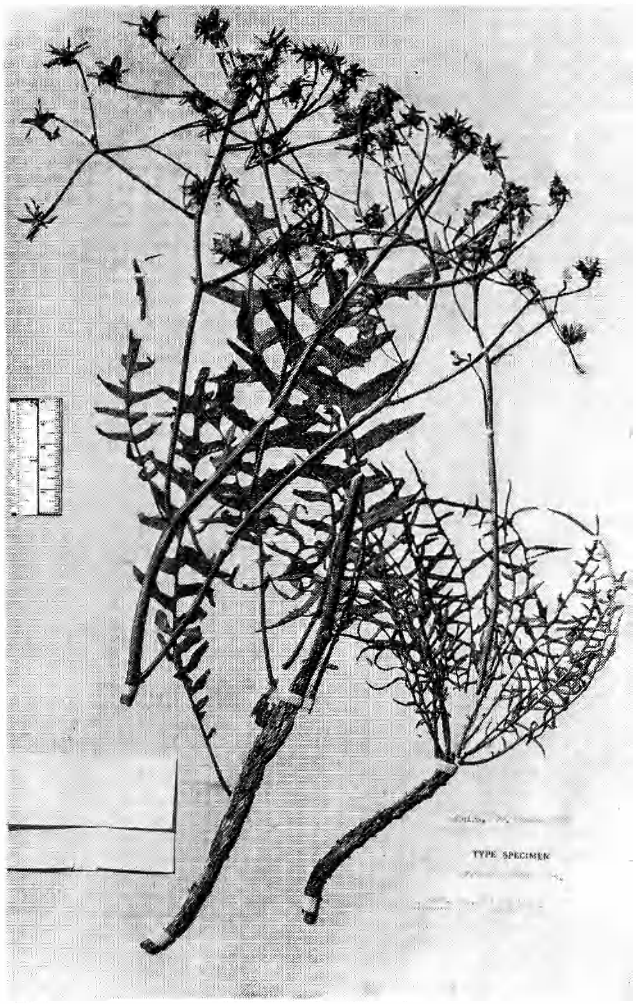

Fig. 27. *Sonchus pinnatus*. Lectotype, Mason s.n. (BM!).

S. pinnatus Ait. 1789 var. *angustiloba* Lowe, Man. Fl. Mad. 1: 551, 1868.

NOMS VERNACULAIRES. *En anglais:* Wing-leaved Sow-thistle — *En allemand:* Gefiederte Gänsedistel.

Arbrisseau, 60—180 cm de hauteur, ramifié, glabre, tiges ± lisses, inflorescence lâche. *Tige* ligneuse, ± lisse, ramifications agées ± cylindriques, pleines, longitudinalement rugueuses avec des traces des feuilles; jeunes tiges florissantes cylindriques et creuses. *Feuilles caulinaires* 5—27×2—10 cm, pennipartites à pinnatiséquées; lobes 0,5—5×0,3—2 cm, triangulaires, linéaires, lancéolés, ± ovoïdes, etc., irrégulièrement séquées, quelquefois entiers, opposés ou alternés, souvent unis par deux, les plus longs et larges au centre de la feuille; nervure médiane jaune-brunâtre, proéminente, 1—3 mm à la base et graduellement atténuée vers le sommet. *Pédoncule* 1—9 cm, à 2—5 bractées. *Capitules* 10×7—8 mm lorsqu'ils sont fermés. Nombre de fleurs 100—150 par capitule. *Écailles de l'involucre* 30—37; les externes 6—8, 2—5×1,5—2 mm; les intermédiaires 6—8, 7—10×2,5—3 mm; les internes 16—22, 9—11×1,5 mm. *Corolle* jaune, 11—13 mm. *Ligule* 5,5—7 ×1,2—1,5 mm. *Tube de la corolle* 5,5—7 mm. *Anthères* 3,5—3,75 mm. *Akènes* 2,25 —2,75×0,8—1 mm, ± elliptiques, comprimés, à 3—4 côtes sur chaque face; deux types d'akènes dans le même capitule: les unes jaunâtres et lisses, les autres brunâtres et transversalement rugueux. *Aigrette* 4—5 mm, caduque.

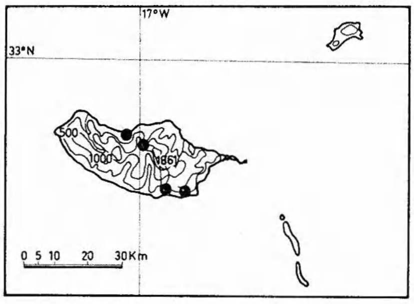

Fig. 28. *Sonchus pinnatus*. Distribution.

DISTRIBUTION. Île de Madère, endémique.

Madère: Pico Grande, Lowe 390 (BM! CGE! G! K! P!) — Caminho Central, Vahl s.n. (C!); 1300—1400 m, Bornmüller 889 (G! LD! LE! P! W!) — Malhada Velha, 1000 —1200 m, Mandon 162 (BM! C! G! K! P! W!) — Près St. Vicente, Lemann s.n. (CGE!) — 1 km E Funchal, Boulos s.n. (B! BM! CAI! MPU! O!) — Entre Funchal et Caniço, Riley 39 (BM! K!) — Ravine (Louros), E Funchal, 300 ft, Murray s.n. (BM!) — s. loc., Webb s.n. (G! K!); Mason 247 (BM! CGE! G! W!); Mason s.n. (Lectotype BM!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Arbrisseau, pousse dans les milieux rocheux, surtout à 1000—1400 m d'altitude. Floraison d'avril à août et fructification de juin à septembre.

CARACTÈRES CARYOLOGIQUES. 2n =18 (Stebbins et al. 1953).

PARTICULARITÉES PALYNOLOGIQUES. Epaississement polaire assez variable (parfois type 1 et 2, le plus souvent 3; Saad 1961).

DISCUSSION. *Sonchus pinnatus* est une espèce endémique de l'île de Madère et caractérisée par ses capitules grands et peu nombreux à pédoncules longs et fixés sur des tiges florifères lâches. Les feuilles sont assez variables (largeur 2—10 cm) et portant presque toujours des lobes irrégulièrement séqués.

Nous considérons les deux variétés *angustiloba* Lowe et *latiloba* Lowe comme simple formes sans valeur taxonomique, car elle sont définies d'après la forme non stable des feuilles, et surtout d'après la largeur des lobes qui sont des caractères peu valables pour établir des variétés nouvelles.

A propos de la valeur taxonomique de ces taxons, Lowe (1868) écrit: «In both these forms (c.-à-d. *angustiloba* et *latiloba*), which pass into each other through numberless gradations, the number of pinnae and all other characters employed by Schultz have no sort of constancy, varying on different branches of the same plant.»

35. **Sonchus palmensis** (Sch. Bip.) Boulos

Boulos in Nytt Mag. Bot. 14: 13, fig. 8, 1967. — Type: non vide.

Sonchus pinnatus Ait. 1789, var. *palmensis* Sch. Bip. in Webb et Berth. Hist. Nat. Iles Canaries 3: 441, T. 130, 1849—1850.

NOMS VERNACULAIRES. *En espagnol:* Lechuga, Lechera de Monte.

Arbrisseau, 1—2,5 m de hauteur, ramifié à partir d'environ 30 cm du collet, feuilles glabres sauf à l'état juvénile, capitules nombreux. *Racine* pivotante, 20—50×2—5 cm, ramifiée. *Collet* ligneux, non ramifié, 4—12 cm diam., lisse. *Tige* ligneuse, cylindrique, pleine, 2—9 cm diam. à la base, longitudinalement rugueuse avec des traces des feuilles proéminentes. *Feuilles caulinaires* 10—40×3—9 cm, pennipartites à pinnatiséquées, tomenteuses à l'état juvénile, autrement glabres; lobes 1—5×0,3—2 cm, ± opposés, ± triangulaires, linéaires-lancéolés, légèrement serrés, sommet aigu; nervure médiane proéminente, 2—3,5 mm diam. à la base, atténuée vers le sommet. *Pédoncule* 2—22 mm à 1—3 bractées. *Capitules* 8—12×3,5—5 mm lorsqu'ils sont fermés, 14—16×20 mm pendant l'anthèse. Nombre de fleurs 36—48 par capitule. *Écailles de l'involucre* 24—29; les externes 8—10, 1,5—3,5×1,5—2 mm; les intermédiaires 6—7, 5—7×1,5 mm; les internes 10—12, 9—10×1—1,5 mm. *Corolle* jaune-orangé, 12—12,5 mm. *Ligule* 6—6,5 mm. *Tube de la corolle* 6 mm. *Anthères* 4—4,25 mm. *Akènes* 2,25—2,75×0,75—1 mm, brunâtres, comprimés, ± elliptiques, très rugueux, à 2—3 côtes sur chaque face. *Aigrette* 6—8 mm, ± caduque.

DISTRIBUTION. La Palma, Îles Canaries; endémique.

La Palma: Mazo, Boulos s.n. (BM! CAI! MPU! O!) — Breña Alta, 400 m, Lid s.n. (O!); Boulos s.n. (B! BM! BR! CAI! G! K! MPU! O! P!); Las Ledas, Breña Alta, Boulos s.n. (CAI! S!) — Breña Baja, Boulos s.n. (B! CAI! MPU! O!); Polvacera, Breña Baja, Boulos s.n. (BM! BR! CAI!) — San Pedro, S Santa Cruz, Boulos s.n. (B! BM! BR! CAI! G! K! LD! MPU! O! P! S!); Près San Pedro, S Santa Cruz, Boulos s.n. (B! CAI! G! K!) — Barlovento, E Bco Tapaciegos, 600 m, Lid s.n. (O!) — 4—5 km W Barlovento, Boulos s.n. (CAI! LD! P!) — Gallegos, c. 9 km W Barlovento, Boulos s.n. (BR! CAI! P! S!) — Bco Herradura, 200 m, Lid s.n. (O!) — Bco de Rio, 400—500 m, Bornmüller 2537 (G!) — Bco La Galga, 700 m, Lid s.n. (O!); Bco Nogales, La Galga, 400 m, Pitard 233 (G! L! P!) — Bco del Agua (Sauces), 430 m, Lid s.n. (O!) — Los Lances, 350 m, Burchard 355 (CGE! E! G!); Kuntze s.n. (K!) — Casa Ferraz (El Granel), 450 m, Lid s.n. (O!) — Los Tilos, Røstad s.n. (LD!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Arbrisseau assez commun

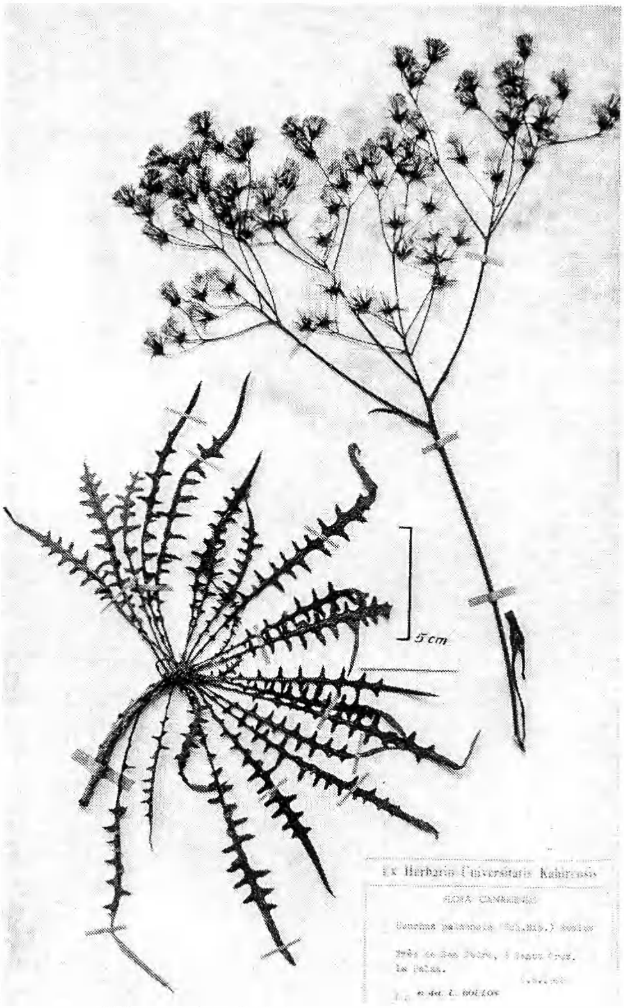

Fig. 29. *Sonchus palmensis*. BOULOS s.n. (CAI!).

sur les bordures des champs cultivés et sur les falaises, entre 200 et 700 m d'altitude. Floraison et fructification de mars à juillet.

CARACTÈRES CARYOLOGIQUES. 2n =18, HENIN in BOULOS (1960); ROUX et BOULOS (1972).

PARTICULARITÉES PALYNOLOGIQUES. Type ordinaire de la section *Pinnati*, mais taille très variable.

DISCUSSION. Nous traitons *Sonchus palmensis* comme une espèce distincte, et non pas comme une variété de *Sonchus pinnatus* pour les raisons suivantes:

1. Le nombre très faible de fleurs par capitule (36—48); c'est le nombre le plus faible parmi les espèces connues du genre *Sonchus*.

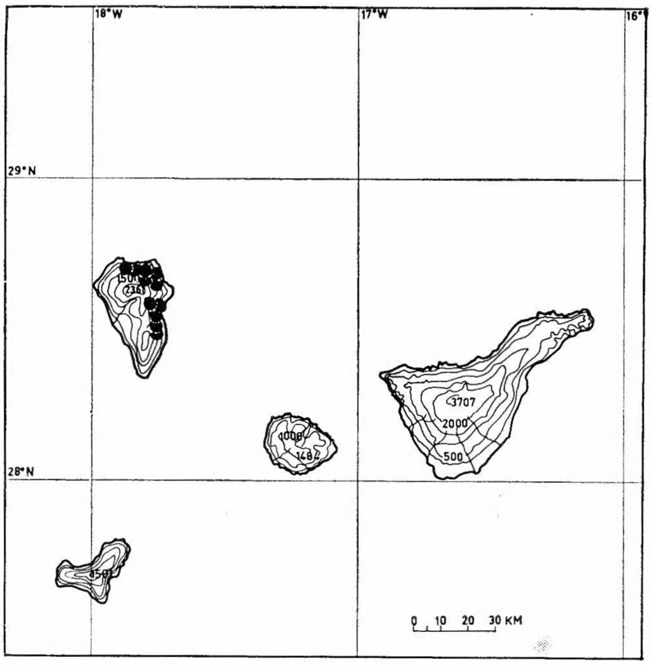

Fig. 30. *Sonchus palmensis*. Distribution.

2. Les pédoncules de *S. palmensis* sont beaucoup plus courts (2—22 mm) que ceux du *S. pinnatus* (1—9 cm). La plupart des pédoncules de *S. palmensis* sont moins de 15 mm de longueur.

3. Les capitules chez *S. pinnatus* sont plus larges et plus volumineux que chez *S. palmensis*.

Les caractères morphologiques de ces deux espèces sont en général trop différents pour que *S. palmensis* puisse être considéré comme variété de *S. pinnatus*.

LOWE (1868) écrit à propos de cette espèce: «The Canarian var. β *palmensis* WB. t. 130, with its much smaller flowers, etc., requires further investigation. It looks like something very different from any of the Madeira plant.»; ce qui est conforme à notre point de vue.

36. **Sonchus canariensis** (SCH. BIP.) BOULOS

BOULOS in Nytt Mag. Bot. 14: 14, 1967. — Lectotype: Bco de la Vierge, Gran Canaria, BOURGEAU 15 (P!).

Fig. 31. *Sonchus canariensis*. Lectotype, BOURGEAU 15 (P!).

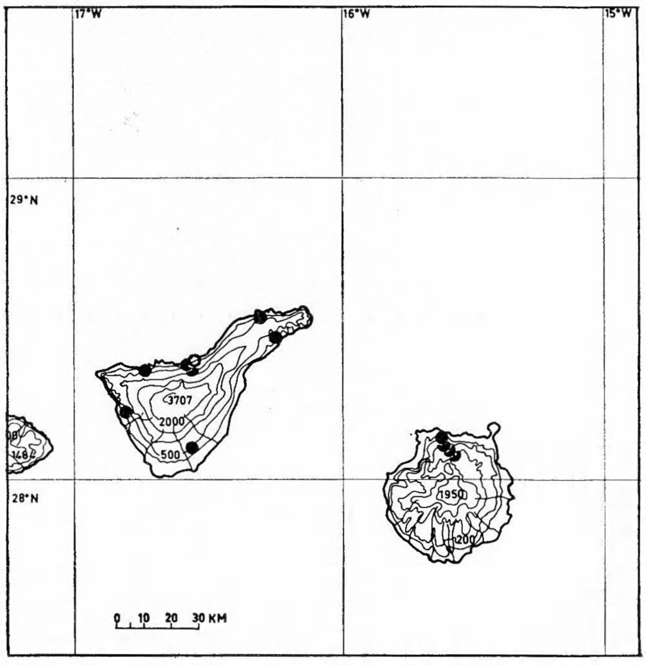

Fig. 32. *Sonchus canariensis*. Distribution. — ○: *S. canariensis* ssp. *orotavensis*.

Sonchus pinnatus AIT. 1789, var. *canariensis* SCH. BIP. in WEBB et BERTH. Hist. Nat. Iles Canar. 3: 411, 1849—1850.

Arbrisseau, 1,5—2,5 m de hauteur, ramifié, feuilles glabres et pinnatiséquées, inflorescence lâche. *Tige* ligneuse, cylindrique, pleine, ramifications âgées rugueuses avec des traces des feuilles, jeunes tiges fleurissantes creuses. *Feuilles caulinaires* 10—40×6—12 cm, souvent auriculées, pinnatiséquées; lobes opposés ou alternés, 1—6×0,3—1,2 cm, ± triangulaires, lancéolés ou linéaires-lancéolés, marges entières ou légèrement denticulées, sommet aigu; nervure médiane proéminente, jaune-brunâtre, large à la base et atténuée vers le sommet. *Pédoncule* 1—7 (3) cm, à 1—2 petites bractées. *Capitules* 10×8 mm lorsqu'ils sont fermés, 12—15×25—30 mm pendant l'anthèse. Nombre de fleurs 90—165 par capitule. *Écailles de l'involucre* 40—57; les externes 10—12, souvent poilues-glanduleuses sur leurs parties médianes, 2—4×1,5—2 mm; les intermédiaires 10—18, moins poilues-glanduleuses que les externes, 6—9×1,5—2 mm; les internes 20—27, glabres, 8—10×0,8—1,5 mm. *Corolle* jaune, 14—15 mm. *Ligule* 7—7,5 mm. *Tube de la corolle* 7—7,5 mm. *Anthères* 3,5 mm. *Akènes* 3—3,2×0,8—1,1 mm, jaune-brunâtres, brunâtres ou noirâtres, comprimés, ± elliptiques, à 1—2 côtes sur chaque face, très rugueux transversalement. *Aigrette* 6—7 mm, caduque.

DISTRIBUTION. Tenerife et Gran Canaria, Îles Canaries; endémique.

Tenerife: Mña Horca, Puerto Orotava, BURCHARD s.n. (Z!); Risco de Oro, Puerto Orotava, BURCHARD 98 (M! MANCH! O!); Malpais, Orotava, PEREZ s.n. (K!) — Entre Mña Chaves et la mer, MURRAY s.n. (BM! K!) — Abona-Granadilla, KUNTZE s.n. (K!) — Guia, ?TRISTRAM s.n. (BM!) — Bco Hoya, S Hidalgo, 300 m, LID s.n. (O!) — Mña Taco, Santa Cruz, BURCHARD 200 (MANCH! O! ZT!) — Domingo, Icod de Los Vinos, SCHRÖTER s.n. (ZT!).

Gran Canaria: Bco de la Virgen, BOURGEAU 15 (Lectotype P!); BOURGEAU 873 (BM! G! K! P!); BOURGEAU s.n. (G!) — SW San Fernando, Moya-Fontanales Rd., c. 800 m, SUNDING s.n. (O!) — Mña Gallego, above Cenobio de Valeron, 360 m, SUNDING 1698 (O!) — Mña Doramas, 800 m, KUNKEL 9845 (M!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Arbrisseau rare, croît dans les vallées protégées, à une altitude de 300 à 800 m. Floraison de mars à mai et fructification d'avril à mai.

PARTICULARITÉES PALYNOLOGIQUES. Epaississement polaire assez archaïque: type 1 (SAAD 1961) très caractéristique.

DISCUSSION. *Sonchus canariensis* est une espèce caractérisée par le grand nombre des écailles de l'involucre (40—57). Les écailles externes et la plupart des intermédiaires sont souvent poilues-glanduleuses. Les lobes des feuilles sont entiers ou légèrement denticulés et ne dépassent pas 1 cm de diam.

En général, l'espèce est polymorphe, surtout en ce qui concerne la forme des feuilles.

36 a. **Sonchus canariensis** (SCH. BIP.) BOULOS subsp. **orotavensis** BOULOS

BOULOS in Nytt Mag. Bot. 14: 15, fig. 9, 1967. — Holotype: Tenerife, Orotava, Bco San Antonio, 250 m, SVENTENIUS s.n. (CAI!).

DISTRIBUTION. Tenerife, Îles Canaries; endémique.

Tenerife: Orotava, Bco San Antonio, 250 m, SVENTENIUS s.n. (Holotype, CAI!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus canariensis* ssp. *orotavensis* est une plante très rare, connue seulement de la collection du type. Elle croît à une altitude de 250 m. Floraison et fructification de mars à mai.

Fig. 33. *Sonchus canariensis* ssp. *orotavensis*. Holotype, SVENTENIUS s.n. (CAI!).

DISCUSSION. Les capitules chez *Sonchus canariensis* ssp. *orotavensis* sont moins grands que chez l'espèce-type. Le nombre de fleurs par capitule est 50 environ; les feuilles sont denses, auriculées, régulièrement pinnatiséquées à lobes ± linéaires et entières.

37. **Sonchus fruticosus** L. FIL.

LINNAEUS FIL., Suppl. Pl. 346, 1781; non *S. fruticosus* JACQ. 1786; non *S. fruticosus* NORONHA, 1790; nom. nud. — Lectotype: Madère, MASON 248 (P!).

Sonchus laevigatus WILLD. Enum. Hort. Berol. Suppl. 54, 1813.

S. lyratus WILLD. Enum. Hort. Berol. Suppl. 53, 1813.

S. squarrosus DC. Cat. Hort. Monsp. 147, 1813.

NOMS VERNACULAIRES. *En anglais:* Shrubby Sow-thistle — *En allemand:* Strauchartige Gänsedistel — *En portugais:* Sarralha.

Arbrisseau, 0,5—2 m de hauteur, ramifié à 20—30 cm de la base, feuilles grandes, larges et glabres, capitules volu-

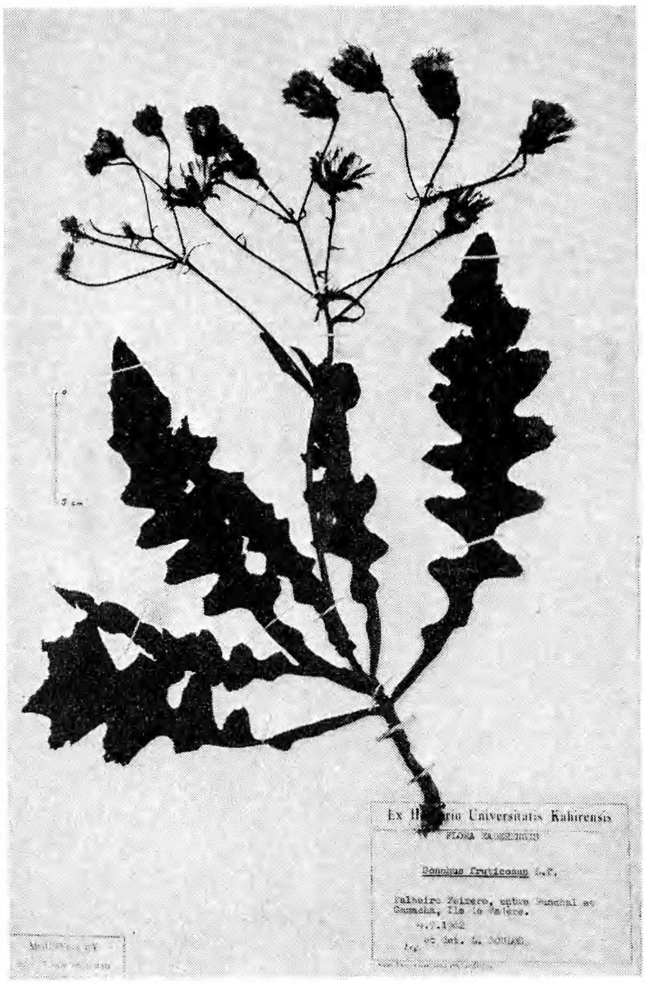

Fig. 34. *Sonchus fruticosus*. BOULOS s.n. (CAI!).

mineux et nombreux. *Racine* ligneuse vers le collet, pivotante. *Collet* ligneux, épais, non ramifié. *Tige* ligneuse, épaisse, ± cylindrique portant les bases des feuilles après leur chute. *Feuilles caulinaires* 20—70×10—18 cm, pennipartites à pinnatiséquées; lobes 4—10 paires, ± triangulaires, 1—8×1—4 cm, marges entières ou irrégulièrement dentées, sommet arrondi, obtus ou aigu, éspaces interlobaires arrondis; nervure médiane proéminente, 4—8 mm à la base, atténuée vers le sommet. *Pédoncule* 2—11 cm, à une bractée à la base. *Capitules* 2,5—3,5×6—8 cm pendant l'anthèse. Nombre de fleurs ± 400 par capitule. *Écailles de l'involucre:* l'involucre est caractérisé par la présence de 4—8 bractées, au-dessous de l'involucre propre, 1—1,5×2—3 mm,

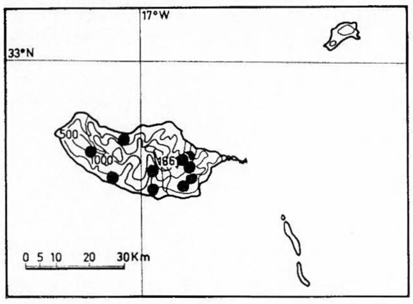

Fig. 35. *Sonchus fruticosus*. Distribution.

coriaces, marges entières, sommet obtus; les écailles propres 60; les externes 15, 12—16×4—6 mm, coriaces; les intermédiaires 11, 16—20×3—5 mm; les internes 34, 19—22×1,5—2 mm. *Corolle* jaune, 20—27 mm. *Ligule* 11—15×2—3 mm. *Tube de la corolle* 9—12 mm. *Anthères* 4—5 mm. *Akènes* 3,5—4,5×1,2 mm, jaune-brunâtres ou ardoises, linéaire-élliptiques, comprimés, à 2—3 côtes principales sur chaque face, transversalement rugueux. *Aigrette* 12—14 mm, ± caduque.

DISTRIBUTION. Île de Madère, endémique.

Madère: Melhada Vhela, 800—1200 m, MANDON 164 (BM! C! G! LE! P! W!) — Rabaçal, 900 m, BORNMÜLLER 888 (G! P! W!) — Camacha, LOWE 371 (G!); LOWE s.n. (G!); BOULOS s.n. (B! BM! CAI! K!) — Grãn Curral, BORNMÜLLER 888 c (LD!) — Ribeiro Frio, LEMANN s.n. (CGE!) — Eira de Fora, 4 km N Camacha, BOULOS s.n. (CAI! MPU! O!) — Yoão Frino, 7 km N Camacha, BOULOS s.n. (CAI! G!) — Palheiro Feirero, entre Funchal et Camacha, BOULOS s.n. (BM! BR! CAI! G! K! P!) — São Vicente, LEMANN s.n. (CGE!) — W Sto Antonio, CLARKE 116 (K!) — Ribeira, VAHL s.n. (C!) — Santa Luzia, LEMANN s.n. (CGE!) — s. loc. NORMAN s.n. (CGE!); MASON 248 (P!); WEBB s.n. (P! UPS!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Arbrisseau croissant dans des stations rocheuses et champs cultivés, entre 800 et 1200 m d'altitude. Floraison et fructification d'avril à août.

CARACTÈRES CARYOLOGIQUES. 2n =18, STEBBINS et al. (1953); ROUX et BOULOS (1972).

DISCUSSION. *Sonchus fruticosus* est une espèce endémique de l'île de Madère et caractérisée par:

1. Ses capitules grands et nombreux.
2. La présence de 4—8 bractées au-dessous de l'involucre.
3. Le grand nombre de fleurs (400 environ), et des écailles d'involucre (60 environ), par capitule.
4. Ses fleurs longues (20—27 mm).
5. Ses feuilles longues (atteignant 70 cm) et larges (atteignant 18 cm).

D'après WEBB et BERTHELOT (1840), *S. fruticosus* existe aux Îles Canaries, mais les échantillons d'herbier appartenant à cette espèce que nous avons examinés ne confirment pas ce dire, car tous les specimens proviennent de l'île de Madère.

38. **Sonchus lidii** BOULOS

BOULOS in Nytt Mag. Bot. 14: 15, fig. 10, 1967. — Holotype: Hierro, El Golfo, Los Llanillos, BORNMÜLLER 2538 (G!); déterminé *Sonchus pinnatus* AIT. var. *Canariensis* SCH. BIP.

Arbrisseau, 80—140 cm de hauteur, feuilles longues, capitules grands et nombreux. *Racine* pivotante, ligneuse et ramifiée. *Collet* ligneux, ± cylindrique, solide, plein, 4—8 cm diam., rarement ramifié. *Tige* ligneuse, pleine, lisse, blanchâtre, ± cylindrique, ± 5 cm diam., moins épaisse vers le sommet; tiges supérieures rugueuses, portant les bases des feuilles après leur chute; tiges florifères presque nues, creuses, richement ramifiées. *Feuilles caulinaires* glabres, coriaces, 30—55×6—14 cm, devenant plus courtes gradualement vers l'inflorescence, pinnatiséquées; lobes ± 12 paires, ± opposés, 3—7×0,5—2 cm, les plus longs au milieu, ± triangulaires ou linéaires-elliptiques, courbés vers le sommet, marges entières, sommet pointu et piquant; nervure médiane proéminente, 3—4 mm diam. à la base. *Pédoncule* 3—8 cm, légèrement tomenteux au-dessous du capitule, plus tomenteux à la base. *Capitules* 2×4 cm pendant l'anthèse. Nombre de fleurs ± 200 par capitule. *Écailles de l'involucre* ± 52; les externes 9, 5—7× 2—3,5 mm; les intermediaires 16, 7—13 ×3—4 mm; les internes 27, 1,2—1,5× 1—2 mm. *Corolle* jaune, 16—18,5 mm. *Ligule* 8—9,5 mm. *Tube de la corolle* 8—9,9 mm. *Anthères* 4—4,5 mm. *Akènes* 3—3,5×1—1,2 mm, brunâtres, oblancéolés, à 2—3 côtes sur chaque face, fortement rugueux transversalement. *Aigrette* 8—10 mm, très caduque.

DISTRIBUTION. Hierro, Îles Canaries; endémique.

Hierro: Los Llanillos, 200—300 m, El Golfo, BORNMÜLLER 2538 (Holotype G!); BOULOS s.n. (B! CAI! G! K! O!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus lidii* croît dans des stations relativement sèches, sur les bordures des champs de vignes dans la région de «El Golfo» de l'île d'Hierro, à une altitude de 200—300 m. Floraison et fructification de mars à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18, ROUX et BOULOS (1972).

DISCUSSION. *Sonchus lidii* est une espèce endémique de l'île d'Hierro et caractérisée par ses feuilles longues, glabres et coriaces; les lobes sont ± opposés; sa ramification florifère à capitules nombreux et des pédoncules longs (3—8 cm) et par le nombre assez élevé des fleurs (± 200) et des écailles d'involucre (± 52) par capitule.

39. **Sonchus gandogeri** PITARD

PITARD in PITARD et PROUST, Iles Canar. Fl. Archipel 260, 1908. — Holotype: Hierro, Riscos de Casitas, PITARD s.n. (P!); isotype (G!).

Fig. 36. *Sonchus lidii.* Holotype, BORNMÜLLER 2538 (G!).

Arbrisseau, 1—1,8 m de hauteur, à tronc volumineux, ramifié, tiges blanchâtres. *Racine* ligneuse, richement ramifiée. *Collet* ligneux, 10—15 cm diam., ramifié. *Tige* ligneuse, irrégulièrement ramifiée, rameaux volumineux, blanchâtres; tiges florifères 30—50 cm, cylindriques, creuses. *Feuilles caulinaires* 10—30×4—10 cm, groupées à l'extrêmité des rameaux, glabres, coriaces, pinnatiséquées; lobes longuement triangulaires-lancéolés, entières ou légèrement dentés, aigus, 2—5×0,3—0,8 cm, espaces interlobaires arrondis; nervure médiane proéminente. *Pédoncule* 5—30 mm, à une petite bractée. *Capitules* nombreux, dans une inflorescence étalée, 15×4—6 mm. Nombre de fleurs ± 60 par capitule. *Écailles de l'involucre* 24—30; les externes 8—10, 2,5—5,5×1—1,5 mm; les intermédiaires 7—8, 8—10×1,5 mm; les internes 9—12, 9—10×0,7—1,2 mm. *Corolle* 6—7 mm. *Tube de la corolle* 6—7 mm. *Anthères* 4,25—4,5 mm. *Akènes* 2,5—2,75×0,8 mm, brunâtres, oblancéolés à elliptiques, à 2—3 côtes sur chaque face, rugueux. *Aigrette* 6—7 mm, caduque.

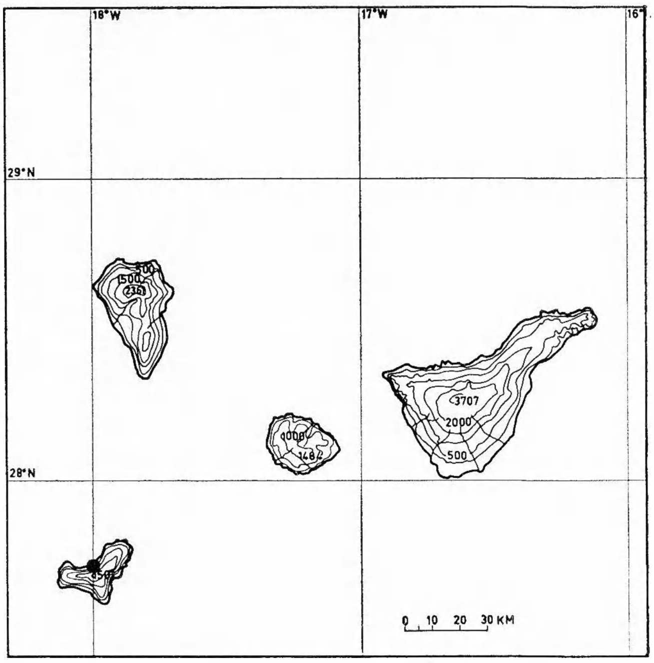

Fig. 37. *Sonchus lidii.* Distribution.

DISTRIBUTION. Hierro, Îles Canaries; endémique.

Hierro: Riscos de Casitas, 50—100 m, El Golfo, PITARD s.n. (Holotype P!, isotype G!) — Las Lapas, El Golfo, BOULOS s.n. (B! BM! CAI! G! K! MPU!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus gandogeri* est une plante, poussant sur les rochers maritimes secs et ensoleillés et sur les bordures des champs de vignes à une altitude de 50 à 300 m. Floraison et fructification de mars à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18, ROUX et BOULOS (1972).

PARTICULARITÉES PALYNOLOGIQUES. Bases des épines très évasées et régulières, et non en escalier comme c'est le cas chez la plupart des espèces du genre.

DISCUSSION. *Sonchus gandogeri* est caractérisé par ses tiges blanchâtres et volumineuses, le nombre faible des fleurs

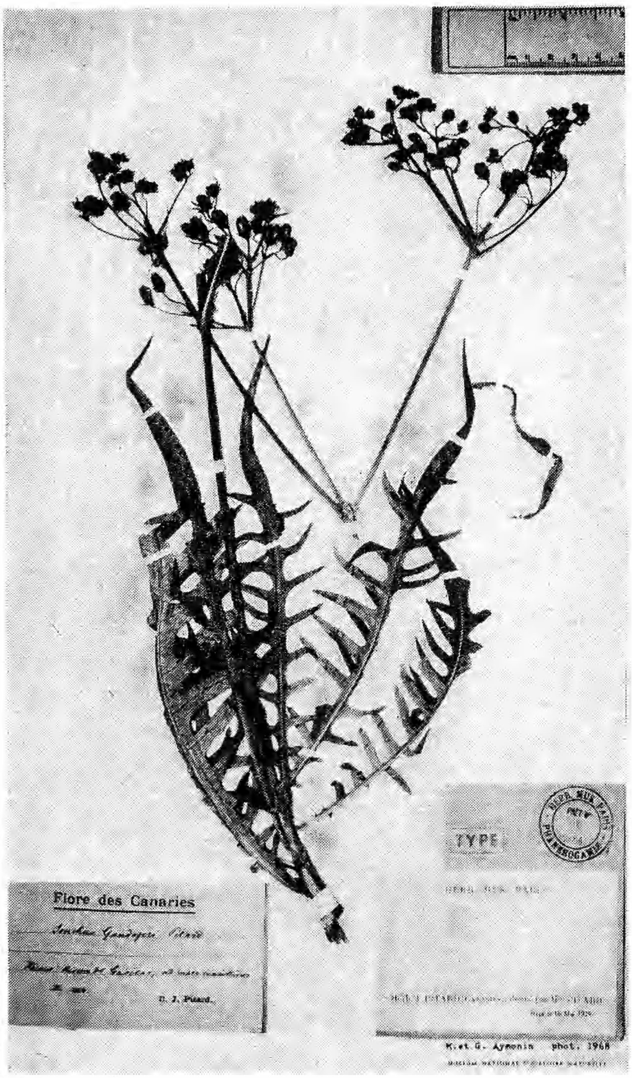

Fig. 38. *Sonchus gandogeri*. Holotype, PITARD s.n. (P!).

(60 environ) et des écailles d'involucre (24—30) par capitule. Les feuilles sont coriaces à lobes longuement triangulaires.

40. **Sonchus pitardii** BOULOS

BOULOS in Nytt Mag. Bot. 14: 17, fig. 11 a, b, 1967. — Holotype: Los Llanillos, El Golfo, Hierro, BOULOS s.n. (CAI!); isotypes (B! BM! BR! CAI! G! K! LD! MPU! O! P!).

Arbrisseau, 1—2 m de hauteur, richement ramifié, inflorescence grande et lâche, feuilles groupées à la base de l'inflorescence, tiges presque nues. *Collet* ligneux, volumineux et richement ramifié. *Tige* grisâtre, ligneuse, pleine, ramifiée, 1—3 cm diam. *Feuilles caulinaires* 10—35×2—8 cm, groupées à l'extrémité des rameaux, glabres sur la face supérieure, légèrement pubescentes sur la face inférieure surtout à l'état juvénile, pinnatiséquées; lobes opposés ou irrégulièrement disposés, triangulaires ou oblongs-lancéolés, 1—4×0,4—0,8 cm, lobe terminal plus long et large, marges entières, rarement à 1—2 mucrons sur la partie supériere. *Pédoncule* à l'aisselle d'une petite bractée, glabre, 0,5—6 cm. *Capitules* nombreux dans une inflorescence 40—70 cm diam. à plusieurs branches, lâche; capitules variables même sur la même plante, 5—12×10—18 mm, plus larges pendant l'anthèse. Nombre de fleurs ± 130 par capitule. *Écailles de l'involucre* ± 35; les externes 12, 3—10×1,5—3 mm; les intermédiaires 10, 14—18×2 mm; les internes 13, 16—18×2 mm. *Corolle* jaunâtre, 15 mm. *Ligule* 7 mm. *Tube de la corolle* 8 mm. *Anthères* 4,5 mm. *Akènes* 2,5—2,75×1 mm, brunâtres, brun-jaunâtres ou crème, oblancéolés, à 2—3 côtes sur chaque face, rugueux. *Aigrette* 6 mm, caduque.

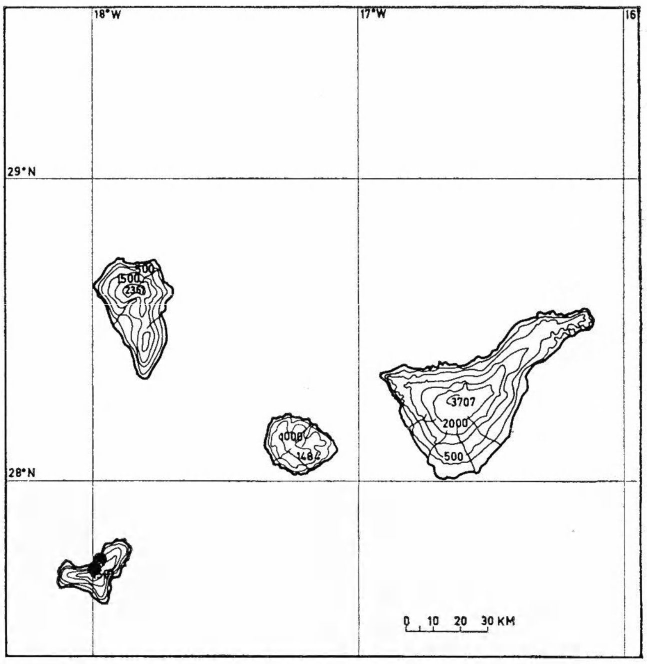

Fig. 39. *Sonchus gandogeri*. Distribution.

DISTRIBUTION. Hierro, Îles Canaries; endémique.

Fig. 40. *Sonchus pitardii*. Holotype, BOULOS s.n. (CAI!).

Hierro: Los Llanillos, El Golfo, BOULOS s.n. (Holotype CAI!, isotypes B! BM! BR! CAI! G! K! LD! MPU! O! P!) — Las Lapas, El Golfo, BOULOS s.n. (CAI! G! K!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus pitardii* est une plante assez commune dans la région de Los Llanillos, El Golfo, île d'Hierro. Elle croît dans des stations sèches sur les bordures des champs, près des maisons rurales à une altitude de 300 m environ. Floraison et fructification de mars à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18, ROUX et BOULOS (1972).

PARTICULARITÉES PALYNOLOGIQUES. L'épaississement polaire présente une extrême hétérogénéitée; le nombre d'épines polaires est très variable; l'épaisseur de crête varie elle même beaucoup. Ces caractères palynologique sont en accord avec notre interprétation concernant la nature hybride de cette espèce (voir la discussion).

DISCUSSION. Il nous semble que *Sonchus pitardii* est une espèce hybride naturelle entre *S. gandogeri* et *S. lidii*. Les caractères morphologiques et palynologiques confirment notre point de vue. En effet, les capitules, les tiges, les feuilles, etc., possèdent des caractères intermédiaires entre *S. gandogeri* et *S. lidii*. Nous avons remarqué aussi qu'un fort pourcentage (plus de 60) des akènes est

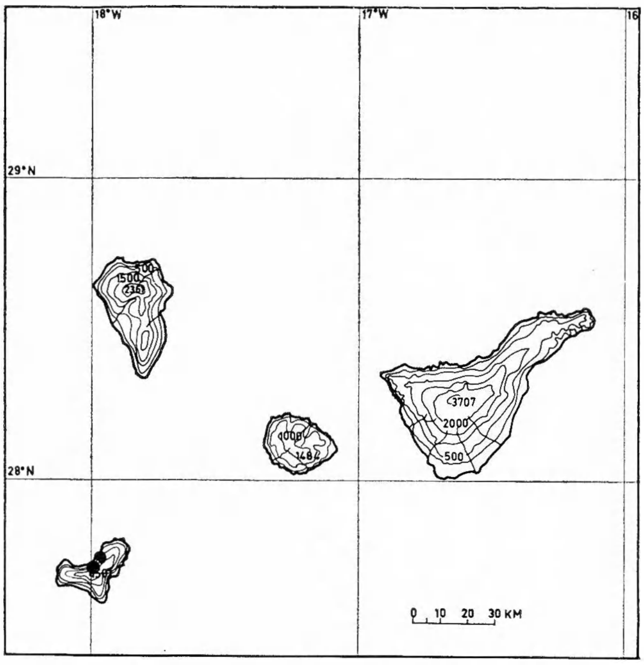

Fig. 41. *Sonchus pitardii*. Distribution.

stérile qui est en faveur de la nature hybride de notre espèce. Dans l'aire occupée par les trois espèces mentionnées ci-dessus, nous avons observé que *S. pitardii* est l'espèce la plus commune. Cette plante est donc, un hybride qui possède des caractères plus favorables, que ceux de ses parents à l'adaptation aux différents milieux.

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Further Additions to the Native Vascular Flora of Tierra del Fuego

D. M. Moore and R. N. P. Goodall

MOORE, D. M. & GOODALL, R. N. P. 1974 03 29. Further additions to the native vascular flora of Tierra del Fuego. — Bot. Notiser 127: 38—43. Lund. ISSN 0006-8195.

Nine species of angiosperms are here reported from Tierra del Fuego for the first time. A further species, the occurrence of which was doubtful, is confirmed. *Phaiophleps lyckholmi* (DUSÉN) R. C. FOSTER is shown to be morphologically and ecologically distinct from the widespread *P. biflora* (THUNB.) R. C. FOSTER.

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Whilst undertaking collections in various parts of Tierra del Fuego as part of a general survey concerned with preparing a modern treatment of the vascular flora of the archipelago a number of species have been discovered which were hitherto unknown from the area. Five species were reported and commented upon by MOORE (1970) and this paper records the occurrence of a further 10 species, only one of which was suspected to be present by earlier workers.

Spergularia marina (L.) GRISEB.

This species is common in coastal and inland saline areas in Europe and the Americas, being recorded as far south as Prov. Santa Cruz in Argentina (MARTINEZ-CROVETTO 1967) and along the Straits of Magellan in Chile (GRISEBACH 1856). It appears likely that a number of Chilean records for *S. media* (L.) PRESL given by ROSSBACH (1943) apply to this species, while the material from the Falkland Islands erroneously ascribed to *S. media* by MOORE (1968) has been shown to belong to *S. marginata* (MOORE 1973). HULTÉN (1971) considers the species to be introduced into South America.

Spergularia marginata has not been definitely recorded hitherto from Tierra del Fuego, although ALBOFF (1897) lists its occurrence but without documentation.

MATERIAL SEEN. Argentina. Tierra del Fuego: Estancia Viamonte, Barrientos Stream, flat muddy area by sea, 10.I. 1971. GOODALL 3311 (BAB, LTR, MICH, NA, RNPG); 16.V. 1972, GOODALL 4263 (LTR, RNPG).

Euphorbia portulacoides SPRENGEL

This very variable species is widespread in temperate South America, being recorded in the literature as occurring southwards to the Straits of Magellan. The southern Patagonian plants are of very reduced stature and were distinguished by SKOTTSBERG (1916) as forma *nana*. DUSÉN (1900) lists the species from east Patagonia but gives no locality and does not comment on its morphology.

The Fuegian material, collected from the south shore of the Straits of Magellan, comprises very reduced cushions partially hidden by the coastal sands. It seems very close to SKOTTSBERG's forma *nana* and appears to correspond to ssp. *major* var. *andensis,* as suggested by CROIZAT (1943). However, as CABRERA (1965) has pointed out, the infraspecific taxonomy of *E. portulacoides* is not very satisfactory and a modern revision is necessary.

MATERIAL SEEN. Chile. Tierra del Fuego: S.W. of Punta Catalina, Cuarto Chorillo, 52°39′S., 68°59′W., open sand and pebbles at top of beach, 7.XI. 1971, MOORE 2354 (K, LTR, UPS).

Lathyrus nervosus LAM.

BURKART (1935) records this species from S. Brazil and Uruguay southwards to Lago Argentino in prov. Santa Cruz, Argentina, while it is cited from just north of the Straits of Magellan in Chile (Cerro Toro, prov. Magallanes) by DUSÉN (1900). Although a rather conspicuous plant, we have only found one population of this species, in contrast to the common occurrence in Tierra del Fuego of the equally widespread *L. magellanicus* LAM.

MATERIAL SEEN. Chile. Tierra del Fuego: 32 km S. of Porvenir on road to Caleta Josefina (Onaisín), steep soil slope near Bahía Inutil, 53°26′S., 70°04′W., 2.XII. 1971, MOORE & GOODALL 2 (BAB, K, LTR, MICH, MU, NA, RNPG, SI).

Androsace pusilla (DUSÉN) LOURTEIG

This species has hitherto been known from the provinces of southern Patagonia in the area Río Negro, Neuquen and Santa Cruz, Argentina, reaching its southern limit in the Río Gallegos valley, prov. Santa Cruz, where it was first collected (DUSÉN 1900; LOURTEIG 1942). It is a minute plant which appears to have a very short growing cycle and, being easily overlooked, is probably more frequent than the few records suggest. In 1971 we carefully searched the area where the species was collected two years previously but could find no trace of it.

MATERIAL SEEN. Chile. Tierra del Fuego: Estancia Lago Gaviota, c. 12 km N. of junction with road from San Sebastian to Caleta Josefina (Onaisín), saline grassland, 29.I. 1969, GOODALL 2197 (RNPG).

Benthamiella patagonica SPEG.

This typically Patagonian genus of chasmophytes has not been previously known to occur in Tierra del Fuego. It was discovered on one of the dry mesetas in the north eastern part of Isla Grande, which present habitats similar to those of the arid Patagonian mesas. It occurred in open soil and rock areas in company with, among others, *Oreopolus glacialis* (POEPP. & ENDL.) RICARDI and *Valeriana sedifolia* D'URV., species which are rare in Fuegia where they are only known with certainty from Estancia Sarmiento, somewhat south of this locality and Estancia Vicuña across the border in Chile. *Benthamiella patagonica* is quite abundant in its only known Fuegian locality and the plants showed some differences from the Patagonian material. Our Fuegian specimens have rather more acute calyx-lobes than typical material, while the leaves are sometimes acute with a wide but not conspicuously amplexicaulous basal sheath. It is possible that these differences will necessitate the recognition of a distinct subspecies in Tierra del Fuego but in view of the few collections of *B. patagonica* studied from mainland Patagonia it might be better to await further information on its variation. The species was previously known from Chubut and N.E. Santa Cruz province in Argentina (SORIANO 1948) so that its discovery in Tierra del Fuego represents a southward extension of its range of some 800 km.

MATERIAL SEEN. Argentina. Tierra del Fuego: Estancia San Julio, Cerro Hongo, 53°40′S., 68°30′W., eroded sandstone hill, c. 150 m, summit area among rocks and open sand, 20.XI. 1971, GOODALL 3956 (AAH, MU, NA, RNPG, UC); MOORE 2563 (H, K, LTR, UPS); BOELCKE 15092 (BAA).

Littorella australis GRISEB. ex SKOTTSB.

This rare species was previously known from the Falkland Islands and from Andean Patagonia between lat. 40°10'S. and lat. 48°50'S. (SKOTTSBERG 1911). Its discovery on both northern and southern coasts of the Isla Grande of Tierra del Fuego consequently represents a southward extension of some 700 km. It has proved to be locally quite abundant in those freshwater lakes and streams where it has been found, tending to occur submerged in water up to 0.6 m deep. Here the plants attain their maximum height of 5—6 cm, being much more stunted in the shallows.

MATERIAL SEEN. Argentina. Tierra del Fuego: Estancia Harberton, Isla Gable, Campos Esquilados and Gaviota, submerged in two lakes, 10.III. 1970, GOODALL 2467 (BAB, LTR, MICH, MU, NA, RNPG, SI, UC, US); Isla Gable, Lago Grande and Lago Triangulo, water margin, 11.III. 1970, GOODALL 2475 (RNPG); Isla Gable, Round Lake, 24.II. 1971, GOODALL 3644 (BAB, LTR, MICH, MU, NA); Estancia Cullen, Río Cullen, on road to Chilean frontier near puesto, 6.I. 1971, GOODALL 3174 (BAB, LTR, MICH, NA, RNPG, SI, UC).

Boopis patagonica SPEG.

Throughout most of the littoral region of north and east Fuegia *Boopis australis* DECNE occurs quite frequently in suitable habitats. *B. patagonica,* which was previously known only from N.E. Santa Cruz province (PONTIROLI 1963), can be distinguished from the widespread species by the corolla being wider at the base, the filaments being joined into a tube, the smaller size of the plant and the rather different arrangement of the flowers. The Fuegian plant agrees with the specimens illustrated by DUSÉN (1907 t. 3, t. 8).

MATERIAL SEEN. Chile. Tierra del Fuego: Estancia Lago Gaviota, N. of San Sebastian, grassy plain near small lake, 29.I. 1969, GOODALL 2054 (LTR, NA, RNPG).

Zannichellia palustris L.

This extremely widespread species, which occurs over much of the Northern Hemisphere, temperate Africa, India and New Zealand, is frequent in South America where it has previously been found as far south as Puerto Deseado, prov. Santa Cruz, Argentina (CORREA 1969) and Ultima Esperanza, prov. Magallanes, Chile (SKOTTSBERG 1926). In one of the two Fuegian localities for the species its habitat appears to be no more than about 10—12 years old, resulting from construction work. There is thus clear evidence for the transport of the species within Tierra del Fuego, even though its apparent absence hitherto probably results from under-collecting rather than recent introduction.

MATERIAL SEEN. Argentina. Tierra del Fuego: Estancia Jose Menendez, Río Grande, new road bridge carrying ruta 3, small pond, 31.XII. 1970, GOODALL 2922 (BAB, LTR, MICH, MU, NA, RNPG, SI, UC); Estancia Viamonte, Duck Pond, 5.II. 1972, leg. M. WELLER, GOODALL 4172 (LTR, RNPG).

Ruppia filifolia (PHIL.) SKOTTSB.

This species of salt or brackish creeks and, less commonly, fresh water, which was described from N. Chile (prov. Atacama), was known in the southern part of prov. Magallanes, Chile, near Seno Skyring (SKOTTSBERG 1916) and near Punta Arenas (DUSÉN 1900). It was recently collected in the Falkland Islands (MOORE 1973) and its discovery in Tierra del Fuego is not altogether unexpected. The species has not

Table 1. The difference between *Phaiophleps lyckholmi* and *P. biflora*.

Character	*P. biflora*	*P. lyckholmi*
Plant-height (cm)	9—70	6—21.5
Basal leaves, number	(1—)2—3(—5)	1—3(—4)
Basal leaves, length, including sheath (cm)	10—29	3 —9.6
Cauline leaves, length (cm)	6.5—22	3.8—6.1
Ridges on leaves and stems	straight, smooth	Usually undulate, tuberculate
Peduncle-length (cm)	up to 11	0—2.5
Flowers, number	1— 7	(1—)3(—4)
Pedicels, length (mm)	25—50	15—29
Corolla, length (mm)	21—37	16—25
Corolla-tube, length (mm)	11—18	7—12
Corolla-tube, width (mm)	4— 8	3— 6.5
Corolla-tube, shape	infundibuliform	± cylindrical
Corolla-lobes, shape	apex acute	apex ± obtuse and apiculate
Corolla-colour	white or cream, with purple stripes	dark burgundy red to reddish-brown
Filament-tube, length (mm)	10 —13	7.5—11.5
Ovary-length (mm)	2.1— 3	3.6— 4.5
Ovary-width (mm)	1.5— 2.2	2—3

been reported from mainland Patagonia (CORREA 1969) but it seems likely to have been overlooked.

The taxonomic status of these plants is still open to further work. They were considered to be distinguished from *R. maritima* L. on their leaf-anatomy by HAGSTRÖM (1911), who gave the austral plants the name *R. obtusa* HAGSTR., but a further study of the variation within *R. maritima* s. lat. is much to be desired.

MATERIAL SEEN. Argentina. Tierra del Fuego: Río Lapataia, 'Laguna Verde', 2.III. 1970, GOODALL 2415 (BAB, LTR, MICH, NA, RNPG, SI, UC); 6.XII. 1970, GOODALL 2627 (BAB, LTR, MICH, MU, NA, SI, UC); Estancia Harberton, Second West Creek, brackish pools and stream, 21.I. 1972, leg. M. WELLER, GOODALL 4162 (RNPG); 19.II. 1972, GOODALL 4185 (AAH, BAB, LTR, MICH, MU, NA, RNPG); Lago Fagnano, small lake on N. side, 4.II. 1972, leg. M. WELLER, GOODALL 4167 (LTR, RNPG); Estancia Jose Menendez, Lago San Luis, 5.II. 1972, leg. M. WELLER, GOODALL 4174 (LTR, RNPG).

Phaiophleps lyckholmi (DUSÉN) R. C. FOSTER

This species was described by DUSÉN (1900) as a member of the genus *Symphyostemon,* only the type collection being known. SKOTTSBERG (1916), in commenting on further collections, also from S. Patagonia, noted that the species might be only an alpine form of the widespread *S. biflora* THUNB. RAVENNA (1964), in the most recent consideration of the species, placed it in synonymy with *Phaiophleps biflora* (THUNB.) R. C. FOSTER.

Material referable to *P. lyckholmi* has been discovered in several localities in Tierra del Fuego, where it was previously unknown, and we have been able to re-examine the question of its status. As a result we have decided that the species described by DUSÉN should be retained, since it differs from *Phaiophleps biflora* in a number of morphological features (Table 1) and in its habitat preferences.

P. lyckholmi seems to have a much more restricted distribution than *P. biflora* (Fig. 1), occurring only on the upper slopes of mountains in the drier parts of

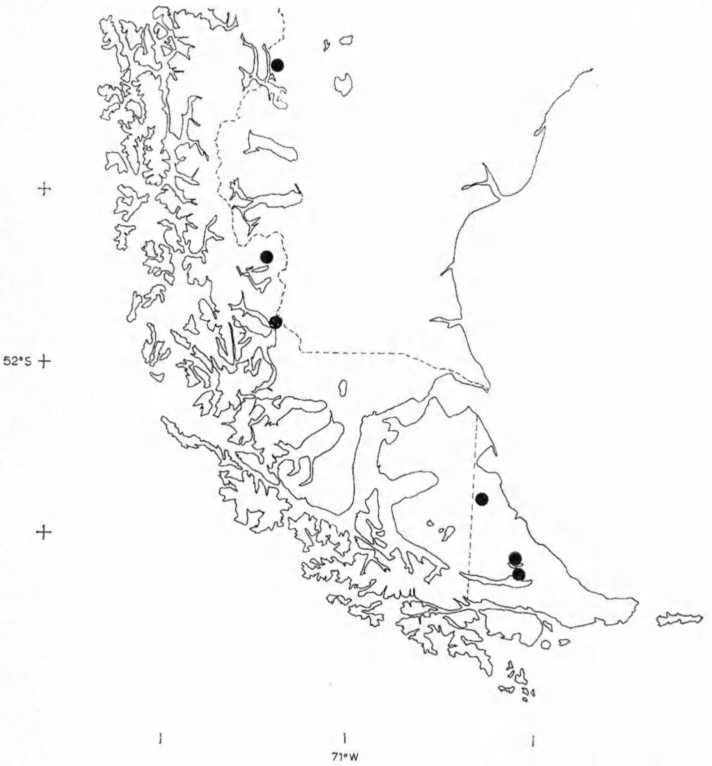

Fig. 1. Map of southern Patagonia and Tierra del Fuego showing the known distribution of *Phaiophleps lyckholmi* (DUSÉN) R. C. FOSTER.

Southern Patagonia and N.E. Tierra del Fuego. Furthermore, it has not been found below about 150 m and usually occurs at much higher altitudes. In all localities *P. lyckholmi* inhabits shallow stony soil or screes, rather bare habitats in which competition is very low or absent. In contrast, *P. biflora* is widespread in Tierra del Fuego, except in the high rainfall areas and on the mountains. It rarely occurs at elevations above 150 m and apparently competes well, being a frequent component of dwarf heath or scrub dominated by *Empetrum, Pernettya* etc.

The two species appear to be generally separated by their habitat preferences. They are sympatric in only one locality (Cerro Hongo, Estancia San Julio, Tierra del Fuego) where *P. lyckholmi* reaches its lowest elevation and even here they seem to retain their ecological separation.

P. lyckholmi was first collected in Tierra del Fuego by Mrs. C. B. GOODALL. She took some plants to her garden in Rio Grande where they grew for about six years, although they only flowered during the first season. No specimens are available but a watercolour of the plant is in Mrs. GOODALL's possession and was published recently (GOODALL 1971).

MATERIAL SEEN. Argentina. Prov. Santa Cruz: Río Fosiles, N. of Lago San Martín, c. 1000 m, 6.I. 1909, SKOTTSBERG 508 (UPS). — Chile. Prov. Magallanes: Cerro Contreras, c. 600 m, 28.XII. 1896, NORDENSKJÖLD s.n. (UPS holotypus); Puerto Natales, Cerro Dorotea, I. 1946, MAGENS (no specimen; painting, C.B.G. coll.). Tierra del Fuego: Mt. Shenolsh, S. summit, 1.I. 1932, C. B. GOODALL (painting, C.B.G. coll.); Cerro Atukoyak, N. summit, c. 650 m, 17.I.1968, MOORE 1553 (K, LTR); Estancia San Julio, Cerro Hongo, summit area, c. 150 m, 20.XI. 1971, GOODALL 3953 (AAH, NA); MOORE 2556 (K, LTR, UPS); BOELCKE 15090 (BAA).

ACKNOWLEDGEMENTS

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Dr. MILTON WELLER kindly made available his collections of *Ruppia* and *Zannichellia* while Dr. A. BURKART, Instituto Darwinión, San Isidro, confirmed the identification of *Lathyrus nervosus*.

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Frequency Mapping of Blackberry Species (Rubus L. Subgen. Rubus) in Sweden

II. Distributional Patterns

Alf Oredsson

OREDSSON, A. 1974 03 29. Frequency mapping of blackberry species (Rubus L. subgen. Rubus) in Sweden. II. Distributional patterns. — Bot. Notiser 127: 44—68. Lund. ISSN 0006-8195.

In a previous paper in this series frequency maps of 18 blackberry species occurring in the southern third of Sweden were presented. The frequency ranges from 1—36 localities per 10 km road investigated in a square of 100 km^2.

In the current paper four levels of frequency are established (rather rare, rather common, common and very common). For each level at which a species is represented a separate map is drawn. Together with neighbouring empty squares the squares in which the frequency level in question is reached form the Range. The position of Clusters with filled squares is described in detail, as is also the case with the Ranges.

With respect to patterns of distribution the blackberries in Sweden can be divided into three main groups. It is shown that the same species in the rest of Europe are distributed as could be expected from conventional divisions of the European flora.

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INTRODUCTION

In a recent paper (OREDSSON 1973) the author described a method of collecting distribution data on plants, the aim being to produce detailed frequency maps of vast areas. The method was applied to the occurrence of blackberries in Sweden, some twenty species in all. The southern third of Sweden was divided into squares of 10×10 km (10 km=6.2 miles), 1,499 in all (Fig. 1). In each square a stretch of road (at least 20 km long) was investigated by car. The locality concept used implies a minimum distance of 150 m between two localities of the same species. For each blackberry species an original frequency map was made, in which every square represented has a symbol, the size of which corresponds to the frequency obtained (OREDSSON 1973, Figs. 5—15). The frequency is the mean number of localities per 10 km.

In the current paper the distribution of the species in Sweden is surveyed, the species are grouped according to distributional patterns, and a comparison with the rest of Europe is made.

STRATIFIED FREQUENCY MAPS

For the current treatment new maps, called stratified frequency maps (Figs. 2—9) have been made on the basis of the original frequency maps as follows:

(1) Four levels of frequency have been fixed, so that each level comprises all the squares of a given species having a frequency equal to, or exceeding the minimum frequency given below. No corre-

sponding maximum frequency has been set up.

Minimum frequency	Level of frequency
1	rather rare (rr)
3	rather common (rc)
6	common (c)
16	very common (vc)

Example: In the case of *plicatus* the Maximum Frequency (see OREDSSON 1973 p. 49) is 27, so that common occurrence of *plicatus* includes all squares with a frequency from 6—27, very common occurrence is 16—27.

Each map shows the distribution of a species at one level of frequency only.

(2) On each separate map squares, in which the species is represented, are shown as:

(a) **Clusters**, a concept reserved for three squares or more, each square joined by at least one side,

(b) **Scattered Squares**, including both solitary squares and pairs.

(3) **Regions** are formed by surrounding each square in which the species is represented by 12 supplementary squares (two in succession from each of the four edges and one in each corner, as in Fig. 9 D). These star-shaped patterns may overlap (or be joined on to another one by at least one side of a square) together forming one Region.

Enclosed squares — solitary and pairs — are included in the area of both Clusters and Regions.

The island of Öland has been treated as a separate unit.

The **Range** of a species is the total area of the Regions at each separate level of frequency.

To simplify the subsequent description of the distribution of species, Clusters and Regions have been divided into classes according to size.

Number of squares in a Cluster	Designation
3— 6	very small
7—12	small
13—24	rather small
25—49	rather large
50—99	large
100—	very large

Number of squares in a Region	Designation
4— 24	very small
25— 49	small
50— 99	rather small
100—199	rather large
200—399	large
400—	very large

DISTRIBUTION IN SWEDEN

Below, Regions and Clusters are described individually at each level of frequency, though in general terms. Names used when specifying the position are to be found in Fig. 1.

In short, a Cluster is a continuous area where a certain minimum frequency is exceeded, whereas the Range (continuous or shared between different Regions) is an area in which this is the case here and there only. Besides burdening the descriptions, Scattered Squares have been omitted here because of the risk that their positions in many cases wholly are fixed at random within a limited geographical area, which the positions of Clusters and Regions probably are not. On the other hand, the investigation of the separate squares can hardly be regarded as so superficial that a general levelling of the individual frequencies would be justified.

On the basis of the original frequency maps published earlier (OREDSSON 1973), alternative treatments can be tested. Anyone wishing to know the situation of localities is welcome to make use of the maps used during the field work, of which a set of duplicates is available at the University Library of Lund.

Rubus bellardii WEIHE & NEES 1825 — Fig. 2 A—C

R. glandulosus BELLARDI 1793

RANGE

Level c. One *very small* Region along the coast of north-eastern Småland.

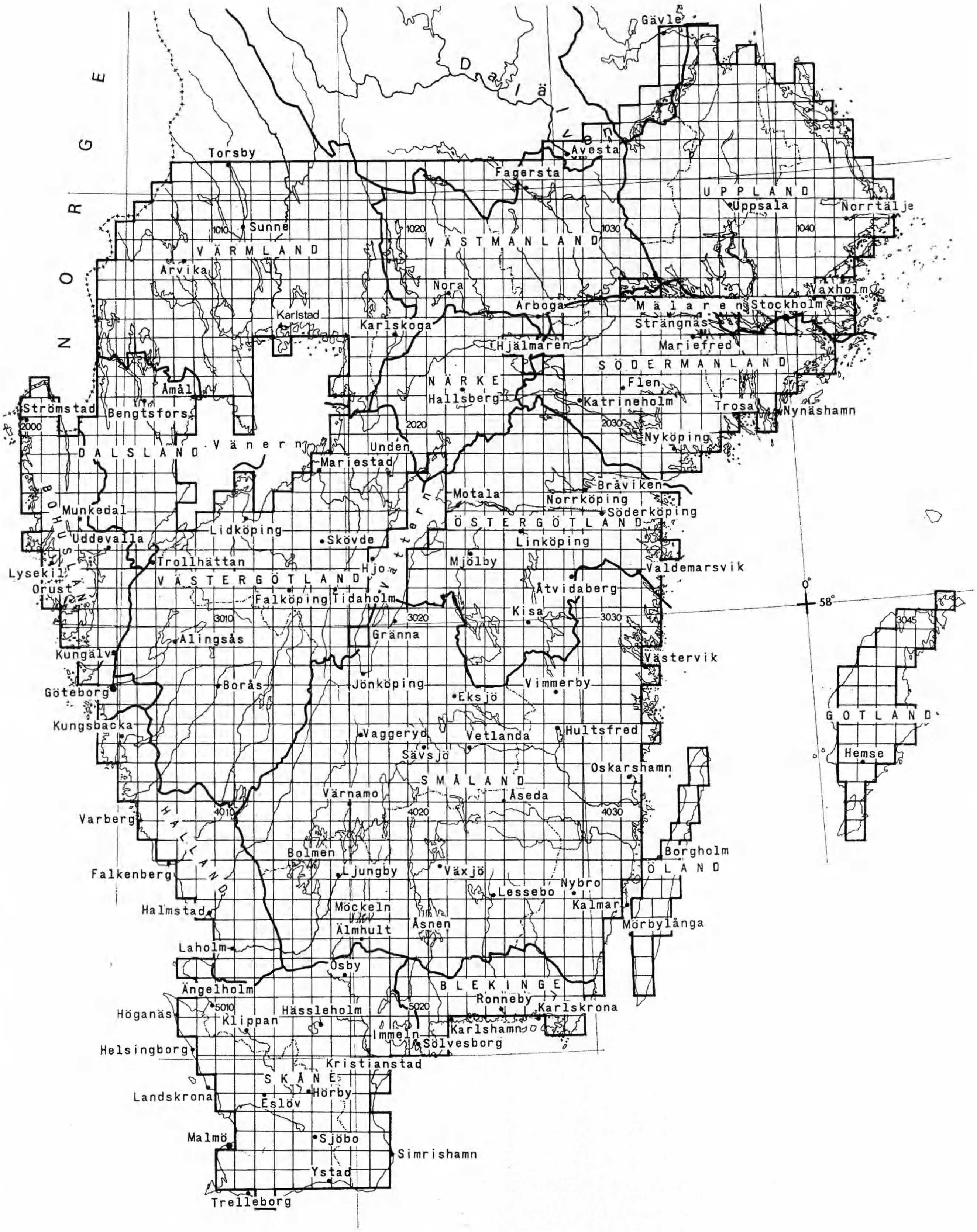

Fig. 1. The area investigated, divided into squares of 100 km². Provinces indicated by capitals and broad boundaries.

Level rc. One *small* Region extending halfway down the coast of Småland and filling the north-eastern corner of the same province, then crossing the border into Östergötland.

Level rr. One *small* Region in Småland only slightly larger than at level rc but in Östergötland now extending along almost the whole of the coast.

CLUSTER

Level rr. One *very small* Cluster in the north-eastern corner of Småland.

Rubus hartmanii GANDOGER ex SUDRE 1905 — Fig. 4 C—D

RANGE

Level rc. One *very small* Region on the coast of eastern Östergötland.

Level rr. One *very small* Region, crossing the border of Småland and also extending somewhat farther inland than at level rc.

CLUSTER

Level rr. One *very small* Cluster comprising the southern half of the coastal strip of Östergötland (with islands).

Rubus fuscus WEIHE & NEES 1825 — Fig. 2 F

RANGE

Level rr. One *very small* Region, including the north-eastern corner of Småland, with the exception of the skerries, inland crossing the boundary into Östergötland.

Rubus scheutzii LINDEBERG 1886 — Fig. 4 A—B

RANGE

Level rc. One *very small* Region halfway up the coast of Småland round Oskarshamn.

Level rr. One *very small* Region, extending somewhat farther inland than at the previous level of frequency.

Rubus sulcatus VEST ex TRATT 1823 — Fig. 2 D—E

RANGE

Level rc. One *very small* Region halfway up the coast of Småland.

Level rr. Two Regions. One *very small* Region situated east of Stockholm, including the archipelago and the neighbouring coastal parts of Uppland and Södermanland. One *rather small* Region along the east coast, stretching from southern Södermanland to south-eastern Småland as far as Nybro.

CLUSTER

Level rr. One *very small* Cluster on the north-eastern coast of Småland.

Rubus thyrsanthus FOCKE 1877 — Fig. 3 A—C

RANGE

Level c. One *very small* coastal Region in north-eastern Småland.

Level rc. Four Regions. One *small* Region, introduced at the previous level of frequency, now extending along the coast to the middle of Småland. Three *very small* coastal Regions: one south-east of Stockholm, another filling central Blekinge, the third in south-eastern Skåne.

Level rr. Five Regions. One *small* Region covering the coastal parts of south-eastern Uppland and north-eastern Södermanland. One *rather large* Region forming a wide belt along the east coast, stretching from southernmost Södermanland to the border between Blekinge and Skåne, reaching farthest inland in southern Östergötland. A *very small* Region in south-eastern Skåne. Two *very small* Regions, introduced at this level of frequency: one isolated Region on the west coast in the middle of Bohuslän, one covering the central part of Öland.

CLUSTERS

Level rc. One *very small* Cluster situated on the north-eastern coast of Småland.

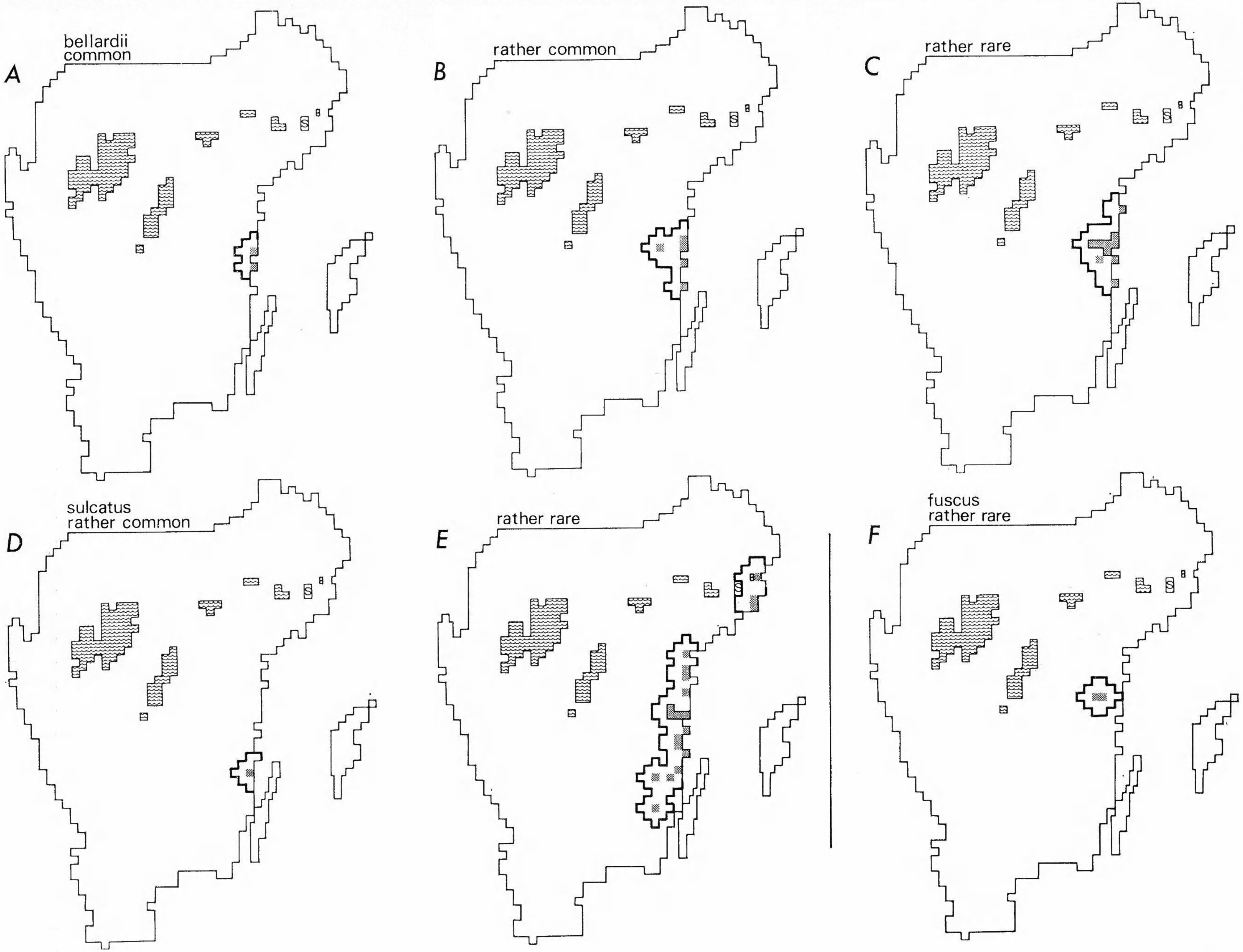

Fig. 2. — Figs. 2—9. Stratified frequency maps. See p. 44. — Clusters (surrounded by a thin line) and Scattered Squares grey. Regions indicated by a broad line.

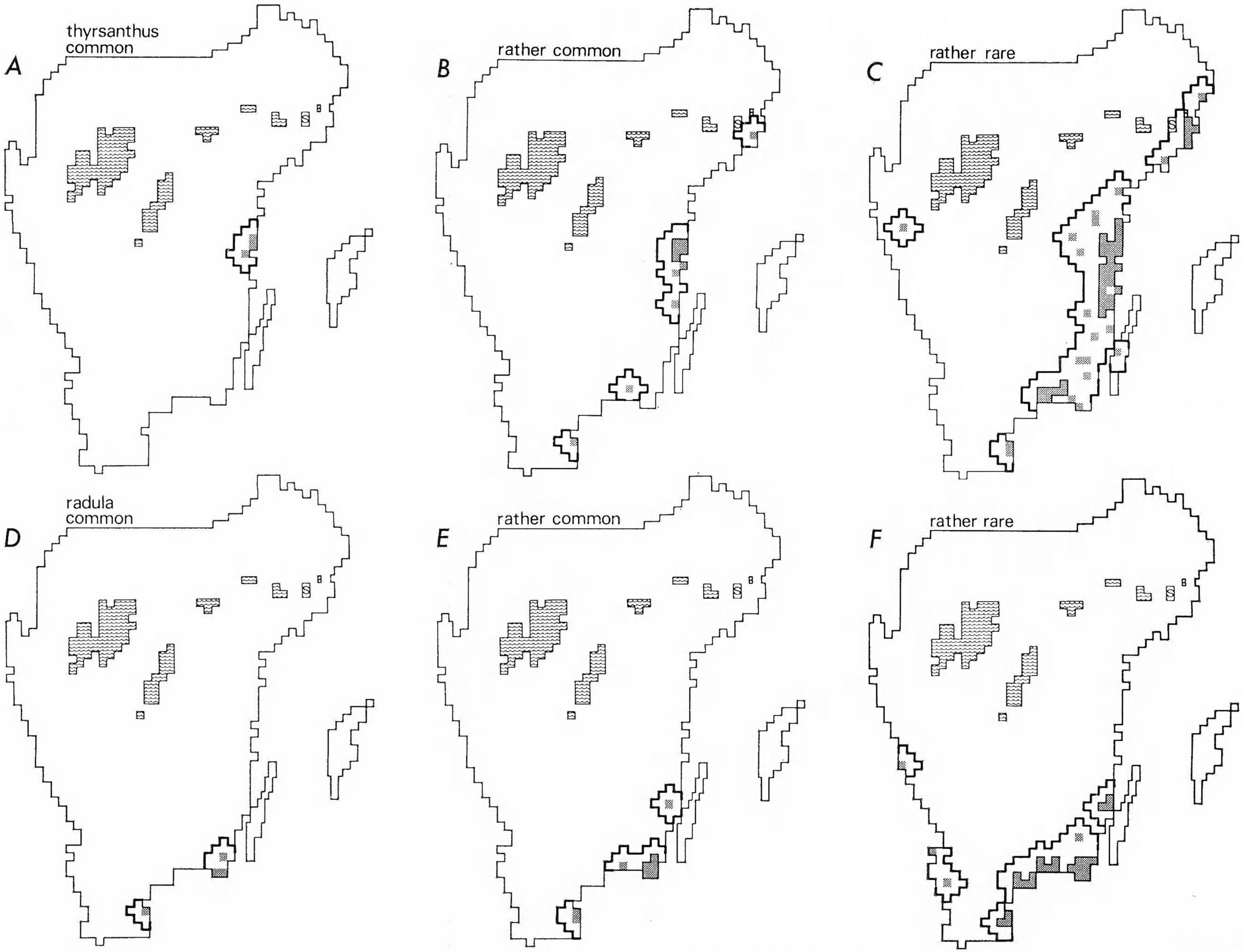
A
thyrsanthus
common
B
rather common
C
rather rare
D
radula
common
E
rather common
F
rather rare

Fig. 3.

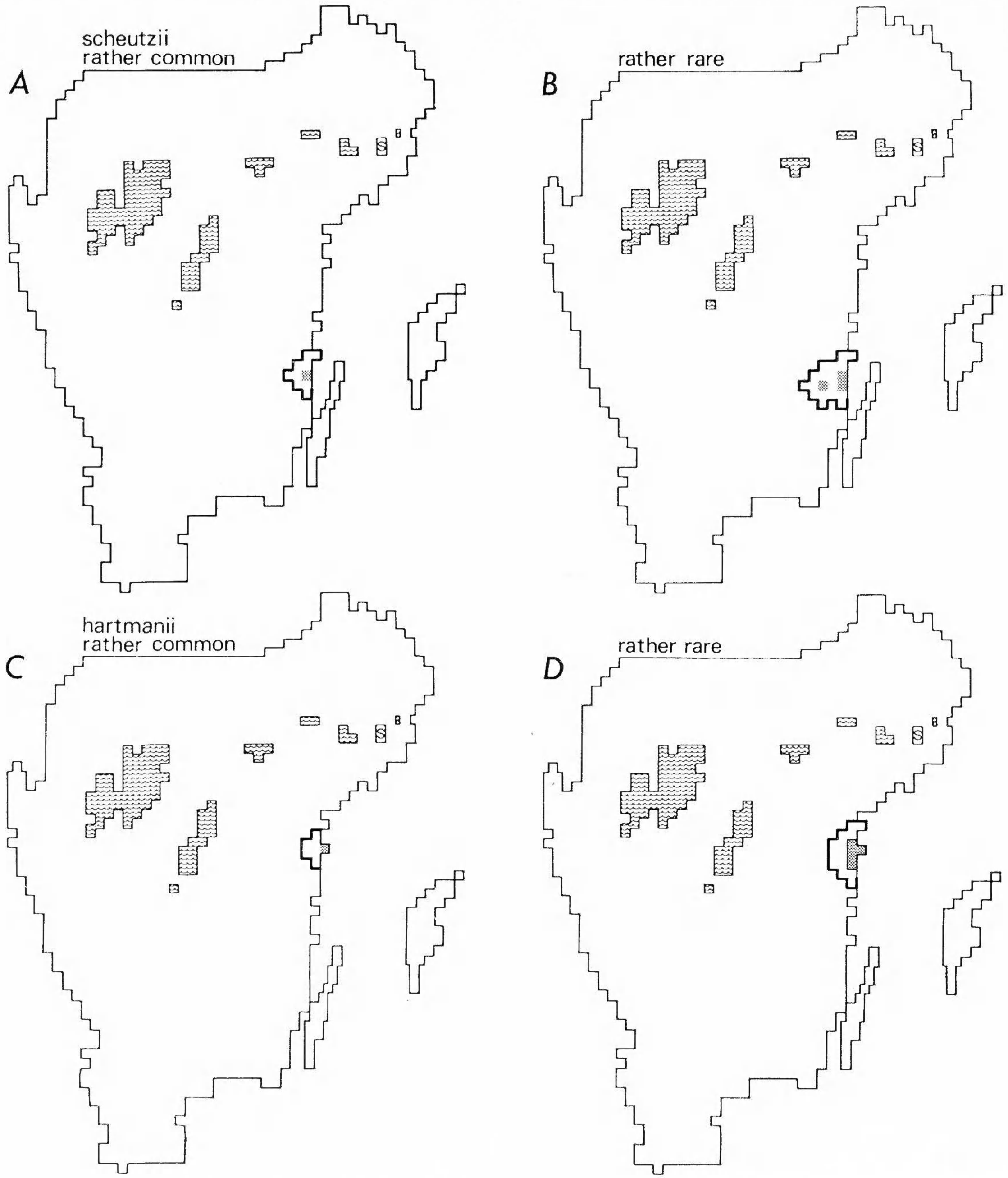
A
scheutzii
rather common
B
rather rare
C
hartmanii
rather common
D
rather rare

Fig. 4.

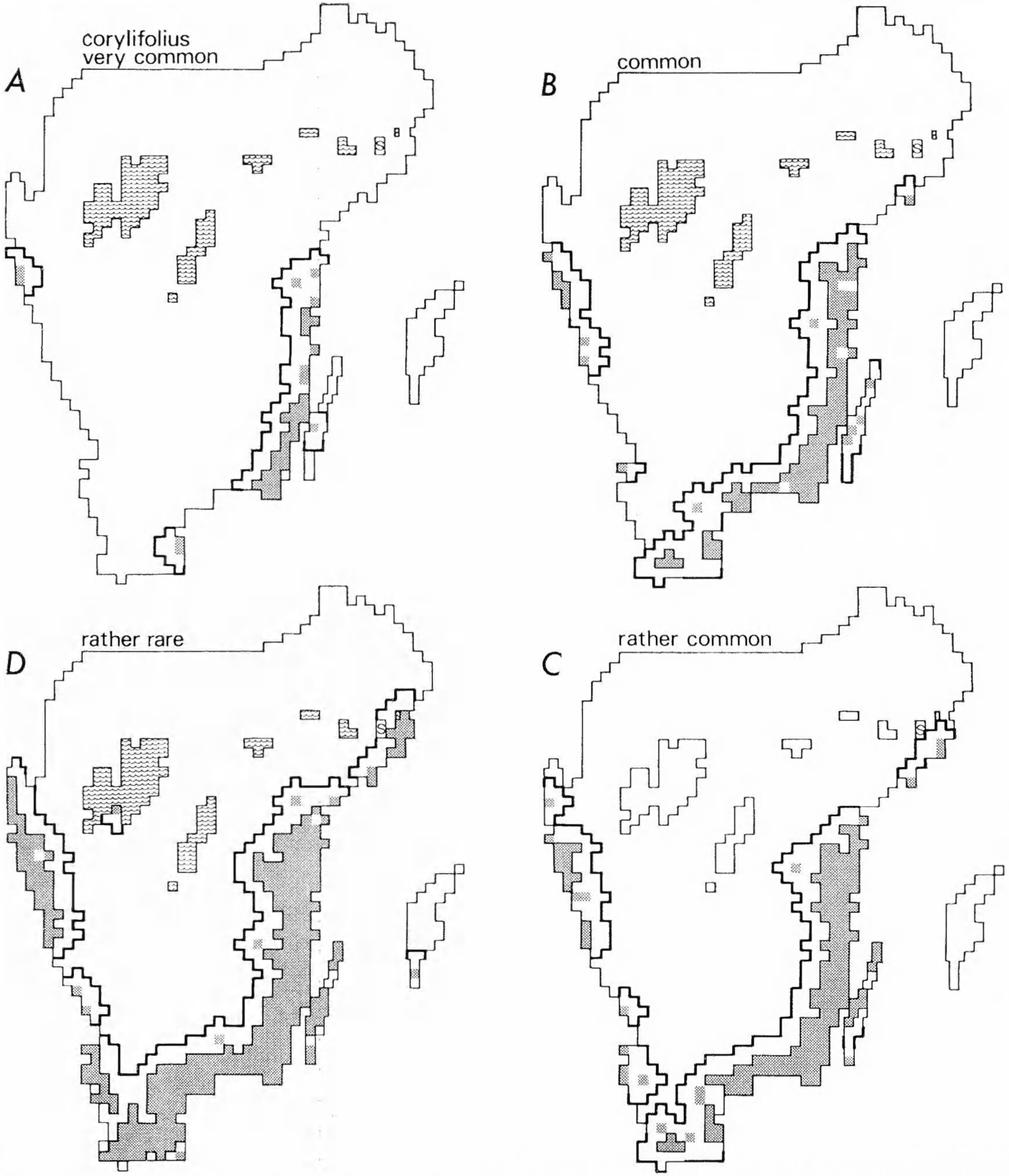
A
corylifolius
very common
B
common
D
rather rare
C
rather common

Fig. 5.

Level rr. Three Clusters, all situated along the east coast. One *very small* Cluster in the southern part of the Stockholm archipelago. One *rather large* Cluster stretching from southern Östergötland to the middle of Småland. One *small* Cluster in central Blekinge.

Rubus corylifolius agg. — Fig. 5

R. grex *Corylifolii* FOCKE 1914, *R. dumetorum* WEIHE 1824

RANGE

Level vc. Four Regions. One *rather small* Region running along the east coast stretching from Östergötland to central Blekinge. Three *very small* Regions: one covering south-easternmost Skåne, another the islands of central Bohuslän, and the third one the central part of Öland.

Level c. Five Regions. One *large* coastal Region, stretching from the border between Södermanland and Östergötland to south-western Skåne. One *small* Region comprising the south-western half of Bohuslän and the northernmost part of Halland. Two Regions introduced at this level of frequency, both *very small:* one in north-westernmost Skåne and the other round Nynäshamn on the coast of Södermanland. The fifth Region is also *very small,* though covering the whole of Öland.

Level rc. Seven Regions. The two largest Regions from common occurrence are unchanged apart from minor inland extensions. Three *very small* Regions on the west coast: one in northern Bohuslän, another in central Halland, and the third, in north-western Skåne, the only one that was introduced at a higher level of frequency. A fourth *very small* Region situated on the north-east coast of Södermanland. Finally, the *very small* Region that is Öland.

Level rr. Seven Regions. Four almost consecutive Regions around the coast: a *small* Region, stretching from south-eastern Uppland to the middle of Södermanland, then a *large* Region reaching as far as southern Halland, a *very small* Region in central Halland and fourthly a *rather small* Region extending from northern Halland to the Norwegian border. One new, *very small* Region, on the tongue of land that protrudes into the lake Vänern in the south, near the town of Lidköping, being the only inland Region for this species. The *very small* Region that is Öland. Finally, the second new-comer, a *very small* Region in the southernmost part of Gotland, representing the only blackberry species on that island.

CLUSTERS

Level vc. Two Clusters, both on the east coast. One *very small* Cluster in north-eastern Småland. One *rather small* Cluster, forming a coastal band stretching from central Småland to eastern Blekinge.

Level c. Five Clusters. One *large* Cluster on the east coast, stretching from Östergötland to western Blekinge. One *very small* Cluster in south-westernmost Blekinge and the adjacent part of Skåne, touching the former Cluster in one corner. Two *very small* Clusters in southern Skåne. A fourth, *very small* Cluster comprising the outer islands of central Bohuslän.

Level rc. Seven Clusters. A *very large* Cluster, along the east coast from Östergötland to north-eastern Skåne. Two Clusters in southern Skåne, both *very small,* the south-western one being the only inland Cluster for this species. One new, *very small* Cluster west of Kungsbacka in northern Halland. One *small* Cluster comprising most of the islands of central Bohuslän. Two *very small* Clusters on Öland, both introduced at this level of frequency: one in the northernmost part of the island, the other central.

Level rr. Six Clusters. The *very large* coastal Cluster from level rc has increased mainly in Östergötland and Skåne — the two Clusters in southern Skåne have been incorporated. One *rather large* Cluster formed by a fusion of the two Clusters from level rc on the west coast, with a northern extension. Another two coastal Clusters, both introduced at this level of frequency: a *rather small* Cluster in north-western Skåne and a *small* one east of Stockholm. Two Clusters on Öland, the northern one *very small,* the central one *small.*

Rubus radula WEIHE 1824 — Fig. 3 D—F

RANGE

Level c. Two Regions, both *very small:* one in eastern Blekinge and the adjacent part of south-easternmost Småland, the other in south-eastern Skåne.

Level rc. Three Regions. One new, *very small* Region in south-eastern Småland. The Region in Blekinge now including the western part of the province, but still *very small.* The *very small* Region in south-eastern Skåne, now slightly larger.

Level rr. Five Regions on the coast. The *very small* Region in south-eastern Småland from level rc. One *rather small* Region covering the whole of Blekinge as well as adjacent parts of Småland and Skåne. Three *very small* Regions: one in south-eastern Skåne and two newcomers in north-western Skåne and northernmost Halland respectively.

CLUSTERS

Level rc. One *very small* Cluster in eastern Blekinge.

Level rr. Five Clusters, all on the coast. One *very small* Cluster in south-eastern Småland. The Cluster in eastern Blekinge, now being *small.* Two *very small* Clusters touching at one corner, one in the middle of Blekinge, the other on the border between Blekinge and Skåne. Lastly, one *very small* Cluster north of Simrishamn, in south-eastern Skåne.

Rubus sprengelii WEIHE 1819 — Fig. 6 C

RANGE

Level rr. Two *very small* Regions remote from each other: one comprising the southern islands of central Bohuslän, the other situated in the south-eastern corner of Skåne.

Rubus taeniarum LINDEBERG 1858 — Fig. 6 A—B

R. infestus auct. mult. non WEIHE 1824

RANGE

Level rc. One *very small* Region comprising some of the islands and skerries of central Bohuslän.

Level rr. One *small* Region covering the whole of central Bohuslän.

CLUSTER

Level rr. One *small* Cluster including parts of the island of Orust and the tongues of land to the north.

Rubus insularis F. ARESCHOUG 1881 — Fig. 6 D—E

RANGE

Level rc. One *very small* Region in the middle of the southern coast of Skåne.

Level rr. Two Regions. One *small* Region formed by a north-easterly extension of the Region at level rc. One new, *very small* coastal Region in north-western Skåne.

Rubus lindebergii P. J. MÜLLER 1859 — Fig. 7 A—C

RANGE

Level c. One *small* coastal Region, which runs from the south-westernmost part of Halland through north-western Skåne to central Skåne.

Level rc. Two Regions. One *small* Region as above, now extending some-

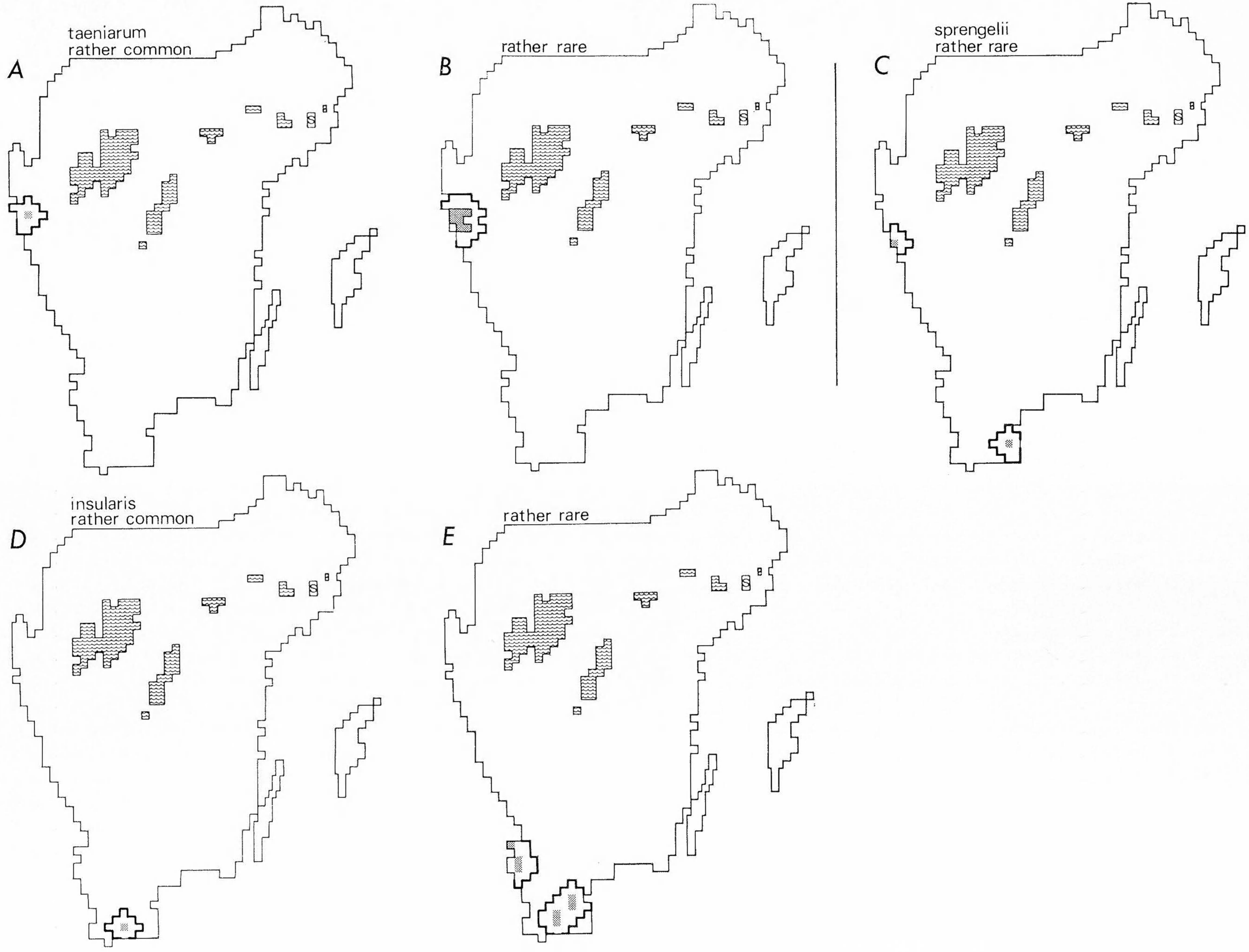
A
taeniarum
rather common
B
rather rare
C
sprengelii
rather rare
D
insularis
rather common
E
rather rare

Fig. 6.

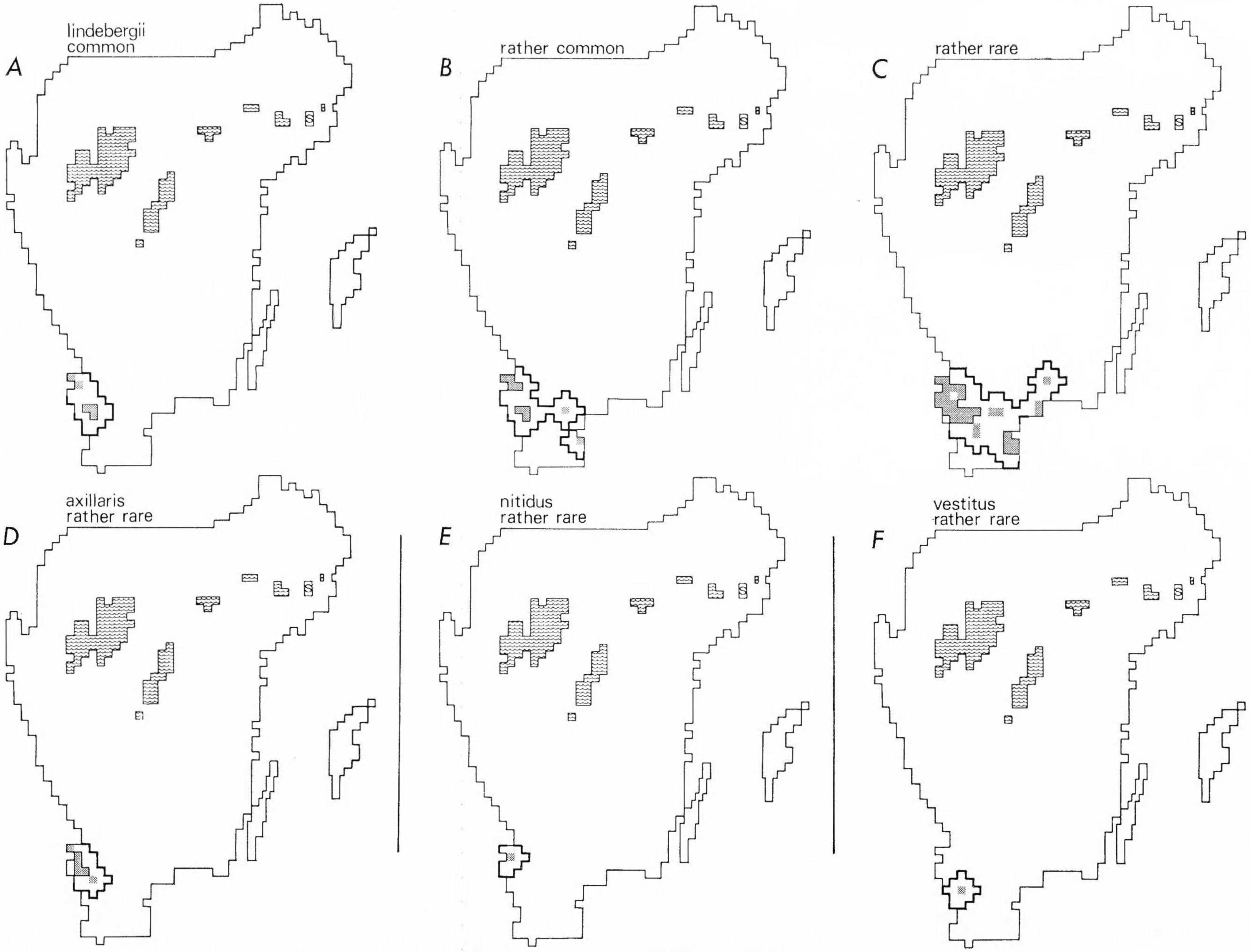
A
lindebergii
common
B
rather common
C
rather rare
D
axillaris
rather rare
E
nitidus
rather rare
F
vestitus
rather rare

Fig. 7.

what farther into south-western Halland and including part of north-eastern Skåne. One new, *very small* coastal Region in south-eastern Skåne touching the former Region at one corner.

Level rr. One *rather large* Region beginning in southern Halland and then forming a wide belt diagonally crossing the province of Skåne in a south-easterly direction, with a north-eastern extension in western Blekinge penetrating into southernmost Småland.

CLUSTERS

Level c. One *very small* Cluster in north-western Skåne, east of the town of Helsingborg.

Level rc. Two Clusters. The above Cluster remaining unchanged. Another *very small* Cluster in north-westernmost Skåne, north of the town of Ängelholm.

Level rr. Two Clusters. One *rather small* Cluster in north-western Skåne, including the two Clusters at level rc. One *very small* coastal Cluster in south-eastern Skåne.

Rubus axillaris LEJEUNE 1831 — Fig. 7 D

R. scanicus F. ARESCHOUG 1881

RANGE

Level rr. One *very small* coastal Region comprising north-western Skåne and the south-westernmost part of the province of Halland.

CLUSTER

Level rr. One *very small* coastal Cluster in north-western Skåne, around the town of Ängelholm.

Rubus vestitus WEIHE & NEES 1825 — Fig. 7 F

RANGE

Level rr. One *very small* coastal Region in the middle of western Skåne.

Rubus nitidus WEIHE & NEES 1822 — Fig. 7 E

R. divaricatus P. J. MÜLLER 1858

RANGE

Level rr. One *very small* Region on the coast in north-westernmost Skåne.

Rubus plicatus WEIHE & NEES 1822 — Fig. 8

RANGE

Level vc. Three Regions. One *rather small* Region including Bohuslän and Halland except for the northern part of the former province and the eastern side of the latter, but protruding into south-westernmost Västergötland. Another *rather small* Region, which from south-westernmost Halland runs through northern Skåne to the middle of Blekinge. One *small* Region covering eastern Blekinge and the south-eastern corner of Småland.

Level c. One *large* coastal Region extending from northern Bohuslän and to the middle of eastern Småland, going farther inland than the separate Regions at level vc as well as extending over almost the whole of the province of Skåne.

Level rc. Four Regions. The *large* coastal Region, only slightly larger than at level c. One *very small* Region in the middle of the eastern shore of the lake Vänern. Two *very small* Regions on Öland, one in the northernmost part and the other in the centre.

Level rr. Four Regions. One *very large* Region formed by an extension of the large coastal Region at level rc, especially in Västergötland and parts of southern Småland, and here reaching the border between Östergötland and Södermanland on the east coast. The same *very small* Region by the lake Vänern as at level rc. One new, *very small* coastal Region east of Stockholm. One *very small* Region extending over the whole of the island of Öland.

CLUSTERS

Level vc. Six Clusters. One *very small* Cluster in the middle of Bohuslän. Another *very small* Cluster in northernmost Halland, also extending into southern Bohuslän. One *small* Cluster in the north-western half of Halland, touching the former Cluster at one corner. One *very small* Cluster in north-eastern Skåne, the only inland Cluster. One *small* Cluster in south-western Blekinge, also going into north-eastern Skåne. Another *small* Cluster comprising easternmost Blekinge and the adjacent part of south-easternmost Småland.

Level c. Six Clusters. One *rather large* Cluster covering the central part of the province of Bohuslän. Another *rather large* Cluster comprising the whole northern part of Halland and most of the central part, also extending into south-westernmost Västergötland. One *large* Cluster with a ribbon-like form, which at its north-western starting-point touches the former Cluster at one corner, then running through northern Skåne and the entire province of Blekinge, ending in south-eastern Småland. Three *very small* Clusters introduced at this level of frequency: one in eastern Småland touching the former Cluster at one corner, and the two others in the southern part of Skåne, the western one lying somewhat inland.

Level rc. Two Clusters. One *very large* Cluster forming a coastal belt by the fusion of five of the six Clusters at level c. One *very small* Cluster in south-western Skåne — the last-mentioned Cluster under common occurrence.

Level rr. Two Clusters. One *very large* Cluster forming a somewhat wider belt than at level rc, on the west coast beginning in northernmost Bohuslän and now covering almost the whole of Skåne. One *very small* Cluster in northernmost Öland introduced at this level of frequency.

Rubus nessensis W. HALL 1794 — Fig. 9 A—C

R. suberectus G. ANDERSSON 1815

RANGE

Level c. Five Regions. One *very small* coastal Region in the northernmost part of Bohuslän. One *large* coastal Region stretching from the western side of the lake Vänern to the coast in the middle of Bohuslän, temporarily leaving it again in the province of Skåne and continuing to north-eastern Småland. Two Regions situated in the inland between the north-eastern end of the large Region and the lake Hjälmaren, the southern one being *very small,* and the other *small.* In the middle of the area investigated, one *rather small* Region along the western side of the lake Vättern, in the north-west reaching the lake Vänern.

Level rc. Two Regions. One *very large* Region forming a wide coastal belt turning inland on a level with the two biggest lakes, Vänern and Vättern, and covering all the five Regions of level c. One *very small* inland Region north of the lake Vänern.

Level rr. Three Regions. One *very large* Region, with the exception of three enclosures in the central part of the area, covering the whole of the mainland south of a line that zigzags through the provinces of Värmland, Västmanland and Södermanland. Two *very small* Regions introduced at this level of frequency, one on the coast north-east of Stockholm, and the other covering the northern part of the island of Öland.

CLUSTERS

Level c. Eight Clusters, all but the last-mentioned below situated within the large coastal Region at level c. One *very small* Cluster north of Göteborg. Two *very small* Clusters touching at one corner, both lying on the border between Halland and Västergötland. One *small* Cluster, also touching its neighbour at one corner, stretching through southern Halland, reaching the coast at Halmstad. One *rather small* Cluster in north-western Skåne, reaching the coast at Ängelholm. One *very small* Cluster in north-western Blekinge

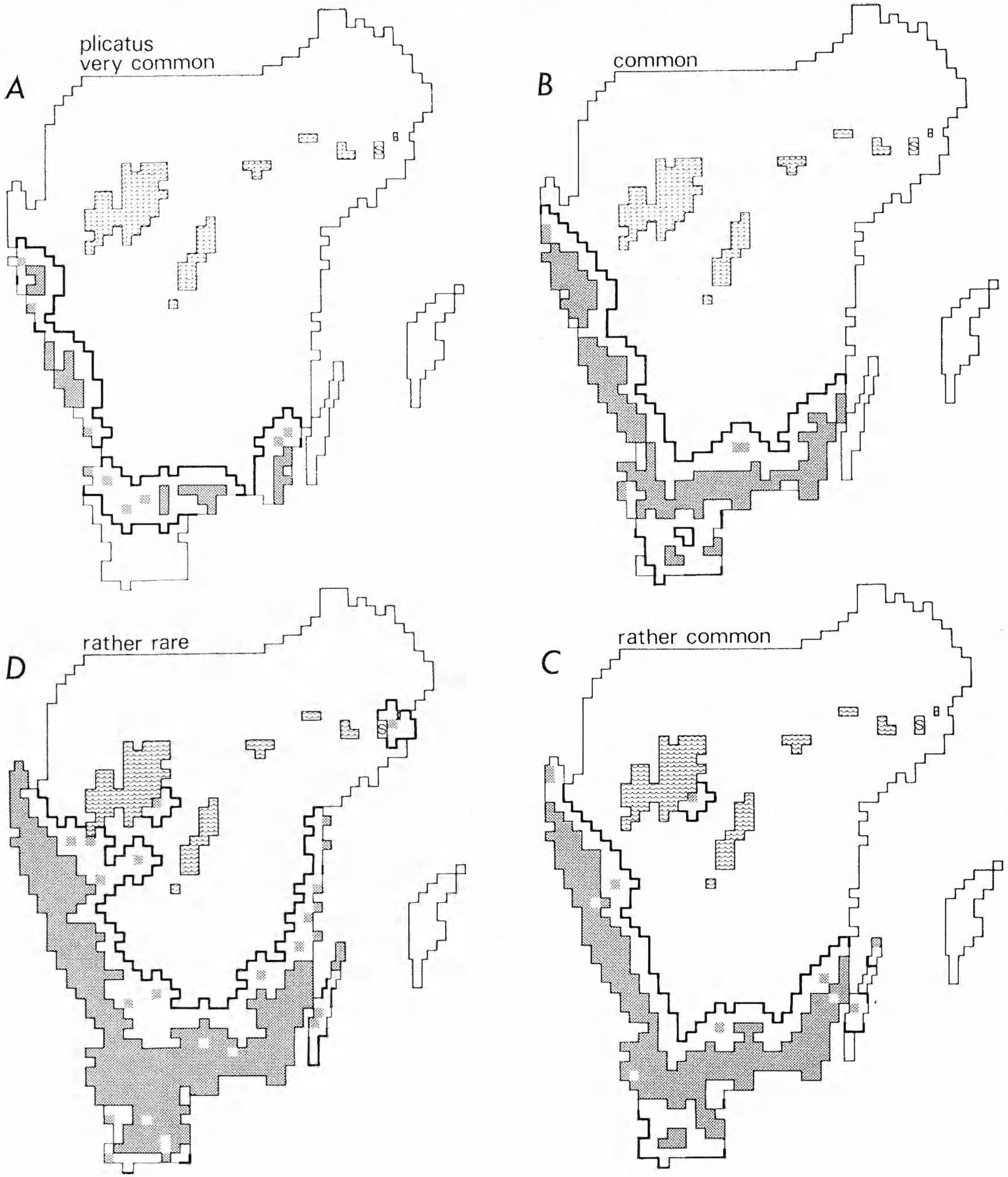
A
plicatus
very common
B
common
D
rather rare
C
rather common

Fig. 8.


A
nessensis
common
B
rather common
C
rather rare
D
scissus
common
E
rather common
F
rather rare

Fig. 9.

and the adjacent part of north-eastern Skåne. One *very small* Cluster attached to the coast of easternmost Blekinge. And the eighth Cluster, *small*, and confined to the north-western side of the lake Vättern.

Level rc. Twelve Clusters. One *large* Cluster, formed by the fusion of four Clusters from level c, i.e. the one in north-western Skåne and the three Clusters covering parts of Halland. Four isolated Clusters, the rest of those introduced at level c, (a further two reaching the coast) which have all become larger, each of them now designated *rather small:* one of them touching the large Cluster at its northern corner, and, from Bohuslän penetrating into the two neighbouring provinces of Dalsland and Västergötland, while the two from Blekinge touch each other, the western one now protruding also into southern Småland. One *very small* coastal Cluster, appearing in northernmost Bohuslän. Another *very small* Cluster, situated in south-western Småland, at the back of the large Cluster on the west coast. Three *small* Clusters along the east coast, the southern one touching the rather small Cluster of eastern Blekinge at one corner, and the northern one lying on the border between Småland and Östergötland, at some distance from the coast. One *very small* Cluster on the north-western side of the gulf of Bråviken, on the border between Östergötland and Södermanland. Finally, a *very small* Cluster, situated on the south-western shore of the lake Vättern, touching the rather small Cluster on the north-western side of the lake at one corner, this latter Cluster now reaching the eastern side of the lake Vänern.

Level rr. Ten Clusters, seven of them introduced at this level. One *very large* horseshoe-shaped Cluster, including nine of the twelve Clusters at level rc, beginning north-west of the lake Vänern and ending in Östergötland, leaving the coast only in the province of Skåne. One *rather large* Cluster mainly in northern Östergötland, but also crossing the borders of Närke and Södermanland, in the latter province reaching the coast. This Cluster was introduced at level rc. One *large* Cluster, touching the former at one corner, filling out the space between Vänern and Vättern, and covering the two remaining level rc Clusters. One *very small* Cluster in the middle of the province of Närke, touching the two last-mentioned Clusters of level rr. Another *very small* inland Cluster situated near the south-westernmost shore of the lake Vättern, touching one corner of the large Cluster described above. A third *very small* Cluster in central Småland, south of the town of Sävsjö. Another three *very small* Clusters all situated in the inland in the northern part of the area investigated, i.e. north of the lake Vänern, in the south-western part of the province of Västmanland, and close to the north-western side of the lake Hjälmaren. The tenth Cluster, *very small* is situated in the northernmost part of Öland.

Rubus scissus W. C. R. Watson 1937 — Fig. 9 D—F

R. fissus auct. mult. non Lindley 1835

RANGE

Level c. One *very small* Region in the interior of northern Skåne.

Level rc. Two Regions. One *small* Region, the one introduced at level c, now reaching central Skåne and to the north penetrating into south-westernmost Småland. One *very small* coastal Region in northern Halland also comprising the adjacent part of south-westernmost Västergötland.

Level rr. Two Regions. One *rather large* south-western Region formed by the merging of the two Regions from level rc, through the province of Halland. Another coastal Region, designated *very small,* including eastern Blekinge and the south-easternmost part of Småland.

CLUSTERS

Level rc. One *very small* Cluster in northern Skåne, stretching from the town of Hässleholm northwards to the border of Småland.

Level rr. Three Clusters. One *rather small* Cluster in northern Skåne, introduced at level rc, now projecting into southernmost Halland. Two *very small* Clusters in central Halland, the more northerly one reaching the coast at Varberg.

PATTERNS OF DISTRIBUTION

As the Range (at the separate levels of frequency) is a moderately simplified representation of the occurrence it has been chosen to group species according to geographical distribution. Three main distributional groups are proposed, which in their turn are divided into ten subgroups (Table 1).

The thyrsanthus Group

SUBGROUP 1. Four species, *bellardii, hartmanii, fuscus,* and *scheutzii* are found exclusively in the middle of the eastern coast of the area investigated, i.e. from the boundary between Södermanland and Östergötland in the north down to the middle of Småland. In the same area two other species, *sulcatus* and *thyrsanthus,* are represented by their only Regions at the highest level of frequency for each species (levels rc and c, respectively). See Figs. 2 A—D, F, 3 A, 4, combined in 10 A.

At their next highest levels of frequency (levels rr and rc respectively), the same two species are both represented within the coastal strip from southern Östergötland to the middle of Småland, as well as in an area south-east of Stockholm. From these common areas the Stockholm Region of *sulcatus* extends northwards to Norrtälje, whereas the major east coast Region of this species (at level rr) stretches northward to southernmost Södermanland and in the opposite direction down to south-eastern Småland. There are no other Regions for *sulcatus.* Besides the two areas common to both species, *thyrsanthus* is represented by two other Regions, one in central Blekinge and another in south-eastern Skåne (Fig. 10 B).

Table 1. The 18 *Rubus* species divided into three main groups of distribution. Subgroups also indicated.

The *thyrsanthus* group (t)	The *radula* group (r)	The *scissus* group (s)
1 *bellardii*	3 *radula*	8 *plicatus*
hartmanii	4 *sprengelii*	9 *nessensis*
fuscus	5 *taeniarum*	10 *scissus*
scheutzii	6 *insularis*	
sulcatus		
thyrsanthus		
2 *corylifolius*	7 *lindebergii*	
	axillaris	
	vestitus	
	nitidus	

At level rr the Range of *thyrsanthus* is divided into five Regions, viz. (1) an elongated coastal strip round Stockholm, (2) a band along the eastern coast, reaching farthest inland in southern Östergötland and stretching from the southernmost part of Södermanland down to the boundary between Blekinge and Skåne, (3) the central part of the island of Öland, (4) the south-easternmost part of Skåne, (5) a Region in the central part of Bohuslän, the only one on the west coast (Fig. 3 C).

SUBGROUP 2. One of the three most frequent blackberry species in Sweden, *corylifolius,* has at level vc a Range similar to that of *thyrsanthus* at level rr (Figs. 5 A and 3 C). It is true that the former Range lacks a counterpart to the Stockholm Region of the latter, but the other Regions more or less overlap. Both Ranges are dominated by one drawn-out Region along the east coast. Two Regions agree exactly, i.e. those on Öland and in south-easternmost Skåne respectively. In the middle of Bohuslän, the Region for *coryli-*

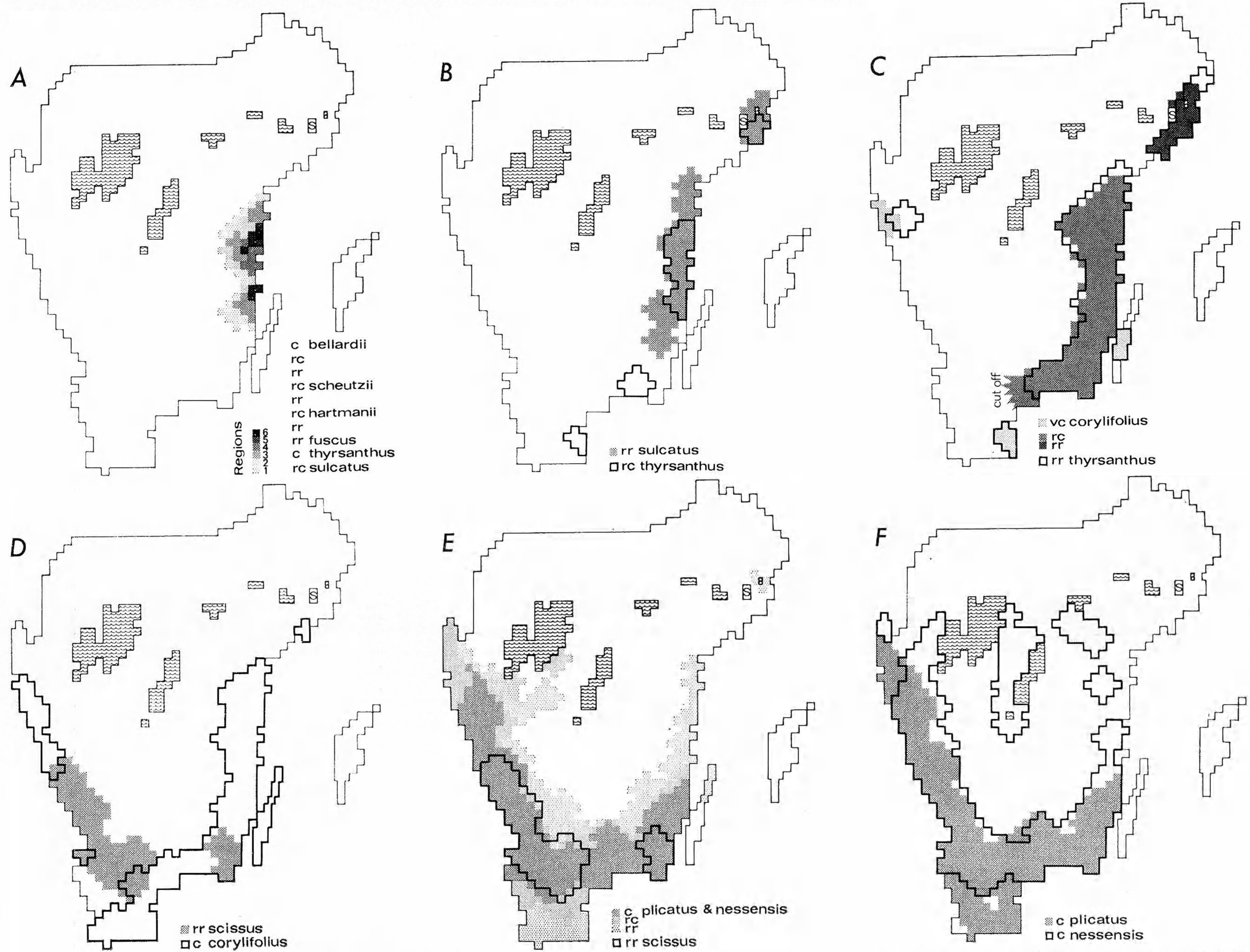

Fig. 10. — Figs. 10—11. The division of the 18 *Rubus* species into 3 main groups and 10 subgroups with respect to distributional pattern, exclusively based on the Range (definition p. 45). See pp. 61 ff. — Levels of frequency: rr=rather rare, rc=rather common, c=common, vc=very common.

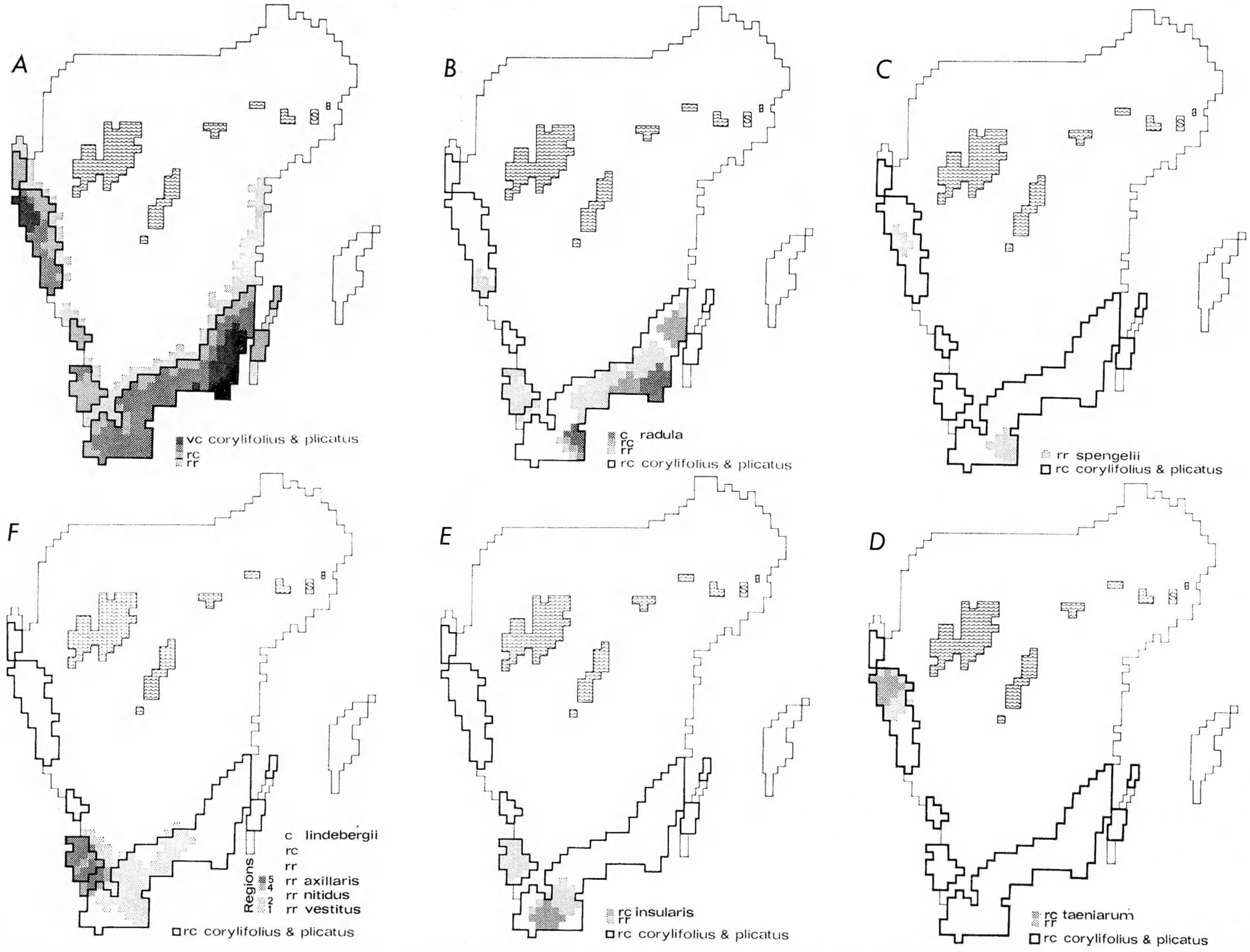
A
vc corylifolius & plicatus
rc
rr
B
c radula
rc
rr
rc corylifolius & plicatus
C
rr spengelii
rc corylifolius & plicatus
F
c lindebergii
rc
rr
Regions
5
4
2
1
rr axillaris
rr nitidus
rr vestitus
rc corylifolius & plicatus
E
rc insularis
rr
rc corylifolius & plicatus
D
rc taeniarum
rr
rc corylifolius & plicatus

Fig. 11.

folius at level vc has a more western location than that of *thyrsanthus* at level rr.

The best agreement between the two species is, however, obtained if the Regions for *thyrsanthus* at level rr are compared with Regions of *corylifolius* from *different* levels of frequency in different parts of the area investigated. Thus, in the Stockholm Region level rr for the latter species agrees best, along the east coast level rc comes closest (but no further than to the boundary between Blekinge and Skåne), whereas, in the remaining parts of the area investigated, the Regions of *corylifolius* at level vc coincide fairly well with those of *thyrsanthus* at level rr, viz. in the provinces of Öland, Skåne and Bohuslän (Fig. 10 C). To the fact that *sulcatus* has a north-eastern character compared with *thyrsanthus* (cf. Fig. 10 B) is now added a gradual lack of agreement between *thyrsanthus* and *corylifolius,* so that from being equally frequent in the north-easternmost part of the area investigated the latter species dominates somewhat along most of the eastern coast, and this becomes more pronounced on the island of Öland and from Skåne all along the west coast. (The complete Range of *corylifolius* at the different levels of frequency is shown in Fig. 5.)

The scissus Group

A pattern of distribution that is the opposite of that of the *thyrsanthus* group is shown by *scissus*, and less distinctly also by *nessensis* and *plicatus,* two of the three most frequent blackberry species in Sweden.

SUBGROUP 10. Though represented at three levels of frequency *scissus* has a Range that overlaps that of any member of Subgroup 1 at level rr only. And what is more, this applies solely to the widest-spread of the six species referred to, i.e. *thyrsanthus* (at levels rc and rr) and with respect to *scissus* to the lesser of two Regions only (Figs. 3 B—C, 9 F).

If the Ranges of *scissus* at level rr and *corylifolius* (Subgroup 2) at level c are compared, the major Region of *scissus,* which fills up the province of Halland and northern Skåne, forms a bridge between the large east-coast Region of *corylifolius* and the small west-coast Region of the same species without overlapping much. On the other hand the minor Region of *scissus,* i.e. eastern Blekinge and south-easternmost Småland, is completely covered by the east-coast Region of *corylifolius* (Fig. 10 D).

SUBGROUPS 8 AND 9. The greatest resemblance to *scissus* is, however, shown neither by *plicatus* nor by *nessensis* whatever the level of frequency, but by a combination of the two species. Thus, the Range of *scissus* at level rr is almost totally covered by the double as large continuous coastal area in which the level c Ranges of *plicatus* and *nessensis* overlap. The area referred to begins in southernmost Dalsland and then runs southwards through Bohuslän, and an adjacent minor part of Västergötland covering the whole province of Halland as well as south-westernmost Västergötland. It then crosses the northern half of Skåne and continues into Blekinge forming a bulge into southern Småland around the lake Åsnen, ceasing half-way up the east coast of Småland (Fig. 10 E).

In addition the Range of *plicatus* (at level c) includes two areas, both connected to the area of overlapping with *nessensis,* viz. the southern half of Skåne and the northern half of the province of Bohuslän, except for the northernmost end.

Outside the area of overlapping, *nessensis* (at level c) is represented here and there along the east coast up to the province of Östergötland, and then farther inland up to the lake Hjälmaren, as well as on the western side of the lake Vättern, in the south-eastern half of Dalsland (west of the lake Vänern), and in northernmost Bohuslän (Fig. 10 F).

Ranges at levels of frequency other than those discussed are illustrated in Figs. 8, 9 and 10 E (combinations).

The radula Group

If we discount minor exceptions it will be found that the Ranges of the eight remaining species are all covered by the area in which *corylifolius* and *plicatus* overlap at level rc. As these two species belong to different main groups of distributional patterns, the eight species thus form an intermediate main group.

There are seven areas of overlapping as above (Fig. 11 A). None of the four smallest (in all 11 % of the total area) contain any intermediate species: two areas on Öland, one in the middle of Halland and one in northern Bohuslän. The three other areas are: One along the south-eastern coast of the area investigated stretching from the middle of Småland to south-western Skåne (62 % of the total intermediate area, 5 intermediate species). The second occupies north-western Skåne (8 %, 6 species), and the third stretches from central Bohuslän to northern Halland (19 %, 3 species).

SUBGROUP 3. At levels c and rc, *radula* is represented in the south-eastern area only, and what is more, only where *thyrsanthus* also occurs, the latter species belonging to Subgroup 1 (Fig. 3). Besides crossing the Range of *thyrsanthus* (at level rr) in the south-eastern intermediate area, *radula* at level rr also appears in north-western Skåne and northern Halland (Fig. 11 B).

SUBGROUPS 4 AND 5. There are another two species which to some extent are connected with *thyrsanthus* with regard to distribution. The two Regions (at level rr) of this species in the western half of the area investigated correspond with the Range of *sprengelii* (represented at level rr only) which consists of two Regions, one in the southern half of Bohuslän and the other in south-easternmost Skåne (Fig. 11 C). Though represented at two levels of frequency *taeniarum* has a Range limited to one Region in the central part of Bohuslän (Fig. 11 D).

SUBGROUP 6. The fourth species belonging to this main group, *insularis,* has two separate Regions at level rr. One Region is in southern Skåne and the other covers the north-western part of the same province. The same species at level rc is met with in southern Skåne only (Fig. 11 E).

SUBGROUP 7. Three species, *axillaris, vestitus* and *nitidus,* are found exclusively in north-western Skåne, while a fourth, *lindebergii,* at level c, is represented here only. It should be observed, however, that the Ranges referred to to some extent all cross the concerned part of the common distributional area of *corylifolius* and *plicatus* at level rc. At levels rc and rr *lindebergii* widens its Range, partly around the Region known from level c, but chiefly eastwards, finally reaching the south-eastern corner of Skåne and the border between Blekinge and Småland (Fig. 11 F).

DISTRIBUTION IN EUROPE

The distribution of the *Rubus* species in Europe has been compiled by HESLOP-HARRISON (1968). With the exception of *corylifolius* (information lacking) Table 2 shows the distribution in other countries of the Swedish blackberry species discussed.

The area in which Swedish blackberry species occur in Europe stretches from the Atlantic coast across the Continent down to the Mediterranean countries (excluding Greece and Turkey) and in the north-east past the Black Sea into the Central division of the U.S.S.R. Of our six neighbouring countries Finland is the

Table 2. The European distribution of the 18 Swedish *Rubus* species treated so far (except for *corylifolius*) according to HESLOP-HARRISON (1968). Main groups and subgroups as in Table 1.

Main group	Subgroup	*Rubus* species	Sweden	Britain	Denmark	Belgium	Germany	Czechoslovakia	Netherlands	France	Hungary	Poland	Romania	Austria	Switzerland	Ireland	Norway	Italy	Jugoslavia	U.S.S.R. Baltic	Portugal	U.S.S.R. South-western	Bulgaria	U.S.S.R. Central	Albania	Spain	Sum, countries per species
t	1	*bellardii*	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	+	+	·	·	+	·	·	+	18
t	1	*thyrsanthus*	+	+	·	·	+	+	·	+	+	+	+	+	+	+	+	·	+	·	·	·	+	·	+	·	15
s	9	*nessensis*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	·	+	·	·	20
s	8	*plicatus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	+	+	·	·	20
t	1	*sulcatus*	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+	·	·	+	·	·	·	·	17
r	7	*vestitus*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	·	·	+	·	·	·	·	·	16
r	3	*radula*	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	·	+	·	·	·	·	·	16
r	7	*nitidus*	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	·	·	+	·	·	·	·	·	15
s	10	*scissus*	+	+	+	+	·	?	+	+	+	+	·	·	·	+	+	·	·	+	·	·	·	·	·	·	12
r	7	*lindebergii*	+	+	+	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	4
t	1	*fuscus*	+	+	+	+	+	+	+	+	+	·	+	+	+	+	·	·	·	·	·	·	·	·	·	·	13
r	4	*sprengelii*	+	+	+	+	+	+	+	+	+	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	11
r	5	*taeniarum*	+	+	+	+	+	+	?	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	7
r	7	*axillaris*	+	+	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	5
r	6	*insularis*	+	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2
t	1	*hartmanii*	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2
t	1	*scheutzii*	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1
Sum, species per country .			17	15	14	12	12	12	11	11	11	10	9	9	9	8	7	6	5	3	3	3	3	2	1	1	

only one lacking blackberries other than *corylifolius*. Britain and Denmark have most of the species referred to.

Six species are found in seven countries or less, all in NW Europe, viz. Sweden, Denmark, Britain, the Netherlands, Belgium, Germany and Czechoslovakia, whereas the remaining eleven species occur in from 11—20 European countries.

In Fig. 12 the distribution in the European countries is shown for each of the three groups of species according to the division into main distributional groups in Sweden.

With the exception of Sweden, the total European distributional area is then divided into eight regions: (1) Norway and Ireland, (2) Denmark, the Netherlands, Belgium and Britain, (3) Germany, Czechoslovakia and Poland, (4) the Baltic, Central and South-western divisions of the U.S.S.R., (5) France, Switzerland, Austria, Hungary and Romania, (6) Spain and Portugal, (7) Italy, (8) Jugoslavia, Albania and Bulgaria.

For each of these eight regions the mean number of species per country is calculated for the three groups of species separately. The mean sums of the separate groups are converted to 30 and the regional means subsequently converted into points for comparison (Fig. 13).

(A) Highest numerical value. The *scissus* group has two maxima, viz. in regions 1 and 2. The highest value of the *radula* group is found in region 2, whereas the highest value for the *thyrsanthus* group is found in region 5.

(B) Central area (regions 2, 3 and 5). In two of the three groups of species the numerical values fall off from region 2—3—5, a trend manifest in the *radula* group and to some extent in the *scissus* group. An opposite but weaker tendency is present in the *thyrsanthus* group.

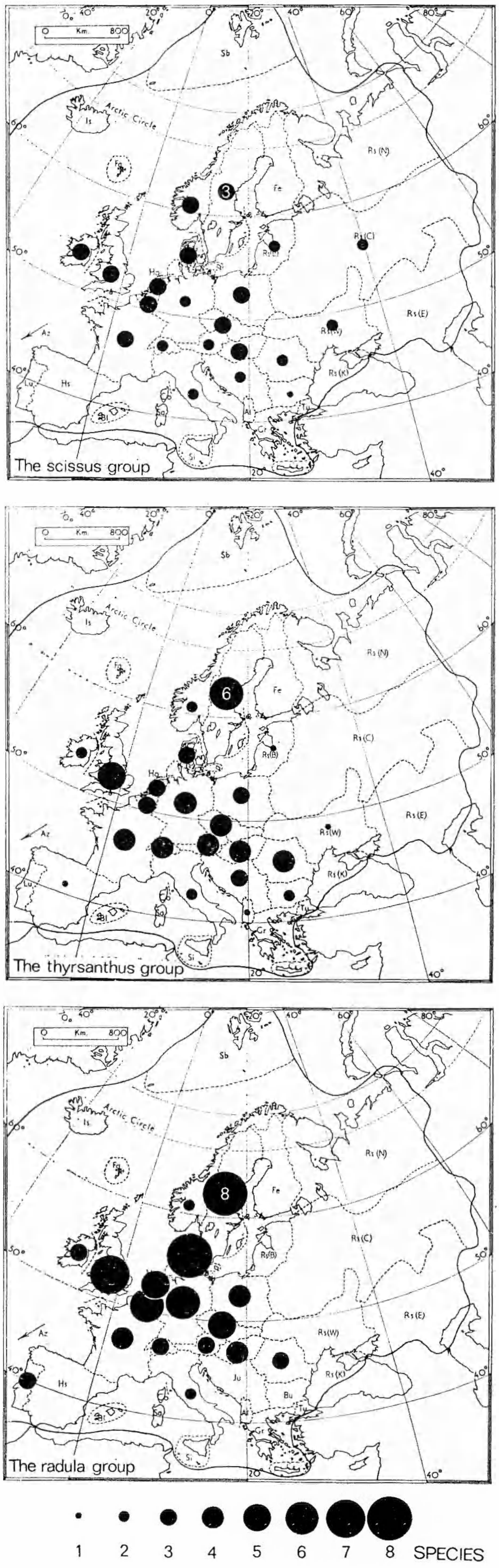

Fig. 12. The European distribution of the 18 *Rubus* species treated so far (except for *corylifolius*) according to HESLOP-HARRISON (1968).

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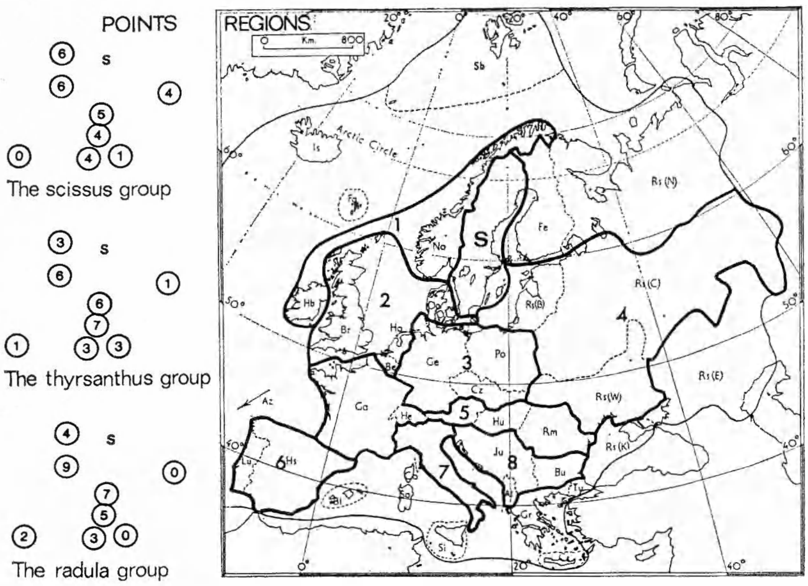

Fig. 13. The data of Fig. 12 as means in eight European regions (Sweden excluded) converted into points making equal sums for the three main groups of species.

(C) The four peripheral regions (1, 4, 6 and 8). The *scissus* group dominates regions 1 and 4, whereas this group is lacking in region 6. The *radula* group is represented in regions 1 and 6 exclusively. The *thyrsanthus* group is found in all the peripheral regions and the sums of the points are the same whether regions 1 and 4 are compared with 6 and 8, or 1 and 6 with 4 and 8.

(D) Italy (region 7). The numerical value for Italy is medium whichever group of species is dealt with.

SWEDISH AND EUROPEAN DISTRIBUTIONS COMPARED

Earlier we saw that both the *radula* and the *scissus* groups in Sweden occur mainly in the south-west, the latter group also being represented inland, while the *thyrsanthus* group dominates along the east coast. To this is now added the fact that the *radula* and the *scissus* groups, as they appear in the rest of Europe, both show Atlantic traits though mixed with a northern trend in the latter group, whereas the *thyrsanthus* group is more evenly distributed, perhaps slightly Central European.

This is in line with the conventional division of the European flora, according to which the western half of Southern Sweden is Subatlantic whereas the eastern half belongs to the Central European region (See Meusel 1965 map 258).

In a future paper the origin of the different patterns of distribution in Sweden will be discussed.

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Karyotypes and Meiosis in Leopoldia Parl. (Liliaceae) from the Southern and Central Aegean (Greece)

Bengt Bentzer

BENTZER, B. 1974 03 29. Karyotypes and meiosis in Leopoldia Parl. (Liliaceae) from the southern and central Aegean (Greece). — Bot. Notiser 127: 69—86. Lund. ISSN 0006-8195.

A survey of the variation in the mitotic karyotypes of *L. weissii, L. cycladica* ssp. *cycladica, L. cycladica* ssp. *subsessilis, L. dionysica* and *L. spreitzenhoferi* is given. The frequency of different meiotic disturbances is briefly discussed. A hypothesis for the evolution of polyploidy in the area is put forward.

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INTRODUCTION

The genus *Leopoldia* PARL. comprises five species and two subspecies in the area investigated, i.e. *L. comosa* (L.) PARL., 2n=18 (27), *L. weissii* (FREYN) FREYN ex HELDR., 2n=18, 36 (54), *L. cycladica* (DAVIS & STUART) GARBARI ssp. *cycladica,* 2n=36, 54, *L. cycladica* (DAVIS & STUART) GARBARI ssp. *subsessilis* BENTZER, 2n=36, *L. dionysica* (RECH. FIL.) BENTZER, 2n=18, 36, *L. spreitzenhoferi* HELDR., 2n=18, 36. Of these taxa *L. comosa* has been treated cytologically in BENTZER (1972 b) and *L. weissii* to a limited extent in BENTZER (1972 a). A general but brief cytological survey of Aegean *Leopoldia* was made in BENTZER (1969). Chromosome numbers of Aegean *Leopoldia* taxa have been published by DAVIS & STUART (1967) and STUART (1970).

As the material studied is comprehensive the presentation in this paper will be limited to a general survey of the variation in the chromosome complements of the various taxa. Features of purely cytological interest will be dealt with elsewhere.

MATERIAL AND METHODS

A total of approximately 500 plants representing about 150 populations from the Aegean have been studied cytologically. A code to the collections used in the present study was given in BENTZER (1973).

Chromosome preparations were made as described in BENTZER (1969 & 1972 a).

Pollen stainability was calculated as in BENTZER (1972 a).

Chromosome slides used in this study are deposited at the Department of Plant Taxonomy, Lund.

Drawings were made with the aid of a binocular camera lucida (Leitz) mounted on a Leitz Orthoplan microscope.

Descriptions of centromeric positions are according to LEVAN et al. (1964).

In this study attention has mainly been focussed on the long (L) chromosomes. Together the (L) chromosomes constitute c. 40 % of the entire chromatin content of a cell.

The size of the chromosomes in the figures can only be compared within the complement since the degree of contraction is slightly different in different cells illustrated.

MITOSIS

General Karyotype

With the exception of *L. comosa* the karyotypes of the different taxa are structurally essentially similar. The basic chromosome number is 9 and a generalized haploid set of chromosomes can be summarized as n(2L+3M+4S) where (L) stands for long chromosomes, (M) for medium and (S) for short chromosomes. Usually the (L), (M) & (S) chromosomes form distinct groups, but occasionally the difference between the (M) and (S) chromosomes is indistinct.

(L) chromosomes: Two different types of (L) chromosomes representing the two pairs of (L) chromosomes at the diploid level, the 8 (L) chromosomes at the tetraploid level and the 12 (L) chromosomes at the hexaploid level can easily be recognized on their arm indices (r-values); one group with r-value c. 3—4 (subtelocentric, st) and one group with r-value c. 7—12 (telocentric, t). In *L. weissii* and in diploid *L. dionysica* the long arm of the (L) st chromosomes tends to be somewhat shorter than the long arm of the (L) t chromosomes. In the other taxa and in tetraploid *L. dionysica,* the length of the long arms of the (L) st and the (L) t chromosomes tend to be similar (Figs. 1 G & H, 2 B, C & D). In addition to these general (L) chromosomes, variant types occur which will be discussed below.

(M) and (S) chromosomes: It is not possible to divide the groups of (M) and (S) chromosomes respectively into homologous pairs by conventional methods. The r-values vary between 1—2 (metacentric-submetacentric, m-sm) in the former group as well as in the latter. The length of the (M) chromosomes are c. 1/3 to 1/2 of that of the (L) chromosomes. The (S) chromosomes are c. 1/2 to 3/4 as long as the (M) ones (Figs. 1 G, 2 A, D & E).

Satellites: The satellites are usually attached to the long arm of either type of (L) chromosomes.

Karyotypes, Satellites and Secondary Constrictions

L. weissii: Populations with different chromosome numbers, i.e. diploids, 2n=18 and tetraploids, 2n=36, tend to be geographically separated (cf. BENTZER 1973 Fig. 28). A case of suspected translocation in the (L) chromosomes was observed in population no. 314 (2x) where one plant had 3 (L) t chromosomes, one with a satellite, and only one (L) st SAT-chromosome (Fig. 1 B 1 & 2). A translocation between the short arm of one (L) st chromosome and the long arm of one (L) t chromosome seems a possible explanation. Pollen stainability was 100 % for this plant.

Satellites are usually small and they are usually attached to the long arm of one or more of the (L) chromosomes. The size of the satellites may, however, sometimes differ considerably between plants in the same population (Fig. 1 A). The number and position of satellites vary (Fig. 3). Only a limited amount of material has been studied from northern Greece but it seems that in plants from the Northern Sporades and northwards satellites are attached to the short arm of the (L) t chromosomes (Fig. 1 E).

Population no. 8 from Kimolos (2x) contained plants with all the four alternative satellite combinations shown in Fig. 3 A. No tetraploid population seemed to contain both SAT-(L) t chromosomes and SAT-(L) st chromosomes (Fig. 3 B). Not more than two alternative satellite combi-

Fig. 1. Long chromosomes in *Leopoldia*; in G the complete karyotype. — A: *L. weissii* (2x, no. 309), two plants with SAT-chromosome heterozygosity. — B: *L. weissii* (2x, no. 314), 1. Normal plant. 2. Plant with 1 (L) st and 3 (L) t chromosomes. — C: *L. weissii* (4x, no. 340), with 4 (L) m-sm chromosomes and 1 extra long (L) t chromosome. — D: *L. weissii* (4x, no. 45), with one extra long (M) chromosome. — E: *L. weissii* (2x, no. 334), with satellites on the short arm. — F: *L. cycladica* ssp. *cycladica* (6x, no. 36). — G: *L. cycladica* ssp. *subsessilis* (4x, no. 433). — H: *L. cycladica* ssp. *subsessilis* (4x, no. 13), two plants with different SAT-chromosomes.

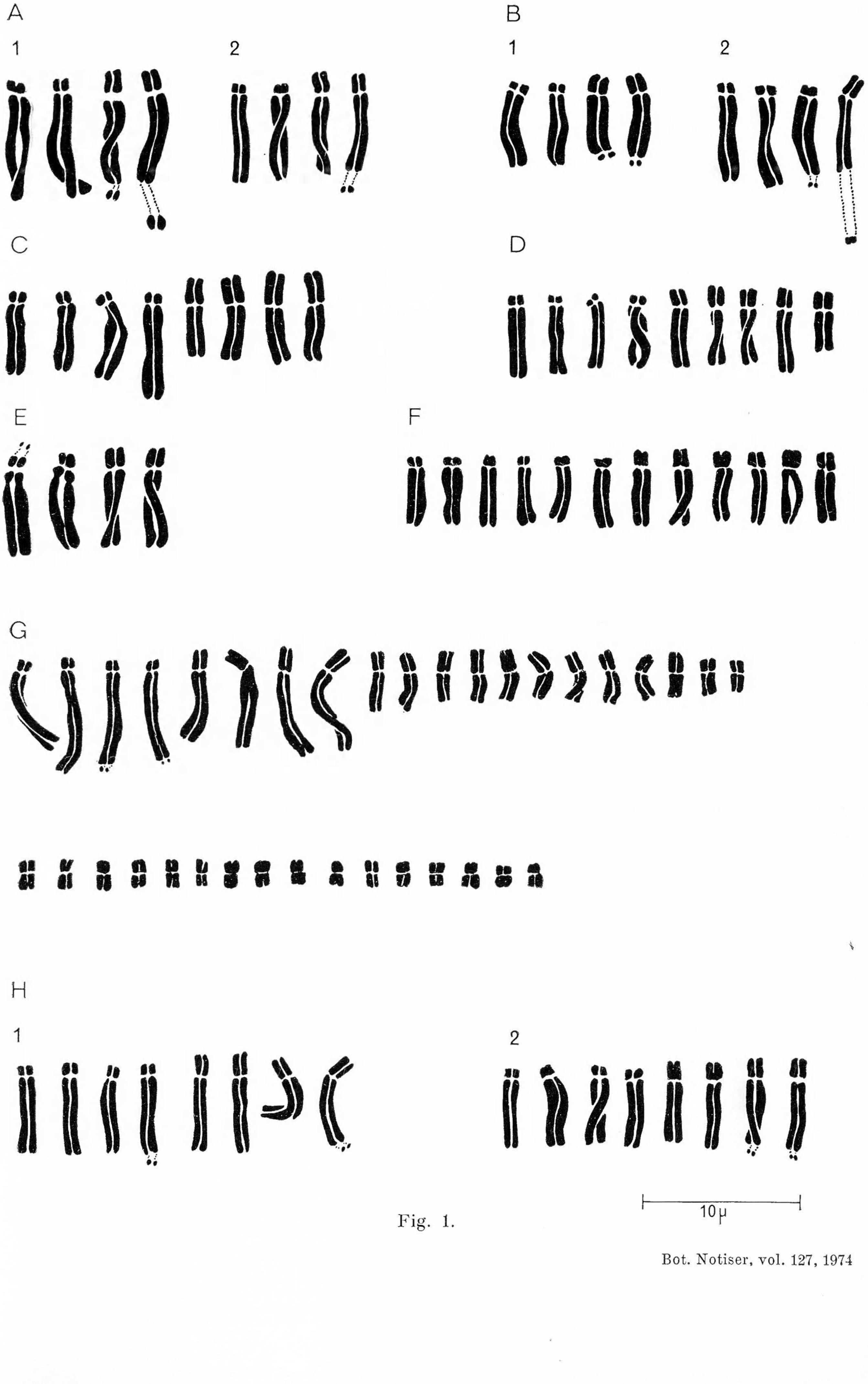

Fig. 1.

nations were found in any tetraploid population.

Secondary constrictions not connected with satellites were only found in one diploid population, viz. no. 334 from Hagion Oros. Here a secondary constriction appeared in the proximal region of the long arms of the (L) t chromosomes (Fig. 1 E).

L. cycladica ssp. *cycladica:* Tetraploid and hexaploid plants were found. On Folegandros both levels of polyploidy were found. The basic karyotypes were similar to those of *L. weissii* (Fig. 1 F). Satellites varied in number from nil (in no. 36 from Santorin, 6x) to 6 (in no. 31 from Folegandros, 6x, BENTZER 1969). Satellites were found attached to the long arm of (L) st chromosomes as well as (L) t chromosomes.

No secondary constrictions besides those connected with satellites were found.

L. cycladica ssp. *subsessilis:* Only tetraploid plants were found. The basic karyotypes agreed in general outline with those of *L. weissii* (Fig. 1 G).

The number of satellites varied between nil and three. They were always attached to the long arm of either the (L) t chromosomes or the (L) st chromosomes. Unlike *L. weissii,* satellites were occasionally found on (L) t as well as on (L) st chromosomes in the same plant (Fig. 1 H). The satellite position sometimes varied between different plants in a population.

L. dionysica: Diploid as well as tetraploid plants were found. In the two diploid populations (nos. 50 from Unia Nisia, W of Karpathos and 97 from Astakidha, W of Karpathos) the satellites were attached to the short arm of the (L) t chromosomes (Fig. 2 A).

The r-values for the four (L) chromosomes varied between 3.5 and 5.0 with the (L) SAT-chromosomes having somewhat higher values than the other (L) chromosomes. The SAT-chromosomes contained a very marked secondary constriction in the proximal region of the long arms (Fig. 2 A). Faint secondary constrictions also occurred on the long arm of some of the (M) chromosomes.

The karyotypes of the tetraploid plants agreed on the whole with those of *L. weissii* (Fig. 2 B). Not more than 2 SAT-chromosomes were recorded from any plant and the satellites were attached to the long arm of the (L) t chromosomes or the (L) st chromosomes.

L. spreitzenhoferi: Diploid and tetraploid plants were found. The basic karyotypes agreed in general outline with those of *L. weissii* (Fig. 2 C & D).

The number of satellites varied between 1 and 3 and they were always attached to the long arm of (L) t chromosomes. Secondary constrictions appeared on the long arm of a varying number of (L) chromosomes in diploid as well as in tetraploid plants (Fig. 2 C).

Deviations from the Normal Karyotype Pattern

ANEUPLOIDY

One population of *L. weissii* (no. 325 from Tinos) constituted a mixture of tetraploids and hexaploids but no triploid or aneuploid plants were found. Although there is a frequent occurrence of structural aberrations particularly in *L. weissii* (see below and BENTZER 1969, 1972 a) as well as occasional hybridization between *L.*

Fig. 2. Long chromosomes in *Leopoldia*; in A, D and E the complete karyotypes. — A: *L. dionysica* (2x, no. 97). — B: *L. dionysica* (4x, no. 84). — C: *L. spreitzenhoferi* (4x, no. 505). — D: *L. spreitzenhoferi* (2x, no. 405). — E: *L. weissii* (2x, no. 313), with a translocation between 2 (M) chromosomes indicated by arrows. — F: Three plants from a hybridogenous population, no. 429 (*L. weissii*, 4x×*L. comosa*, 2x). 1. Diploid *L. comosa* with aberrant satellite position and aberrant (L) m-st chromosomes indicated by arrow. 2. Triploid hybrid with one aberrant (L) *L. weissii* chromosome indicated by arrow. 3. Tetraploid *L. weissii* with one (L) m-sm chromosome indicated by arrow.

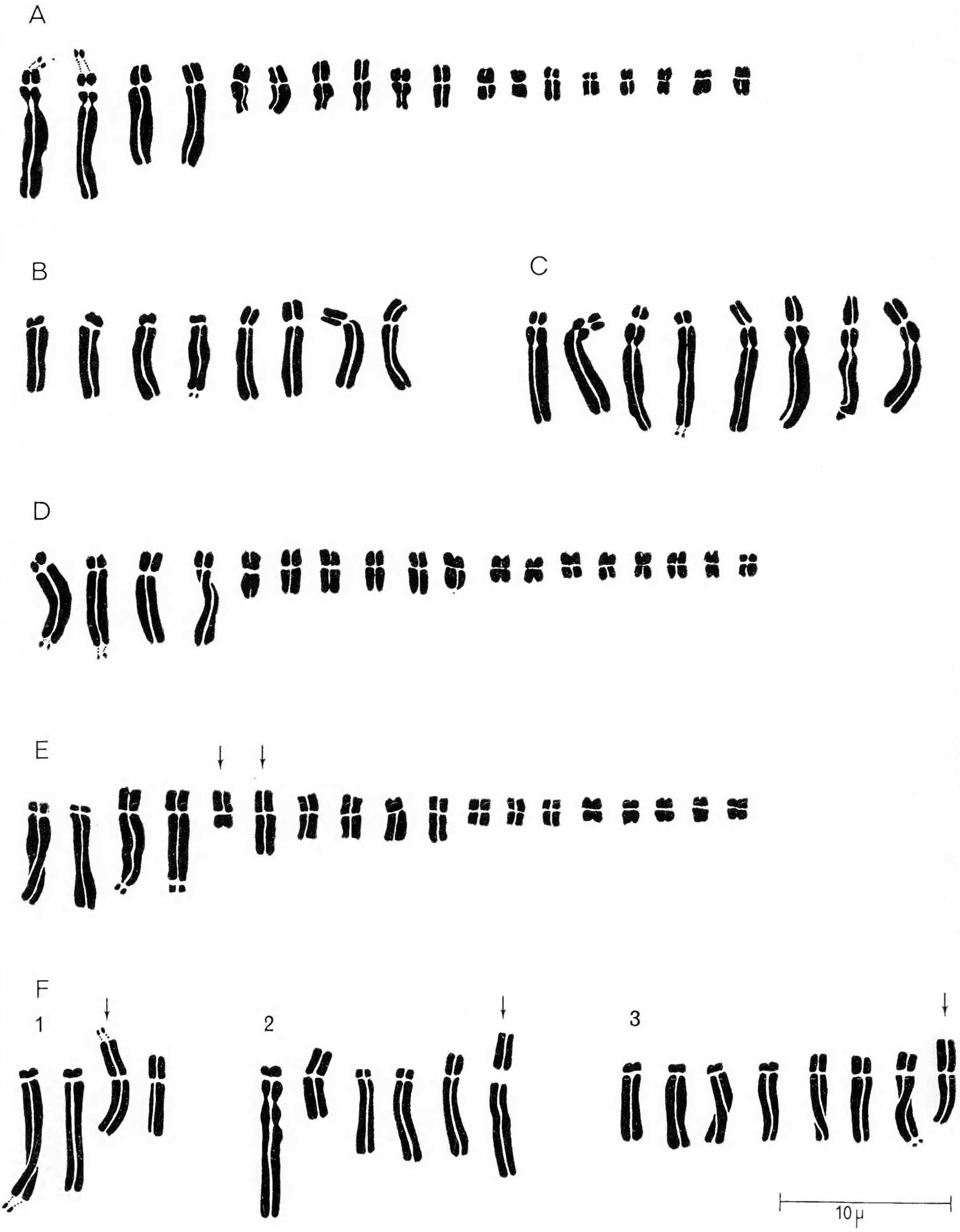

Fig. 2.

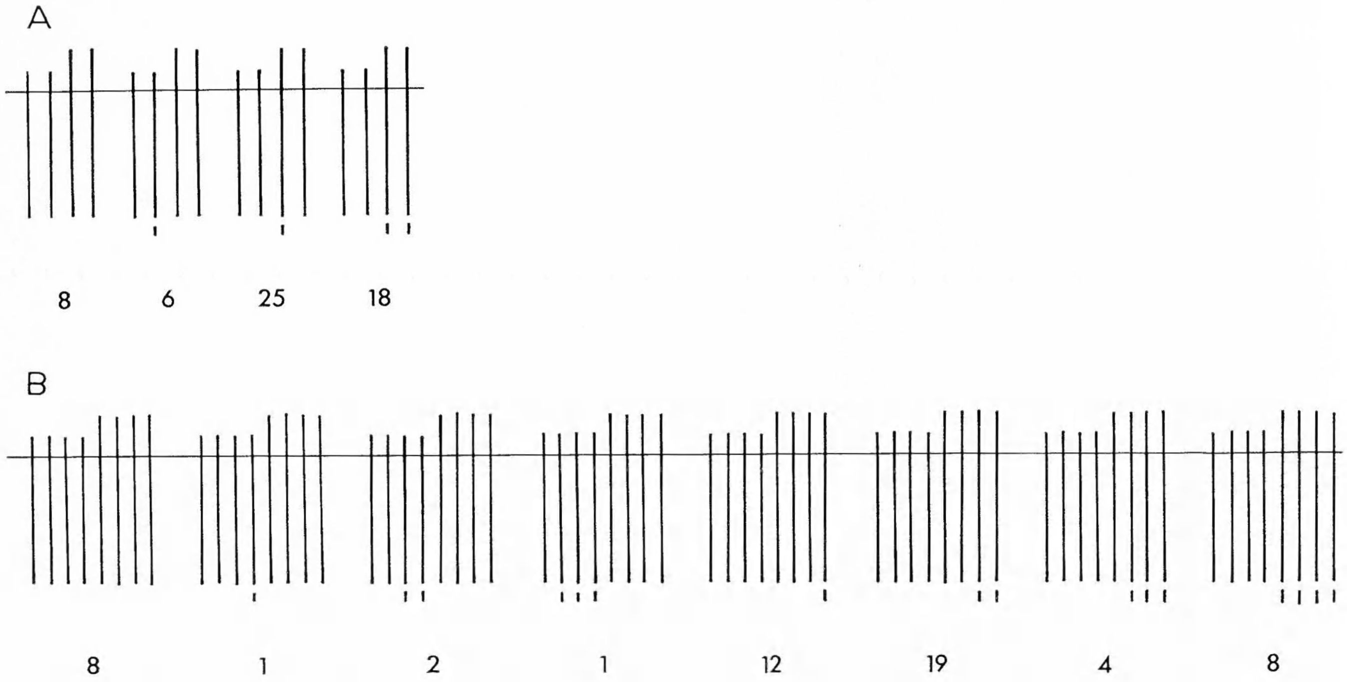

Fig. 3. Generalized sets of long chromosomes in *L. weissii* showing the alternative combinations of satellite number and position on the long arms. All satellites have been generalized to an equal size. The number of plants with each combination is given. — A: Diploid plants from 17 populations. — B: Tetraploid plants from 20 populations.

weissii (4x) and *L. comosa* (2x) (BENTZER 1972 b) aneuploid chromosome numbers were only exceptionally found in tetraploid *L. weissii* and never in diploid. In no. 41 from Kimolos one plant lacked one (L) t chromosome while another plant had an additional (L) t chromosome. Five plants in the population were normal, i.e. 2n=26. The plant that lacked one chromosome had a pollen stainability of 90 %.

In no. 61 from Kimolos one plant lacked one (L) t chromosome (pollen stainability 85 %) and in no. 67 from Karpathos one plant had an additional (L) t chromosome.

In *L. cycladica* ssp. *cycladica, L. cycladica* ssp. *subsessilis, L. dionysica* and *L. spreitzenhoferi* no plants were found with aneuploid chromosome numbers.

CHANGE OF CENTROMERIC POSITION IN (L) st CHROMOSOMES

In a number of plants of *L. weissii* (4x), *L. cycladica* ssp. *cycladica* (4x), *L. cycladica* ssp. *subsessilis* (4x) and *L. dionysica* (4x) one or more of the (L) st chromosomes had become metacentric to submetacentric (m-sm) with an r-value of c. 1.5—2.0. The length of the rearranged chromosome was similar to that of normal (L) st chromosomes. The (L) m-sm chromosome was essentially similar in geographically separated populations (Fig. 4).

L. weissii: C. 15 % of the tetraploid populations contained one or more plants with one or more (L) m-sm chromosomes. Diploids were not found with (L) m-sm chromosomes of this kind. In the tetraploids, the karyotypes were usually normal apart from the (L) m-sm chromosome and the chromosome numbers were unaltered, i.e. 2n=36.

In populations nos. 19 and 87 from Amorgos and 32 from Rodhos the 6 plants studied had 1 (L) m-sm chromosome each. In the other populations heterozygous plants were found together with normal ones.

In population no. 44 from Naxos, one

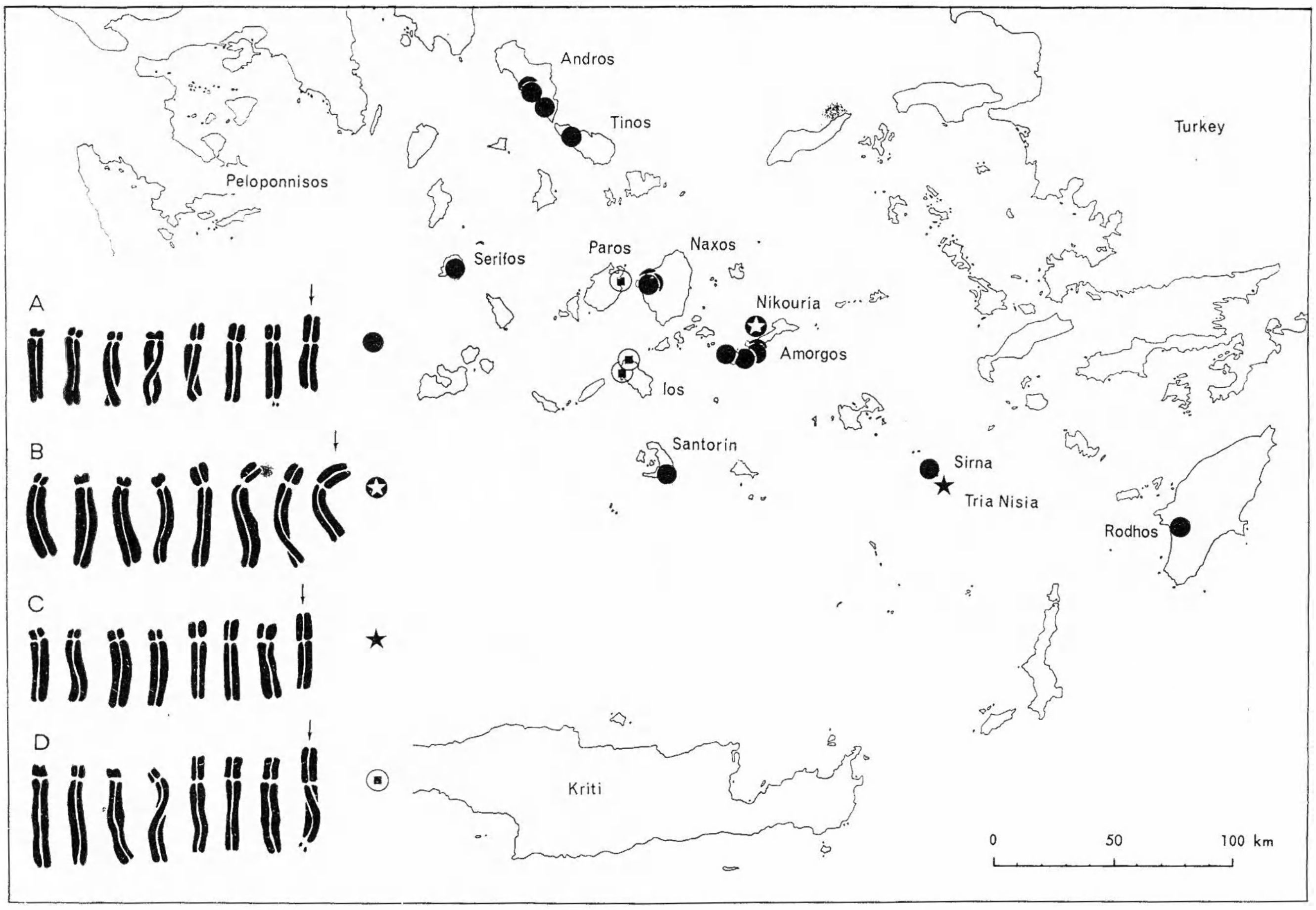

Fig. 4. Distribution of (L) m-sm chromosomes in Aegean *Leopoldia*. The eight (L) chromosomes in four tetraploid taxa of *Leopoldia* have been drawn. Arrows indicate the (L) m-sm chromosome. — A: *L. weissii*. — B: *L. cycladica* ssp. *cycladica*. — C: *L. dionysica*. — D: *L. cycladica* ssp. *subsessilis*.

homozygous, one heterozygous and one normal plant as regards the (L) m-sm chromosome were recorded. In populations nos. 5 from Santorin and 66 & 74 from Sirna plants with 2 (L) m-sm chromosomes were found, in no. 346 from Andros which grew intermixed with *L. comosa* one plant with 3 (L) m-sm chromosomes was found and finally, in population no. 340 from Andros one plant with 4 (L) m-sm chromosomes was found (Fig. 1 C). The latter plant also had one (L) t chromosome that was longer than the rest. Pollen stainability was not particularly reduced owing to the presence of one or more (L) m-sm chromosomes (Tab. 1).

L. cycladica ssp. *cycladica:* Only in

Table 1. Percentage stainable pollen in plants with (L) st chromosomes altered to r-value c. 1.5—2.0 and in plants with one extra long (M) chromosome. *L. weissii, L. cycladica* ssp. *cycladica, L. cycladica* ssp. *subsessilis* and *L. dionysica* are represented.

No. of plants with	Percentage stainable pollen							
	65	70	75	80	85	90	95	100
(L) m-sm chromosomes .... No. of (L) m-sm's within parentheses			1 (1)	1 (3)	2 (1)	1 (2) 2 (1)	1 (4)	14 (1)
Extra long (M) chromosome		1						4

population no. 17 from Nikouria (N of Amorgos) was one plant with one (L) m-sm chromosome found (Fig. 4 B) together with 3 normal ones.

L. cycladica ssp. *subsessilis:* In three populations plants with one (L) m-sm chromosome each were found (Fig. 4 D).

L. dionysica: In population no. 42 from Tria Nisia (SE of Astipalaia) three out of four plants contained one (L) m-sm chromosome each (Fig. 4 C).

EXTRA LONG (M) CHROMOSOME IN L. WEISSII

In some geographically separated tetraploid populations of *L. weissii,* i.e. no. 3 from Naxos, no. 6 from Naxos, no. 10 from Serifos, no. 45 from Kimolos, no. 422 from Anafi and no. 426 from Amorgos, plants were observed with one (two in no. 422) chromosome intermediate in size between the ordinary (L) and (M) chromosomes (Fig. 1 D). In populations nos. 3 and 6 this extra long (M) chromosome occurred with the structurally rearranged (L) st chromosome mentioned above. In populations nos. 10 and 45, 8 normal (L), 10 normal (M) and 17 (S) chromosomes were found with the extra long (M) chromosome. An unequal translocation between 2 normal (M) chromosomes seems to be a possible explanation for the origin of the extra long (M) chromosome in these populations. In the other populations, i.e. nos. 3, 6, 422 (containing hybrids between *L. weissii* and *L. comosa*) and 426, each extra long (M) chromosome replaces one normal (M) chromosome without any other visible change in the karyotype. Pollen stainability does not seem to be reduced in spite of the presence of an extra long (M) chromosome (Tab. 1).

An extra long (M) chromosome was also found in one diploid plant in population no. 313, in which *L. weissii* grows intermixed with *L. comosa* (Fig. 2 E). The karyotype indicates an unequal reciprocal translocation between two (M) chromosomes. Pollen stainability was 95 %.

Hybrids between L. weissii and L. comosa

Hybrids between *L. comosa* and other members of *Leopoldia* in the Aegean region are easily identified on their chromosome complements. Three plants from one hybridogenous population (*L. weissii,* 4x×*L. comosa,* 2x) are shown in Fig. 2 F.

In the diploid karyotype (Fig. 2 F: 1) one of the (L) m-st chromosomes of *L. comosa* was abnormally long and had a satellite attached to the short arm. One of the (L) t chromosomes of *L. comosa* had a satellite on the long arm. The normal karyotype of *L. comosa* was given in Bentzer (1972 b).

In the triploid karyotype (Fig. 2 F: 2) the two (L) *L. comosa* chromosomes were normal apart from an extra secondary constriction on the long arm of the (L) t chromosome. One of the (L) st *L. weissii* chromosomes was abnormally long and had an r-value of c. 2.7 (pollen stainability 20 %).

The tetraploid karyotype (Fig. 2 F: 3) consisted of 7 normal (L) chromosomes and one (L) m-sm chromosome similar to those described on p. 74 (pollen stainability 95 %).

In a number of cases hybridization seems to imply a change in morphology for one or other of the chromosomes, e.g. in population no. 422, where 2 extra long (M) chromosomes occurred, in nos. 425 and 429 where one (L) m-sm chromosome occurred and in no. 74 and 66 (Bentzer 1969), where one or two (L) m-sm chromosomes occurred along with other changes, etc.

MEIOSIS

Meiosis was studied in a limited amount of material, i.e. c. 50 plants representing all taxa. If carried out on a greater number of plants meiotic analyses would be of value in elucidating possible explanations of observed mitotic irregularities, e.g.

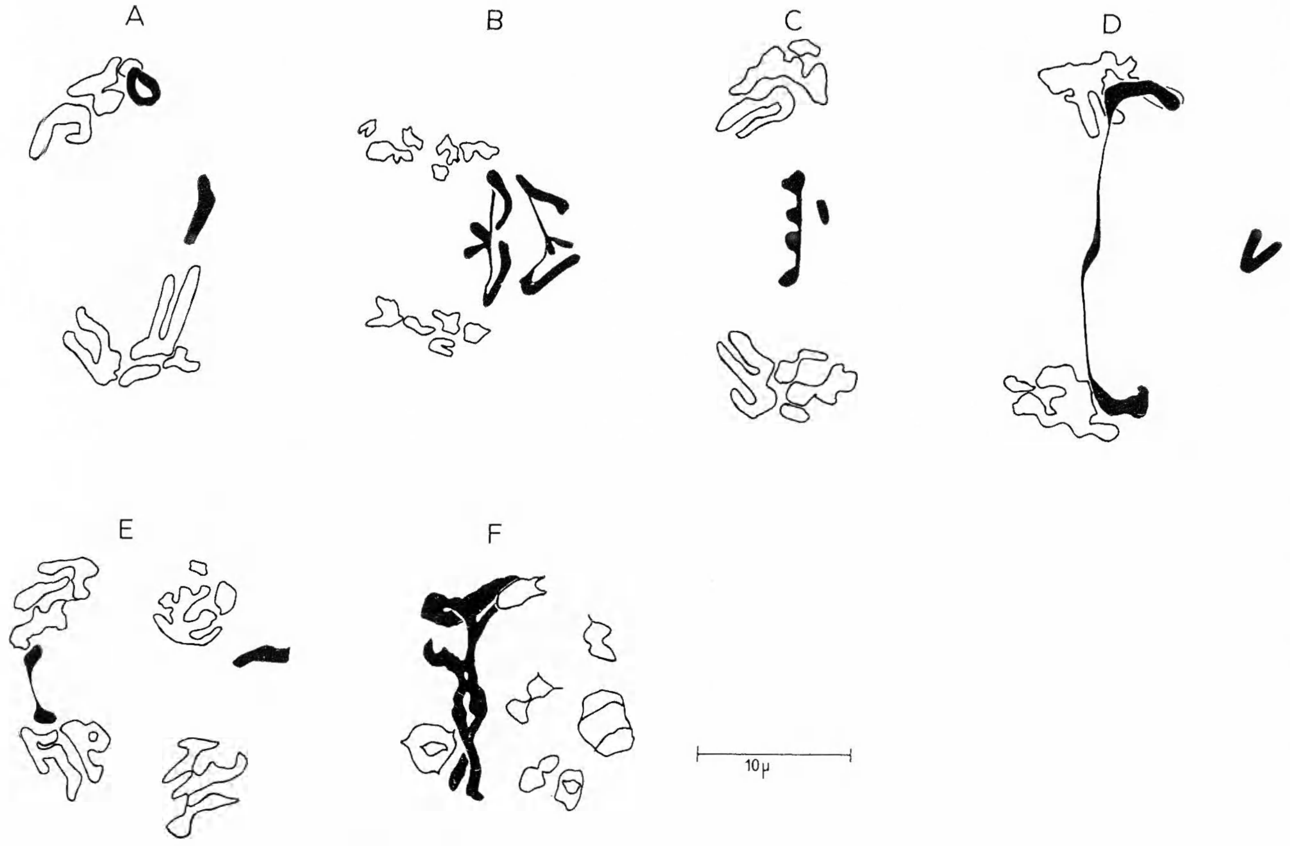

Fig. 5. Disturbances during meiosis in diploid *L. weissii*, A—D: Anaphase I. E: Anaphase II. F: Diakinesis. — A: Loop and fragment involving (L) chromosomes (no. 303). — B: Two side-arm bridges in (L) chromosomes (no. 411). — C: (BF) in (M) chromosomes (no. 330). — D: (BF) in (L) chromosomes (no. 330). — E: (B) in (M) chromosomes and (F) from (L) chromosomes (no. 310). — F: Quadrivalent involving (L) chromosomes (no. 330).

structural heterozygosity, aneuploidy, etc. In most cases, however, it has not been possible to obtain acceptable preparations from those plants of which meiotic analyses were most urgently needed.

Diakinesis and Metaphase

PAIRING

In diploid plants of *L. weissii* and *L. spreitzenhoferi* the pairing of homologous chromosomes was usually very good. Diploid *L. dionysica* was not investigated. In *L. weissii* (2x), in one plant in each of populations nos. 310, 330 and 334 there was a tendency for the (L) chromosomes to be associated in quadrivalents at diplotene-diakinesis (Fig. 5 F). In no. 334 the quadrivalents were maintained to metaphase indicating a reciprocal translocation, but in the other two plants the quadrivalents had usually become bivalents at metaphase, which may nevertheless indicate the presence of reciprocal translocations without ability to form chiasmata in the homologous segments.

Failure of apparently homologous chromosomes to pair properly was observed in one plant of *L. weissii* (2x) from population no. 333 from Tinos where 2—4 univalents of (M) and (S) chromosomes were frequently found. The pollen stainability of this plant was 55 %.

One quadrivalent involving 2 (S) and 2 (M) chromosomes was observed in some cells of one diploid *L. spreitzenhoferi*, no. 406 (Fig. 6 O). A reciprocal translocation seems likely although the mitotic karyotype did not support a translocation.

In tetraploid plants of all taxa a

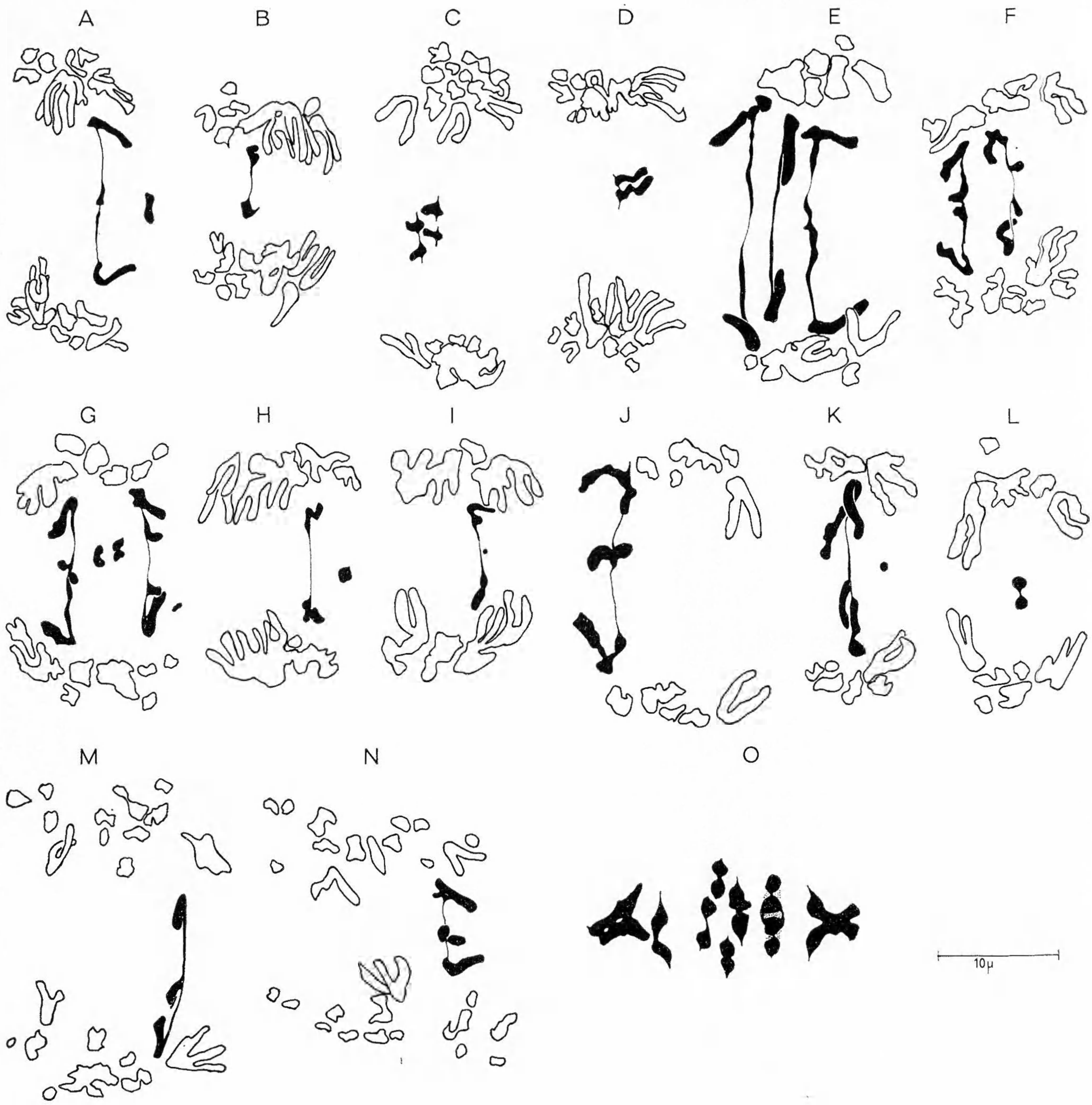

Fig. 6. Anaphase I aberrations in *Leopoldia*; in O metaphase I. — A—D: *L. cycladica* ssp. *cycladica* (4x, no. 416 b), A: Bridge and fragment (BF) in (L) chromosomes. B: Bridge (B) in (M) chromosomes. C: Lagging (M) chromosomes. D: One lagging bivalent of (L) chromosomes. — E—G: *L. cycladica* ssp. *subsessilis* (4x), E: Three (B) in (L) chromosomes in no. 75. F: Two side-arm bridges in (L) chromosomes in no. 433. G: Two side-arm bridges in (L) chromosomes, two lagging (S) bivalents and one fragment in no. 433. — H—I: *L. dionysica* (4x, no. 30), H: (BF) in (M) chromosomes. I: (BF) in (M) chromosomes. — J—L: *L. spreitzenhoferi* (2x, no. 406), J: Side-arm bridge in (L) chromosomes. K: (BF) in (L) chromosomes. L: Lagging bivalent of (S) chromosomes. — M—N: *L. spreitzenhoferi* (4x, no. 402), M: Side-arm bridge in (L) chromosomes. N: Side-arm bridge in (L) chromosomes. — O: *L. spreitzenhoferi* (2x, no. 406), metaphase I with one quadrivalent involving (M) and (S) chromosomes.

Table 2. *L. weissii* (4x). Distribution of quadrivalents involving (L), (M) and (S) chromosomes. n=number of cells studied.

Population no.	n	Min., mean and max. values for number of quadrivalents/cell			% stainable pollen
		(L)	(M)	(S)	
328	5	0—0.60—1	1—1.80—2	0—0.80—1	100
339	18	0—0.72—2	0—1.11—3	0—0.39—1	100
341	6	0—0.50—1	0—1.00—2	0—0.50—1	100
342	12	0—0.58—1	0—1.33—3	0—0.92—2	100
351	17	0—1.41—2	0—1.12—2	0—0.53—3	70

comparatively large number of multivalents, particularly quadrivalents were regularly found. The quadrivalents always contained homologous chromosomes and they appeared to orientate at random at M I. Quadrivalents involving non-homologous chromosomes may exist but have in that case escaped notice owing to the relative difficulty in analysing 36 chromosomes at meiosis.

Quadrivalents generally seem to involve (M) chromosomes more frequently than other chromosomes (Tab. 2). In one plant from no. 351 of *L. weissii* (4x) quadrivalents involving (L) chromosomes prevailed (Tab. 2). The pollen stainability of this plant was 70 %, while in those plants where (M) quadrivalents prevailed the pollen stainability was 100 %.

Occasionally a few hexavalents and octovalents of (L) as well as (M) chromosomes were found, indicating interchanges between non-homologous chromosomes.

CHIASMATA

In diploid *L. weissii* the number of chiasmata in the (L) chromosomes varied between 1.5 and 3.5 per bivalent (Tab. 3). (L) bivalents with one chiasma were only occasionally observed. The chiasmata in the (L) bivalents were apparently distributed at random (Fig. 8). An average of 0.7 chiasmata per bivalent were terminal (Tab. 3).

The (M) bivalents of *L. weissii* (2x) regularly had 1—2 chiasmata, usually terminal or almost terminal.

The (S) bivalents were difficult to analyse as to number of chiasmata formed per bivalent. It seems, however, as if 1 terminal chiasma per bivalent prevails.

In tetraploid *L. weissii* the frequency of chiasmata per pair of (L) chromosomes was reduced in comparison with diploid *L. weissii* (Tab. 3). The frequency of terminal chiasmata per pair of (L) chromosomes was greater in the tetraploids as compared with the diploids (Tab. 3). The reason for decreased chiasma fre-

Table 3. Chiasmata number and distribution per chromosome pair in the (L) chromosomes of diploid and tetraploid *L. weissii.*

Plant no.	No. of cells studied	Min., mean and max. values for	
		Chiasma frequency	Frequency of terminal chiasmata
Diploid			
64—2	15	2.0—2.5—3.5	0.0—0.7—1.0
73—5	15	2.0—2.5—3.5	0.0—0.9—1.5
73—15	31	2.0—2.6—3.0	0.0—0.7—1.5
318—3	7	1.5—2.1—2.5	0.0—0.5—1.0
318—4	13	1.5—2.3—3.0	0.0—0.7—1.5
318—5	9	2.5—2.9—3.5	0.5—0.8—1.0
326—1	33	1.5—2.3—3.0	0.0—0.9—2.0
330—3	23	1.5—2.2—3.0	0.0—0.3—1.0
Mean:		1.8—2.4—3.1	0.1—0.7—1.3
Tetraploid			
328—4	5	1.5—2.1—2.5	0.5—0.9—1.3
339—4	18	1.8—2.0—3.0	0.3—1.0—1.8
341—2	6	1.3—1.7—2.0	0.3—0.8—2.0
342—4	12	1.3—1.7—2.0	0.0—0.8—1.5
351—1	17	1.5—2.1—2.5	0.0—1.1—2.0
Mean:		1.5—1.9—2.4	0.2—0.9—1.7

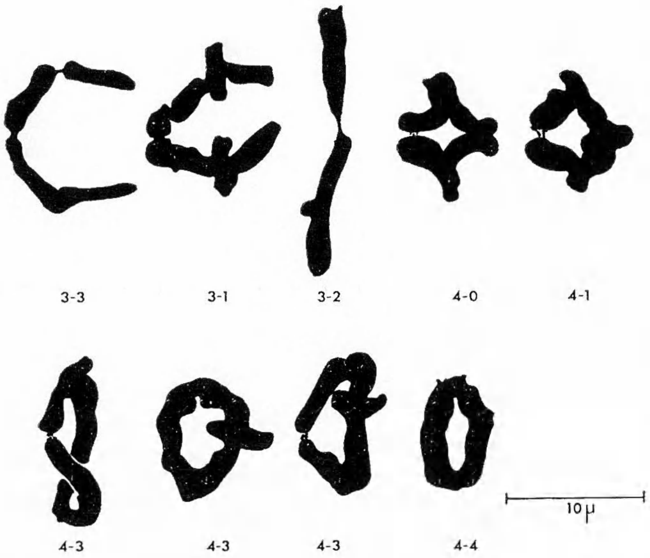

Fig. 7. *Leopoldia weissii* (4x, no. 451). Total number of chiasmata and number of terminal chiasmata in quadrivalents of (L) chromosomes from different cells of one plant.

quency is the common formation of quadrivalents. Different chiasma positions in (L) quadrivalents are given in Fig. 7.

Only terminal positions for chiasmata were found between (M) chromosomes in tetraploid *L. weissii* as well as in the other tetraploid taxa (Fig. 8).

The chiasma positions in (S) associations seemed to be terminal in tetraploid taxa.

Two plants of *L. weissii* (4x) each having one (L) m-sm chromosome were analysed. The (L) m-sm chromosome paired with the other (L) chromosomes in a normal way.

L. cycladica ssp. *cycladica* (4x), *L. cycladica* ssp. *subsessilis* (4x), *L. dionysica* (4x) and *L. spreitzenhoferi* (4x) all appear to have a frequency and distribution of quadrivalents and chiasmata similar to that in *L. weissii* (4x).

ANAPHASE I

In diploid *L. weissii* 3 out of 16 plants were found with no disturbances at A I. In these 3 plants comparatively few cells were analysed (Tab. 4). Although A I was normal in no. 64—2 (Tab. 4) this plant had the lowest pollen stainability of all plants studied at A I, i.e. 60 %. In all plants of diploid *L. weissii* studied more than 90 % of the cells were normal. The most frequent disturbances were bridges and fragments, and laggards (cf. BENTZER 1972 a, where sub-chromatid bridges were the most frequent aberration in population no. 318 of *L. weissii*). In one plant from population no. 330 of *L. weissii* (2x) 5 cells with bridge & fragment were observed; 3 bridges involved (L) chromosomes, 1 (M) and 1 (S) chromosomes.

In tetraploid *L. weissii* the frequency of disturbances was much higher than in diploid *L. weissii*. Only 2 out of 9 plants studied had more than 90 % normal cells (Tab. 4). The most frequent disturbances were bridges & fragments, and laggards. Side-arm bridges were common in one plant from no. 332 of *L. weissii* (4x) where in some cells as many as 3 side-arm bridges occurred. Laggards were found in all plants of *L. weissii* (4x) with varying frequency. Bridges and fragments were formed by all kinds of chromosomes, i.e. (L), (M) and (S) chromosomes. Bridges involving (L) chromosomes were commonest.

Almost all laggards were of similar size and appearance, resembling a bivalent of (S) chromosomes (Fig. 6 L) and staining a weaker colour than the other chromosomes. One (L) chromosome was found lagging in a few cells. Although A I in tetraploid *L. weissii* in most cases was severely disturbed, the pollen stainability was only reduced in 3 plants (Tab. 4).

In the other taxa the A I was essentially similar to that of *L. weissii* (Tab. 5). Particularly in *L. cycladica* ssp. *subsessilis* (no. 75) a high frequency of chromatid bridges without fragments was observed (Fig. 6 E). In *L. cycladica* ssp. *cycladica* (no. 416 b, 4x) bridges & fragments were found involving (L) as well as (M) chromosomes. Two different fragment sizes together with the (M) chromosome bridges were observed. In *L. dionysica* (4x) also two different fragment sizes occurred

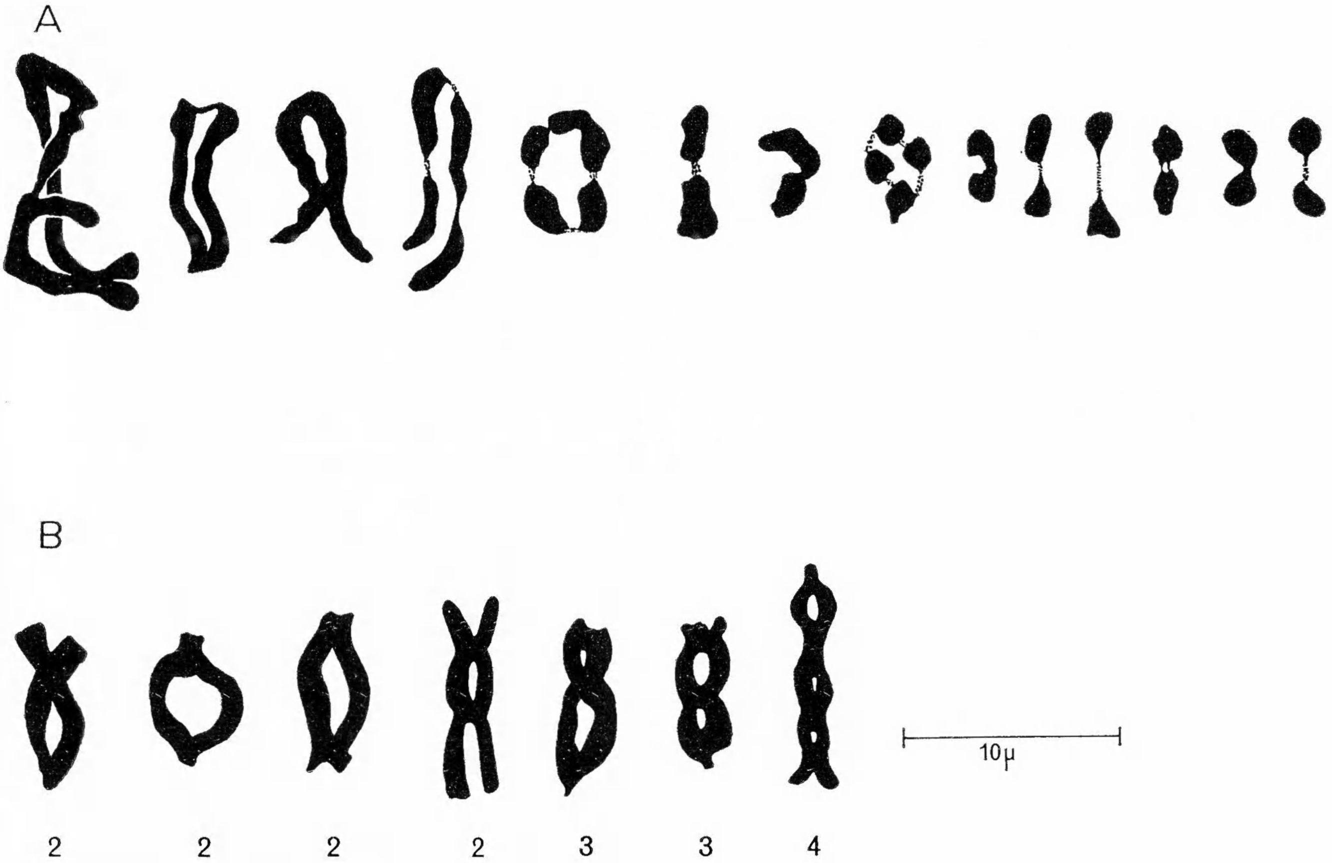

Fig. 8. Pairing configurations at diakinesis. — A: *Leopoldia cycladica* ssp. *subsessilis* (4x, no. 96) showing one (L) chromosome quadrivalent, two (M) chromosome quadrivalents and one (S) chromosome quadrivalent. — B: *L. weissii* (2x, no. 306) showing different chiasma positions and numbers in (L) bivalents from different cells. Number of chiasmata indicated.

with (M) chromosome bridges (Fig. 6 H & I).

In *L. spreitzenhoferi* (no. 402, 4x) 3 different sizes of fragments were found with (L) chromosome bridges in one plant.

ANAPHASE II

In diploid plants of all taxa A II was usually almost perfect with only exceptional cases of laggards, bridges & fragments (Fig. 5 E) and non-disjunction.

In tetraploid plants of all taxa the frequency of disturbances was somewhat higher but it was still usually less than 1 % of the cells that were disturbed. The most extreme disturbances were found in one plant of *L. weissii* (4x) from population no. 361 where 60 % of the cells contained bridges (n=46).

DISCUSSION

In *L. comosa* (L.) PARL., BENTZER (1972 b) described a case of widespread heteromorphism in the (L) m-st chromosome pair. The origin of that heteromorphism was presumed to be a pericentric inversion. Possible reasons for the persistance of the rearranged chromosome were discussed.

The present case of widely distributed heteromorphism in the (L) st chromosomes, i.e. the presence of one or more (L) m-sm chromosomes in several tetraploid plants from various taxa is parallel to that of *L. comosa* (BENTZER op. cit.).

The origin of the (L) m-sm chromosome cannot be proved but a few indications support an origin by pericentric inversion: (1) The length of the (L) m-sm chromosome was similar to that of the

Table 4. Percentage of various disturbances at A I in *L. weissii* (2x, 4x).

Population no.	No. of cells	Normal	Bridges & Fragments			Loops	Laggards	Side-arm bridges	% stainable pollen
			1	2	3				
L. weissii (2x)									
49—6	212	97	1	—	—	—	2	—	95
49—7	100	100	—	—	—	—	—	—	95
49—14	125	98	1	—	—	—	—	1	100
64—2	16	100	—	—	—	—	—	—	60
64—11	151	97	1	—	—	—	2	1	90
73—11	51	98	2	—	—	—	—	—	95
73—15	177	94	5	—	—	—	1	1	95
303—1	37	100	—	—	—	—	—	—	100
303—2	152	99	1	—	—	1	—	—	95
303—5	94	98	—	—	—	—	2	—	100
310—1	160	96	2	—	—	—	2	—	—
326—1	104	96	3	—	—	—	1	—	95
326—3	315	94	3	—	—	—	3	—	95
330—3	316	98	2	—	—	—	—	—	90
350—3	248	98	2	—	—	—	—	—	95
411—2	143	91	8	—	—	—	—	1	70
L. weissii (4x)									
59—1	98	92	3	—	—	—	5	—	65
300—1	43	84	5	—	—	—	12	—	100
301—1	94	10	3	—	—	—	87	—	60
332—9	243	52	10	6	3	—	22	8	90
340—2	32	81	13	—	—	—	6	—	100
341—2	57	88	—	—	—	—	12	—	100
346—2	209	97	1	—	—	—	1	1	100
346—7	102	77	5	—	—	1	18	—	100
357—4	152	63	11	—	—	—	26	—	100

normal (L) st chromosomes. — (2) In some plants a satellite was attached to the long arm of the (L) m-sm chromosome (Fig. 4 D, Bentzer 1969 pp. 469, 472). Since satellites normally appear in this position in normal plants one may conclude that the distal part of the long arm has remained intact and the possibility of a shift seems less tenable. — (3) The (L) m-sm chromosome paired with the other (L) chromosomes in a normal way during meiosis. It seems therefore unlikely that the (L) m-sm chromosome originates from another taxon, e.g. *L. comosa*.

Pericentric inversions are difficult to demonstrate cytologically especially when the chiasma frequency is reduced, which is the case in the tetraploids, or when chiasmata tend to be formed outside the presumably inverted segment, i.e. in terminal positions, which is also the case in the tetraploids. No efforts have been made to go any further in analysing the origin of the (L) m-sm chromosome.

To explain the extensive occurrence and wide distribution of the (L) m-sm chromosome one could speculate a little. Hybridization between *L. weissii* (4x) and *L. comosa* (2x) has been well proved in a number of localities (Bentzer 1973). Hybridization between other taxa is also probable although it has not been proved. As pointed out by Walters (1957), Mangelsdorf (1958) and Moav et al. (1968) for example, hybridogenous populations often seem to have an increase of chromosome morphological diversity which may be due to the break-down of balanced cytogenetic systems. One may

Table 5. Percentage of disturbances at A I and A II in *L. cycladica* ssp. *cycladica* (4x), *L. cycladica* ssp. *subsessilis* (4x), *L. dionysica* (4x) and *L. spreitzenhoferi* (2x, 4x).

Taxon	A I								A II					% Pollen stain-ability
	No. of cells	Normal	Bridges			Bridge & Fragm.	Lag-gards	Side-arm bridges	No. of cells	Normal	Bridge	Bridge & Fragm.	Lag-gards	
			3	2	1									
L. cycladica ssp. *cycladica* (4x)														
416b—2	113	89	—	—	—	5	5	—	—	—	—	—	—	—
L. cycladica ssp. *subsessilis* (4x)														
75—1	186	35	39	23	3	1	—	—	—	—	—	—	—	100
80—3	72	89	6	—	—	1	4	—	—	—	—	—	—	100
96—1	—	—	—	—	—	—	—	—	314	89	4	1	5	75
433—1	207	66	3	—	—	8	16	6	—	—	—	—	—	—
L. dionysica (4x)														
30—2	136	87	5	—	—	3	5	—	—	—	—	—	—	100
L. spreitzenhoferi (2x, 4x)														
406—7 (2x)	181	96	—	—	—	1	2	1	200	100	—	—	—	—
402—1 (4x)	146	88	—	—	—	5	—	8	179	98	2	—	—	—
404—1 (4x)	—	—	—	—	—	—	—	—	548	85	5	—	10	—

suspect that if there are some "weak spots" on the (L) st chromosomes, the risk of breaks on such sites would increase with hybridization. The tendency for spontaneous mutations to be localized to particular regions has been shown by GILES (1940) in *Tradescantia* and WALTERS (1957) in *Bromus*, for example.

Hybridization may consequently generate new chromosome types which in some cases may prove selectively positive or completely neutral, in both cases with a fair chance of being established. In those localities where plants with one or more (L) m-sm chromosomes were found, *L. comosa* also occurred in the neighbourhood and hybridization would be at least theoretically possible.

Another possible explanation of the extensive distribution of the (L) m-sm chromosome is of course that it has a monophyletic origin dating back to the times when the islands of the Aegean were still connected with each other and with the mainlands of Greece and Anatolia, i.e. in Pliocene to Pleistocene times.

Those extra long (M) chromosomes which cannot be directly explained by translocation may possibly originate from hybrid swarms between *L. weissii* and *L. comosa*, for example in a way similar to that discussed for the (L) m-sm chromosomes.

The irregular shape, number and position of satellites in diploid as well as tetraploid (and hexaploid) plants of *Leopoldia* spp. is difficult to explain (BENTZER 1972 b). HENEEN and RUNEMARK (1962, 1972 b) pointed to a very extensive variation in the satellite chromosomes of *Elymus rechingeri* (RUN.) RUNEMARK and *Elymus striatulus* RUNEMARK from the Aegean which is comparable to that described in the present paper. HENEEN and RUNEMARK (1962) also discussed possible modes of the preservation of the SAT-chromosome polymorphism. In *Elymus rechingeri* SAT-chromosome polymorphism was associated with morphological diversity while in *E. striatulus* such morphological diversity was not met with. In *Leopoldia* there certainly is an extensive morphological variation (Bentzer 1973), but it does not seem to be directly correlated with SAT-chromosome polymorphism nor to other forms of structural chromosome heterozygosity, i.e. a plant with a given chromosome morphological abnormality was not also necessarily morphologically divergent.

The meiotic disturbances which occurred at A I were most extensive in the tetraploid plants. To what extent the bridges with or without fragments are caused by paracentric inversions cannot be determined. A bridge and fragment is certainly not sufficient indication of a paracentric inversion (cf. Lewis & John 1963). Brandham (1969) pointed out that bridges and fragments formed by other means than by crossing-over within an inversion loop are almost invariably found in plants which also show sub-chromatid bridges at A I. In the present material a number of sub-chromatid bridges were observed mainly involving (L) chromosomes which were also those chromosomes which had most bridges and fragments. As a rule there were too few bridges and fragments observed to give a sufficient number of measurements of fragment sizes. However, in at least three cases (pp. 80—81) fragments of different sizes occurred thus indicating breakage and defective reunion of chromatids. It can be suspected that several of the observed bridges and fragments have been formed in a similar way. One possible means by which such irregularities may arise is through crossing-over malfunction (for references, see Heneen 1972 p. 434). Some of the bridges and fragments are probably caused by crossing-over within paracentric inversion loops. Inversions may be a common feature in segments which are not frequently involved in crossing-over, i.e. in proximal parts of the chromosomes of tetraploid plants in particular. The comparatively infrequent occurrence of bridges and large fragments and other indications of inversion heterozygosity suggests such putative localizations. The formation of quadrivalents and the tendency of terminal chiasmata in tetraploids may, in fact, be a very effective way of disguising inversions and other irregularities in proximal chromosome segments.

Autopolyploidy

With the possible exception of *L. dionysica* (4x) polyploidy in *Leopoldia* in the Aegean seems to be a case of autopolyploidy. The indications for such an origin are: (1). Morphologically more or less indistinguishable diploids and tetraploids of *L. weissii,* tetraploids and hexaploids of *L. cycladica* ssp. *cycladica* and diploids and tetraploids of *L. spreitzenhoferi.* The levels of polyploidy are to a certain extent distinguishable on seed size and pollen size (Bentzer 1973). — (2). The very close agreement in appearance between the basic karyotypes of diploids, tetraploids and hexaploids. — (3). The high frequency of apparently randomly orientated multivalents including homologous chromosomes at meiosis in the tetraploids and the high percentage of stainable pollen in spite of numerous quadrivalents. Evidence has accumulated that in general the formation of multivalents in itself does not cause a reduction in the fertility of an autopolyploid (for references see Stebbins 1950 pp. 305—306). Roseweir and Rees (1962) using induced autotetraploid Rye as an example suggest that quadrivalents may even be selectively positive, since severe cytological disturbances are mainly caused by non-disjunction owing to the formation of univalents and trivalents. Along with a presumed positive selection for quadrivalents another selection may operate to localize chiasmata terminally and in that way avoid separation difficulties at A I. Although the present material is very limited the results agree well with the suggestions of Roseweir and Rees (op.

cit.). — (4). The occurrence of mixed levels of polyploidy in the same population, e.g. no. 325 of *L. weissii* from Tinos (4x, 6x) and the occurrence of different levels of polyploidy of the same taxon on the same island (BENTZER 1973). The absence of pentaploids in no. 325 and triploids on islands with diploids as well as tetraploids may well be a result of what MARKS (1966) called a "triploid block" and which he claims is a common phenomenon. — (5). The relative ease of establishment of a polyploid deriving from a diploid which already has a means of vegetative propagation and which can be considered as preadapted with respect to polyploidy (DARLINGTON 1956). Vegetative propagation in *Leopoldia* was discussed in BENTZER (1973). — (6). Autopolyploidy could be a means of preserving favourable structural heterozygosity in cross-fertilizers which were probably forced to inbreeding in systems of small isolated populations (HENEEN & RUNEMARK 1972 a). The possibility of oscillations in population size during past times was discussed in BENTZER (1973).

There is close morphological agreement between the chromosomes of tetraploid plants of *L. dionysica* and those of normal *L. weissii* (4x), *L. cycladica* ssp. *cycladica* (4x), *L. cycladica* ssp. *subsessilis* (4x) and *L. spreitzenhoferi* (4x). The chromosomes of the diploid plants of *L. dionysica* are morphologically different from the tetraploid ones and resemble more those of *L. weissii* from the Northern Sporades and northwards. Since there are also morphological differences between the diploids and tetraploids (BENTZER 1973), the origin of the polyploidy in this taxon is not clear.

SUMMARY

(1) The karyotypes of *L. weissii* (2x, 4x), *L. cycladica* ssp. *cycladica* (4x, 6x), *L. cycladica* ssp. *subsessilis* (4x), *L. dionysica* (2x, 4x) and *L. spreitzenhoferi* (2x, 4x) all are essentially similar.

(2) The satellites are usually attached to the long arm of (L) chromosomes. The size, number and position of the satellites can vary considerably within a population. *L. dionysica* (2x) is similar to *L. weissii* (2x) from Northern Sporades and northwards in having satellites attached to the short arm of (L) chromosomes.

(3) Structural heterozygosity of varying types is a common phenomenon in the various taxa, particularly in *L. weissii* which has also been most studied.

(4) A particular case of widespread and common structural heterozygosity in the (L) st chromosomes is described. The same basic heterozygosity is found in four taxa.

(5) A frequent occurrence of quadrivalents of homologous chromosomes at diakinesis — M I is taken as an indication of an autopolyploid origin of the polyploidy. All types of chromosomes can form quadrivalents.

(6) Sub-chromatid bridges are found at A I in *L. weissii* (2x, 4x), *L. cycladica* ssp. *subsessilis* (4x) and *L. spreitzenhoferi* (2x, 4x). The other taxa were too superficially studied at A I to state whether subchromatid bridges occur or not.

(7) Bridges and fragments were found at A I. They are presumed to be caused by breakage and defective reunions of chromatids as well as by crossing-over within paracentric inversion loops.

(8) The percentage of stainable pollen does not generally seem to be reduced in spite of the structural heterozygosity in tetraploids and to the frequent occurrence of laggards at A I in tetraploids (*L. weissii*).

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Chromosome Morphology in Scilla hyacinthoides L.

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CARLSSON, M. et al. 1974 03 29. Chromosome morphology in Scilla hyacinthoides L. — Bot. Notiser 127: 87—88. Lund. ISSN 0006-8195.

The karyotype of a population of Scilla hyacinthoides L. from Greece, with 2n=20 and structural heterozygosity is presented.

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Three plants from one population were studied. The material originates from Greece, Northern Sporades: Skopelos, roadside and olive grove at Elios, 0—10 m, BOTHMER, 22.4 1972 (B 43159). The usual squash method with Feulgen staining was employed (cf. BOTHMER 1970). The root-tips were pretreated for about 2 hours in a mixture of 0.6 % colchicine and 2mM 8-hydroxyquinoline. Drawings were made with the aid of a Leitz binocular camera lucida.

The chromosome number in the present material was found to be 2n=20. The same number has also been reported by SATO (1935, 1942), BATTAGLIA (1959) and GIMENEZ MARTIN (1959). MACKENNEY (1898) and HEITZ (1926) reported the number 2n=16.

It has not been possible to separate the entire karyotype into pairs of homologous chromosomes because of the minute differences in length and in arm indices. Only one long chromosome with a secondary constriction on the short arm was observed (Fig. 1). BATTAGLIA (1959) in Israelian material and SATO (1935, 1942) reported one pair of such chromosomes. The latter author also reported one pair of short satellited chromosomes, not observed by BATTAGLIA (op. cit.) and the present authors. In a few cases, however, we observed a weak secondary constriction in one of the medium-sized chromosomes (Nos 2—4 in Fig. 1). The 5th chromosome (Fig. 1) is intermediate in size between the groups 2—4 and 6—7. The length decreases gradually from 6—7 to

Fig. 1. Karyotype of *Scilla hyacinthoides*. In this karyotype chromosome number 8 is longer and has a larger arm index than usual.

chromosome No 20 (Fig. 1). The smallest chromosomes were in most cells markedly shorter then the others.

The structural heterozygosity in our material may possibly be the result of various structural rearrangements. Owing to the limited cytological variation and the fact that only one long satellite chromosome was observed in all plants one may suspect that the present material constitutes one clone. The natural growth habit also favours a clone hypothesis (collector's information).

The origin of the 2n=20 karyotype of *S. hyacinthoides* from a presumed 16-chromosome ancestor by fragmentation, deletion and duplication was discussed by SATO (1935, 1942).

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The European Genera of the Family Brachytheciaceae (Bryophyta) and Chromosome Numbers Published in the Genus Brachythecium

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Delimitation of the family Brachytheciaceae and the genus *Brachythecium* is discussed and a key to the European genera recognized in the family is given. Views on the subdivision of the genus *Brachythecium* are discussed.

Chromosome numbers published for the species in the genus *Brachythecium* are listed and the basic chromosome numbers in the genus are discussed.

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INTRODUCTION

In Japan and adjacent areas the genus *Brachythecium* has been studied by TAKAKI (1955 b) and a generic revision of the family Brachytheciaceae in North America has been published by ROBINSON (1962). In Europe, however, no modern investigation of the family Brachytheciaceae or the genus *Brachythecium* has been carried out. Studies on certain species complexes in the genus have been published and these investigations will be discussed in future papers.

It is the purpose of the present author to investigate the Scandinavian species of the moss genus *Brachythecium* from a cytotaxonomical point of view. This paper mainly deals with the delimitation of the genus *Brachythecium* and the chromosome numbers reported for the genus.

The geographical concept Scandinavia can be defined in different ways but is here taken to comprise Denmark, Finland, Norway and Sweden.

The Scandinavian moss flora has been fairly thoroughly investigated. A modern Flora covering the whole Fennoscandian area has been published by NYHOLM (1954—1969). In this Flora the genus *Brachythecium* is treated in an excellent way, but the author pointed out several taxonomical problems which could not be solved with the help of traditional morphological studies. NYHOLM wrote: "In Scandinavia *Brachythecium* is a genus of extraordinary complexity and it seems, with many intermediate forms."

NYHOLM (l.c.) recognized 22 species of *Brachythecium* which will further be discussed in a series of papers. One paper has already been published on the systematical position of *B. geheebii*, which is transferred to the genus *Homalothecium* (WIGH 1973 b). The other species will be grouped in as natural and well-delimited groups as possible. These groups can be said to roughly comprise a section in the genus and each group will be discussed in a separate paper.

Two different methods are used by the author when studying the taxonomical problems in *Brachythecium:* (a) cytological studies to ascertain the chromosome complements in the species, and (b) modification experiments to determine which characters prove to modify extensively and are thus of less importance in the taxonomical treatment of the genus, and which characters show the highest degree of morphological constancy. About 2,000 gatherings of Scandinavian species of *Brachythecium* have hitherto been studied cytologically and a number of gatherings have been cultivated in different types of environments to study the modifications. These studies will be discussed in future papers.

The taxonomical treatment of the genus *Brachythecium* is difficult. Modification studies show that a number of characters modify extensively which makes it difficult to delimit them morphologically. As no modification experiments have previously been carried out in the genus it has not been possible to evaluate the taxonomical availability of the different morphological characters.

THE RELATIONS BETWEEN BRACHYTHECIACEAE AND SOME OTHER FAMILIES

As has already been pointed out by ROBINSON (1962) Brachytheciaceae was given family status by GROUT (1897) but was first described by BROTHERUS (1909).

It is not the purpose of the present author to try to give a description of the family Brachytheciaceae or to try to give it a more natural delimitation. Our knowledge about several important problems concerning morphology, cytology, evolution and so on is much too meagre for that. Only a few examples of the difficulty in delimiting some pleurocarpous families will be discussed here. There are by no means any clear-cut distinctions between many of the moss families in the order Hypnobryales and they cannot be said to be naturally delimited taxa.

There is a long series of pleurocarpous moss families with indistinct delimitation. As examples can be mentioned: Leskeaceae—Lembophyllaceae—Amblystegiaceae Brachytheciaceae—Entodontaceae—Hypnaceae. In all these families there are a number of genera with a controversial taxonomical position. For instance the genus *Ishibaea,* described as a monotypic genus endemic to Japan, was placed in the family Brachytheciaceae by BROTHERUS and OKAMURA (1915). The genus has later been transferred to the family Leskeaceae, and according to TAKAKI (1955 a) and NOGUCHI (1972) it is not a valid genus but should be united with the genus *Lescuraea* in the family Leskeaceae.

Another example is the genus *Isothecium* by some authors placed in the family Lembophyllaceae and by others in the family Brachytheciaceae. Still another one is *Platyhypnidium* sometimes placed in Brachytheciaceae and sometimes in Amblystegiaceae, as is the genus *Kurohimehypnum. Scleropodium* is also alternatively placed in two families, viz. Brachytheciaceae or Entodontaceae and the genus *Pleurozium* in Hypnaceae or Entodontaceae.

The family Hypnaceae has been divided into a number of subfamilies by several authors. By some bryologists these subfamilies have been given the taxonomical status of families. Such is the case with Climacioideae and Hylocomioideae for instance. Some authors have, however, done the reverse and treat Amblystegiaceae and Brachytheciaceae as subfamilies of Hypnaceae.

Formerly, the characters of the sporophytes were almost the only ones regarded as useful in the delimitation of taxa of higher rank. Later the cell structure of the gametophyte and other gametophytic characters were also taken into consideration. More detailed morphological studies and particularly cytological studies combined with cultivation experiments and chemotaxonomical studies will undoubtedly solve a number of problems connected with the delimitation of families.

As the mosses are so uniformly built up morphologically certain characters have doubtless been over-emphasized in the taxonomical treatment of a group.

A very illustrative example of the difference between the earlier and modern taxonomical delimitation of families is the family Pylaisaeceae. According to BRUCH et al. (1852) this family comprises the following accepted genera: *Pylaisia, Homalothecium, Platygyrium, Lescuraea, Orthothecium, Entodon, Pterigynandrum* and *Pterogonium.* Nowadays the family Pylaisaeceae is often treated as a subfamily of Hypnaceae and the genera within the family taxonomically delimited according to BRUCH et al. (l.c.) have been placed in various other families, viz. following NYHOLM (1954—1969), *Pylaisia* and *Platygyrium* in Hypnaceae, *Homalothecium* in Brachytheciaceae, *Lescuraea* in Leskeaceae, *Orthothecium* and *Entodon* in Entodontaceae, *Pterigynandrum* in Lembophyllaceae and *Pterogonium* in Leucodontaceae.

Even in more recent studies of the delimitation of families there are often great differences between different authors. A number of pleurocarpous families are probably still incorrectly delimited and many genera and species are grouped together with unrelated taxa. A number of new combinations must be made before a natural system can be established.

THE EUROPEAN GENERA OF THE FAMILY BRACHYTHECIACEAE

Many pleurocarpous mosses were described by HEDWIG (1801) as belonging to the genus *Hypnum.* This large genus, however, soon proved to be very heterogeneous and in the middle of the 19th century it was split into a number of genera.

Just as there are no clear-cut distinctions between a number of families in the order Hypnobryales, it is difficult to delimit several genera in the family Brachytheciaceae.

TAKAKI (1955 a) recognized 13 genera in Japan and adjacent areas and ROBINSON (1962) 11 genera in North America. The generic concept of these two authors, however, diverges considerably, for instance, ROBINSON divided the genus *Brachythecium* into two genera, *Brachythecium* in a narrower sense and *Chamberlainia.* This in contrast to TAKAKI who only recognized *Brachythecium* in a broader sense.

The genera *Homalothecium* and *Camptothecium* are treated as two genera by TAKAKI, while ROBINSON united them in *Homalothecium. Cratoneurella* is a genus described by ROBINSON. It is a monotypic genus with the species *C. uncinifolia* (BROTH. & PAR.) ROBINS., treated by TAKAKI (1955 b) as a species of *Brachythecium.* This illustrates how different the generic concepts are between authors.

Key to the European Genera of the Family Brachytheciaceae

1.	Autoecious or synoecious species	2
	Dioecious species	5
2.	Small plants, leaves lanceolate	*Rhynchostegiella*
	Robust plants, leaves ± ovate	3
3.	Nerve ending at back of branch leaves in a spine-like projection	*Eurhynchium*
	Nerve gradually disappearing	4
4.	Seta smooth	*Rhynchostegium*
	Seta ± rough	*Brachythecium*
5.	Cells at back in the upper part of the leaves with projecting ends	*Bryhnia*
	Cells smooth	6
6.	Leaves strongly plicated, ± straight, not narrowed into a filiform point	*Homalothecium*
	Leaves not plicated or ± strongly plicated. If strongly plicated leaves ending in a ± filiform point. Leaves not straight	7
7.	Lid conical, without or with a short beak	8
	Lid ± obliquely rostrate or rostellate	9
8.	Leaves strongly concave, imbricate, abruptly or gradually narrowed into a short point	*Scleropodium*
	Leaves plane or slightly concave, with an elongated point	*Brachythecium*

Bryhnia KAUR.

The genus *Bryhnia* comprises only one European species, *B. novae-angliae* (SULL. et LESQ.) GROUT. It is distinguished from the other genera of Brachytheciaceae in having cells with projecting ends.

ROBINSON (1962) transferred to the genus *Bryhnia* the species *Eurhynchium stokesii* (TURN.) B. S. G. in order to simplify the delimitation of *Eurhynchium*. As has already been pointed out by WIGH (1972 b) *E. stokesii* is neither morphologically nor cytologically closely related to the majority of species in the genus *Eurhynchium*, but it is not a good solution to place the species in the genus *Bryhnia*. *Eurhynchium stokesii* has the chromosome number n=9 (WIGH 1972 b), as opposed to the type species of the genus *Bryhnia*, *B. novae-angliae*, which has the chromosome number n=11 according to YANO (1957 b), SANNOMIYA (1958), ARAKI (1963) and INOUE (1967). *E. stokesii* has smooth cells as opposed to *B. novae-angliae*.

If *E. stokesii* was placed in the genus *Bryhnia* the genus *Eurhynchium* would be more clearly delimited, but the genus *Bryhnia* would then be more heterogeneous. The genus *Eurhynchium* and related genera are in need of further morphological and cytological investigation. The Scandinavian species of these complexes are being studied by I. ALMGREN, working at this Institute.

Cirriphyllum GROUT

The genus *Cirriphyllum* is distinguished from the other genera of the family Brachytheciaceae solely on the leaves, which narrow suddenly to form an elongated tip. By some authors, e.g. DIXON (1924), this genus is included in the genus *Eurhynchium*, and by others, e.g. ROBINSON (1962) it is included in the genus *Brachythecium*. This is one more example of the difficulty in delimiting the genera in the family Brachytheciaceae. Two Scandinavian species of *Cirriphyllum*, viz. *C. piliferum* (HEDW.) GROUT and *C. cirrosum* (SCHWAEGR.) GROUT have strongly concave leaves, and a very long and well-delimited leaf tip. The two species *C. tenuinerve* (LINDB.) WIJK et MARG. and *C. crassinervium* (TAYL.) LOESKE et FLEISCH. have less developed leaf points and *C. reichenbachianum* (HÜB.) WIJK et MARG. poorly developed leaf-points and much less concave leaves. The genus thus shows great variation as to gametophytic characters. This has also been pointed out by NYHOLM (1954—1969), who considers *C. reichenbachianum* to be a species intermediate between the genera *Cirriphyllum* and *Rhynchostegiella*. All European species of *Cirriphyllum* are dioecious.

Chromosome numbers are known for two species: *C. piliferum* has the chromosome number n=6 or 7 according to HOLMEN (1958) and n=11 according to WIGH (1972 b). *C. crassinervium* has the chromosome number n=11 (WIGH unpublished). In the former species 14 populations have been studied by the present author, some of the results have not yet been published, and all populations proved to have n=11. The chromosome complement in this species has been studied by means of a squash method as compared with the population studied by HOLMEN, who embedded the sporophytes in paraffin and sectioned by a microtome. Whether the difference in cytological methods can afford an explanation of the discrepancy in results obtained or whether chromosome races of the species exist requires further study. *Cirriphyllum piliferum* is a morphologically constant species which is easily recognized, so that the divergent chromosome numbers reported are presumably not due to taxonomic misdetermination.

Only one European species of *Brachythecium* is known with the chromosome number n=11, viz. *B. ryanii* KAUR., p. 100. Cytological information indicates that *Cirriphyllum* is not closely related to most species of *Brachythecium,* and should be treated as a separate genus. The species of *Cirriphyllum* have also been placed in the genus *Eurhynchium.* In this latter genus the present author has found n=11 in two European species, viz. *E. angustirete* (BROTH.) KOPONEN and *E. striatum* (HEDW.) B. S. G., (WIGH 1972 b). The leaves of these two species are of quite a different shape and the nerves end in a spine-like projection at the back of the branch leaves, whereas the nerve of the branch leaves in *Cirriphyllum* gradually disappears. A good basis for the delimitation of the genus *Cirriphyllum* is to recognize in the genus dioecious species with long pointed and more or less concave leaves, in combination with the chromosome number n=11.

The species *Brachythecium ryanii* KAUR. has also been treated in the genus *Cirriphyllum.* Some characters show resemblance to species in this genus, viz. the long pointed leaves, the rough seta in combination with the dioecious state and the chromosome number n=11, p. 100. This species is in need of further study.

Eurhynchium B. S. G.

The genus *Eurhynchium* is both morphologically and cytologically heterogeneous. Some authors have divided the genus into a number of genera, e.g. *Oxyrrhynchium* and *Scorpiurium,* while others have transferred species to other genera. Some authors treat *Eurhynchium* in a very broad sense and unite *Eurhynchium* with the genera *Cirriphyllum, Rhynchostegium* and *Rhynchostegiella* etc. Cytological information available indicates, however, that it seems justifiable to treat the genus *Eurhynchium* in a narrower sense. Several species of the genera *Cirriphyllum, Rhynchostegium* and *Rhynchostegiella* have the chromosome number n=11 in common. According to some authors *Rhynchostegium* and *Rhynchostegiella* are represented in Europe by autoecious species and *Cirriphyllum* by dioecious species. In the genus *Eurhynchium* treated in a narrower sense two European species have the chromosome number n=11, viz. *E. angustirete* and *E. striatum,* see under "Cirriphyllum". These species are easily distinguished from the remaining European species and should perhaps be placed in a separate genus.

The relationships between *Eurhynchium stokesii* and the genus *Bryhnia* are discussed on p. 93.

All European species of *Eurhynchium* are dioecious, except for *E. speciosum* which is autoecious or synoecious. This species is closely related to *E. praelongum.* Only one population of *E. speciosum* has been studied cytologically (NYHOLM & WIGH 1973), and it proved to have the same chromosome complement as *E. praelongum.* Further cytological information is necessary before this relationship can be discussed in greater detail.

The taxonomic position of *E. pumilum* is discussed under "Rhynchostegiella".

Rhynchostegium B. S. G.

In the genus *Rhynchostegium* MÖNKEMEYER (1927) recognized four species, *R. megapolitanum* (WEB. & MOHR) B. S. G., *R. murale* (HEDW.) B. S. G., *R. confertum* (DICKS.) B. S. G. and *R. rotundifolium* (BRID.) B. S. G. *R. riparioides* (HEDW.) CARD. was included in this genus by NYHOLM (1954—1969). Chromosome numbers are known for all these species. Cytological information indicates two dominating basic chromosome numbers, n=10 and 11. The former number has been reported in three species and the latter in all five species. Most populations studied have the chromosome number n=11. In *R. riparioides* n=8 and n=6—8 have also been reported by SMITH & NEWTON (1967) and HEITZ (1928) respectively.

Accessory chromosomes are known in *R. megapolitanum* (NYHOLM & WIGH

1973). The chromosome number n=11+1 m has been reported by SMITH & NEWTON (l.c.) for *R. murale*. This m-chromosome should probably be regarded as an accessory chromosome. Cytologically the genus *Rhynchostegium* is fairly uniform and should be excluded from the genus *Eurhynchium* on both morphological and cytological grounds, cf. p. 94.

Rhynchostegiella (B. S. G.) LIMPR.

In the genus *Rhynchostegiella* in the sense of MÖNKEMEYER (1927) five species are recognized. Chromosome numbers are known in three of the species, viz. *R. curviseta* (BRID.) LIMPR. with the chromosome number n=11 (WIGH 1972 a), *R. pumila* (WILS.) WARB. n=10 (SMITH & NEWTON 1968) and *R. tenella* (DICKS.) LIMPR. n=11 (SMITH & NEWTON 1966 and RAMSAY 1969) and n=22 (RAMSAY 1969).

Rhynchostegiella pumila is treated by NYHOLM (1954—1969) in the genus *Eurhynchium* and this is justifiable on several grounds. Cytologically this species is not related to the other species that have been studied karyologically. It has 10 chromosomes as opposed to the other species, which have 11 chromosomes, and it is dioecious as against the others. The nerve which ends in a spine-like projection at the back of the branch leaves clearly indicates that *R. pumila* is more closely related to species in the genus *Eurhynchium* than to species in the genus *Rhynchostegiella*.

Scorpiurium SCHIMP.

In the genus *Scorpiurium* only one European species has been studied cytologically, viz. *S. circinatum* (BRID.) FLEISCH., which has the chromosome number n=11 (WIGH 1972 a). This species has often been placed in the genus *Eurhynchium*, but as it is neither morphologically nor cytologically related to species in this genus it should be placed in a separate genus.

Conclusions

Several problems connected with the delimitation of the genera in the family Brachytheciaceae are discussed by the present author from a cytological point of view. The most common chromosome number in the European species of the family is n=11, a number reported for all genera. This indicates that the family is a natural one at least from most points of view.

The present author thus recognizes the following 9 European genera in the family Brachytheciaceae, viz. *Brachythecium, Bryhnia, Cirriphyllum, Eurhynchium, Homalothecium, Scleropodium, Rhynchostegium, Rhynchostegiella* and *Scorpiurium*. A number of problems in connection with the delimitation of the genera remain to be solved, and this study is not intended as a generic revision of the family, but only an attempt at the delimitation of the European genera.

In several aspects the key is in accordance with MÖNKEMEYER (1927) and NYHOLM (1954—1969). It diverges from that used by NYHOLM in that it includes *Tomenthypnum* in the genus *Homalothecium* and that the key also comprises the genus *Scorpiurium,* a non-Scandinavian genus. It also diverges somewhat in the delimitation of the genus *Brachythecium*. It diverges from the key in MÖNKEMEYER's Flora in the delimitation of the genera *Rhynchostegium, Eurhynchium, Rhynchostegiella, Brachythecium* and in treating *Scorpiurium* as a separate genus.

As has already been discussed the genera treated in this key are neither naturally nor clearly delimited. It will probably be necessary to make several transformations and perhaps also to describe new genera before the genera can be naturally delimited. The author is also aware that forms of some species do not key out well.

Table 1. The subdivision of the genus *Brachythecium* into sections. Abbreviations: *Cirriph.* = *Cirriphyllopsis*, *Pseudoc.* = *Pseudocamptothecium*. Species not treated by the authors have been marked with —.

Species	Authors			
	NYHOLM (1954—1969)	MÖNKEMEYER (1927)	TAKAKI (1955 b)	SZAFRAN (1961)
B. collinum	*Reflexa*	*Velutina*	—	*Julacea*
B. glaciale	,,	*Reflexa*	*Reflexa*	*Reflexa*
B. reflexum	,,	,,	,,	,,
B. starkei and *B. curtum*	,,	,,	,,	,,
B. latifolium	,,	*Rutabula*	—	*Rutabula*
B. velutinum	*Velutina*	*Velutina*	*Velutina*	*Velutina*
B. trachypodium	,,	,,	—	,,
B. populeum	,,	,,	*Cirriph.*	*Cirriph.*
B. plumosum	,,	*Cirriph.*	,,	,,
B. erythrorrhizon	*Albicans*	*Salebrosa*	—	—
B. albicans	,,	,,	—	*Salebrosa*
B. groenlandicum	,,	,,	—	—
B. ryanii	,,	,,	—	—
B. geheebii	,,	,,	—	*Pseudoc.*
B. mildeanum	*Rutabula*	,,	—	*Salebrosa*
B. rivulare	,,	*Rutabula*	*Rutabula*	*Rutabula*
B. rutabulum	,,	,,	,,	,,
B. campestre	,,	*Salebrosa*	*Salebrosa*	*Salebrosa*
B. salebrosum	*Salebrosa*	,,	,,	,,
B. glareosum	,,	,,	,,	,,
B. turgidum	,,	,,	—	,,

THE SUBDIVISION OF THE GENUS BRACHYTHECIUM

Only some problems connected with the subdivision of the genus *Brachythecium* will be discussed here. The discussion is mainly restricted to the European species and in particular to those recognized in the Scandinavian flora, see Table 1.

Brachythecium is the largest genus in the family Brachytheciaceae and more than 200 species have been described. Most of them are restricted to the Northern Hemisphere.

In order to make this large genus easier to handle it has been divided into a number of sections or subgenera and even genera.

As this study is based on NYHOLM (1954—1969) it is in place to discuss the subdivision of the genus *Brachythecium* in this Flora. NYHOLM recognizes 22 species and a number of varieties in Fennoscandia. The genus is divided into five sections. As the present study began with a cytological investigation of the species and since cytological information is of great use in solving a number of taxonomical problems in the genus, the chromosome numbers observed by the present author are given at the end of each section or species. Only a few of these numbers have formerly been published. Chromosome numbers published by other authors are given in Table 2. The following subdivision has been used by NYHOLM:

1. Section *Reflexa* LIMPR. Stem leaves triangular or ovate, plane or concave, hardly plicated; angular cells quadrate or rectangular, forming a large group which is longly decurrent in a broad or narrow band, cells in the middle of the leaf short, only in *B. curtum* and *B. latifolium* as long as 70 to more than 100 µ. Seta ± rough, cilia of the inner peristome ± appendiculate.

Chromosome numbers: $n=10$, 11 and 22.

Table 2. Chromosome numbers published in the genus *Brachythecium*. Accessory chromosomes are abbreviated Acc.

Taxon	n	Authors
B. albicans (Hedw.) B. S. G.	6 or 7	Holmen (1958).
	7	Wigh & Strandhede (1971), Wigh (1972 a), Nyholm & Wigh (1973).
	9	Vaarama (1950), Ho (1956).
B. austro-salebrosum (C. Müll.) Par.	10	Newton (1972).
B. brotheri Par.	11, 22	Yano (1954, 1957 b).
B. buchananii (Hook.) Jaeg.	10	Sannomiya (1955), Inoue (1967).
	11, 22	Chopra & Kumar (1967).
as var. *japonicum* Card.	10	Yano (1954, 1955, 1957 b).
B. campestre (C. Müll.) B. S. G.	7	Lazarenko et al. (1971).
	11	Visotska (1967), Lazarenko et al. (1971).
	12	Vysotskaya & Fetisova (1969), Lazarenko et al. (1971).
	16—17	Lazarenko et al. (1971).
	17	Lazarenko et Lesnyak (1966), Lazarenko et al. (1971).
B. coreanum Card.	11	Yano (1954, 1957 b).
B. curtum (Lindb.) Limpr.		
as *B. starkei* (Brid.) B. S. G. subsp. *curtum* (Lindb.) Amann	20	Vaarama (1950).
B. frigidum (C. Müll.) Besch.	6	Ireland (1967).
B. glareosum (Spruc.) B. S. G.	6	Holmen (1958).
	9, 9+2, 3 Acc.	Wigh (1972 a, 1973 a).
	10	Tsutsumi et al. (1973).
	14	Steere (1954 a, b).
B. helminthocladum Broth. et Par.	11	Inoue (1964).
as *B. tsunodae* Broth.	18	Yano (1954, 1957 b).
B. kamounense (Harv.) Jaeg.	11	Chopra & Kumar (1967).
B. kuroishicum Besch.		
as *B. decurrentifolium* Broth.	10	Yano (1954, 1955, 1957 b).
B. leibergii Grout	10	Ireland (1967).
B. mildeanum (Schimp.) Schimp.	14	Visotska (1967), Lazarenko et al. (1971).
B. piligerum Card.	18	Yano (1954, 1957 b).
B. plumosum (Hedw.) B. S. G.	10	Ireland (1965), Smith & Newton (1967), Lazarenko et al. (1971), Wigh & Strandhede (1971).
	11	Anderson & Al-Aish (1963), Inoue (1967), Chopra & Kumar (1967), Wigh & Strandhede (1971).
as *B. flagellare* (Hedw.) Jenn.	11	Inoue (1964).
B. populeum (Hedw.) B. S. G.	9	Vaarama (1950).
	10	Vaarama (1950), Yano (1955, 1957 b), Visotska (1967, 1970), Smith & Newton (1967), Vysotskaya & Fetisova (1969), Lazarenko et al. (1971), Wigh & Strandhede (1971).
	11	Inoue (1964, 1967), Chopra & Kumar (1967), Bryan (1973).
B. procumbens (Mitt.) Jaeg.	10	Chopra & Kumar (1967).
B. reflexum (Stark.) B. S. G.	10	Lazarenko et al. (1971).
	11	Wigh & Strandhede (1971).
	20	Lazarenko et al. (1970, 1971).
B. rhynchostegielloides Card.	10	Yano (1957 a, b).

Table 2 (continued).

Taxon	n	Authors
B. rivulare B. S. G.	6	Holmen (1958), Smith & Newton (1968), Vysotskaya & Fetisova (1969), Lazarenko et al. (1971), Wigh & Strandhede (1971), Wigh (1972 a).
	11	Inoue (1967).
	12	Fetisova & Visotskaya (1970), Lazarenko et al. (1971), Wigh & Strandhede (1971).
	13	Visotska (1967, 1970), Lazarenko et al. (1971).
	16	Anderson & Bryan (1958).
B. rutabulum (Hedw.) B. S. G.	5	Holmen (1958).
	6	Lazarenko et al. (1971).
	10	Moutschen (1955), Holmen (1958).
	11	Sinoir (1952), Chopra & Kumar (1967), Bryan (1973).
	12	Wilson & Burnett (1961), Smith & Newton (1967), Visotska (1967, 1970), Ramsay (1969), Vysotskaya & Fetisova (1969), Lazarenko et al. (1971), Wigh & Strandhede (1971).
	13	Visotska (1967), Lazarenko et al. (1971).
	20	Ramsay (1969).
	22	Lazarenko et al. (1971).
as *B. eurhynchioides* (Limpr.) Loeske	6	Visotska (1967), Lazarenko et al. (1971).
	12	Visotska (1967), Lazarenko et al. (1971).
B. sakuraii Broth.	12	Inoue (1967).
B. salebrosum (Web. et Mohr) B. S. G.	11	Lazarenko et al. (1970, 1971).
	13	Vaarama (1950), Lazarenko & Lesnyak (1966), Visotska (1967), Lazarenko et al. (1971), Bryan (1973).
as var. *longisetum* B. S. G.	13	Lazarenko et al. (1971).
B. salebrosum var. *vineale* (Mild.) Podp.		
as *B. vineale* Mild.	11	Lazarenko et al. (1971).
B. starkei (Brid.) B. S. G.	10	Ireland (1965), Lazarenko et al. (1971).
	20	Fetisova & Vysotskaya (1970), Lazarenko et al. (1971).
B. trachypodium (Brid.) B. S. G.	10	Visotska (1967), Lazarenko et al. (1971).
B. turgidum (Hart.) Kindb.	14	Lazarenko & Lesnyak (1966), Lazarenko et al. (1971).
B. velutinum (Hedw.) B. S. G.	10	Marchal & Marchal (1911), Ho (1956), Lazarenko & Visotska (1964), Visotska (1967), Smith & Newton (1968), Newton (1971), Lazarenko et al. (1971), Wigh & Strandhede (1971), Wigh (1973 a), Nyholm & Wigh (1973).
	10+ 2 Acc.	Wigh (1973 a).
	11	Vaarama (1950), Bryan (1973).
	12	Smith & Newton (1968).
as var. *praelongum* B. S. G.	12	Lazarenko et al. (1971).
as *B. condensatum* (B. S. G.) Loesk.	18	Lazarenko et al. (1968, 1971).
B. velutinum var. *salicinum* (B. S. G.) Moenk.		
as *B. salicinum* B. S. G.	10	Lazarenko et al. (1971).
B. wichurae (Broth.) Par.	10	Inoue (1965, 1967).

Species: *B. collinum* (C. MÜLL.) B. S. G., *B. glaciale* B. S. G., *B. reflexum* (STARKE) B. S. G., *B. starkei* (BRID.) B. S. G., *B. curtum* (LINDB.) LIMPR., *B. latifolium* KINDB.

2. Section *Velutina* DE NOT. Stem leaves mostly elongate, triangular or ovate, ± concave, not or slightly plicate; angular cells in a short or slightly oval group, sometimes reaching from the margin to the nerve, mostly shortly decurrent, only in *B. plumosum* long decurrent, cells in the middle of the leaf about 35—80 μ long. Seta ± rough; cilia of the inner peristome ± appendiculate.

Chromosome number n=10 in all species. In a few populations of *B. velutinum* there are accessory chromosomes.

Species: *B. velutinum* (HEDW.) B. S. G., *B. trachypodium* (BRID.) B. S. G., *B. populeum* (HEDW.) B. S. G., *B. plumosum* (HEDW.) B. S. G.

3. Section *Albicans* NYH. Stem leaves ovate-lanceolate, concave, plicate; angular cells quadrate or rectangular, forming an oval marginal group, usually decurrent in a broad band, cells in the middle of the leaf up to 30—80 μ long. Seta smooth or rough; cilia of the inner peristome nodose.

Chromosome numbers and species: *B. erythrorrhizon* B. S. G. n=7, *B. albicans* (HEDW.) B. S. G. n=7, *B. groenlandicum* (C. JENS.) SCHLJAK n=7, *B. ryanii* KAUR. n=11, *B. geheebii* MILDE n=10.

4. Section *Rutabula* LIMPR. Stem leaves ± rounded-ovate, concave, often slightly plicate; angular cells rectangular, sometimes inflated, ± decurrent; cells in the middle of the leaf about 70 to more than 100 μ long. Seta rough or smooth; cilia of the inner peristome nodose.

Chromosome numbers and species: *B. mildeanum* (SCHIMP.) SCHIMP. n=13, *B. rivulare* B. S. G. n=6, *B. rutabulum* (HEDW.) B. S. G. n=12, *B. campestre* (BRUCH) B. S. G. n=17.

5. Section *Salebrosa* BROTH. Stem leaves ovate-lanceolate, strongly plicate; angular cells ± quadrate, somewhat decurrent, cells in the middle of the leaf 70 to more than 100 μ long. Seta smooth; cilia of the inner peristome nodose.

Chromosome numbers and species: *B. salebrosum* (WEB. et MOHR) B. S. G. n=13, *B. glareosum* (BRUCH) B. S. G. n=9 and besides in some populations accessory chromosomes, *B. turgidum* (HARTM.) KINDB. n=14.

The morphological differences between the sections are thus only small and there are no clear-cut distinctions between them.

Section **Reflexa** LIMPR.

This section is perhaps taxonomically the most complex of all five sections. The three species *B. reflexum*—*B. starkei*—*B. curtum* form a natural group (*B. curtum* is often regarded as a variety or synonym of *B. starkei,* so that they are placed together in Table 1). In this group the chromosome numbers n=11 and 22 have been observed. The species are characterized by the plane leaves.

The species *B. glaciale* and *B. collinum* differ from the other species in their concave leaves. The latter species shows cytological relationship with species in the section *Velutina* and it has been placed in that section by MÖNKEMEYER (1927), Table 1.

B. latifolium differs from the other species in the well-developed angular cells and it shows resemblance to *B. rivulare* in the section *Rutabula.* This has also been pointed out by MÖNKEMEYER (1927) and SZAFRAN (1961), Table 1.

Section **Velutina** DE NOT.

This section is the only one which is cytologically homogeneous. All species have the basic chromosome number n=10. The accessory chromosomes in *B. velutinum* have been discussed in a previous paper (WIGH 1973 a).

The species in this section can be

divided into two groups. One comprises *B. velutinum* and the closely related *B. trachypodium* and the other *B. plumosum* and *B. populeum*. The last two species have often been placed in the section *Cirriphyllopsis,* Table 1.

Section **Albicans** NYH.

The section *Albicans* is morphologically and cytologically heterogeneous and can be divided into three groups. One comprises the species *B. albicans* and the closely related *B. groenlandicum* and *B. erythrorrhizon*. All have the chromosome number n=7.

B. ryanii seems to be most closely related to *B. campestre,* see below. As has already been mentioned it has also been treated in the genus *Cirriphyllum,* p. 94.

B. geheebii is not related to any other species in the genus *Brachythecium,* but to species in the genus *Homalothecium* (WIGH 1973 b). That it differs from the other species in the genus *Brachythecium* has also been pointed out by SZAFRAN (1961) who placed it in a new section, *Pseudocamptothecium,* Table 1.

Section **Rutabula** LIMPR.

All the species in the section *Rutabula* have different chromosome numbers. The taxonomical position of *B. mildeanum* has been discussed by NYHOLM (l.c.). She pointed out that it shows relationship with species in the section *Reflexa* and in *Salebrosa.* The chromosome number also shows that *B. mildeanum* is neither related to the other species in the section *Rutabula* nor to species in the section *Reflexa,* but shows some resemblance to *B. salebrosum* in the section *Salebrosa.* There are morphological intermediates between *B. salebrosum* and *B. mildeanum.*

B. ryanii, in the section *Albicans,* has the chromosome number n=11 and *B. campestre* n=17. Nevertheless they seem to be related, or at least morphologically alike. Both species are uncommon in Scandinavia and *B. ryanii* is considered to be endemic to this area. This, however, does not seem to be true. *B. ryanii* has probably been mistaken for *B. campestre* in other areas. This is supported by the chromosome numbers published for *B. campestre* by LAZARENKO et al. (1971). They reported among other numbers both n=11 and n=17 for this species, Table 2. *B. campestre* does not seem to be closely related to *B. rutabulum* or *B. rivulare* and should probably be excluded from this section. It has been placed by several authors in the section *Salebrosa,* Table 1.

Section **Salebrosa** BROTH.

This section is cytologically heterogeneous and all Scandinavian species have different chromosome numbers. It can often be very difficult to distinguish *B. turgidum* from *B. groenlandicum* in the section *Albicans* and small forms of *B. glareosum* can be difficult to separate from robust forms of *B. albicans.* This explains why most authors unite the section *Albicans* with the section *Salebrosa* into one section, which, however, is heterogeneous.

Conclusions

It is not the intention of the present author to attempt a more natural subdivision of the genus *Brachythecium.* This cannot be done until most species have been carefully studied both morphologically and cytologically.

GROUT (1928) divided the genus *Brachythecium* into two genera: *Brachythecium* in the narrower sense and *Chamberlainia.* The differences between these two genera are discussed on p. 92. This splitting of the genus *Brachythecium* is perhaps taxonomically justified. ROBINSON (1962), however, transferred several other species to the genus *Chamberlainia.* The genus *Chamberlainia* in the sense of ROBINSON can be said to correspond roughly to the sections *Salebrosa, Velutina* and *Albicans* of the genus *Brachythecium.* This division of the genus *Brachythecium* is not a good solution of the taxonomical problems within the genus. The genus *Chamberlainia* cannot be said to be more natural than the genus *Brachythecium* in the broad sense. This division has not been generally accepted and in a later paper Robinson (1965 p. 315) wrote: "To use the name *Chamberlainia* on a worldwide basis would require innumerable new combinations. In face of the increasing difficulty in finding a clear distinction on a worldwide basis, I would rather abandon the name."

It would be of great interest to compare a number of related species from Asia, Europe and North America to determine whether all the species reported are good species. This has, however, not been done. In such a study cytological information would be of great use. In the Scandinavian species the following chromosome numbers have been observed: n=6, 7, 9, 10, 11, 12, 13, 14, 16, 17 and 22.

CHROMOSOME NUMBERS PUBLISHED IN THE GENUS BRACHYTHECIUM

The chromosome numbers reported for the genus *Brachythecium* are given in Table 2. As views on the subdivision of the genus are so divergent the species have not been arranged according to taxonomical affinity but in alphabetic order.

Basic Chromosome Numbers in the Genus Brachythecium

A number of basic chromosome numbers are known in the genus *Brachythecium*. Lazarenko et al. (1971) gave the basic numbers x=5, 6 and 7. The chromosome number n=5 was published for *B. rutabulum*. This count is, however, presumed by the present author to be incorrect, as will be discussed in a future paper. x=5 must be regarded as the basic number for some autoecious species with n=10 and 20.

The chromosome number n=6 is known for some species and is the basic number for species with n=12.

The basic chromosome number x=7 is uncommon, but exists in *B. albicans* and some related species, see above.

Besides these basic chromosome numbers some other must be added, viz. x=8, 9 and 10. No species with n=8 is known in the genus, but an unidentified Scandinavian species of the genus has the number n=16. This number has also been reported for *B. rivulare* and *B. campestre,* Table 2. These species have probably arisen from species with n=8.

The basic number x=9 is also uncommon but has been found for *B. glareosum* and species with n=18.

The chromosome number n=10 for dioecious species of the genus should probably be regarded as a basic number, as against n=10 in autoecious species, which probably originate from forms with n=5. The same is the case with dioecious species with n=11. In such species the chromosome number 11 can be regarded as the basic number.

In the genus *Brachythecium* the following basic chromosome numbers are thus recognized, viz. x=5, 6, 7, 8, 9, 10 and 11. If chromosome numbers higher than 11 are basic numbers or not can only be revealed by more detailed cytological studies.

In Scandinavian species of *Brachythecium* the basic numbers x=5, 6, 7, 8 and 9 are known. Three Scandinavian species are controversial as to their basic chromosome number, viz. *B. ryanii, B. turgidum* and *B. campestre*. The first species has the chromosome number n=11 and is dioecious. It has also been regarded as a species in the genus *Cirriphyllum,* see above. In this genus dioecious species with n=11 are known (Wigh 1972 b).

B. turgidum has 14 chromosomes and has by some authors been reported as dioecious and by others as autoecious.

B. campestre is said to be both dioecious, autoecious and polyoecious. Some chromosome numbers are known in this species, Table 2. The chromosome numbers indicate that it is a heterogeneous species and the different chromosome numbers reported perhaps refer to different taxa. It seems likely from a morphological point of view that the number n=11 can refer to *B. ryanii,* or closely related species, see above. The chromosome numbers n=12 and 17 may refer to autoecious or polyoecious cytotypes.

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Cobana, a New Genus of Central American Iridaceae

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RAVENNA, P. 1974 03 29. Cobana, a new genus of Central American Iridaceae. — Bot. Notiser 127: 104—108. Lund. ISSN 0006-8195.

A re-examination of characters in *Eleutherine guatemalensis* STANDL. revealed that the species represents a separate genus. Anther, pollen and chromosome morphology exclude it from *Eleutherine*. The name *Cobana* is proposed for the new genus.

In addition, *Cobana guatemalensis* is reported for the first time from Honduras.

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INTRODUCTION

During a journey through Latin America, in 1963, I had the opportunity of examining and collecting the species described as *Eleutherine guatemalensis* STANDL. Plants were subsequently cultivated in Buenos Aires (Argentina) where they flowered during the summers of 1964 and 1965. In a brief treatment (RAVENNA 1965 pp. 314—315), I gave reasons for retaining the species in *Eleutherine,* since it had been incorrectly transferred to *Calydorea* by FOSTER (1945, p. 46). At that time, however, some characters of generic importance were overlooked. This especially concerns the anther, pollen, and chromosome morphology. Under the present re-examination of the status of *Eleutherine guatemalensis* it seems clear that it represents a new genus.

Cobana gen. nov.

Flores cernui albi. Ovarium clavatum triloculare; ovula in loculis plura. Tepala oblanceolata, interiora exterioribus valde minora. Filamenta libera brevissima. Antherae erectae luteae e foramini dehiscentes. Pollinis granuli subglobosi vel late aellyptici sulcis duis propinquis notati. Stylus perbrevis. Styli rami e basi antherarum patentes vel erectopatentes filiformes ad apicem subulato-incurvi. Stigma in summo styli ramorum punctatus. Capsula clavata breviter trivalvata. Semina angulata ochracea. Chromosomata 2n=28 paribus duobus majoribus caeteris parvis.

Plantae bulbosae. Bulbus tunicatus ovato-oblongus tunicis exterioribus paucis obtectus. Folia plicata lineari-ensiformia flaccida. Caulis floriferus teres folium basalibus simile sed brevius instructus. Spathae usque tres saepe longe pedunculatae sed a folio caulinari saepe superatae quinqueflorae; valvae subaequilongae herbaceae.

Typus generis: *Cobana guatemalensis* (STANDL.) RAV. (*Eleutherine guatemalensis* STANDLEY).

One species on the northern slopes of the Sierra Madre, Guatemala. The genus name commemorates the small town of Cobán, in whose vicinity the plant is found.

GENERIC RELATIONSHIPS

GENERAL HABIT. This does not show any exclusive feature. Bulb, leaves, stem, and spathe, are similar to those in several genera of American plaited-leaved Iridaceae, such as *Mastigostyla, Tigridia* and *Gelasine*. A several-flowered spathe is found in the last two genera as well.

FLOWER. Its position is cernuous in the same manner as in *Sessilanthera*.

PERIGONE. On account of the flat, white perigone, as in *Eleutherine,* the species was included in this genus by

STANDLEY. This resemblance is, in my opinion, superficial. The inner tepals are smaller and more acute than the outer. The white color turns bluish as soon as the flower begins to wither.

STAMENS. The filaments are free and extremely short, which is an interesting characteristic, but not valid for distinguishing genera. Although connate in a column, *Sessilanthera* bears filaments of a similar length. In the anthers, however, is found the most peculiar and exclusive feature in the new genus: dehiscence is apically foraminal. Here again we can draw a parallel between *Cobana* and *Sessilanthera*. Anthers in the latter genus dehisce only by a short extrorse furrow in the upper part of each loculus. In nature the anthers of *Cobana* are partially eaten by a small beetle, which apparently aids pollen shedding.

STYLE AND STYLE ARMS. The style is extremely short, as in *Sessilanthera,* but style arms show substantial differences: in *Sessilanthera* they are trifid, with two long divisions, and a short mucro between them; *Cobana* has simple, filiform-subulate arms. In the latter character it resembles *Eleutherine*.

The structure of the androecium and gynoecium, especially that of the style arms, is important for defining genera but often loses its usefulness when used for grouping genera. Marked differences in these organs do not necessarily imply remote relationship. Of course some allied genera do have similar floral organs; nevertheless, when observations are extended to other obviously close genera such as, for instance, *Trimezia* and *Pseudotrimezia,* we see that there is no apparent similarity in the morphology of the floral organs as a whole.

An extreme case of this peculiarity is found in *Cipura,* where style and style arms show fundamental variations from one species to another. If these species are considered singly differences could be thought of as being of generic importance.

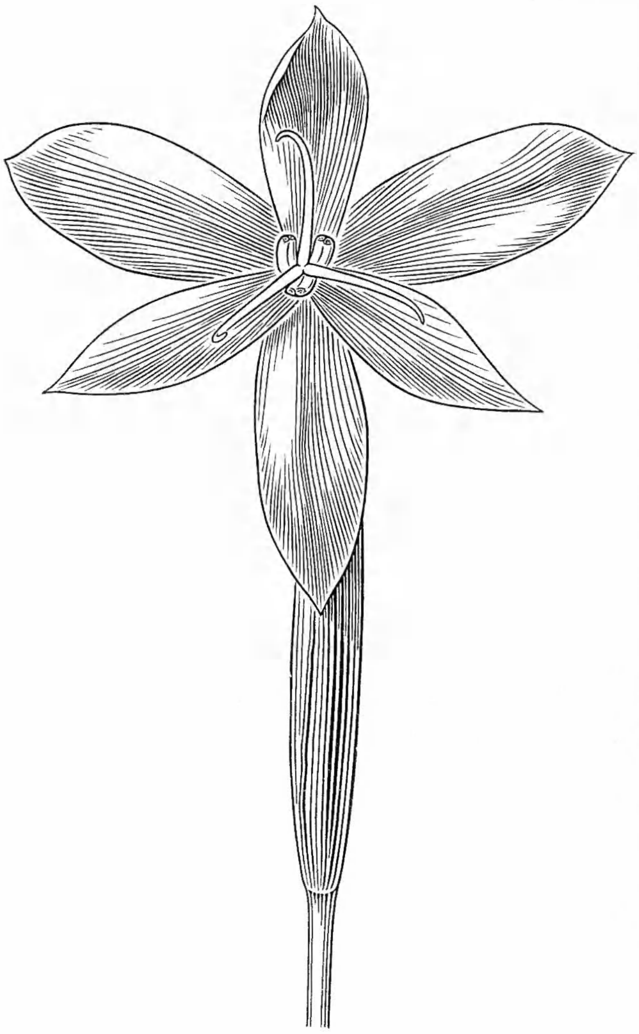

Fig. 1. *Cobana guatemalensis* (STANDL.) RAV., flower (×1.5). P. RAVENNA del.

The stigmas in *Cobana* are placed at the summit of the three style arms, as in *Eleutherine*. In *Sessilanthera* we find six stigmas, each at the top of the long divisions of the style arms.

POLLEN MORPHOLOGY. Pollen was observed under the microscope. No special technique was employed. Externally the grains appeared unusually round and their size fairly uniform (about 50 μ long, 46 μ wide).

All the grains show a two-furrowed face and an unfurrowed face; the latter is apparently slightly flat. The furrows are rather close to each other. The whole

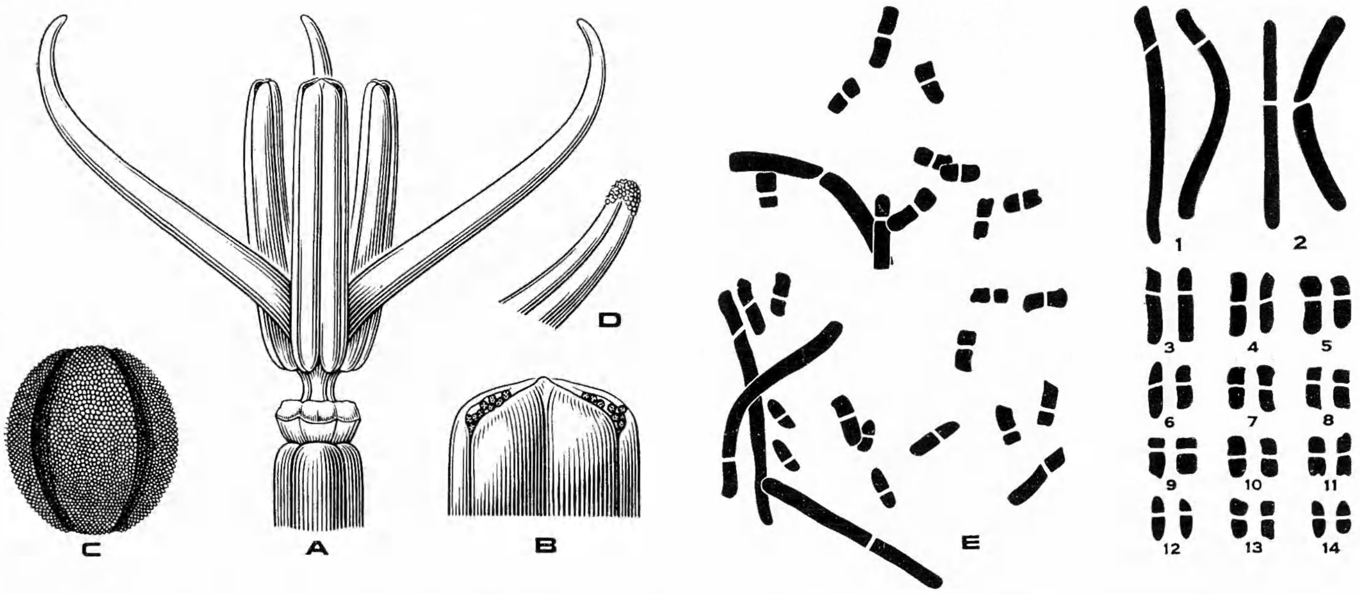

Fig. 2. *Cobana guatemalensis* (STANDL.) RAV. — A: Flower with tepals removed to show androecium and gynoecium (×4). — B: Apex of anther showing foraminal dehiscence (×20). — C: Pollen grain (×300). — D: Detail of stigma (×13). — E: Chromosomes as they appeared in the cell selected for the illustration (×1000); to the right, the karyotype. — P. RAVENNA del.

surface of the grain is covered by minute subconical protuberances.

The morphology of pollen grains in *Cobana* differs from that in *Eleutherine, Calydorea,* or the other exclusively South American genera already examined. Pollen grains of *Eleutherine* are ellipsoid to rather round, but they are one-furrowed (inedit datum). The two-furrowed character has been found, so far, only in *Tigridia* (including *Rigidella*), *Fosteria* and *Sessilanthera*; but in these genera each furrow is located on a different face. The pollen grains, in the American genera hitherto examined, are reported to be peroblate, ellipsoid, or fusiform and slightly flattened in the one-furrowed form (inedit datum).

CAPSULE AND SEEDS. Similar to several species of *Tigridia, Mastigostyla* and other genera.

CYTOLOGY

Material and Methods

Root tips were cut from five bulbs that were initiating their activity. Prior to fixation they were immersed for 4—5 hours in para-2-chlorobenzene, then fixed with Carnoy's fixative for at least 48 hours. Tips were macerated in 2N HCl for about ten minutes, washed and squashed in a drop of acetic-orceine solution. Before making slides permanent about twenty cells were selected and drawn with the aid of a camera lucida apparatus; one of these is illustrated in Fig. 2. Permanent slides were made by freezing, separating slide and cover-slip with absolute ethanol, adding a drop of Mayer's albumin, and mounted.

Results

CHROMOSOME NUMBER. 2n=28, the same complement as in *Tigridia, Eustylis,* and *Sessilanthera.*

SHARMA and TALUKDAR (1969 pp. 68—69), found 2n=14 chromosomes in *Eleutherine bulbosa* (as *E. plicata*). According to these authors, the material was collected from plants growing in India; they did not say, however, whether the species was found growing under culture, as an escape, or growing naturally in the field; nor do they quote the exact locality of the collection. *Eleutherine* is a genus of the New World.

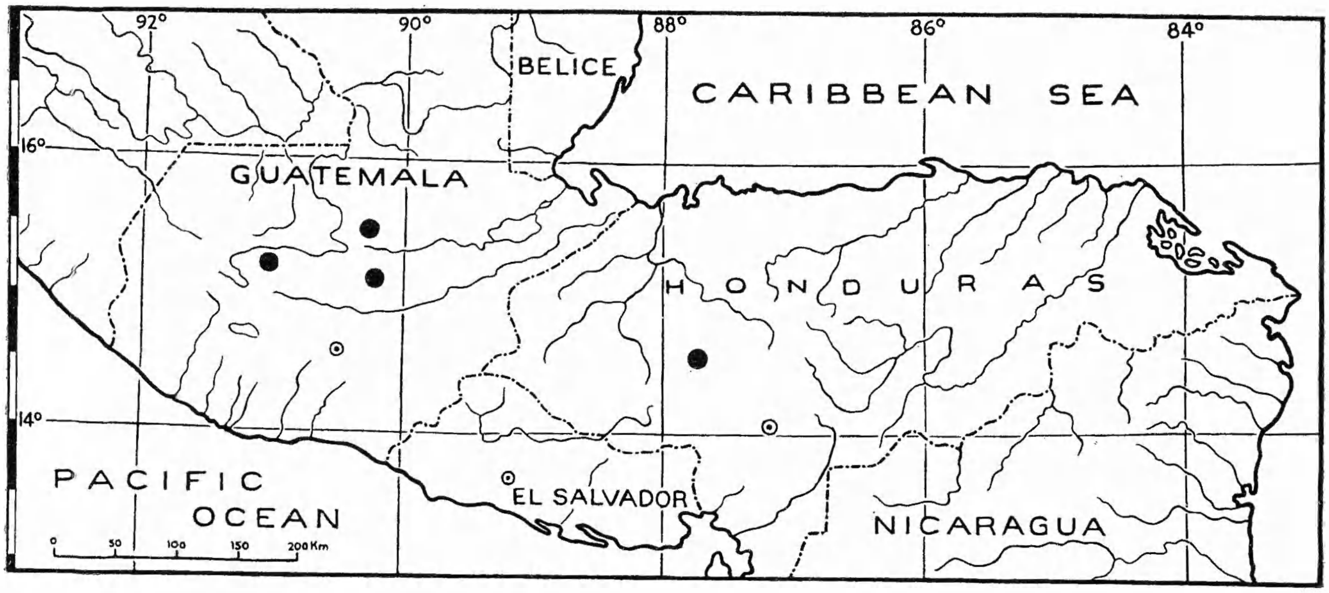

Fig. 3. Collecting sites (dots) of *Cobana guatemalensis*. — From left to right: Santa Rosa, Cobán, Salamá, and Cascada El Chorrito.

CHROMOSOME MORPHOLOGY. The karyotype of *Cobana* shows a similar kind of bimodality as that found by LEWIS and OLIVER (1961) in *Eustylis,* and by MOLSEED (1970 pp. 20—23) in *Tigridia:* two pairs of long chromosomes and the rest very short. Secondary constrictions and satellites were not observed.

The karyotype of *Eleutherine bulbosa,* as illustrated by SHARMA and TALUKDAR (1959 Fig. 5 a), shows substantial differences from that of *Cobana guatemalensis.*

The two large pairs, in *Cobana,* show differences in size and shape as well. Chromosomes of pair 1 measure 18.7 μ, bearing an acrocentric constriction; those of pair 2 are 16.73 μ long, with a submetacentric constriction. The other twelve pairs vary less in size, but differences can, in most cases, be seen: pair 3 with chromosomes 6.1 μ long, and acrocentric constriction; pair 4, 5.02 μ long, metacentric or almost so; pair 5, 4.52 μ long, subterminal; pair 6, 4.41 μ long, submetacentric to subterminal; pair 7, 3.52 μ long, submetacentric; pair 8, 3.52 μ long, submetacentric to subterminal; pair 9, 3.22 μ long, subterminal; pair 10, 3.22 μ long, metacentric; pair 11, 3.29 μ long, metacentric or submetacentric; pair 12, 3.45 μ long, submetacentric to subterminal; pair 13, 3.18 μ long, submetacentric; pair 14, 2.92 μ long, metacentric or submetacentric.

The measurements given were made with the aid of a micrometrical ocular lens. They are the maximum lengths recorded in the twenty cells studied. No consideration was paid to the other measurements since curvature of chromosome arms or the projection from different levels of the whole chromosome could give a false impression of a smaller size. On the other hand pretreatment often produces different shortening effects in the chromosomes of different cells.

CONCLUSIONS

From the facts presented here, it is assumed that *Cobana* is related to the group that includes *Tigridia, Fosteria* and *Sessilanthera,* but that it is closer to the last-mentioned genus. The similarity to *Eleutherine* appears to be superficial.

Cobana guatemalensis (STANDL.) RAVENNA, comb. nov. — Fig. 1, 2

Basionym: *Eleutherine guatemalensis* STANDLEY, Publ. Field. Mus. Nat. Hist. Chicago, Bot. Ser. 4: 200 (1929). — *Calydorea guatemalensis* (STANDL.) R. C. FOSTER, Contr. Gray Herb. Harv. Univ. 155: 46 (1945).

Plant up to 40—60 cm high. Bulb oblong-ovoid, about 40 mm long, 20 mm wide, covered with few, pale brown coats. Basal leaves at anthesis two, linear-ensiform, plicate, flaccid, often lax, green or slightly glaucescent, about 30—40 cm long, 15—20 mm broad, gradually narrowed toward the apex. Stem cylindrical, with a single leaf 18—22 cm long, 12—17 mm broad. Spathes as many as three, peduncled, often overtopped by the caulinar leaf, bearing five flowers or less, up to 50—55 mm long; valves subequal, narrowing upwards. Flowers matutinal, cernuous. Ovary obovoid. Perigone flat, white, turning bluish with age, about 35—40 mm in diameter. Outer tepals oblanceolate, about 20—25 mm long, 5.5—6.8 mm broad, apiculate. Inner tepals smaller than the outer, oblanceolate, 12—20 mm long, 3.2—8.9 mm broad, the apicule 1—2.5 mm long. Filaments free, yellow, about 0.7 mm long. Anthers erect, linear-oblong, yellow, about 4.9—7 mm long, 1—1.3 mm broad; dehiscence apically foraminal. Pollen grains subglobose or widely elliptic, 2-colporate, about 50 μ long, 46 μ wide. Style 1.1—1.5 mm long. Style branches filiform, subulate, white, ascending, up to 8—11 mm long, incurving moderately at the apex. Stigma punctiform, apical. Capsule clavate 10—14 mm long. Seeds angular, brown, up to 2—3 mm long. Karyotype bimodal, 2n=28, two pairs long, the rest small.

HABITAT. In clearings in woods of *Liquidambar styraciflua* and *Quercus* sp. (or sometimes of *Quercus* sp. and *Pinus* sp.), especially on both sides of the road Cobán—San Juan Chamelco, in Guatemala; altitude 1000—1500 m.

SPECIMENS. Guatemala, Alta Vera Paz, Cobán, alt. 1350 m; leg. H. von Tuerckheim II 1885, VI. 1907 (US 933801, type). — Idem ibid. Cobán, 6 km ad vian San Juan Chamelco; leg. Ravenna 265, 21. VIII. 1963 (Herb. Ravennae, K, topotype). — Honduras, dept. Comayagua, matorrales de Cascada El Chorrito, 16 km al S.O. de Siguatepeque, 1500 m; leg. A. Molina R., 19.VII. 1962 (Herb. Esc. Agr. Panam. 10904, NY).

Standley's original description says nothing about flower morphology, tepals, androecium, gynoecium or seeds. These are defined here for the first time.

Cobana guatemalensis is formally reported in the flora of Honduras. The addition of this element is interesting since the country is apparently poor in Iridaceae.

ACKNOWLEDGEMENTS

I am obliged to the Department of Botany (US), United States National Museum, Washington, DC., for lending me the type specimen of *Eleutherine guatemalensis*; the New York Botanical Garden (NY), Bronx, New York, U.S.A., for its constant cooperation; Instituto de Botánica Darwinion (SI), San Isidro, Argentina; and to Dr Vincent Santilli, Dept. of Biology, State University of New York, Buffalo, U.S.A., for revising the English text.

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Studies in African Cyperaceae X

New Taxa and Combinations in Fuirena Rottb.

Kåre Arnstein Lye

LYE, K. A. 1974 03 29. Studies in African Cyperaceae X. New taxa and combinations in Fuirena Rottb. — Bot. Notiser 127: 109—112. Lund. ISSN 0006-8195.

Three new species and one new variety are described, viz. *Fuirena zambesiaca* K. LYE, sp. nov. from Mozambique, *F. sagittata* K. LYE, sp. nov. and *F. microcarpa* K. LYE, sp. nov., both from Tanzania, and *F. pubescens* KUNTH var. *abbreviata* K. LYE, var. nov. from Uganda.

Two new combinations are coined, viz. *F. angolensis* (SCHINZ) K. LYE, syn. *F. ciliaris* (L.) ROXB. var. *angolensis* SCHINZ and *F. pubescens* KUNTH var. *major* K. LYE, syn. *F. pachyrrhiza* RIDL.

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Fuirena zambesiaca K. LYE, sp. nov.

Herbae annuae, pubescentes. *Culmus* 10—30 cm altus et 0.5—1.4 mm latus. *Folia* culmi 1—10 cm longa et 2—5 mm lata. *Spiculae* 4—8 mm longae et 2—3 mm latae, multiflorae. *Squamae* dense imbricatae oblongolanceolatae, 2.2—2.6 mm longae; apice mucronatae. *Perigonium* 6. *Setae* hypogynae 3, ciliolatae. *Squamellae* hypogynae 3, latae, stipitatae, membranaceae; apice mucronatae. *Stamina* 3. *Stylus* longus; stigmata 3. *Nux* oblonga, triquetra, conspicue apiculata, breviter stipitata, pallida demum brunnea.

TYPUS SPECIEI: PEDRO & PEDROZAD n. 4222, 10.XI.1948. Mozambique, Marrupa Div., 4 km from Maua (Holotype EA).

Fuirena zambesiaca K. LYE (Fig. 1) is a slender erect annual with a minute root system. Culms leafy, 10—30 cm long and 0.5—1.4 mm in diameter, longitudinally ridged and densely set with short, spreading or recurved white hairs. Leaves flat, densely set with short white hairs, the largest 4—10 cm long and 2—5 mm wide; the lower leaves usually very short; leaf-sheaths densely hairy.

Inflorescence with 1—2 stalked spikelet clusters from the upper leaf-sheaths, the uppermost ones subsessile and confluent into one or two irregular heads. Peduncles up to 6 cm long and 0.5—0.6 mm in diameter, densely set with spreading white hairs. Spikelets sessile, 4—8 mm long and 2—3 mm wide, ovate to lanceolate, with slightly spreading glumes. Glumes 1.7—2.1 mm long excluding an about 0.5 mm long mucro, ovate, grey to reddish-brown, minutely pubescent but occasionally with larger white spreading hairs on the paler 3-nerved excurrent midrib. Perianth-segments 6; the outer 3 filiform, pubescent, of the same length or shorter than the nutlet; the inner three 1.1—1.4 mm long (excluding the about 0.5 mm long excurrent midrib) with a squarish blade with cuneate base and emarginate apex, almost glabrous except for the filiform pubescent excurrent midrib. Stamens 3. Style 3-branched. Nutlet 0.7—0.8 mm long (including the cuneate base, but excluding the persistent filiform style-base) and 0.4 mm wide, elliptic, yellowish-brown, strongly triangular.

On grey sandy soil (dambo). Known only from Mozambique and southern Tanzania.

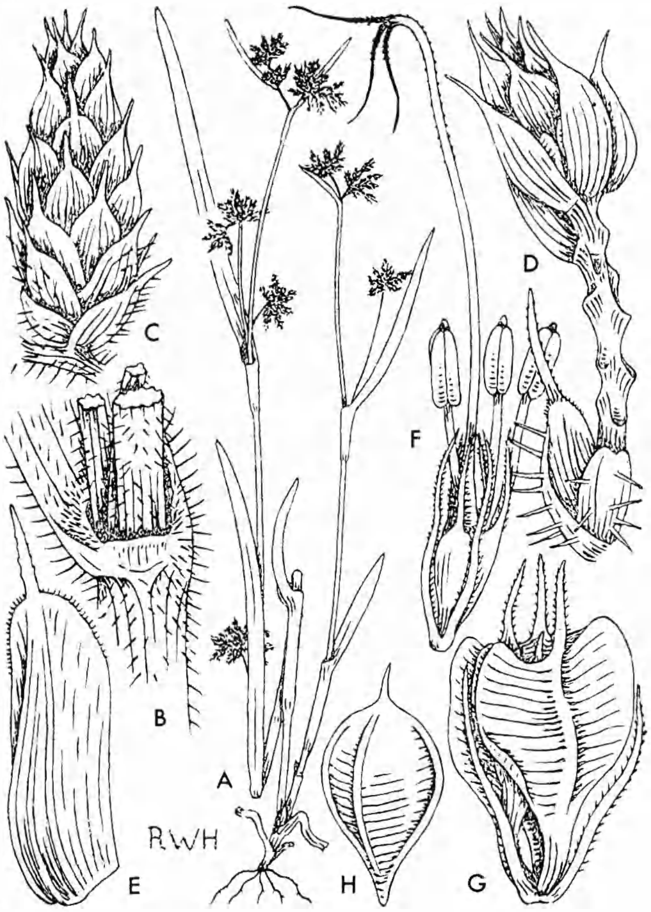

Fig. 1. *Fuirena zambesiaca* K. LYE. — A: Habit, reduced. — B: Leaf-base with throat and two peduncles. — C: Spikelet. — D: Mature spikelet with many fallen glumes. — E: Glume. — F: Flower. — G: Nutlet with persistent perianth-segments. — H: Nutlet with perianth-segments removed. — Drawn from PEDRO & PEDROZAD 4222 (near Maua, Mozambique; the holotype). — Original by RICHARD WHEELER HAINES.

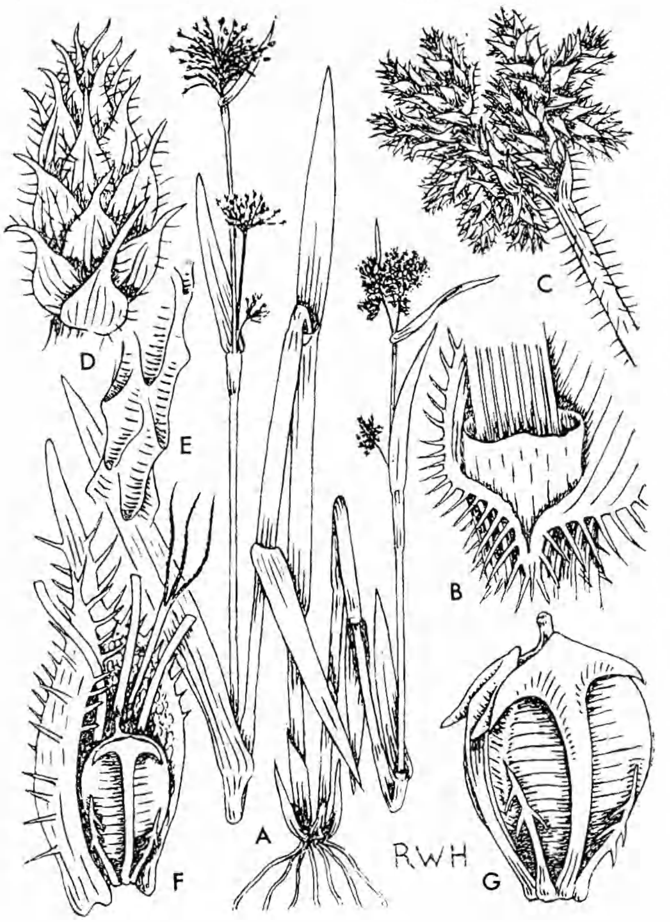

Fig. 2. *Fuirena sagittata* K. LYE. — A: Habit, reduced. — B: Leaf-base and ligule. — C: Inflorescence-detail. — D: Spikelet. — E: Spikelet-axis. — F: Glume and young nutlet with persistent perianth-segments, filaments and style. — G: Nutlet with persistent perianth-segments. — Drawn from GREENWAY 780 (S of Dodoma, Tanzania; the holotype). — Original by RICHARD WHEELER HAINES.

Fuirena sagittata K. LYE, sp. nov.

Herbae annuae, pubescentes. *Culmus* 20—45 cm altus et 1—2 mm latus. *Folia* culmi 2—15 cm longa et 3—10 mm lata. *Spiculae* 3—12 mm longae et 2—3 mm latae, multiflorae. *Squamae* dense imbricatae oblongo-lanceolatae, 1.9—2.3 mm longae; apice mucronatae. *Perigonium* 6. *Setae* hypogynae 3. *Squamellae* hypogynae 3, stipitatae, sagittatae.

TYPUS SPECIEI: P. J. GREENWAY n. 780, 16.VIII.1928. Tanzania, Mwitikera, 29 miles S of Dodoma, 1080 m (Holotype EA).

Fuirena sagittata K. LYE (Fig. 2) is a rather robust annual with a tufted base. Culms 20—45 cm long and 1—2 mm in diameter (but wider across the leaf-sheaths), longitudinally ridged, hairy or almost glabrous below. Leaf-blades flat, hairy, the largest 8—15 cm long and 6—10 mm wide; leaf-sheaths rather wide, hairy; ligule prominent, reddish-brown.

Inflorescence with an irregular terminal head consisting of numerous crowded spikelet-clusters and 1—2 pedunculate spikelet-clusters from one or two of the leaf-sheaths immediately below the main spikelet-group. Peduncles up to 4 cm long and 0.5—0.7 mm in diameter, hairy. Spikelets sessile, 3—12 mm long and 2—3 mm wide, ovate-lanceolate with spreading

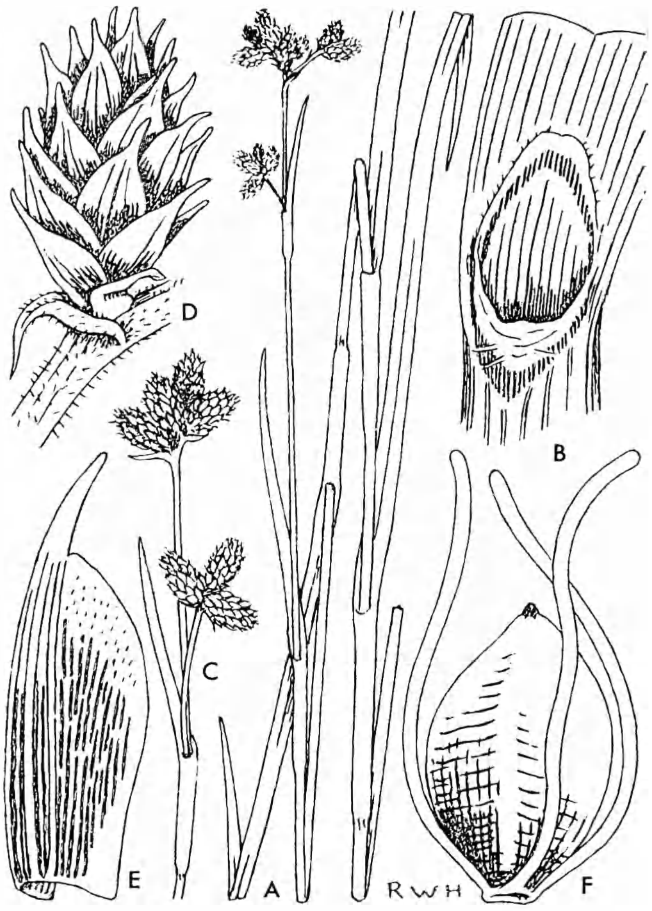

Fig. 3. *Fuirena pubescens* Kunth var. *abbreviata* K. Lye. — A: Habit, reduced. — B: Leaf-throat and ligule. — C: Inflorescence. — D: Spikelet. — E: Glume. — F: Nutlet with persistent filaments. — Drawn from Langdale-Brown 2356 (Teso, Uganda; the holotype). — Original by Richard Wheeler Haines.

mucros. Glumes 1.4—1.6 mm long excluding an 0.5—0.7 mm long mucro, ovate, densely hairy. Perianth-segments 6; the outer 3 filiform with scattered recurved spines, shorter than the nutlet; the inner three arrow-shaped (sagittate) with a much swollen apex, as long as the nutlet. Nutlet 0.9—1.1 mm long and 0.5—0.6 mm wide, obovate with distinctly cuneate narrow base and a short apiculus, sharply triangular, greyish-yellow with slightly darker ribs.

In a waterhole (but not eaten by stock of any kind), 1080 m. Known only from Tanzania.

Fuirena microcarpa K. Lye, sp. nov.

Herbae annuae, pubescentes. *Culmus* 5—20 cm altus et 0.2—1.0 mm latus. *Folia* culmi 0.5—8.0 cm longa et 0.2—2.0 mm lata. *Spiculae* 4—8 mm longae et 2—3 mm latae, multiflorae. *Squamae* dense imbricatae oblongo-lanceolatae, 1.7—2.2 mm longae; apice mucronatae. *Perigonium* nullum. *Nux* 0.4—0.5 mm longa et 0.3—0.4 mm lata, oblonga, triquetra, pallida.

TYPUS SPECIEI: R. Wingfield n. 1638, 11.VIII.1972. Tanzania, Manzese pond, Morogoro road, Dar es Salaam (Holotype DAR ES SALAAM UNIV. HERB.).

Fuirena microcarpa K. Lye is a slender erect annual with a minute root-system. Culms leafy, 5—20 cm long and 0.2—1.0 mm thick, longitudinally ridged and densely set with spreading white hairs. Leaves flat, hairy; the largest 1—8 cm long and 0.5—2.0 mm wide.

Inflorescence of 1—2 pedunculate or subsessile spikelet-clusters from the 2—3 uppermost leaf-sheaths. Peduncles up to 4 cm long and 0.2—0.3 mm thick, hairy. Spikelets sessile, 4—8 mm long and 2—3 mm wide, ovate to lanceolate; spikelet-axis strongly notched. Glumes 1.0—1.3 mm long excluding an 0.7—0.9 mm long ciliate mucro, ovate, grey to reddish-brown, hairy; midrib 3-nerved. Perianth-segments absent. Nutlets 0.4—0.5 mm long and 0.3—0.4 mm wide, elliptic, triangular with rounded angles and faces, grey to yellowish-grey, smooth.

In sandy rice-field at pond edge, 30 m. Known only from Tanzania.

Of the three new species described above *Fuirena zambesiaca* K. Lye does not show any close relationship to any other species, although obviously belonging to the *F. ciliaris* (L.) Roxb. group of species. *F. sagittata* K. Lye is possibly most closely related to *F. ciliaris* (L.) Roxb. s. str., but it differs in its much larger nutlet and different shape of the inner perianth-segments. *F. microcarpa* K. Lye is related to *F. leptostachya* Oliv. var. *nudiflora* C. B. Cl. from which it differs in its smaller and paler nutlet with rounded (and not flat) faces.

Fuirena pubescens KUNTH var. **abbreviata** K. LYE, var. nov.

Herbae perennes, pubescentes. *Culmus* erectus pubescentes. *Spiculae* multiflorae. *Squamae* dense imbricatae oblongae; apice mucronatae, 0.7 mm longae. *Perigonium* nullum. *Nux* ovata, triquetra, alba.

TYPUS: LANGDALE-BROWN n. 2356. Uganda, Teso district, 10 miles ESE of Soroti, 1050 m (Holotype KAW).

Fuirena pubescens KUNTH var. *abbreviata* K. LYE (Fig. 3) differs from var. *pubescens* in having glumes with only 0.7 mm long mucros. The glumes are also less hairy, and pale green or greyish with longitudinal reddish stripes. The nutlet is white and slightly longer than in var. *pubescens*.

In permanently water-logged valley swamp, 1050 m. Known only from central Uganda.

NEW COMBINATIONS

The following new combinations of *Fuirena* are needed for "The Sedges of Uganda and Kenya":

Fuirena angolensis (SCHINZ) K. LYE, comb. nov., syn. *Fuirena ciliaris* (L.) ROXB. var. *angolensis* SCHINZ in Bull. Herb. Boiss. iv. Append. iii, p. 31.

Fuirena pubescens KUNTH var. *major* K. LYE, nom. nov., syn. *Fuirena pachyrrhiza* RIDL. in Trans. Linn. Soc. Ser. II. ii, p. 161 (1884) and in Flora of Tropical Africa 8, p. 464 (1902).

Coronopus zambiensis (Cruciferae), a New Species from Tropical Africa

Bengt Jonsell

JONSELL, B. 1974 03 29. Coronopus zambiensis (Cruciferae), a new species from tropical Africa. — Bot. Notiser 127: 113—118. Lund. ISSN 0006-8195.

Coronopus zambiensis JONSELL sp. nov. (Cruciferae) is described from Zambia, Kalabo Distr., Liuwa Plain. It is close to *C. integrifolius* (DC.) SPRENG., differing particularly in its large, verrucose and pointed siliculae. *C. zambiensis* is thus far known only from the type locality.

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Coronopus is a small genus in the Cruciferae containing about 10 species, some of which are well known as cosmopolitan weeds. The genus is above all characterized by its indehiscent, two-seeded, dorsiventrally compressed siliculae. The whole silicula with its two seeds (e.g. in *C. squamatus* (FORSK.) ASCH.), or a one-seeded nutlet derived from one half of the silicula (e.g. in *C. didymus* (L.) SM.), may constitute the diaspore. *Coronopus* is certainly closely related to *Lepidium,* which has two-seeded but dehiscent siliculae. The possibility that *Coronopus* comprises the results of parallel trends towards indehiscent fruits evolving from within *Lepidium* was first suggested by MUSCHLER (1908), whose work is the only monographic treatment of the genus so far.

The only *Coronopus* species previously known to be indigenous in tropical and southern Africa is *C. integrifolius* (DC.) SPRENG. It is characterized by simple, lanceolate to linear cauline leaves, and didymous, emarginate siliculae (Fig. 1 J) splitting into spheroidal, reticulate or finely rugose nutlets. The plant is up to 40 cm high, ascending or prostrate and richly branching from the base and all along the stems, which in some specimens are woody in the basal parts. Thus it seems able to perennate, although most of the material was obviously collected in annual state. Descriptions with illustrations are to be found in EXELL and WILD (1960) and CODD et al. (1970). *C. integrifolius* grows in moist depressions, dried up river-beds, pools and pans, often in salt steppe. It may also occur as a weed (LAMBRECHT No. 294; cf. also CODD et al. 1970). It is rather widespread in South and South-West Africa, has scattered occurrences in Botswana, Rhodesia, Mozambique, southernmost Zambia and northern Tanzania (cf. Appendix), and is known from Madagascar by the type specimen collected by COMMERSON (cf. DE CANDOLLE 1799). It has been introduced into some other warmer regions of the world (e.g. Japan). *Coronopus englerianus* MUSCHLER (1908 p. 139) was described from a collection by PETERS from the mouth of the Zambesi River (in PETERS 1862 p. 169, as *C. integrifolius*) mainly on account of its shorter pedicels. The type collection, still extant in the Berlin herbarium, clearly shows that *C. englerianus* is conspecific with *C. integrifolius* (cf. EXELL & WILD 1960 p. 193).

For a revision of Tropical African crucifers in general I have investigated or searched through *Coronopus* material in the herbaria of B, BM, BR, COI, EA, FI, K, LISC, LISU, P, S, SRGH, UPS. The perusal of herbarium sheets of *C. integrifolius* revealed a plant from western Zambia (Liuwa Plain in Kalabo District; DRUMMOND & COOKSON 6458) with highly divergent siliculae, which is here described as *Coronopus zambiensis* sp. nov. (Fig. 3). The fruit is distally produced into two bifid beaks (one at each side of the style) from which two prominent parallel, wavy ridges continue along the lateral margin of the fruit. The fully ripe fruits are prominently verrucose all over the surface (Fig. 1 I, 2 A, C). This kind of sculpture is reminiscent of *C. squamatus,* but in contrast to that species the fruit-halves are united only for a short and narrow area (Fig. 2 A) and fall apart readily at maturity. The tubercles on the surface of each half often grow big enough to meet in the median plane (Fig. 2 A). The adaxial and abaxial fruit surfaces may be somewhat dissimilar, but there is no constant dissimilarity between them as in e.g. *C. niloticus* (DEL.) SPRENG. The siliculae of *C. zambiensis* are much bigger than those of *C. integrifolius* (only 0.9—1.2×1.8—2.2 mm in the latter, cf. description below and Figs. 1 I, J; 2 C, D). The unfertilized gynoecia seem to be impossible to distinguish from those of *C. integrifolia,* but the special fruit characters develop very early (Fig. 1). The material of *C. zambiensis* seen by me comprises 29 single individuals, which invariably show the same type of silicula. In *C. integrifolius* the fruits vary little in shape between the collections but the surface pattern may vary from reticulate to rugose (Figs. 1 J, 2 B). No trend towards the *C. zambiensis* type of fruits was observed.

There are a few other less spectacular differences between the two species. The seeds (Fig. 2 E, F), as may be expected, are bigger in *C. zambiensis* than in *C. integrifolius* (0.8—1.2×0.6—0.8 mm in the latter). In *C. integrifolius* the stem hairs are linear, falcate or clavate (the latter especially in S.W. African collections), 0.1—0.2 mm long and most of them recurved or even retrorse. In *C. zambiensis* they are more slender, up to 0.3 mm long, straight and only rarely at all curved. The pedicels of ripe fruits are in *C. zambiensis* about 0.2 mm thick, in *C. integrifolius* 0.10—0.15 mm.

In all other characters studied *C. zambiensis* falls within the variation range of *C. integrifolius,* to which it is certainly very closely related. Both have very reduced flowers with only two stamens which are already dehisced in bud, features that suggest strong autogamy in both species. This means that a population such as that of *C. zambiensis* might have been established rather rapidly and have few genic differences against *C. integrifolia.* The divergent fruits (remarkable also when seen in the context of the genus as a whole) in combination with the other slighter differences mentioned, warrant, in my opinion, the recognition of the Liuwa Plain population as a separate species. Its locality is outside the known range of *C. integrifolia.* The nearest finds of the latter species occur some 700 km to the E.S.E. and S.E., in Zambia (Lusitu at the Zambesi River, FANSHAWE 5231) and in Botswana at Nata River (DRUMMOND & SEAGRIFF 5168). Liuwa Plain is in westernmost Zambia not far from the Angolan border. No *Coronopus* has hitherto been reported from Angola, or from the rather close Katanga area in Zaïre. Whether it is a narrow endemic, a western-distributed element of the Flora

Fig. 1. Development from ovaries to ripe fruits in *Coronopus zambiensis* (left row) and *C. integrifolius* (right row). — A, B: Unfertilized ovaries (×c. 30). — C, D: Very young fruits (×c. 30). — E, F: Half ripe fruits (×c. 15). — G, H: Nearly ripe fruits (H at a somewhat younger stage than G; ×c. 15). — I, J: Ripe fruits (×c. 15). — The collections represented are DRUMMOND & COOKSON 6458 (SRGH) and FANSHAWE 5231 (SRGH) resp.

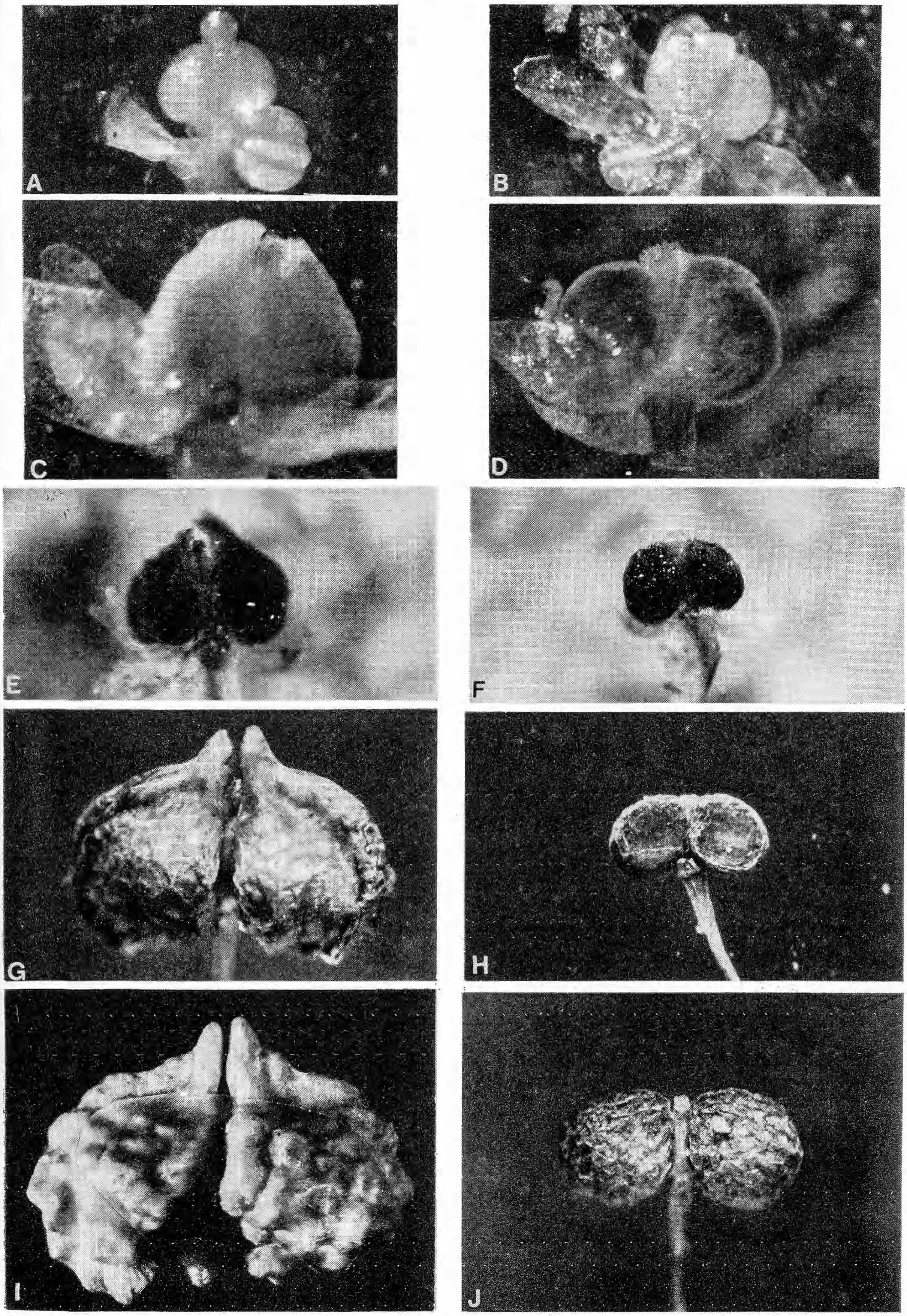

Fig. 1.

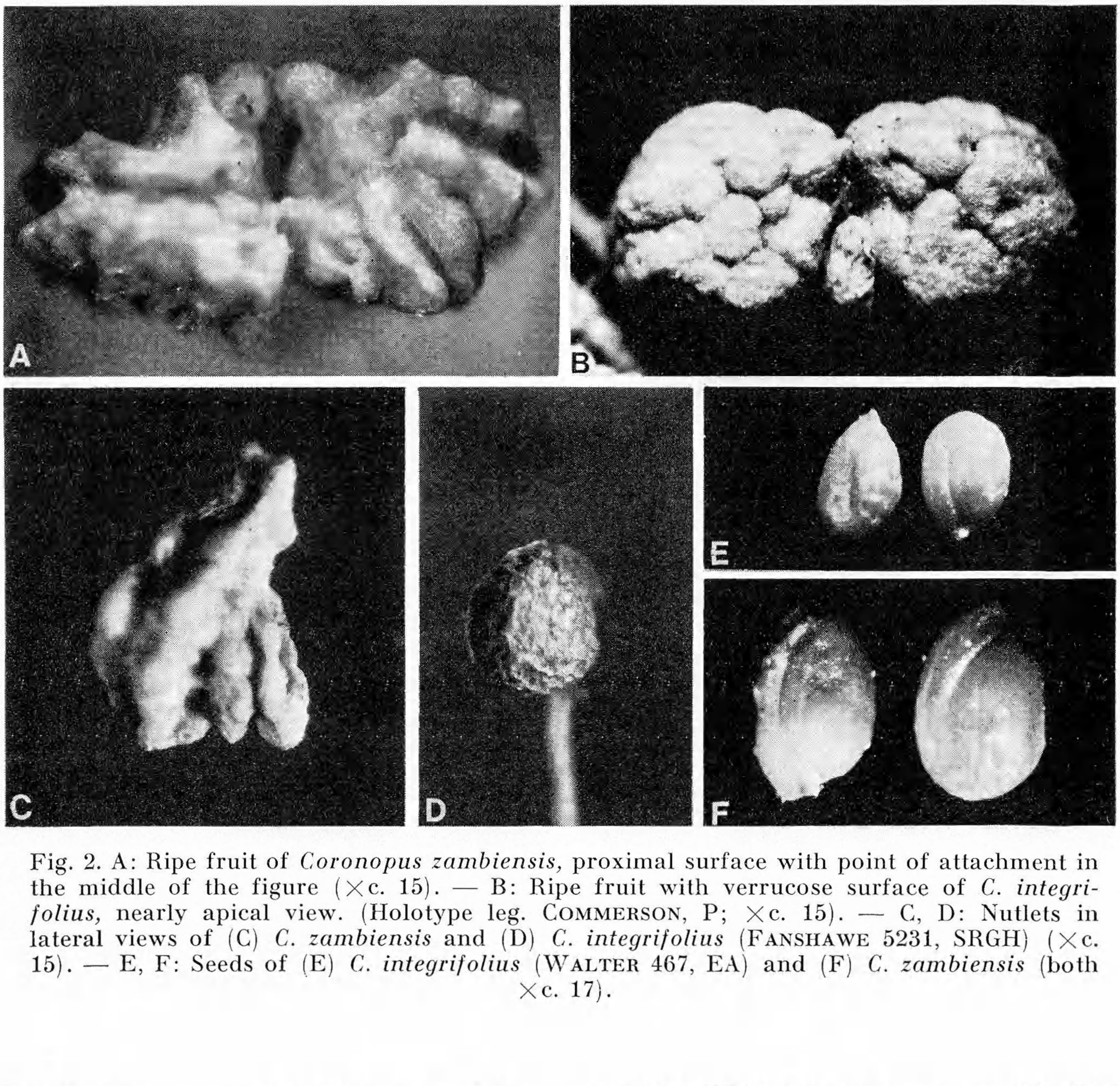

Fig. 2. A: Ripe fruit of *Coronopus zambiensis,* proximal surface with point of attachment in the middle of the figure (×c. 15). — B: Ripe fruit with verrucose surface of *C. integrifolius,* nearly apical view. (Holotype leg. Commerson, P; ×c. 15). — C, D: Nutlets in lateral views of (C) *C. zambiensis* and (D) *C. integrifolius* (Fanshawe 5231, SRGH) (×c. 15). — E, F: Seeds of (E) *C. integrifolius* (Walter 467, EA) and (F) *C. zambiensis* (both ×c. 17).

Zambesiaca area (cf. Exell & Wild 1961), or whether it has some other phytogeographical connection is of course impossible to tell.

Coronopus zambiensis Jonsell sp. nov.

Species nova *Coronopo integrifolio* (DC.) Spreng. affinis, a quo pilis caulium rectioribus longioribusque, seminibus longioribus et praesertim siliculis verrucosis, distaliter in duos processus bifidos protrusis, lateraliter duabus sinuatis cristis parallelis munitis differt.

ORIG. COLL.: Zambia, Kalabo Distr., Liuwa Plain, Paramount Chief's Game Reserve c. 45 km N. of Kalabo, in profusion at margin of small pan, 14.IX.1959. Drummond & Cookson 6458 (BM holotype; isotypes in BR, COI, LISC, SRGH).

Annual herb, richly branched from the base. *Stems* 7—13 cm high, ascending to prostrate, richly and diffusely branched, moderately puberulous with fine, mostly straight hairs, up to 0.3 mm long. *Racemes* ebracteate, numerous, terminal and axillary, often more or less leaf-opposed, in flower very small and densely corymbose in flower, narrowly cylindrical and rather dense in fruit. (Rosette leaves not observed). *Cauline leaves* usually simple (lower ones sometimes with one or two narrow lobes), of rather firm consistency and with a coriaceous tip, al-

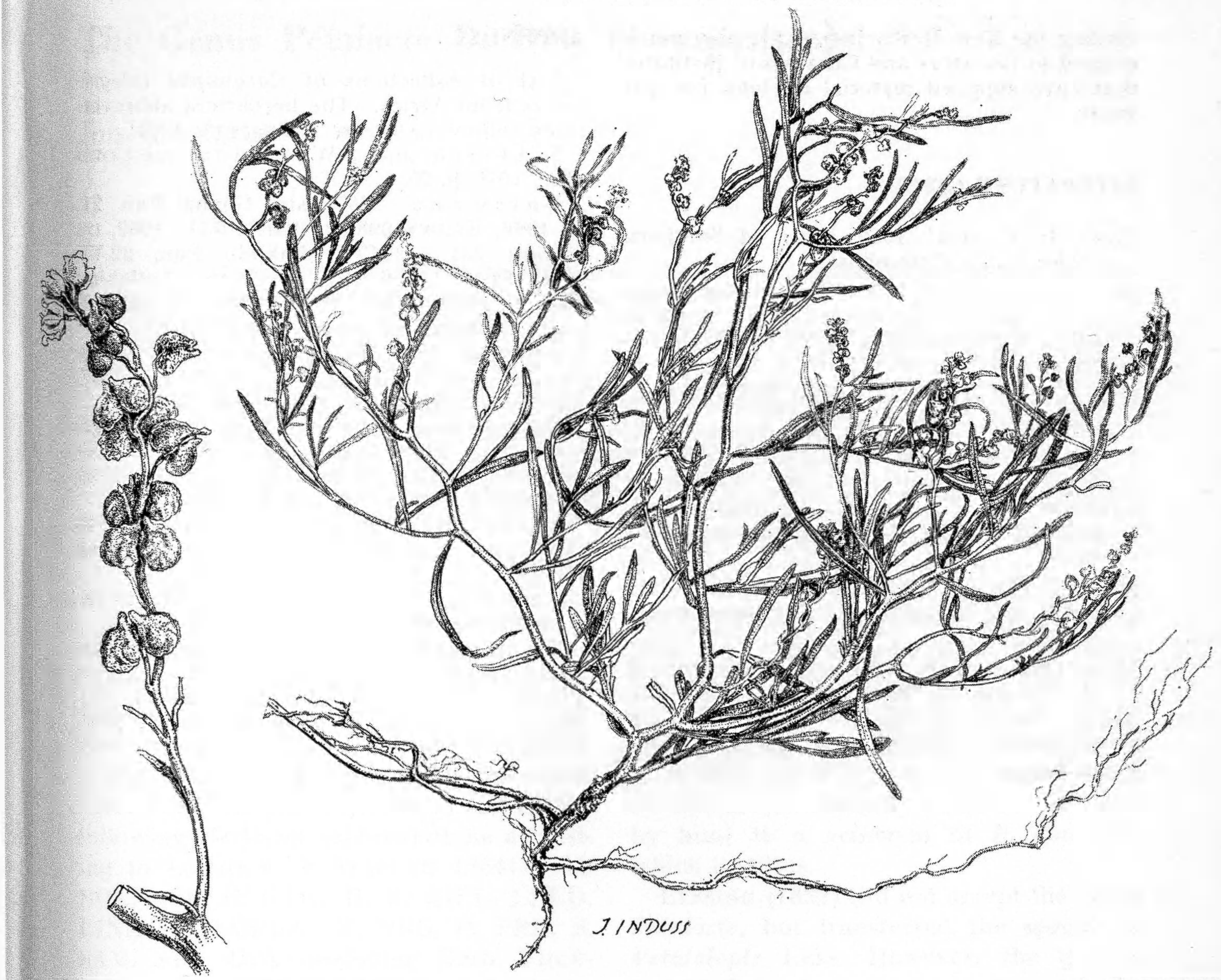

Fig. 3. *Coronopus zambiensis,* a specimen from the isotype collection in SRGH (×c. 0.8). Detail: Inflorescence with ripe fruits (×c. 2.4).

most sessile, narrowly lanceolate to linear, entire, sparsely puberulous on the upper side especially towards the base. *Sepals* elliptic c. 0.9 mm long, greenish with hyaline margins. *Petals* narrowly spathulate, c. 1.0 mm long, white. *Stamens* 2, median, with linear filaments; one flat, triangular, nectarial gland c. 0.2 mm long at each side of the base of each filament. *Ovary* transversely elliptic. *Silicula* 2.0—2.3 mm long, 3.2—4.2 mm broad, didymous, two-seeded, with a very short and narrow septum, emarginate, cordate, prominently verrucose. Each half of the silicula distally produced into a bifid beak, and with two parallel, wavy ridges along the lateral margin. Style in ripe fruits c. 0.2 mm long. Seeds 1.3×1.0 mm, flattened, elliptic in outline, with a smooth light-brown testa. *Pedicels* erecto-patent, 2.0—2.3 mm long, c. 0.2 mm thick.

ACKNOWLEDGEMENTS

My thanks are due to Dr B. Bergh, Inst. of Classical Languages, Uppsala, for checking the Latin diagnosis, Mr A. O. Chater, Univ. of Leicester, for revising the English text and for other useful suggestions, Mr J. Induss, Uppsala, for his excellent drawing, and Mr M. Thulin, Inst. of Systematic Botany, Uppsala, for perusal of some material while visiting the Kew Herbarium. I am also much obliged to Directors and Curators of institutes that have supplied material on loan for this study.

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APPENDIX

List of collections of *Coronopus integrifolius* from Africa. (The herbarium abbreviations follow LANJOUW & STAFLEU 1964).

S. Africa and S.W. Africa: see CODD et al. 1970, p. 95.

Botswana: SW distr., Ghanzi Pan, 21. X. 1969, BROWN 6985 (SRGH); 9.IV. 1969, DE HOOGH 231 (LISC); Chukudu Pan, 22.VI. 1955, STORY 4956 (K). SE Distr., Letlaking Valley, 16.II. 1960, WILD 4965 (SRGH). E Distr., Gaberones, main square, 14.IX. 1967, LAMBRECHT 294 (SRGH). N Distr., Mumpwe Pan, 40 km NNW of Nata R., 21.IV. 1957, DRUMMOND & SEAGRIFF 5168 (K, SRGH).

Rhodesia: Sebungwe Distr., near Binge, 6.XI. 1958, PHIPPS 1362 (EA, LISC, SRGH). Melsetter Distr., Chimaniwami, 26.X. 1959, GOODIER & PHIPPS 300 (EA, SRGH).

Mozambique: Zambesi Estuary, PETERS (B). Expedition I, VIII. 1858, KIRK (K).

Zambia: Lusitu, at Zambesi R., 26.IX. 1959, FANSHAWE 5231 (BM, SRGH).

Tanzania: Arusha Distr., Ngoro Kalende, 25.XI. 1901, UHLIG 707 (EA); Lekururi Village, 5.XII. 1969, RICHARDS 24895 (K). Musoma Distr., E of Nabi Hill, 10.V. 1961, GREENWAY 10161 (K).

Madagascar: COMMERSON (P).

The Genus Petalacte D. Don (Compositae)

Jan Lundgren

LUNDGREN, J. 1974 03 29. The genus Petalacte D. Don (Compositae). — Bot. Notiser 127: 119—124. Lund. ISSN 0006-8195.

The genus *Petalacte* D. DON (Compositae--Inuleae—Gnaphalinae) is endemic to the southwestern part of the Cape Province, South Africa. Only one species, *P. coronata* (L.) D. DON is now referred to the genus. This species is superficially similar to the species of the genus *Anaxeton,* the chief difference being that the florets of *P. coronata* are subtended by paleae. The pappus, too, offers distinguishing characters. The investigation is based on herbarium material only.

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Petalacte D. DON belongs to Compositae —Inuleae—Gnaphalinae. The generic name is derived from the Greek πεταλον (a petal) and ἀκτίς (a ray), and alludes to the petal-like involucral bracts.

The present investigation is based on herbarium material borrowed from the following Herbaria (abbreviations according to LANJOUW & STAFLEU 1964): BM, BOL, CGE, G, G-DC, H, K, KIEL, L, LD, LINN (microfiche), M, NBG, P, PRE, S, SAM, STE, UPS (including Herb. THUNBERG), and Z. The cooperation of the directors and curators of the listed Herbaria is gratefully acknowledged. The material studied is presented in Fig. 4. Collections without precise localities have been omitted. The data from which the map is prepared are preserved at the Museum of Natural History, Section for Botany, Stockholm, Sweden, in the form of a stencil.

The methods and terminology used follow LUNDGREN (1972 pp. 6—18).

The first species of the present genus *Petalacte* to be known was *Gnaphalium coronatum* L. It was described in 'Systema naturae' (LINNAEUS 1759).

The genus *Petalacte* was established by D. DON (1826) and included two species, *P. coronata,* based on *G. coronatum* L., and *P. bicolor,* described for the first time. The main differences between these two species were the shape of the leaves and the colour of the involucral bracts. Later on HARVEY (1865 p. 288) found these differences very trifling and reduced *P. bicolor* (erroneously named *P. discolor* by him) to a synonym of *P. coronata,* which it still is.

LESSING (1832) did not accept the genus *Petalacte,* but transferred the species to *Petalolepis* LESS. However, the generic name *Petalolepis* has been used by CASSINI (1817 p. 138) for quite different species, so that *Petalolepis* LESS. must be considered a later homonym and thus illegitimate.

DE CANDOLLE (1837) re-established the genus *Petalacte,* and added a new species, *P. canescens.* He also split the genus into two sections, *Eupetalacte* and *Amphilasia,* and placed *P. canescens* alone within the latter, mainly on account of its peculiar pappus. Furthermore, two new varieties of *P. coronata* were described.

HARVEY (1865) only recognized two taxa, *P. coronata* and *P. canescens,* in 'Flora Capensis' and his treatment of the genus has been the standard work up to now.

My attention was drawn to the genus

when revising the genus *Anaxeton* GAERTN. (LUNDGREN 1972). The two genera are superficially similar, the chief difference being that the florets of *Petalacte* are subtended by paleae. In *Anaxeton* paleae are always lacking. Another reliable character is the pappus, which in *Anaxeton* consists of barbellate bristles with small lateral teeth. In *Petalacte coronata* the bristles are distinctly subplumose at the apex. In *P. canescens,* too, the receptacle is epaleate. The presence or absence of paleae has frequently been used in characterizing genera and even subtribes within the Compositae. Therefore it is remarkable that DE CANDOLLE (1837) and later on HARVEY (1865) referred *P. canescens* to *Petalacte*. In the present paper only *P. coronata* (L.) D. DON is acknowledged as a valid species of *Petalacte*.

The mistake made by DE CANDOLLE and HARVEY had already been pointed out by BENTHAM & HOOKER (1873 p. 314) who discussed the transfer of *P. canescens* to *Anaxeton* but without making the actual combination. However, as has previously been established (LUNDGREN 1972 p. 56), the species is not considered to belong to *Anaxeton* either, mainly on account of the entirely different pappus morphology and the indumentum of the leaves.

The final systematic position of *P. canescens* requires further investigation.

PETALACTE D. DON

DON 1826 p. 552; DE CANDOLLE 1837 p. 267 p.p.; HARVEY 1865 p. 288 p.p.; 1868 p. 193 p.p.; BENTHAM & HOOKER 1873 p. 314; HOFFMANN 1890 p. 188; BAILLON 1891 p. 542; LEVYNS 1950 p. 788; PHILLIPS 1951 p. 793 p.p.; LEVYNS 1966 p. 277.

Gnaphalium L. p.p.; LINNAEUS 1759 p. 1210; auct. mult. seq.

Petalolepis LESS., nom. illeg.; LESSING 1832 p. 357 (non *Petalolepis* CASS. 1817 p. 138= *Helichrysum* MILL. emend. PERS.); auct. seq. as synonym of *Petalacte*.

Petalacte coronata (L.) D. DON

DON 1826 p. 553. — *Gnaphalium coronatum* L.; LINNAEUS 1759 p. 1210; 1763 p. 1191; auct. mult. seq. — *Petalolepis coronata* (L.) LESS., nom. illeg.; LESSING 1832 p. 357; DE CANDOLLE 1837 p. 267, and HARVEY 1865 p. 288 (as synonym of *Petalacte coronata*). — Lectotype: Herb. LINNAEUS 989: 6 (LINN microfiche only seen).

Evax involucratus SCHRANK; SCHRANK 1824 p. 171; DE CANDOLLE 1837 p. 267 (as synonym of *Petalacte coronata*). — Orig. coll.: BREHMIUS, ex herb. SCHRANK (M lectotype).

Petalacte bicolor D. DON; DON 1826 p. 553; DE CANDOLLE 1837 p. 267; HARVEY 1865 p. 288 (sphalm. *P. discolor*; as synonym of *Petalacte coronata*). — *Petalolepis discolor* (D. DON) LESS., nom. illeg.; LESSING 1832 p. 358; DE CANDOLLE 1837 p. 267 (as synonym of *Petalacte bicolor*). — Orig. coll.: Not traced.

Gnaphalium achilleae SIEB. ex DC., nom. nud.; DE CANDOLLE 1837 p. 267 (as synonym of *Petalacte coronata*). — Orig. coll.: SIEBER, Fl. capensis no. 14 (G, G-DC, H, K, KIEL, L, M, P).

Petalacte coronata (L.) D. DON var. β. *minor* DC.; DE CANDOLLE 1837 p. 267. — Orig. coll.: C.B.S., FORBES (G-DC lectotype).

Petalacte coronata (L.) D. DON var. γ. *subrosea* DC.; DE CANDOLLE 1837 p. 267. — Orig. coll.: Clanwilliam, am Fluss Olifantrivier und bei Villa Brakfontein, ECKLON & ZEYHER 76. (1237) (G-DC lectotype).

ILLUSTR.: KIDD 1950, Plate 46: 9.

Suffrutex, erect, moderately branched. Flowering branches leafy to the corymb or nearly so, densely woolly, older parts glabrous and nude and marked with leaf-scars. — *Leaves* alternate, sessile, ± closely set and imbricated, erect—patent, coriaceous, narrowly elliptic—narrowly obovate—spathulate, (0.5—)1.5—2.5(—3.5) cm long and 2—6(—10) mm wide, entire, distinctly mucronate with a dark apex, densely tomentose—woolly with white or brownish hairs on both sides. — *Corymb* compact or ± loosely composed, (1.5—)2—4(—6) cm wide. Peduncles 0.5—3(—5) cm long, densely woolly. — *Capitula* small, densely clustered, heterogamous, discoid, 8—15(—20)-flowered with 1—2 of the marginal florets female and the rest male. Florets subtended by paleae, the female one(s) often quite embraced. — *Involucral bracts* 10—20, imbricated, stipitate; claw narrowly

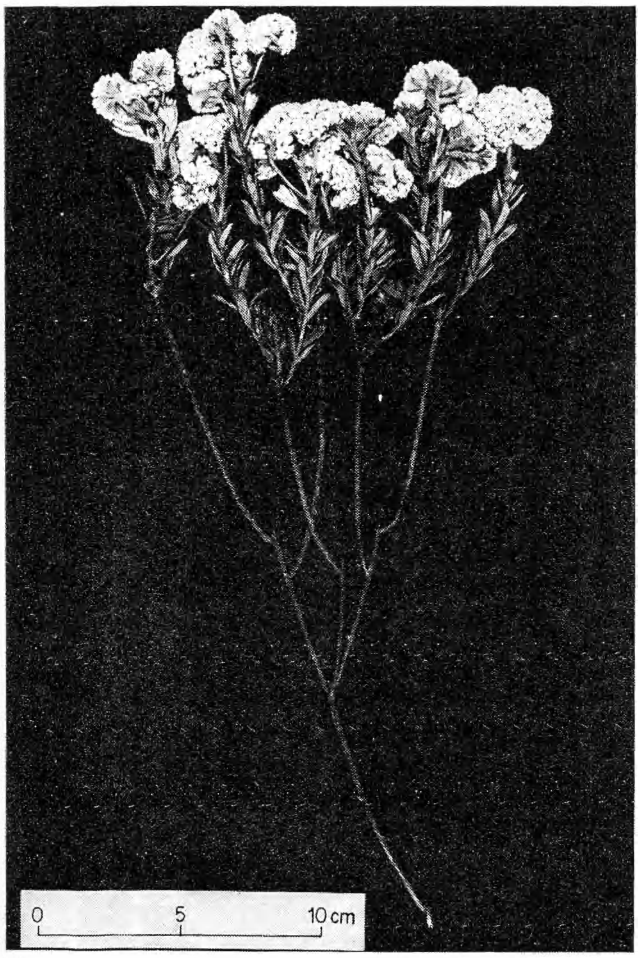

Fig. 1. *Petalacte coronata,* portion of plant. — BARKER 10657.

elliptic—narrowly oblanceolate, 3—4 mm long and c. 1 mm wide, brownish, membranaceous, outside and margins densely (sericeous—)woolly; lamina broadly elliptic—circular, 1.5—3 mm long and 1.5—2.5 mm wide, white, opaque, obtuse. — *Receptacle* flat or somewhat convex, paleate. — *Paleae* stipitate, similar to the innermost involucral bracts in shape, size, and hair-covering. — *Female floret(s)*: Corolla filiform—tubular, 2—3 mm long, slightly widening above, minutely 5-toothed and glandular at the apex, brown—purplish (when dry). Pappus as in male florets, but more poorly developed. Style terete, bifurcate; style-branches flattened, linear, 1—1.5 mm long, apically fringed with hairs and obtuse—truncate. Achene narrowly elliptic, (1—)1.5—2.2 mm long and 0.3—0.8 mm wide, brownish, glabrous, beakless, often subtended by a short, scarious, apically laciniate scale. — *Male florets:* Corolla tubular, 2.5—3.5 mm long, narrowly campanulate above, 5-lobed and glandular at the apex, brown—purplish (when dry). Pappus bristles 10—15, as long as or slightly longer than the corolla tube, white, slender, sparsely barbellate with small lateral teeth below and subplumose with thick and spreading teeth at the apex, free at the base. Style terete, filiform, simple, c. 2.5 mm long, apically fringed with hairs, apex and base club-shaped. Stylophore very distinct, c. 0.2 mm long. Stamens 5; anthers linear, caudate, 1—1.5 mm long excluding tails, but including the sterile, triangular and acute(—obtuse) apical appendage.

FLOWERING PERIOD: May—December, but most flowering specimens collected in August—September.

VERNACULAR NAME: Wildesewejaartjie (SMITH 1966).

COMMENTS

P. coronata is a distinct species, most easily recognized by its tomentose—woolly leaves, densely woolly involucral bracts, and especially by its pappus bristles which are sparsely barbellate below and subplumose at the apex.

The leaves vary a great deal in size and outline (Fig. 3). Normally they are narrowly obovate—spathulate and more or less distinctly narrowed to the base. In some collections (e.g. BAYLISS 1656) from the vicinity of Darling the leaves are narrowly elliptic with a sharp apex. A collection from Bredasdorp (COMPTON 9049) has extremely small and closely set leaves. These extreme forms are connected with more typical *coronata* by transitional forms.

In *Petalacte* the receptacle is paleate, and the paleae are very similar to the involucral bracts in size, shape, and indumentum (Fig. 2 A—B). The marginally situated female floret is often em-

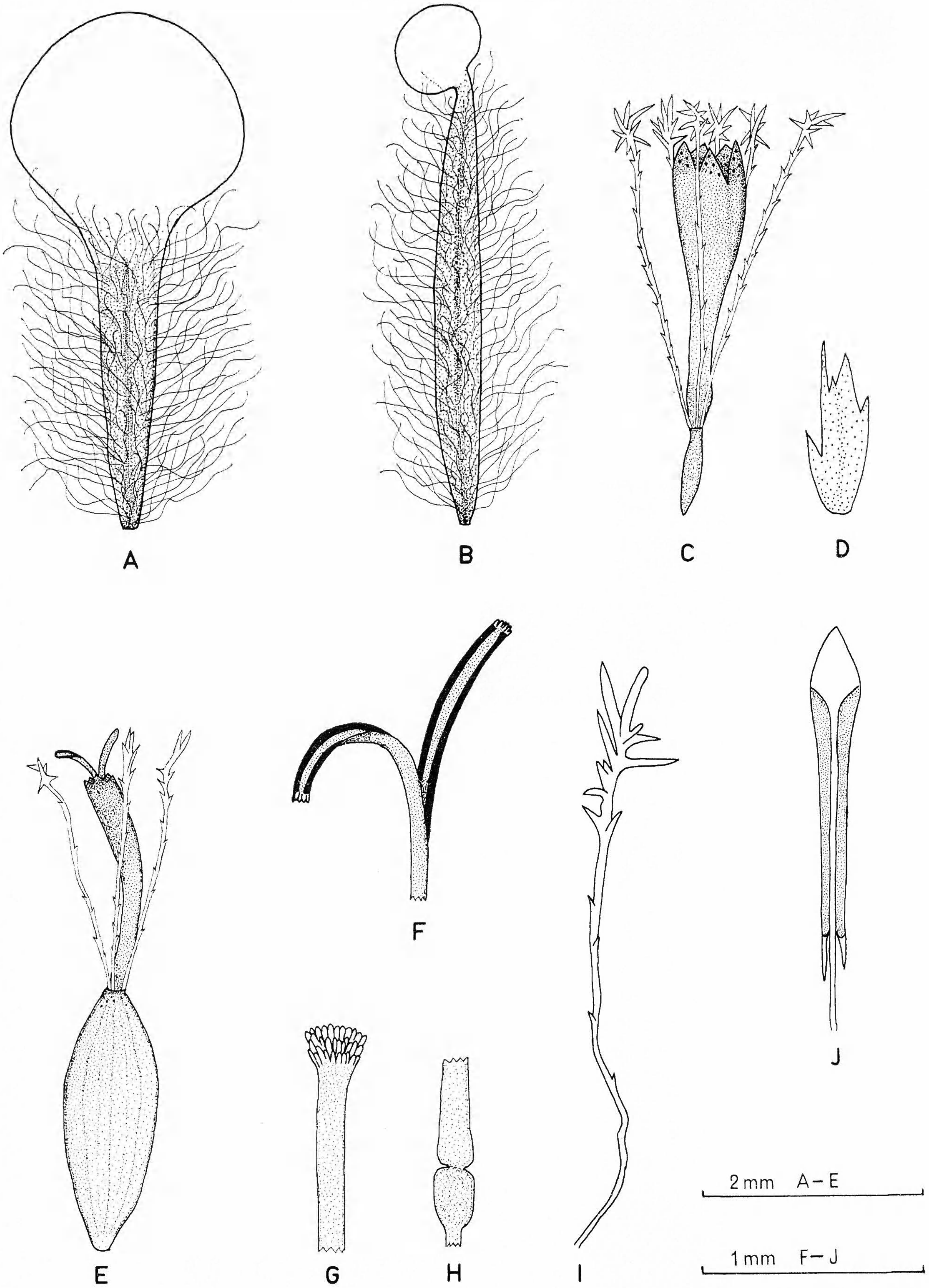

Fig. 2. *Petalacte coronata.* — A: Outer involucral bract. — B: Palea. — C: Male floret, with c. 1/2 the number of pappus bristles. — D: Scale from base of achene. — E: Female floret, with c. 1/2 the number of pappus bristles. — F: Style apex (female floret). — G: Style apex (male floret). — H: Style base with stylophore (male floret). — I: Pappus bristle (male floret). — J: Anther. — WALL 29.11. 1938, mountains above Muizenberg.

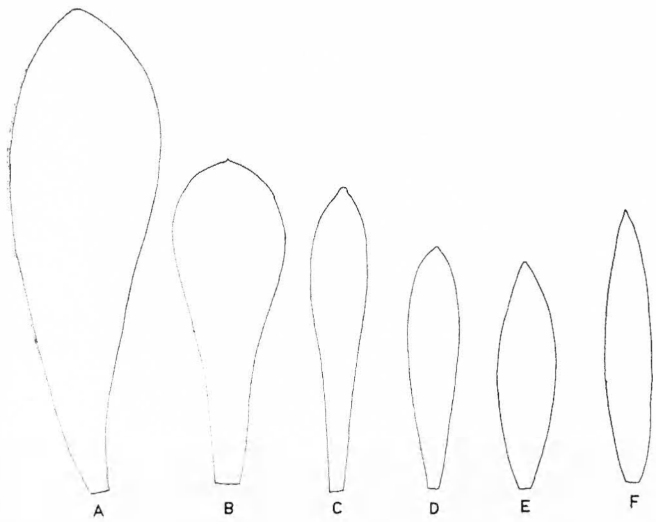

Fig. 3. *Petalacte coronata.* — Variation in leaf outline (without indumentum). — All ×1.75. — A: ECKLON & ZEYHER 77.9; B: WALL 29.11. 1938 (Muizenberg); C: ANDREAE 551 (along Muizenberg); D: ROGERS 29835 (Clovally); E: EDWARDS 156 (Piquetberg); F: BAYLISS 1656 (Darling).

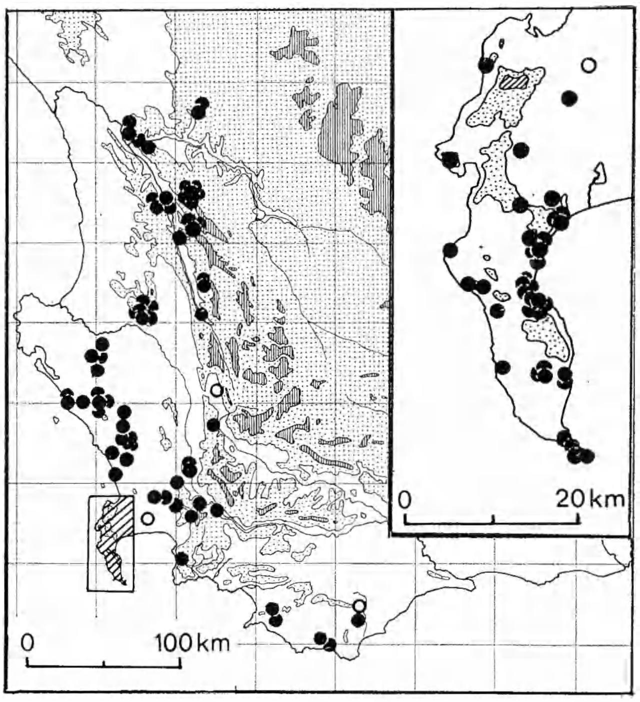

Fig. 4. Distribution of *Petalacte coronata* (○ = inexact locality). — Hatched area (Cape Peninsula) enlarged.

braced or enclosed by its subtending bract, the achene being quite hidden. There is some doubt as to whether this bract belongs to the innermost row of involucral bracts or to the outermost row of receptacular paleae. Homologically the two are one and the same thing, but I find it most appropriate to call all bracts that are outside the florets involucral bracts and those within the outermost row of florets paleae.

At the very base of the achene, opposite the subtending bract, a small, scarious, and apically laciniate scale can be observed (Fig. 2 D).

The variation in floral details seems to be insignificant.

DISTRIBUTION

P. coronata has a western distribution, ranging from the Cape Peninsula in the south northwards through the Olifants River valley to the Giftberg (Van Rhynsdorp Division) and Lokenberg (Calvinia Division), and eastwards to Bredasdorp Division. The species seems to have a wide ecological amplitude, occurring on sandy soils from low altitudes close to the sea up to c. 1000 m above sea level.

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Evolutionary Trends in the Atriplex triangularis Group of Scandinavia

III. The Effects of Population Size and Introgression on Chromosomal Differentiation

Mats Gustafsson

GUSTAFSSON, M. 1974 03 29. Evolutionary trends in the Atriplex triangularis group of Scandinavia. III. The effects of population size and introgression on chromosomal differentiation. — Bot. Notiser 127: 125—148. Lund. ISSN 0006-8195.

In *A. longipes* ssp. *praecox* 80 % of the populations investigated are small or very small, whereas most populations of other taxa are medium-sized to very large. Male fertility has been investigated (1) within populations of varying size, (2) within introgressive and normal populations respectively. Plants showing reduced fertility are most frequent in some small *praecox* populations. In *A. longipes* ssp. *longipes* and *A. triangularis* plants with reduced fertility are commoner in introgressive populations than in normal ones. Crossing experiments have been carried out (1) between populations of varying size, (2) between introgressive and normal populations respectively. Crosses between small *praecox* populations show a much higher frequency of reduced fertility than crosses small×medium-sized *praecox* populations and than crosses between all other taxa. In *A. triangularis* 85 % of the crosses between normal populations and 50 % of the crosses between introgressive populations show reduced fertility. Investigations of meiosis indicate that reduced fertility is to a great extent due to heterozygosity for paracentric inversions. Inversion polymorphism seems to be most pronounced in small *praecox* populations, less in medium to large *praecox* populations and within *A. triangularis,* and of little significance in the other taxa. In *A. triangularis* chromosomal differences are commoner between non-introgressive than between introgressive populations.

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INTRODUCTION

This paper forms part of the investigation on morphological and cytological differentiation within the *Atriplex triangularis* group in Scandinavia. In a previous paper (GUSTAFSSON 1973 a) the author discussed the frequency of reduced male fertility in different populations, as well as the degree of hybrid sterility in intra- and interspecific crosses. In certain populations of *A. longipes* ssp. *praecox* and *A. triangularis* there is a high frequency of plants with reduced fertility. In *A. longipes* this reduction is most pronounced in small populations (GUSTAFSSON 1972). Population crosses carried out within *A. longipes* ssp. *praecox* and within *A. triangularis* result in a high frequency of both F_1 and F_2 progenies with reduced fertility. This is, in fact, about as high as in crosses between the five taxa, i.e. between *A. calotheca, A. glabriuscula, A. longipes* ssp. *longipes,* ssp. *praecox* and *A. triangularis.* Investigations of meiosis, carried out both in plants grown from seeds of natural populations and in artificially produced hybrids, indicate a high degree of correlation between the formation of bridges at

Table 1. Sizes of populations in the taxa of the *A. triangularis* group. n indicates the number of populations investigated.

Taxon	Population size (number of individuals)					n
	1 — 100	100 — 300	300 — 1,000	1,000 — 3,000	>3,000	
	very small	small	medium-sized	large	very large	
A. calotheca	—	1	1	3	4	9
	—	11	11	33	44	%
A. glabriuscula	—	1	7	3	—	11
	—	9	64	27	—	%
A. longipes ssp. *longipes*	—	2	5	8	8	23
	—	9	22	35	35	%
A. longipes ssp. *praecox*	13	13	5	1	1	33
	39	39	15	3	3	%
A. triangularis	—	1	6	6	14	27
	—	4	22	22	52	%

anaphase I and reduced male fertility. The formation of bridges is probably due to heterozygosity for paracentric inversions. The hybrid fertility in intraspecific crosses seems to be correlated neither with geographical distance separating parent populations, nor with the differentiation of morphological types.

Gene exchange between taxa occurs mainly in the western part of Scandinavia and in the northernmost part of Norway where reproductive isolation is weak. The reproductive capacity of natural hybrids can be lowered either by the reduction of male fertility or by decrease in germination capacity. Morphological segregation of hybrid offspring towards the parent species is not combined with a simultaneous restoration of fertility (Gustafsson 1973 b).

MATERIAL

The experimental work is based upon the following number of populations of each taxon: *A. calotheca* (Rafn) Rafn & Fries: 9, *A. glabriuscula* Edmondst.: 12, *A. longipes* Drej. ssp. *longipes:* 27, ssp. *praecox* (Hülph.) Turess.: 33, and *A. triangularis* Willd.: 52. The origin of the populations is presented in Gustafsson 1973 a. The code to the crossing experiments is preserved at and available from the Botanical Library, the University of Lund, Sweden.

Table 2. Frequency (%) of plants with different fertility values in populations of different Introgressive populations of *A. longipes* ssp.

Taxon	*A. longipes* ssp. *praecox*				*A. longipes* ssp. *longipes*			
Population size	1 — 100	100 — 300	300 — 1,000	>1,000	1 — 100	100 — 300	300 — 1,000	>1,000
Fertility %								
50— 60	3	1	4	—	—	—	—	—
60— 70	13	4	—	5	—	—	—	1
70— 80	10	6	—	5	—	—	3	1
80— 90	7	6	8	9	—	4	3	3
90—100	67	84	88	82	—	96	95	95
n	30	86	24	22	—	23	39	103
N	3	7	2	2	—	2	3	7

MORPHOLOGICAL AND CYTOLOGICAL VARIATION WITHIN AND DIFFERENCES BETWEEN POPULATIONS OF VARYING SIZE

The importance of population size and structure on the evolutionary processes has been discussed by numerous workers, e.g. WRIGHT (1940), STEBBINS (1950) and GRANT (1963). They are agreed that medium-sized and large populations are the most usual in plants. STEBBINS and GRANT consider that in small periodically isolated populations, new gene combinations and structural changes can be advantageous. WRIGHT considers that the evolutionary possibilities of a small population system are restricted, that a high degree of inbreeding may result in almost complete homozygosity and both morphological and cytological invariability. However, many authors have pointed out that heterozygosity can be maintained in small populations (e.g. HENEEN & RUNEMARK 1962, SNOGERUP 1967).

The present investigation deals with three main problems: The effects of population size on, (1) the frequency of structural heterozygosity within populations, (2) hybrid fertility and chromosomal differences between populations, (3) degree of morphological variation.

Population Size

In all, the size of 103 populations has been investigated and the results are summarized in Table 1. In the main, populations representing different parts of the area of distribution have been selected. Population size has been divided into five categories (cf. Table 1) based on the maximum size of a population during the years 1969 to 1972, with the exception of Norwegian populations of *A. longipes* ssp. *praecox* which were investigated in 1968 only. The decided differences between taxa are rather remarkable. Most populations of *A. calotheca, A. longipes* ssp. *longipes* and *A. triangularis* are made up of a large number of individuals, 90 to 95 % of these populations being medium-sized or large, i.e. comprising more than 300 individuals. The majority of populations of *A. glabriuscula* are of medium size and only one of the eleven is small. By contrast, most populations of *A. longipes* ssp. *praecox* are small or very small, only 7 of 33 are of medium or large size.

The difference in population size is probably conditioned by differential ecological preference. *A. longipes* ssp. *praecox* generally grows in open, more or less ephemeral areas, with little or no vegetation, in the lower parts of sea-shore

size. n indicates the number of individuals and N the number of populations investigated.
longipes and *A. triangularis* have been excluded.

A. calotheca					*A. glabriuscula*				*A. triangularis*			
1—100—300 —1,000—>1,000					1 —100 —300—1,000 —>1,000				1 —100 —300—1,000 —>1,000			
—	—	—	—		—	—	—	—	—	—	—	1
—	—	—	—		—	—	1	—	—	—	—	—
—	—	—	—		—	—	1	—	—	—	—	—
—	—	—	9		—	—	5	—	—	—	6	4
—	—	100	91		—	100	92	100	—	100	94	95
—	—	13	70		—	14	74	15	—	13	71	124
—	—	1	5		—	1	4	1	—	1	4	7

meadows. These areas are usually rather small in size and the populations consequently limited. The remaining taxa usually inhabit more stable biotopes such as communities dominated by *Scirpus maritimus,* belts of *Phragmites,* and the upper and middle parts of marshes. These biotopes are usually fairly extensive and the populations large and probably remain so over a considerable period of time.

Fertility in Populations of Varying Size

The frequency of plants with reduced fertility in relation to size of populations is summarized in Table 2. The results are based on data from all populations within the *A. triangularis* group investigated, except those of *A. longipes* ssp. *longipes* and of *A. triangularis* which have been shown to be influenced by hybridization and introgression. The results are similar to those observed within *A. longipes* (Gustafsson 1972). In very small populations of *A. longipes* ssp. *praecox* as many as 33 % of the plants display reduced fertility (less than 90 % stainable pollen). The corresponding figure for small, medium-sized and large *praecox* populations is much lower, 16 %, 12 %, and 18 % respectively. The distribution of fertility values within *praecox* populations is shown in Table 3. In two populations (G 87 and G 89), both originating from the archipelago of Åland, reduction in fertility is extremely common, about one half of the plants having less than 80 % stainable pollen. All populations where 15 % or more of the plants have reduced fertility, are small or very small except for population G 109, originating from Öland. It is possible that the high frequency of reduced fertility has been maintained in population G 109, as the increase in size, from about 100 to 3,000 individuals occurred very rapidly during the period 1969 to 1972. Two small populations, one from Åland (G 88) and one from Norway (G 160), are composed solely of plants with high fertility values.

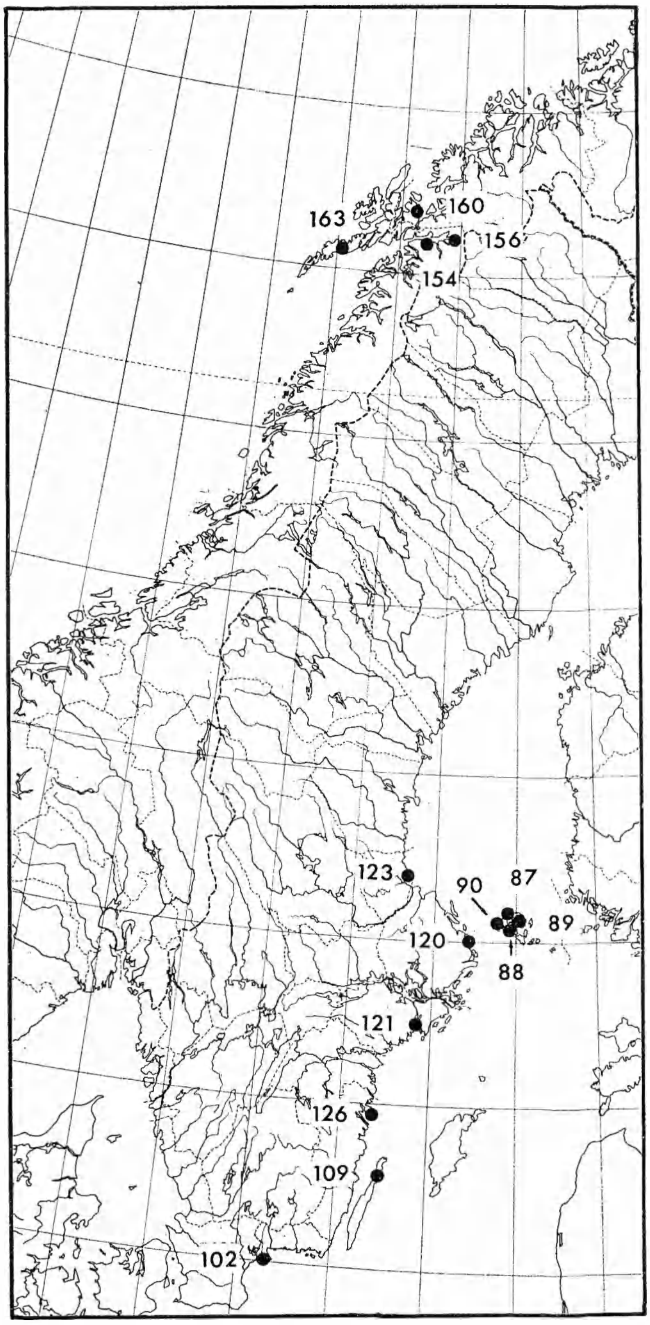

Fig. 1. The origin of the populations of *A. longipes* ssp. *praecox* accounted in Table 3.

In all other taxa the frequency of plants with reduced fertility is less than 10 % independent of population size.

Hybrid Fertility in Relation to the Size of the Parent Populations

In the *A. triangularis* group chromosomal differences between populations can only be estimated by means of reduced hybrid fertility as the somatic chromo-

Table 3. Distribution of fertility values in populations of varying size within *A. longipes* ssp. *praecox*. n indicates the number of individuals investigated. To the right the frequency of individuals with fertility values less than 90 % has been calculated.

Population		Fertility %					n	% plants with reduced fertility
code	size	50 — 60	— 70	— 80	— 90	— 100		
G 89	Very small	—	3	2	—	4	9	56
G 120	,,	—	1	—	2	7	10	30
G 163	,,	1	—	1	—	9	11	18
G 87	Small	—	2	3	—	5	10	50
G 88	,,	—	—	—	—	9	9	0
G 121	,,	—	—	2	1	8	11	27
G 123	,,	—	1	—	2	9	12	25
G 126	,,	1	—	—	—	12	13	8
G 154	,,	—	—	—	2	14	16	13
G 160	,,	—	—	—	—	15	15	0
G 90	Medium	—	—	—	1	8	9	11
G 156	,,	1	—	—	1	13	15	13
G 102	Large	—	—	1	—	9	10	10
G 109	,,	—	1	—	2	9	12	25

somes are too small for detailed analysis. The degree of reduced fertility in crosses between populations of different size has been investigated in intraspecific as well as in interspecific crossing combinations. In addition the meiotic behaviour of F_1 hybrids has been investigated. Crosses with populations of *A. longipes* ssp. *praecox* have been divided into two main groups. The first group comprises crosses with small populations i.e. not exceeding 300 individuals. In all, nine small populations from the Baltic region and four from Norway have been used. The second group represents crosses with four medium-sized to large populations originating from both the Baltic region and Norway.

INTRASPECIFIC CROSSES. The crossing experiments carried out within *A. longipes* ssp. *praecox* comprise the combinations small×small populations and small×medium to large populations. Crossing between large *praecox* populations has not been carried out. However, the degree of hybrid sterility in crosses between medium to large populations within *A. longipes* ssp. *longipes* and within *A. triangularis* are given as comparisons. All crosses with populations affected by introgression have been excluded. The results are shown in Table 4 and Fig. 2. In crosses between small populations of *A. longipes* ssp. *praecox* most of the combinations have low fertility values, in fact no cross has a mean fertility exceeding 90 %. In 19 crosses of 21 pollen stainability is less than 80 % and in as many as 9 crosses less than 50 %. The degree of hybrid sterility in population crosses within regions seems to be as high as that in crosses between regions. The mean fertility in crosses between the small population G 121 and eight other small populations is shown in Fig. 2 A. The highest mean fertility value (81 %) is found in the cross between G 121 and the most distant population (G 160). In the cross between G 121 and the nearest population (G 120) the fertility value is as low as in crosses with more distant populations.

Reduced fertility is much less frequent in all other crossing combinations. In crosses small×medium to large *praecox* populations pollen stainability in 9 of 13 is less than 80 %, but in no cross is it less than 50 %. In the majority of crosses

Table 4. Distribution of mean fertility values in intraspecific crosses in relation to the size of the parent populations. n indicates the number of crosses investigated. In *A. longipes* ssp. *praecox* the crossing combination small×small populations has been divided into groups according to the geographic origin of the parent populations. Sw.=Sweden, No.=Norway, Fi.=Finland.

Crosses within	Size of parent populations	Origin	Male fertility % in F_1 30—40	40—50	50—60	60—70	70—80	80—90	90—100	n
A. longipes ssp. *praecox*	Small×Small	E Sw.×E Sw.	—	3	4	1	—	—	—	8
		No.×No.	1	—	—	—	—	—	—	1
		E Sw.×Fi.	—	—	1	1	—	1	—	3
		E Sw.×No.	—	5	—	1	1	1	—	8
		Fi.×No.	—	—	1	—	—	—	—	1
	Total		1	8	6	3	1	2	—	21
			5	38	29	14	5	10	—	%
	Small×Medium —Large		—	—	4	2	3	—	4	13
			—	—	31	15	23	—	31	%
A. longipes ssp. *longipes*	Medium×Medium —Large —Large		—	—	1	—	2	8	13	24
			—	—	4	—	8	33	54	%
A. triangularis	Medium×Medium —Large —Large		—	—	—	4	4	8	3	19
			—	—	—	21	21	42	16	%

between medium to large populations within *A. longipes* ssp. *longipes* and within *A. triangularis* fertility values are relatively high, only 3 and 8 crosses respectively having a mean fertility of less than 80 %, none less than 50 %.

INTERSPECIFIC CROSSES. The interspecific crosses have been divided into two main groups, small *praecox* populations×other taxa and medium to large *praecox* populations×other taxa. The results are shown in Table 5 and Fig. 2 C, and correspond remarkably well with those observed in intraspecific crosses. In the crossing combinations small populations of *A. longipes* ssp. *praecox*×other taxa 49 crosses of 63 have fertility values of less than 80 %, and 14 crosses less than 50 %. The corresponding figures for the crossing combinations medium to large *praecox* populations×other taxa are 10 and 3 respectively of 20 crosses. In crosses between all other taxa (*A. calotheca, A. glabriuscula, A. longipes* ssp. *longipes* and *A. triangularis*) the degree of reduced hybrid fertility is much less, 10 crosses of 49 having less than 80 %, but only one cross less than 50 % stainable pollen.

The results indicate that in crosses between small populations within *A. longipes* ssp. *praecox* reduced fertility is commoner than in crosses between all the other taxa.

Variation Patterns in Male Fertility and Chromosomal Changes in F_1 Progenies

Variation patterns in male fertility and the disturbances found at meiosis within F_1 progenies of *A. longipes* are shown in Fig. 3. Three types of variation pattern can be distinguished: (1) crosses where all F_1 hybrids show reduced fertility, (2) crosses composed of highly fertile hybrids as well as hybrids showing reduced fertility, (3) crosses where all F_1 hybrids have high fertility values. The meiotic behaviour of crosses with reduced fertility demonstrates that the formation of bivalents is quite normal, while bridges and laggards have been observed at anaphase. Correlation between the number of bridges formed at anaphase I and the frequency of reduced fertility is high. The

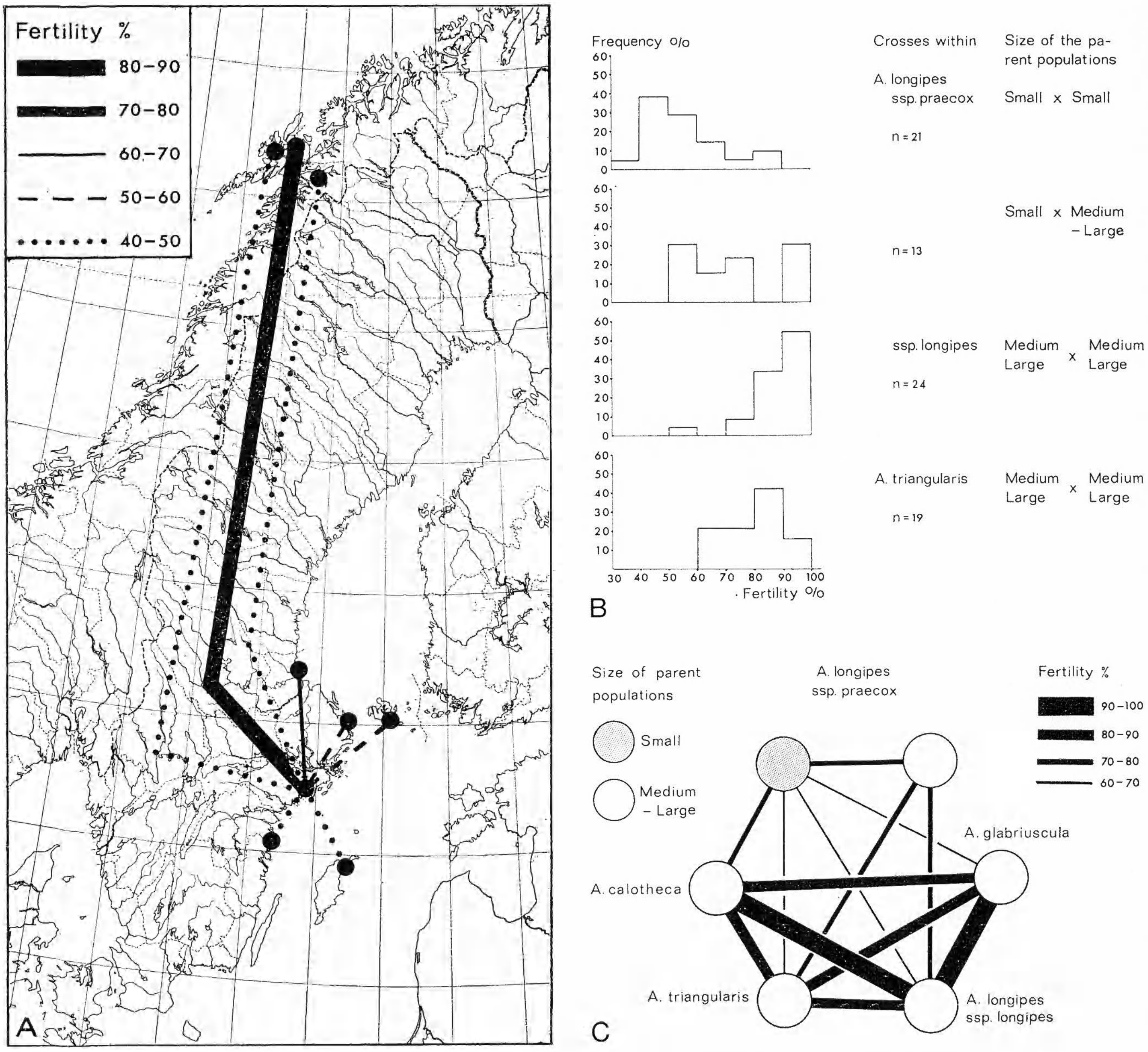

Fig. 2. Mean fertility values in intra- and interspecific crosses between parent populations of varying size. — A. Crosses within *A. longipes* ssp. *praecox*. Mean fertility values in crosses between the small population G 121 and eight other small populations. — B. Crosses within *A. longipes* ssp. *praecox,* within ssp. *longipes* and within *A. triangularis*. Distribution of mean fertility values in relation to the size of the parent populations. n indicates the number of crosses investigated. All crosses with introgressive populations have been excluded. — C. Crossing polygon indicating mean fertility values of interspecific crosses in relation to the size of the parent populations. The data are based on all crosses carried out within the *A. triangularis* group.

formation of bridges is probably due to heterozygosity for paracentric inversions (cf. GUSTAFSSON 1973 a). Thus the occurrence of different variation patterns in fertility is probably due to diversity in the state of the inversions displayed in the parents. (1) In the six crosses between small populations all the F_1 progenies are composed exclusively of hybrids with reduced fertility. This kind of variation indicates that one parent is homozygous for at least one inversion the other parent being either normal, heterozygous or homozygous for at least

Table 5. Distribution of mean fertility values in interspecific crosses in relation to the size of the parent populations. n indicates the number of crosses investigated.

	Male fertility % in F_1								n
	20—30	30—40	40—50	50—60	60—70	70—80	80—90	90—100	
Small *praecox* populations × other taxa									
praecox × *longipes*	1	4	7	8	10	11	4	8	53
praecox × *triangularis*	—	—	2	—	2	1	1	—	6
praecox × *calotheca*	—	—	—	1	—	—	1	—	2
praecox × *glabriuscula*	—	—	—	—	1	1	—	—	2
Total	1	4	9	9	13	13	6	8	63
%	2	6	14	14	21	21	10	13	
Medium—Large *praecox* populations × other taxa									
praecox × *longipes*	—	—	2	2	2	2	4	3	15
praecox × *triangularis*	—	1	—	—	—	1	2	1	5
Total	—	1	2	2	2	3	6	4	20
%	—	5	10	10	10	15	30	20	
Crosses between other taxa									
calotheca × *glabriuscula*	—	—	—	—	—	—	1	1	2
calotheca × *longipes*	—	—	—	—	—	1	1	3	5
calotheca × *triangularis*	—	—	—	—	1	—	2	5	8
glabriuscula × *longipes*	—	—	—	—	—	—	2	3	5
glabriuscula × *triangularis*	—	—	—	1	—	1	1	4	7
longipes × *triangularis*	—	—	1	3	—	2	5	11	22
Total	—	—	1	4	1	4	12	27	49
%	—	—	2	8	2	8	25	55	

one other inversion. This is also the case in most crosses between small and medium to large populations. (2) Cross number Gk 29, representing small × medium to large populations, show a variation in fertility from 70 % to 100 %. The same variation has also been observed in crosses Gk 3 and Gk 4, representing crosses between medium to large populations. The wide range of variation can be accounted for by different chromosomal rearrangements in the parents. Presumably one of the parents is heterozygous for at least one inversion the other being normal, homozygous for the same inversion, or heterozygous for the same or some other inversion. (3) In crosses where all the F_1 hybrids are highly fertile (Gk 65, Gk 7, Gk 15 and Gk 97), both the parents are either normal or homozygous for the same inversion. However, as the crosses have been performed between rather distant and well-isolated populations, it seems unlikely that the parents should be homozygous for the same inversion.

The distribution of these variation patterns differs somewhat in the different crossing combinations. In the six crosses between small populations at least one half of the parents seem to be homozygous for at least one inversion. But this is probably also true of most of the 21 crosses performed between small populations (Table 4). The fertility of more than 80 F_1 hybrids has been checked and only one individual has a fertility value exceeding 90 % (cross number Gk 73). Two other crosses (Gk 70 and Gk 80) have hybrid plants with a fertility of between 80 and 90 %, but all the other 18 crosses are composed of hybrids that are fertile to less than 80 %. This may indicate that in 18 crosses of 21 at least one of the parents is homozygous for one or more paracentric inversions.

In crosses small × medium to large populations all three types of variation patterns are observed. Most parents of

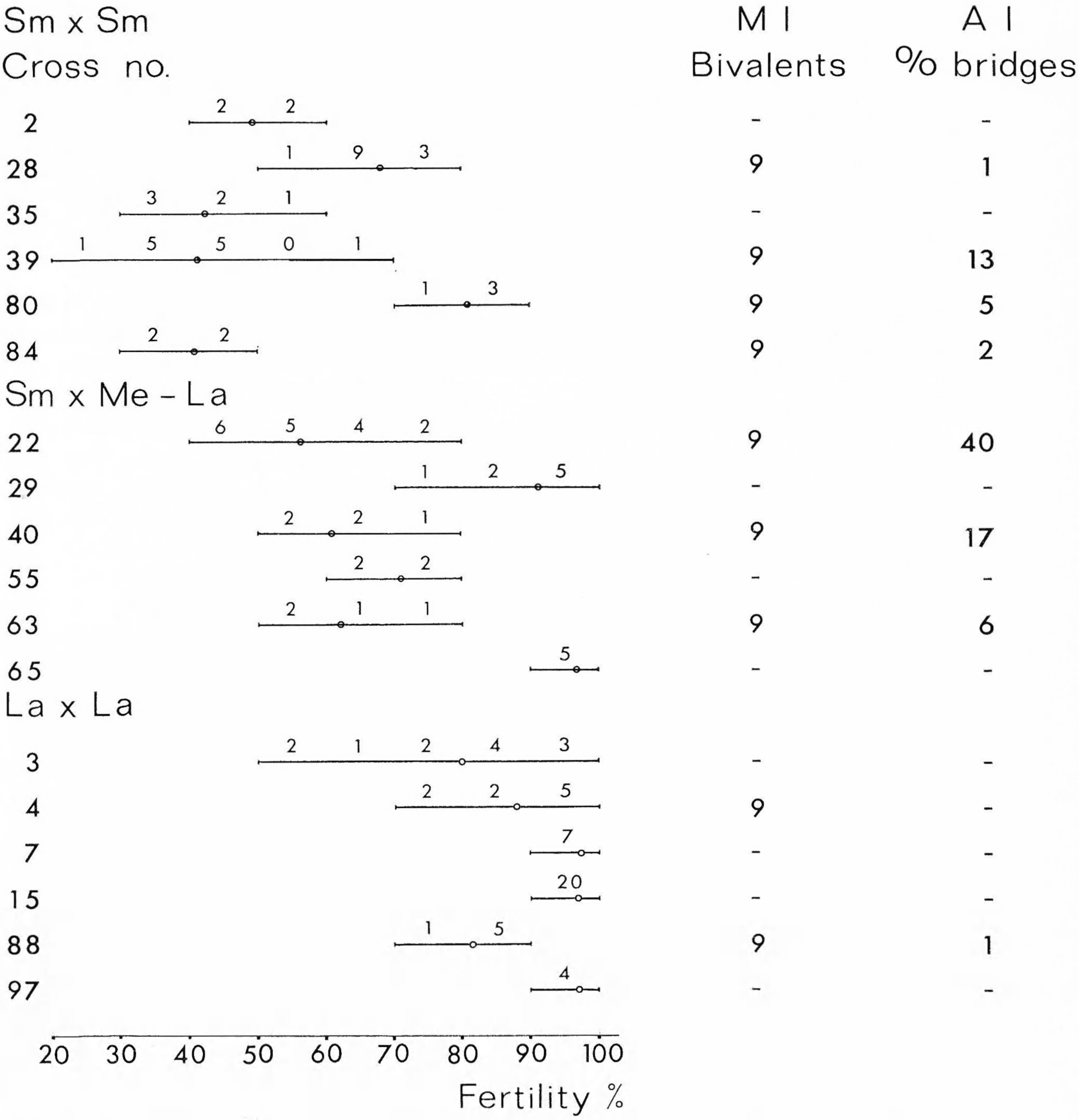

Fig. 3. Variation in fertility and meiosis within F_1 families in relation to the size of the parent populations. Crosses 2—84 represent small×small populations of *A. longipes* ssp. *praecox*, crosses 22—65 small×medium to large *praecox* populations, and crosses 3—97 large×large populations of *A. longipes* ssp. *longipes*.

crosses between larger populations are probably normal or heterozygous for one or more inversions.

Distribution of Inversions in Small Populations

Investigations of meiosis and the distribution of male fertility values within populations indicate that plants showing reduced fertility, to a great extent probably due to heterozygosity for inversions, are more frequent in some small populations than in others (cf. Table 1). The question is whether the total number of structural changes is greatest in populations displaying a high degree of heterozygosity,

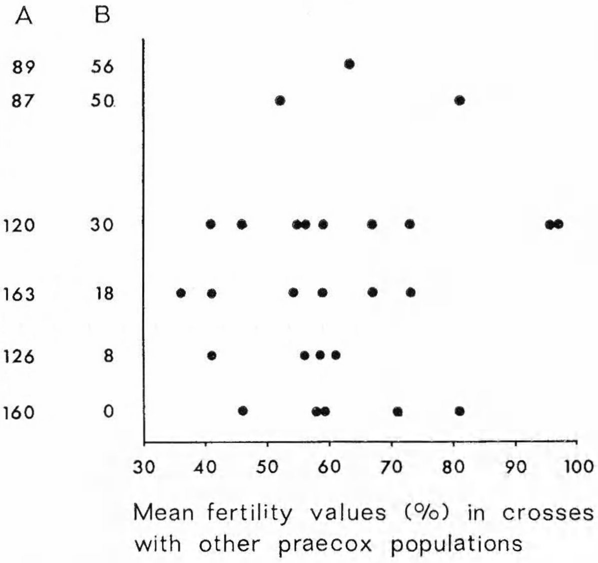

Fig. 4. Relation between the frequency (%) of plants with reduced fertility within seven small populations of *A. longipes* ssp. *praecox* and distribution of mean fertility values (%) in crosses with other *praecox* populations. — A: Population code. — B: % plants with reduced fertility (less than 90 %) within the populations G 89—G 160 respectively.

or if it is about equally distributed in the small populations. The relation between mean fertility values in crosses with different small *praecox* populations and the frequency of individuals with reduced fertility within these populations has been summarized in Fig. 4. It is obvious that no correlation exists and most of the crosses have fertility values of less than 80 %. The cross between populations G 88 and G 160, both showing a low degree of heterozygosity, displayed a fertility value as low as 58 %. The results of the crossing experiments indicate that structural changes, probably mainly inversions, are distributed in all or most of the small populations independent of (1) the origin of the populations and (2) whether the frequency of heterozygous structural changes is high or low. However, the number of crosses is too small to determine whether the total number of structural changes is about equally distributed or not.

Morphological Variation in Small, Medium-sized and Large Populations

The morphological variation within populations of varying size has been investigated in *A. longipes* ssp. *praecox,* as this taxon shows a large range of variation from very small to large populations. The other taxa have very few small populations so that they must be left out of account in this case. Morphological variation in four characters, viz. height, lamina length, length of bracteoles and seed size is shown in Fig. 5. The populations shown have been selected to illustrate the variation patterns in small, medium-sized and large populations. In general 20 individuals from each population have been measured on populations cultivated in the Botanical Gardens, Lund. The range of variation is equal to the difference between the highest and the lowest value.

The small populations are generally less variable in most characters than the larger populations. However, populations G 89 and G 123 diverge conspicuously from the other small populations in having a morphological variation similar to that of larger populations.

Isolation between Populations

Local populations of *A. longipes* are usually spatially isolated from each other by a number of unsuitable biotopes, such as cliffs, sandy shores and belts of *Phragmites.* Further, island populations are separated to a greater or lesser extent

Fig. 5. Variation in four morphological characters within populations of *A. longipes* ssp. *praecox* in relation to population size. The data are based on 20 individuals from each population and the range of variation is equal to the difference between the highest and the lowest value. Mean values are indicated by rings. The material has been cultivated in the Botanical Gardens, Lund.

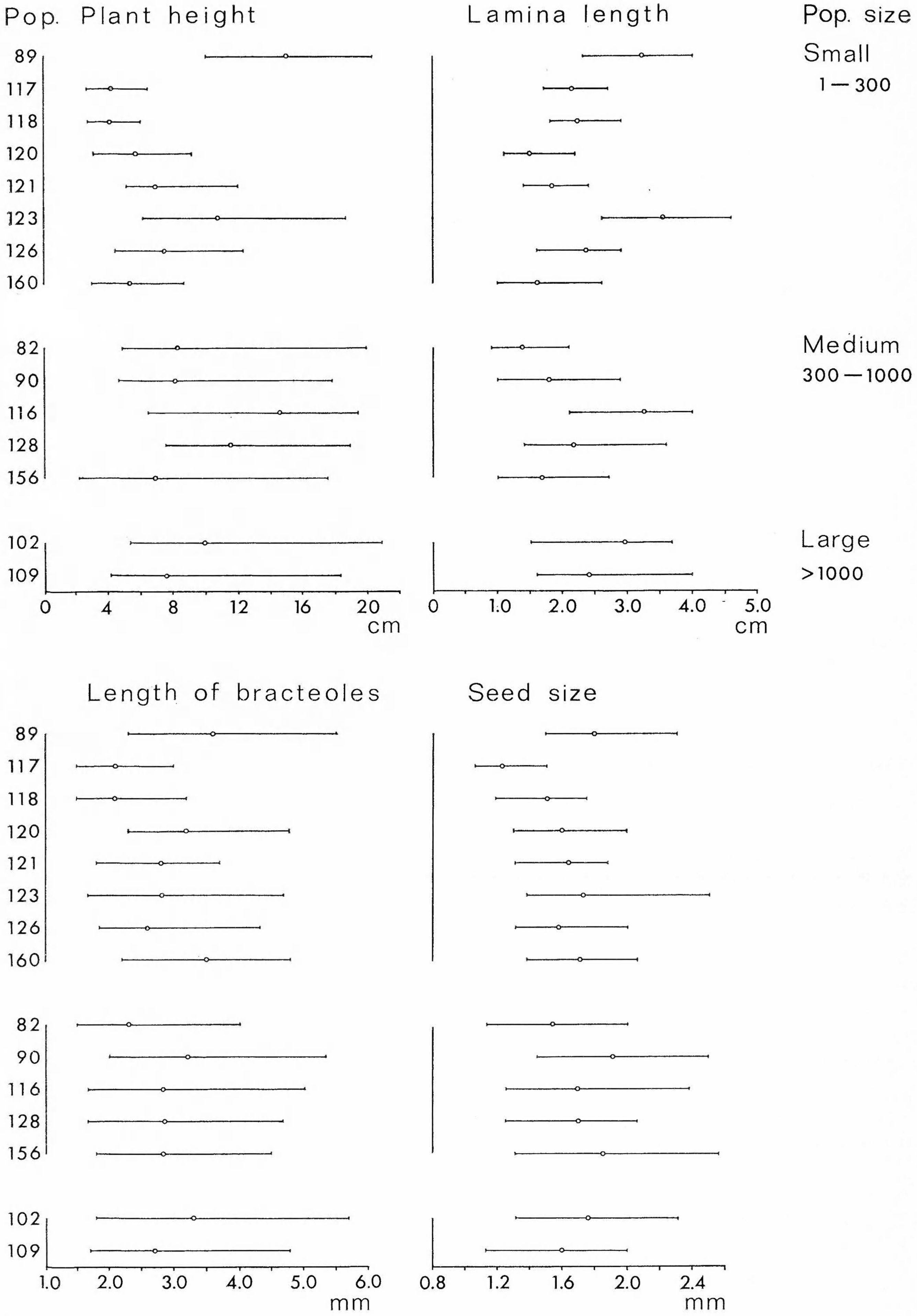
Pop.
Plant height
Lamina length
Pop. size
Small
1—300
Medium
300—1000
Large
>1000
89
117
118
120
121
123
126
160
82
90
116
128
156
102
109
0
4
8
12
16
20
cm
0
1.0
2.0
3.0
4.0
5.0
cm
Length of bracteoles
Seed size
1.0
2.0
3.0
4.0
5.0
6.0
mm
0.8
1.2
1.6
2.0
2.4
mm

Fig. 5.

from populations inhabiting the neighbouring islands and the mainland. Most populations are separated by a distance of several kilometres. Thus, the degree of gene flow between populations depends to a great extent on the dispersal range of the fruits and a successful establishment of the dispersed seeds. Floating experiments indicate that the floating capacity of the fruits is sufficient to allow dispersal over at least short distances. The dispersal range is probably large enough to allow a certain gene flow between adjacent populations. However, crossing experiments show that hybrid sterility in crosses between adjacent populations is as great as in crosses between more distant populations (GUSTAFSSON 1973 a), indicating that even adjacent populations are fairly isolated from each other.

The area of distribution of *A. triangularis* is more continuous as this taxon inhabits most kinds of littoral biotopes. Under favourable environmental conditions the distance separating the populations of *A. triangularis* may decrease and they may even come into contact.

THE EFFECTS OF INTROGRESSION

Introgressive hybridization (ANDERSON 1949) may result in a more or less continual gene flow from one species to another, particularly through repeated back-crossing. The extent and the effects of introgression are mainly determined by the kind and strength of reproductive isolation, by crossability and hybrid vigour. But genes can be transferred from one taxon to another even via partially sterile hybrids (cf. ANDERSON 1949 and GRANT 1971). The degree of reproductive isolation between the taxa in the *A. triangularis* group has been discussed in a previous paper (GUSTAFSSON 1973 b). The frequency of hybridization varies in different parts of Scandinavia. In the western parts spontaneous hybrids are frequently formed between *A. calotheca* and *A. triangularis* as well as between *A. longipes* ssp. *longipes* and *A. triangularis*. In addition hybrids may arise at times between other taxa in this region. In the northernmost parts of Norway transitional populations are common between *A. longipes* ssp. *praecox* and *A. triangularis*, whereas hybridization between the taxa in the Baltic area occurs only occasionally.

Introgression of Morphological Traits

Introgression within the *A. triangularis* group, leading to a transfer of morphological traits from one species to another, is exemplified in Fig. 6, i.e. *A. calotheca, A. glabriuscula* and *A. triangularis* have been exposed to introgression of genes from *A. longipes* ssp. *longipes*. The plants illustrated are similar in most morphological characters to the parental species *A. calotheca, A. glabriuscula* and *A. triangularis*. However, certain morphological traits such as the somewhat cuneate bases of lower leaves and stalked, axillary bracteoles probably arise due to the action of genes transferred from *A. longipes*. The figure illustrates introgression from *A. longipes* to the other species only, but hybrid derivatives have been observed in most other directions as well. A continual gene flow probably exists between *A. calotheca* and *A. triangularis,* between *A. longipes* ssp. *longipes* and *A. triangularis,* and between *A. longipes* ssp. *praecox* and *A. triangularis,* at least in some parts of the sympatric areas of distribution. Gene exchange between other taxa is less common, but is probably sufficient to cause some degree of gene flow.

The Effect of Introgression on Male Fertility

The effect of introgression on male fertility has been investigated in populations of *A. longipes* ssp. *longipes* and *A. triangularis*. Seeds have been collected from natural populations affected by introgression as well as from normal (non-

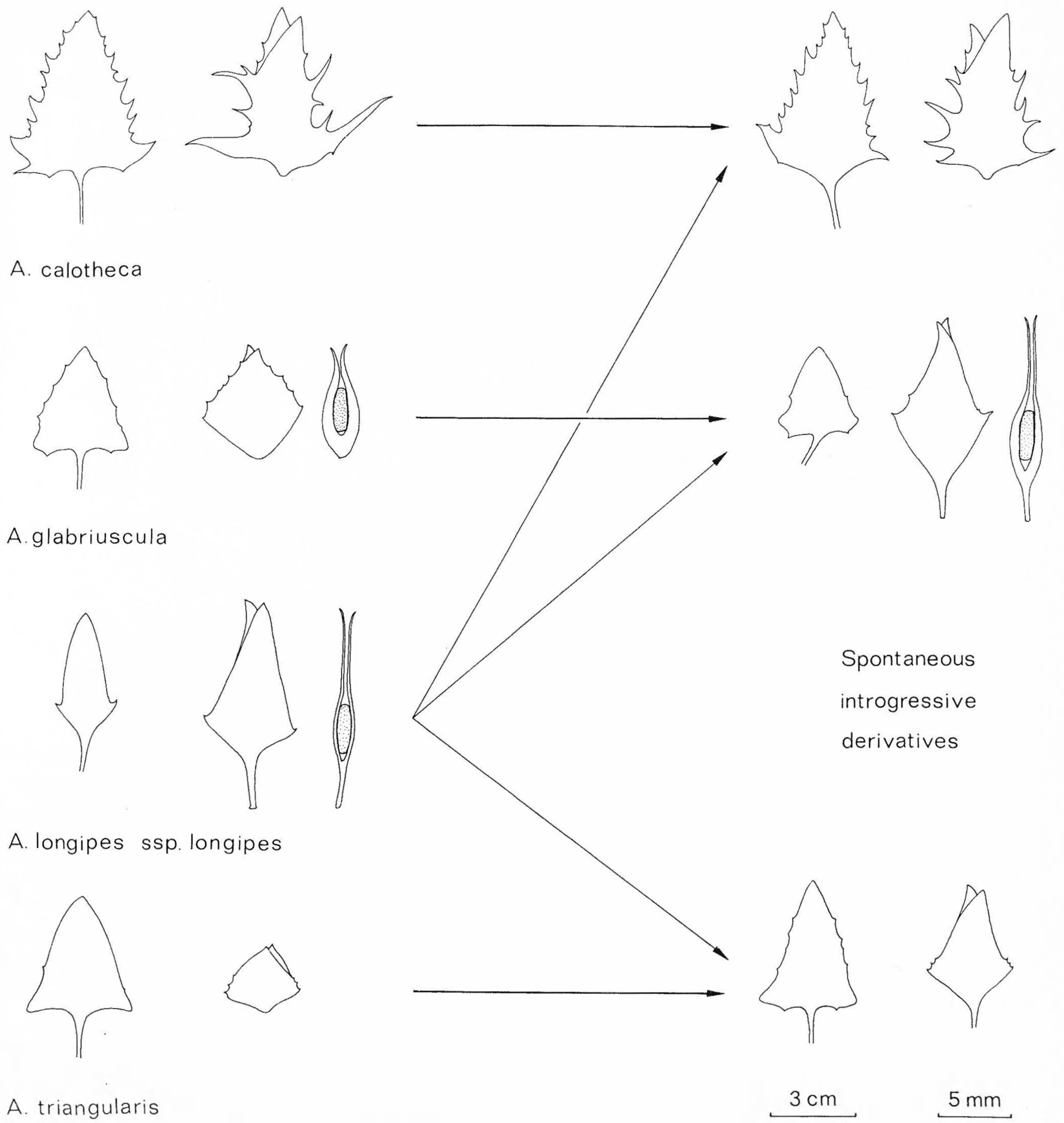

Fig. 6. Introgression of genes, leading to transfer of morphological traits, from *A. longipes* ssp. *longipes* into *A. calotheca, A. glabriuscula* and *A. triangularis*. The figure is based on introgressive derivatives observed in natural habitats.

introgressive) ones. A population is considered introgressive when any kind of hybrid derivative at all has been observed during the period 1968 to 1970. However, in most introgressive populations hybrid derivatives have been common during the entire period. Seed samples of *A. longipes* ssp. *longipes* were collected in 1968 and those of *A. triangularis* in 1970. All the seed samples were sown in pots and placed outdoors in the Botanical Gardens, Lund. In the springtime the seedlings were transplanted into individual pots and placed in greenhouses. The general appearance of the plants was carefully examined and all the individuals used were found to be

Table 6. Distribution of plants with different fertility values in normal (non-introgressive) and introgressive populations of *A. longipes* ssp. *longipes* and *A. triangularis*. n indicates the number of individuals and N the number of populations investigated.

Taxon	Origin	Male fertility %					n	N
		50 — 60	— 70	— 80	— 90	— 100		
A. longipes ssp. *longipes*								
Introgressive populations	W Sweden	—	1	1	13	69	84	4
	%	—	1	1	16	82		
Normal populations	W Sweden	—	—	1	1	10	12	1
	E Sweden	—	—	1	3	84	88	6
	Denmark	—	1	—	1	63	65	5
	Total	—	1	2	5	157	165	12
	%	—	1	1	3	95		
A. triangularis								
Introgressive populations	W Sweden	2	—	3	14	121	140	7
	%	1	—	2	10	86		
Normal populations	W Sweden	—	—	—	—	16	16	1
	E Sweden	—	—	—	4	86	90	5
	Denmark	1	—	—	5	96	102	6
	Total	1	—	—	9	198	208	12
	%	0	—	—	4	95		

morphologically indistinguishable from *A. longipes* ssp. *longipes* and *A. triangularis* respectively. The results are summarized in Table 6 and Fig. 7.

A. longipes ssp. *longipes:* The frequency of individuals with reduced fertility (less than 90 % stainable pollen) within 16 populations is shown in Fig. 7. In normal populations from Denmark and E. Sweden the frequency of reduced fertility is relatively small, usually less than 10 %. However, in population G 119 (from E. Sweden) about 15 % of the plants display reduced fertility. In W. Sweden the normal population G 135 as well as the populations affected by introgression (G 214—G 242) display a fairly high frequency of reduced fertility, between 14 and 23 %.

On the whole introgressive populations have about 10 % greater frequency of plants with reduced fertility than non-introgressive ones have (cf. Table 6).

A. triangularis: The degree of reduced fertility within 19 populations is shown in Fig. 7. In normal populations from Denmark and E. Sweden the frequency of plants with reduced fertility is usually small, being in population GAG (from E. Sweden) 10 % and in GDH (from Denmark) 11 %, in all the others 8 % or less. In the normal population from W. Sweden (GBC) all the individuals have more than 90 % stainable pollen. All the introgressive populations have plants with reduced fertility, the frequency in one population (G 233) is 6 % and in the six other populations 10 to 20 %.

Generally speaking fertility in about 95 % of plants in normal populations exceeds 90 %. The corresponding figure for introgressive populations is 86 %. The results are similar to those for *A. longipes* ssp. *longipes.*

Fig. 7. The frequency (%) of plants with reduced fertility (less than 90 % stainable pollen) in normal and introgressive populations of *A. longipes* ssp. *longipes* and *A. triangularis*.

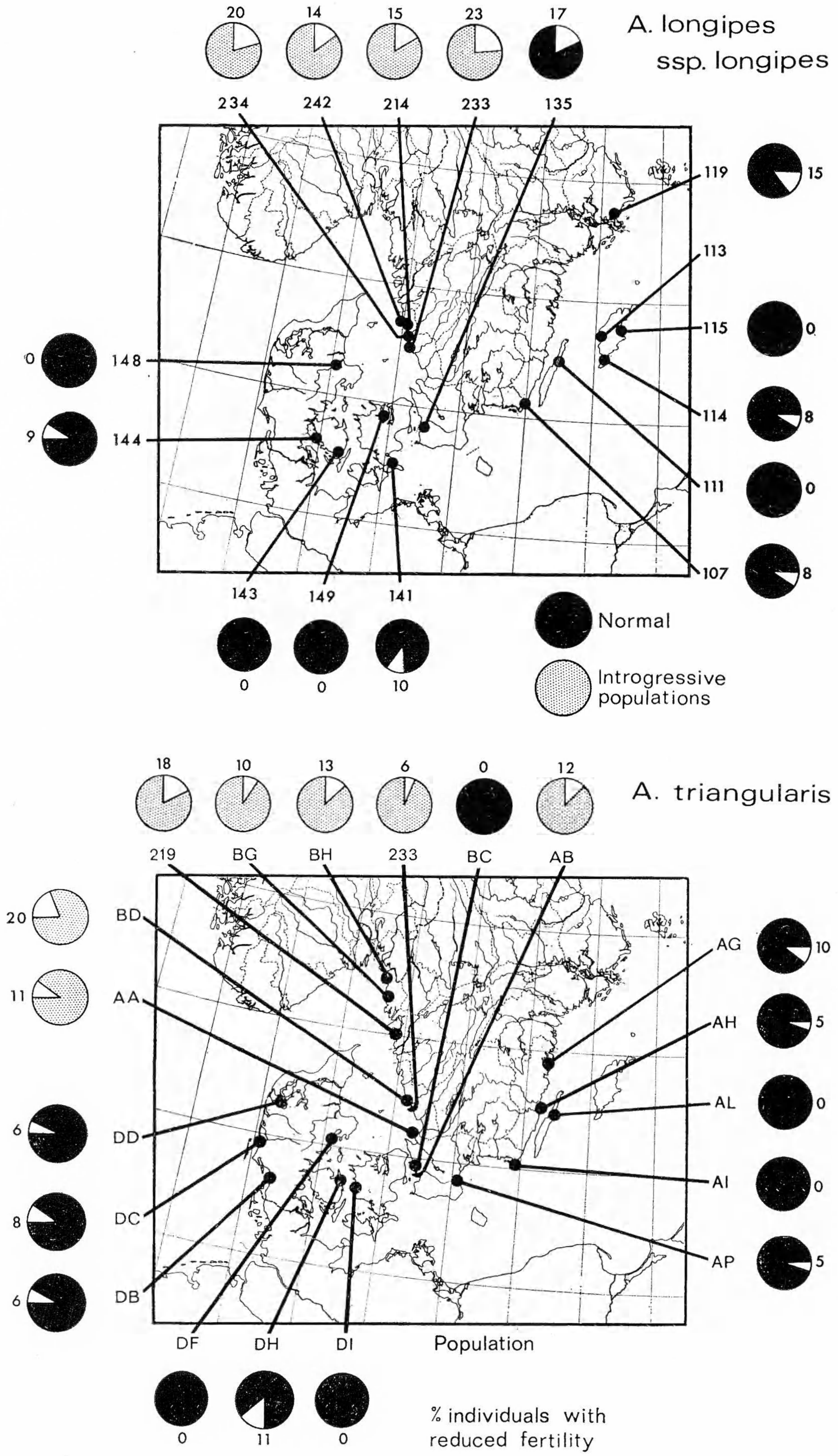
A. longipes ssp. longipes
20
14
15
23
17
234
242
214
233
135
119
15
113
115
0
114
8
111
0
107
8
0
148
9
144
143
149
141
0
0
10
Normal
Introgressive populations
A. triangularis
18
10
13
6
0
12
219
BG
BH
233
BC
AB
20
BD
11
AA
6
DD
8
DC
6
DB
AG
10
AH
5
AL
0
AI
0
AP
5
DF
DH
DI
0
11
0
Population
% individuals with reduced fertility

Fig. 7.

Table 7. Distribution of mean fertility values in crosses within and between six introgressive populations of *A. triangularis,* originating from the western part of Sweden. n indicates the number of crosses investigated.

	Male fertility % in F_1					n
	50—	60—	70—	80—	90—100	
Crosses within populations						
G 166	—	—	—	1	1	2
G 167	—	1	—	1	3	5
G 219	—	—	—	1	1	2
G 221	—	1	—	—	1	2
G 233	1	—	—	—	6	7
G 236	—	—	—	2	1	3
Total	1	2	—	5	13	21
%	5	10	—	24	62	
Crosses between populations						
G 166×G 167	—	—	—	1	—	1
G 166×G 221	—	—	2	—	—	2
G 166×G 233	—	—	—	—	2	2
G 167×G 233	—	—	—	—	1	1
G 167×G 236	1	—	3	1	2	7
G 219×G 236	—	—	—	—	1	1
G 221×G 233	—	2	1	1	6	10
G 233×G 236	—	—	—	—	1	1
Total	1	2	6	3	13	25
%	4	8	24	12	52	

The Effects of Introgression on Hybrid Fertility

Crossing experiments have been carried out within *A. longipes* ssp. *longipes* and *A. triangularis.* All the plants used in the crossing experiments were morphologically identical with *A. longipes* ssp. *longipes* and *A. triangularis.*

HYBRID FERTILITY IN CROSSES WITHIN AND BETWEEN INTROGRESSIVE POPULATIONS OF A. TRIANGULARIS

The investigation of male fertility indicates that in introgressive populations from the Swedish west coast there are a large number of plants with reduced fertility. In order to analyze the degree of chromosomal diversity within populations from this region crossing experiments have been carried out between plants originating from the same population. In all, crossing experiments have been carried out within six populations. In addition representatives of these six populations have been crossed with one another. The results are summarized in Table 7. In thirteen crosses of 21 performed within populations the fertility values are higher than 90 %, but in all the populations investigated there is at least one cross with reduced fertility. The results must be interpreted with discretion, as the variation is largely due to the effects of introgression. The results cannot be applied to *A. triangularis* populations from other parts of Scandinavia.

The degree of reduced hybrid fertility in crosses between the six populations is of about the same magnitude as that within populations. In 13 crosses of 25 fertility values exceed 90 %. Thus in W. Sweden the frequency of chromosomal diversity within introgressive populations seems to be about as high as chromosomal differences between the populations.

Table 8. The number of germinated and non-germinated crosses in the combinations introgressive×introgressive, introgressive× normal and normal×normal populations. n indicates the number of crosses.

Crossing combination	Germinated crosses	Non-germinated crosses	n
A. longipes ssp. *longipes*			
Introgressive×Introgressive	4	0	4
Introgressive×Normal	7	2	9
Normal×Normal	37	11	48
A. triangularis			
Introgressive×Introgressive	32	8	40
Introgressive×Normal	27	7	34
Normal×Normal	16	0	16

Table 9. Distribution of mean fertility values in intraspecific crosses between introgressive ×introgressive, introgressive×normal and normal×normal populations. n indicates the number of crosses investigated. The parent populations have been put together in groups representing different regions of Scandinavia.

Crossing combination	Male fertility % in F_1					n
	50 — 60	60 — 70	70 — 80	80 — 90	90 — 100	
A. longipes ssp. *longipes*						
Introgressive × Introgressive						
W. Sweden × W. Sweden	—	—	—	2	2	4
Introgressive × Normal						
W. Sweden × W. Sweden	—	—	—	—	1	1
W. Sweden × Other regions	1	1	1	—	3	6
Total	1	1	1	2	6	11
%	9	9	9	18	55	
Normal × Normal						
Within regions	1	—	1	7	11	20
Between regions	—	1	1	3	12	17
Total	1	1	2	10	23	37
%	3	3	5	27	62	
A. triangularis						
Introgressive × Introgressive						
W. Sweden × W. Sweden	1	2	7	7	15	32
%	3	6	22	22	47	
Introgressive × Normal						
W. Sweden × W. Sweden	—	—	2	4	9	15
W. Sweden × Other regions	—	1	1	7	6	15
Total	—	1	3	11	15	30
%	—	3	10	37	50	
Normal × Normal						
Within regions	—	3	—	4	2	9
Between regions	—	2	6	7	2	17
Total	—	5	6	11	4	26
%	—	19	23	42	15	

HYBRID FERTILITY IN CROSSES WITH NORMAL AND INTROGRESSIVE POPULATIONS

The degree of reduced hybrid fertility and to a certain extent also of germination has been tested in crosses with normal and introgressive populations. Unfortunately the germination capacity of individual hybrid progenies has not been tested, but a certain amount of information is available on the relationship between germinated and non-germinated hybrid seeds (Table 8). The crosses have been divided into three main groups, one representing introgressive×introgressive populations, one normal×introgressive populations, and a third group is composed of crosses between normal populations. The degree of reduced fertility in the different crossing combinations is summarized in Table 9.

A. longipes ssp. *longipes*

Germination: In about 20 % of the crosses representing normal×normal and normal×introgressive populations the

Table 10. Male fertility within populations and hybrid fertility in crosses between populations within *A. longipes* and *A. triangularis* in relation to population size and main evolutionary factors. — [1] The figure is based on both the crossing combinations introgressive × introgressive and introgressive × normal populations (cf. Table 8). — [2] The figure is exclusively based on the crossing combination introgressive × introgressive populations.

Taxon	Population size	Fertility within populations. % plants with a fertility		Hybrid fertility between populations. % crosses with a mean fertility		Main evolutionary factors
		< 80 %	> 90 %	< 80 %	> 90 %	
A. longipes ssp. *praecox*	Small	15	79	90	0	Genetic drift Selection
	Medium—Large	7	85	69	31	Selection
ssp. *longipes*	Medium—Large	2	82	27	55[1]	Introgression Selection
	Medium—Large	2	95	11	62	Selection
A. triangularis	Medium—Large	4	86	31	47[2]	Introgression Selection
	Medium—Large	0	95	42	15	Selection

hybrid seeds did not germinate at all. All crosses between introgressive populations (4) yielded seeds that germinated.

Fertility: The number of crosses is too small for definite conclusions. However, all four crosses between introgressive populations have high fertility values.

A. triangularis

Germination: In crosses involving introgressive populations germination seems to be highly reduced. In about 20 % of the crosses the hybrid seeds did not germinate. By contrast, all crosses between normal populations yielded seeds that germinated.

Fertility: The distribution of the fertility values varies somewhat in the different crossing combinations. The highest frequency of reduced fertility is observed in crosses between normal populations, 22 crosses of 26 have fertility values of less than 90 %. The corresponding figures for introgressive × introgressive populations and for normal × introgressive populations are 17 crosses of 32 and 15 crosses of 30 respectively. Thus the frequency of reduced fertility is about three times higher in crosses representing normal × normal populations than in the crossing combinations introgressive × introgressive and normal × introgressive populations.

RESULTS

The effects of evolutionary factors on the frequency of plants displaying highly reduced fertility (< 80 %) within populations, and the degree of highly reduced hybrid fertility (< 80 %) in crosses between populations are summarized in Table 10.

In normal plants as well as in hybrids, reduced male fertility is probably caused by structural rearrangements in a heterozygous state rather than by the effects of fertility decreasing genes. Meiosis has been investigated in plants from 8 and 9 populations of *A. longipes* and *A. triangularis* respectively and in addition an analysis has been made of meiosis in 26 crosses within taxa and 18 between taxa. All individuals display the same type of meiotic behaviour. The formation of bivalents seems to be quite normal and nine bivalents are almost always formed. Multivalents have not been observed at all. At anaphase bridges and laggards have been observed in individuals with a fertility of less than 85 %. Correlation between number of bridges formed at anaphase I and degree of reduced fertility is high, the lower the fertility value the higher the frequency of bridges. In the *A. triangularis* group reduced fertility and the formation of bridges are presumably due to heterozygosity for paracentric inversions. The distribution of the fertility values in F_2 indicates that the parent genomes, giving rise to semi-fertile hybrids, in the main differ from each other by at least two inversions (GUSTAFSSON 1972, 1973 a). In the *A. triangularis* group translocations are probably of subordinate importance as indicated by the regular formation of bivalents and by the high degree of correlation between reduced fertility and the frequency of bridges at A I.

Thus, if one assumes that reduced fertility (< 80 %) is largely due to heterozygosity for paracentric inversions the following can be inferred:

(1) Crossing experiments indicate that paracentric inversions are differently distributed in the taxa. Inversion polymorphism seems to be most pronounced in *A. longipes* ssp. *praecox,* less pronounced in *A. triangularis,* and of relatively little significance in *A. longipes* ssp. *longipes,* probably also in *A. calotheca* and *A. glabriuscula.*

(2) In *A. longipes* ssp. *praecox* the distribution of the inversions varies according to the size of the population. Reduced male fertility and probably heterozygosity for inversions occur in most *praecox* populations. But this heterozygosity is generally more extensive in very small to small populations than in medium to large populations. In all 21 crosses between small populations fertility values are less than 90 %. The corresponding figure for crosses small × medium to large *praecox* populations is 9 out of 13. The results obtained in interspecific crosses are similar. Crosses with small *praecox* populations have a higher frequency of low fertility values than crosses with medium to large *praecox* populations. All the results indicate that structural changes, mainly in the form of inversions, are commoner in small populations than in medium to large populations. Chromosomal differences between adjacent populations seem to be as large as those between more widely separated populations. Polymorphism for inversions probably occurs in most of the small populations investigated, i.e. in populations originating both from the Baltic region and from Norway.

(3) In *A. triangularis,* where most of the populations are large, structural heterozygosity is most pronounced in introgressive populations. The fertility values in intraspecific crosses vary with the parent populations involved. In crosses within introgressive populations low fertility values are about as common as in crosses between introgressive populations. But there are more cases of reduced fertility in crosses between normal populations than between introgressive populations. Thus chromosomal differentiation, mainly in the form of inversions, seems to be most pronounced in crosses between normal populations. In interspecific crosses with *A. triangularis* the mean fertility values are generally high (cf. p. 32 and GUSTAFSSON 1973 a), presumably due to the large number of introgressive populations used.

(4) In introgressive populations of *A. longipes* ssp. *longipes* there are slightly more plants with reduced fertility than in normal ones. The number of crosses between introgressive populations is too small to allow definite conclusions to be formed. However, in most interspecific as well as intraspecific crosses with *A. longipes* ssp. *longipes* mean fertility values are greater than 80 %. These results indicate that structural changes are relatively rare within and between populations of *A. longipes* ssp. *longipes.*

DISCUSSION

In the *A. triangularis* group structural chromosomal changes seem to largely consist of paracentric inversions, both in a homozygous and a heterozygous state. However, the frequency of the inversions differ between taxa as well as between populations of different sizes. Some probable reasons for the striking differences will be discussed below.

ESTABLISHMENT OF SMALL PRAECOX POPULATIONS

There are two ways in which the small populations of *A. longipes* ssp. *praecox* may have been established. A new population may arise from a few original founders with only a minor part of the total genetic variation of the parental populations (cf. MAYR 1963). When a small population is established in this way it will result in reduced morphological and cytological variation, due to the small number of original founders and extensive inbreeding. Reduced morphological variation has been observed in some small *praecox* populations, but in others variation is almost as great as in larger ones. This indicates that at least some of the small populations have arisen in another way. LEWIS (1962) has pointed out that an entire population or part of it can be eliminated by the effects of "catastrophic" natural forces. "Catastrophic selection", occurring in ecologically marginal populations, has probably played an important part in the speciation of the genus *Clarkia* (LEWIS 1962). Similar results have also been obtained in the genus *Gilia* (GRANT 1971). In *Allium commutatum,* which exclusively inhabits islets, the extinction of some populations and the random survival of others has probably occurred as a result of oscillations of the sea-level (BOTHMER 1974). The biotopes inhabited by *A. longipes* ssp. *praecox* are often subject to drastic changes. Heavy storms are characteristic of these biotopes, particularly during spring and autumn. It is not unusual for whole plants to be covered by water during anthesis or for part of a population to be washed away before seed is set. A great number of seeds are probably also washed away during heavy storms. Further, entire populations will disappear or decrease conspicuously when the open biotopes inhabited by *A. longipes* ssp. *praecox* become covered by denser vegetation or when there is a period of extreme drought.

INTERACTION BETWEEN SELECTION AND GENETIC DRIFT

The rate and direction of evolutionary changes are mainly regulated by selection and/or genetic drift. Interaction between selection and genetic drift in populations of different sizes has been investigated by WRIGHT in particular (1921, 1931 and 1940). The importance of genetic drift as a factor in the evolution of small populations has been verified by numerous investigations on animals (cf. MAYR 1942, LAMOTTE 1959 and DOBZHANSKY 1970), on plants (cf. GRANT 1963, SNOGERUP 1967 and STRID 1970) and on human populations (CAVALLI-SFORZA et al. 1964 and CAVALLI-SFORZA 1969).

In large populations of the taxa in the *A. triangularis* group, the occurrence of different genes, gene-blocks and chromosomal rearrangements is mainly regulated by selection, but in small populations of *A. longipes* ssp. *praecox* evolutionary changes are probably influenced by genetic drift at least for shorter periods of time. In these small populations one may expect to find increased homozygosity and reduced variability, due to the frequent occurrence of inbreeding. The majority of genes and structural chromosomal changes will either be fixed in a homozygous state or lost, owing to the action of genetic drift. The fixation—loss process will occur at random and effect all genes.

MORPHOLOGICAL VARIATION AND STRUCTURAL HETEROZYGOSITY IN SMALL POPULATIONS

In *A. longipes* ssp. *praecox* morphological variation is limited in some smallsized populations, but extensive in a few others. Similar observations have been made on populations of the taxa in *Erysimum* sect. *Cheiranthus* (SNOGERUP 1967). SNOGERUP explains the variability in small populations by an increased degree of mutability. "In large populations, a selection for mutation suppressors, i.e. genes underlying a great constancy in the reproduction of genes, is probably normal. . . . Thus in species consisting of constantly large populations, there will often be established gene systems giving the highest possible degree of genic stability. In the small isolated populations, such systems can hardly be built up and if they ever existed in the material, they will probably be broken down by genetic drift." This may also be true of the *praecox* populations, but morphological variability in some small populations may also be due to the fact that the small-population system has been developed a too short period of time.

In small populations one may also expect to find that structural rearrangements occur in a homozygous state at least to a large extent. But in fact in some small *praecox* populations there are a considerably greater number of plants with reduced fertility than in medium-sized to large populations of *A. longipes* and *A. triangularis*. In all, eight small populations of ten have individuals displaying reduced fertility. In the *A. triangularis* group reduced fertility (below 80 %) is probably caused exclusively by heterozygosity for paracentric inversions, which indicates that structural heterozygosity is higher in some small populations than in larger ones. Heterozygosity for structural rearrangements has also been observed in small populations of *Elymus rechingeri* (HENEEN & RUNEMARK 1962), of *Erysimum* sect. *Cheiranthus* (SNOGERUP 1967) and in inbred lines of rye (MÜNTZING & PRAKKEN 1941, AKDIK & MÜNTZING 1949, HRISHI et al. 1969). In fact the relation between homokaryotypes and heterokaryotypes may be altered in different ways despite a relatively high degree of inbreeding:

(1) The entire process of cell division, both mitotic and meiotic, is probably controlled by some genes or gene-blocks. One function of such a system is probably to maintain cytological stability within individuals and their progenies. But normal meiotic behaviour can be altered by the effects of other genes. A fairly large number of meiotic disturbances caused by different gene actions have been observed, giving rise to a lot of aberrations, e.g. deficiencies, duplications, translocations and inversions (for references see DARLINGTON 1937 and SWANSON 1965).

The "stabilizing" genes are probably of great selective advantage in large populations, as they maintain the number of functional gametes at a high level. But in small populations these genes as well as others are exposed to fixation or loss. Break-down in the stabilizing systems is to be expected to some extent in some populations and it seems to be one of the possible reasons for increased heterozygosity in the small populations of *Erysimum* sect. *Cheiranthus* (SNOGERUP 1967).

(2) Effects of structural alterations and their adaptive significances have been investigated principally in species of *Drosophila* (for references see DOBZHANSKY 1970). In *Drosophila* at least, polymorphism for structural changes has a number of positive effects: (a) Many populations are polymorphic for different inversions and the composition of the inversions is probably due to the ability to adapt themselves to particular ecological niches. (b) The frequencies of the inversions may undergo cyclic, seasonal changes depending on the adaptive value of a certain inversion to different climatic conditions. (c) The fitness of inversion heterozygotes seems to be superior to that of homozygotes. (d) Polymorphic populations, i.e. populations with several in-

versions, seem to have a higher reproductive capacity than monomorphic ones. (e) Heterozygous paracentric inversions may act as supergenes, i.e. bring together gene-blocks, which will be inherited more or less intact. The shorter the inversion the less probable will recombination be and the greater the probability that a segment of genes will be inherited intact.

Information on the adaptive values of structural changes in plants is more limited. In *Cyrthanthus* a certain pericentric inversion probably causes an increase in fertility and seed production (ISING 1969). In *Leopoldia comosa* the same balanced, structural alteration is maintained in several populations. Since heteromorphism is distributed over large areas and includes populations of different kinds, inhabiting different biotopes, it may be of adaptive significance (BENTZER 1972).

(3) The maintenance of heterozygosity in small populations may also be due to the effects of lethal and semilethal genes whether balanced or not. In *Oenothera* and in *Campanula persicifolia* the elimination of homokaryotypes through the action of a balanced lethal system has been observed (CLELAND 1936, DARLINGTON & GAIRDNER 1937, DARLINGTON & LA COUR 1950). Varying lethal conditions of homozygotes have also been observed in populations of *Drosophila* (cf. CARSON 1967). However, the elimination of homozygotes is not necessarily restricted to a balanced lethal condition. A large number of deleterious recessive genes have been observed in plants, in *Drosophila* species, in domestic animals as well as in man (CRUMPACKER 1967) indicating that a number of lethal genes probably exist in most species populations. The effects of these lethal genes will be particularly evident in small populations. The high degree of inbreeding will cause increased homozygosity for lethal genes as well as for others, resulting in a certain elimination of homozygotes.

(4) The frequent occurrence of heterozygotes may also be the result of gene exchange between different homokaryotypic plants. Analysis of the crossing experiments indicates that many of the parents from small populations are homozygous for at least one inversion, probably two or more. The frequency of inversions within the populations is probably rather high, as almost all crosses between small populations display reduced fertility. According to HARDY-WEINBERG's law one may expect to find a large number of heterozygotes derived from fertilization between different inversion homozygotes as well as between these and plants with "normal" genomes.

It seems impossible to refer the high degree of heterozygosity in populations of *A. longipes* ssp. *praecox* to any one particular factor, probably it is a combination of several factors. The adaptive values of different inversions are of subordinate importance in small populations, due to the random fixation—loss process. But, a certain variation in population size has been observed in some populations and during periods where there is a medium to large population size, selection will favour the most adaptive plants whether they are homozygotes or heterozygotes. Increased inversion polymorphism due to the break-down of gene systems "stabilizing" the process of meiosis is less probable. Such a break-down would certainly cause a large number of different structural rearrangements, not only paracentric inversions. In fact, chiasma frequency and bivalent formation are completely regular, indicating that genes determining the normal actions of these processes are still functional. It seems more probable that the proportions of the stabilizing and the mutability inducing genes have changed and that cytological "instability" of the small populations is due to an increased number of fixed genes inducing chromosomal changes.

A balanced system of lethality associated with inversions has not been observed at all in the *A. triangularis* group, neither in cultivated spontaneous material nor in hybrid progenies. However, this does not exclude the possibility of a certain elimination of plants homozygous for recessive, lethal or semilethal genes. On the whole inversion polymorphism, both in a heterozygous and homozygous state, is several times higher in small populations than in medium to large ones. The genetic system of the small populations of *A. longipes* ssp. *praecox* has led to a unique chromosomal differentiation within the *A. triangularis* group. This differentiation is probably conditioned by genetic drift combined to some extent with selection.

EFFECTS OF INTROGRESSION

In the *A. triangularis* group the effects of introgression, i.e. increased chromosomal heterozygosity and transfer of morphological traits from one taxon to another, are similar to those found in most other investigations (for references see ANDERSON 1949, STEBBINS 1950 and GRANT 1971). In *A. triangularis* most of the crosses between normal populations have reduced fertility values. The genome differences between normal populations, leading to reduced hybrid fertility, are probably largely homozygous, as indicated by the low degree of structural heterozygosity within these populations. These genome differences may at least partly consist of paracentric inversions. Reduced hybrid fertility is much less common in crosses within and between introgressive populations. However, seeds derived from crosses between introgressive populations show decreased germination. But it seems unlikely that the differences in hybrid fertility are due to decreased seed germination and that crosses involving severe cytological disturbances are exclusively represented by non-germinating seeds. In fact, the low correlation between germination of hybrid seeds and hybrid fertility indicates that germination and male fertility are not controlled by the same genetic systems (GUSTAFSSON 1973 a). The degree of reduced hybrid fertility is about equal in crosses within introgressive populations and in crosses between these populations, which indicates that evolution of chromosomal differences between introgressive populations seems to be rather small.

All these facts indicate that structural changes are and/or have been established in normal populations of *A. triangularis*. In introgressive populations structural changes are established to a minor extent, or if they have existed, can even be broken down. The establishment of structural changes in introgressive populations is probably counteracted by strong karyotypic selection. But, the degree of heterozygosity will probably remain high as long as hybridization and introgression occur in these populations. It is rather remarkable that introgression, mainly from *A. longipes* ssp. *longipes,* affects the degree of chromosomal differentiation between introgressive populations of *A. triangularis*.

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Rhipidoglossum paucifolium, a New African Species of Orchidaceae

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JOHANSSON, D. 1974 03 29. Rhipidoglossum paucifolium, a new African species of Orchidaceae. — Bot. Notiser 127: 149—151. Lund. ISSN 0006-8195.

The new species *Rhipidoglossum paucifolium* D. JOHANSS. from the Nimba Mts in Liberia is described.

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Rhipidoglossum paucifolium D. JOHANSS. sp. nov.

Herba epiphytica; caulis brevissimus, circiter 0.5—1.0 cm longus. Folia pauca, oblonga —anguste oblonga, ad 65 mm longa et 22 mm lata, apice inaequaliter et acute bilobulata. Inflorescentiae descentes, usque ad 8 cm longae, dense multiflorae.

Flores pallide virides. Sepalum intermedium late oblongum, subacutum, 3.5—4×2.5—3 mm; sepala lateralia ovato-lanceolata, acuta, 4.5—5×2 mm. Petala triangularia, acuta, 3—3.5 mm longa, prope basin 2.5 mm lata; omnia tepala trinervia. Labellum leviter recurvatum, convexum, late triangulare, trilobatum, 4—5×6.5—7 mm (lobo intermedio triangulari, 1 mm longo; lobis autem lateralibus obtuso-rotundatis) prope basin ante ostium calcaris callo humili lunato instructum; calcar cylindricum, leviter incurvatum, circiter 9—10 mm, apice inflatum.

Columna horizontalis, truncata, 2—2.5 mm longae; rostellum porrectum, trilobatum.

Epiphytic herb; stem extremely short, about 5—10 mm with numerous very long flattened unbranched roots, about 2—3 mm broad, greyish. Leaves few, oblong—narrowly oblong, up to 65 mm long and 22 mm broad, acute, shortly bilobed, dull green.

Inflorescences descending, up to 80 mm long, densely many-flowered; peduncle up to 20 mm long, with a few sheaths; rachis flexuous, terete; bracts 3—5 mm apart, 1—2 mm long, obtuse. Flowers pale green; pedicel including ovary about 4 mm long. Median sepal broadly oblong, acute, 3.5—4 mm long, 2.5—3 mm broad; lateral sepals ovate-lanceolate, acute, 4.5—5 mm long, 2 mm broad. Petals triangular, acute, 3—3.5 mm long, near base 2.5 mm broad; all tepals three-nerved. Labellum slightly recurved, convex, broadly triangular, trilobed, 4—5 mm long, 6.5—7 mm broad; median lobe triangular, 1 mm long, lateral lobes obtusely rounded, at the mouth of the spur with a low crescent-shaped callus; spur slightly incurved, cylindrical, about 9—10 mm long.

Column truncate, 2—2.5 mm long, androclinium slightly excavate, anther hemispherical, truncate; pollinia globular, stipes linear-obovate, about 1 mm long, viscidia separate, elliptical; rostellum directed forwards, trilobed, 1—1.2 mm, median lobe club-shaped, very short, lateral lobes obtusely rectangular.

ORIG. COLL.: Liberia. Nimba Co. Saniquelle Distr. Nimba Mts, Seka Valley 700 m. Epiphyte on a tall tree close to a stream. 10th August 1969. DICK JOHANSSON 572. UPS holotype; isotype in K.

The genus *Rhipidoglossum* was established by SCHLECHTER in 1918. It was included in *Diaphananthe* as a section (Section 2, *Rhipidoglossum*) by SUMMERHAYES 1960, but re-established as a new genus by GARAY in 1972.

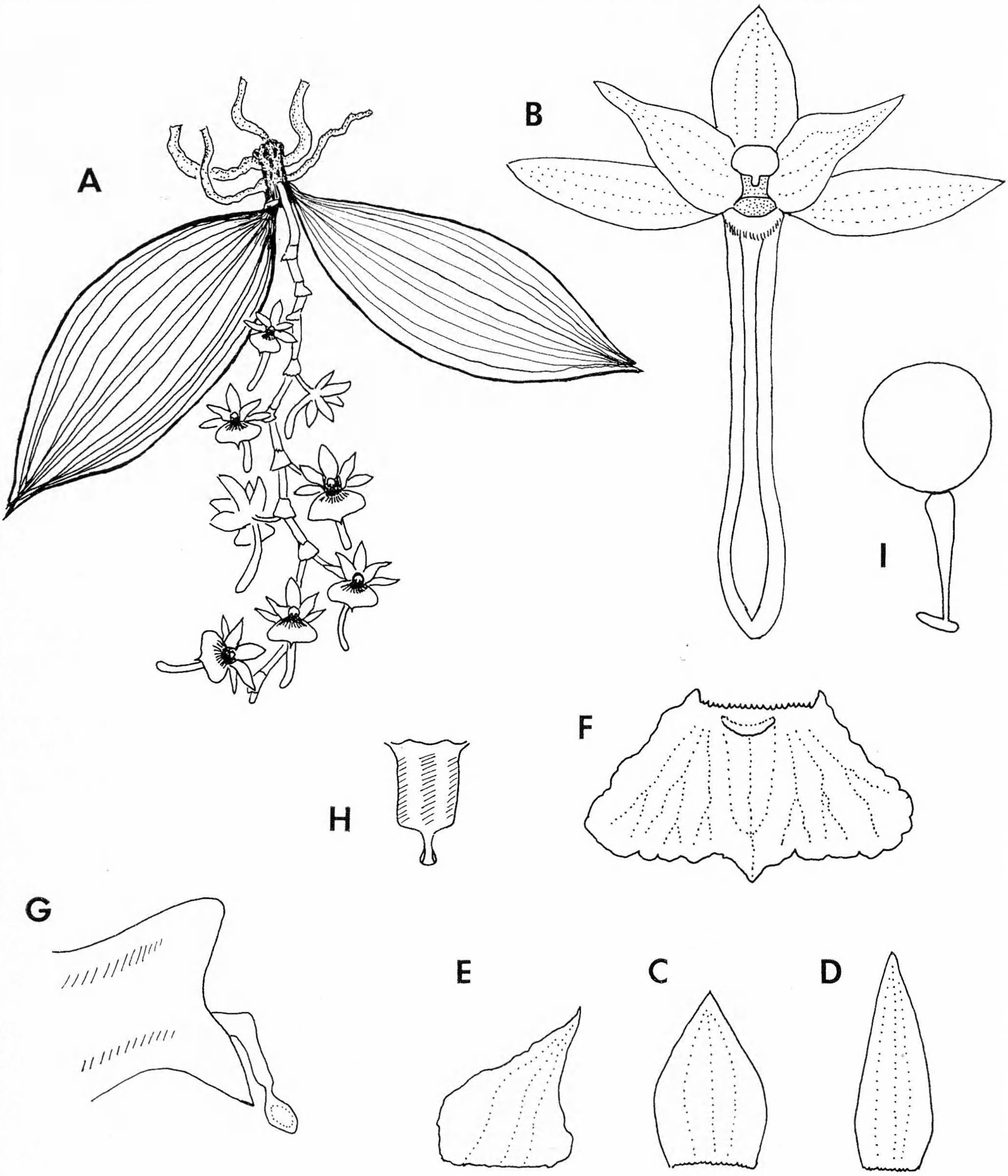

Fig. 1. *Rhipidoglossum paucifolium* DICK JOHANSS. sp. nov. (DICK JOHANSSON 572). — A: Flowering plant, ×6/7. — B: Flower with lip removed, front view, ×7. — C: Dorsal sepal, ×7. — D: Lateral sepal, ×7. — E: Petal, ×7. — F: Lip, ×7. — G: Column with anther cap and pollinia removed, side view, ×12. — H: Rostellum, front view, ×14. — I: Pollinium, ×17.

R. paucifolium was found in the basal parts of the trunk of a tall tree, 1.5 m from the ground in a fairly open environment close to a stream in a rain forest. This small and rather inconspicuous plant is easily overlooked in the heap of climbers and debris that is often found at the base of the trunks. This rare plant has only been observed in the type of habitat described above.

ACKNOWLEDGEMENTS

Prof. emer. J. A. NANNFELDT and Dr Ö. NILSSON have been of great help in the preparation of this paper. Dr E. WIKÉN has kindly improved the Latin diagnosis.

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Botanical Literature

NILSSON, S. (ed.): World Pollen and Spore Flora 1—2. 1. Fouquieriaceae (12 pp.) by J. HENRICKSON, and 2. Menyanthaceae (19 pp.) by S. NILSSON and R. ORNDUFF. — The Almquist & Wiksell Periodical Co., Stockholm. Price, see below.

The late Professor GUNNAR ERDTMAN had great hopes for this floral project during the last years of his life. In fact a forerunner to it, "World Pollen Flora", appeared in 1970. Four families were published: Batidaceae, Coriariaceae, Globulariaceae and Gyrostemonaceae, i.e. they were small families as are Fouquieriaceae and Menyanthaceae, the first two to appear in "World Pollen and Spore Flora".

If the "old" and "new" floras are compared it is not difficult to find a common denominator: the aspiration to deal with small families with a problematical taxonomic position. Among families soon to be published in "World Pollen and Spore Flora" are Dichapetalaceae, Didieraceae, Lecythidaceae (a somewhat larger family) and Rhoipteleaceae. This effort to tackle in the first place taxonomic difficulties is of great value. It makes the flora a source of interesting and useful information to the taxonomist with a relatively limited expenditure of work and money. That useful characters from pollen morphology can be used in taxonomy for larger families as well has been shown by various authors, for example for Lamiaceae by R. WUNDERLICH.

The publication of this flora has been preceded by much planning by specialists. As a result the contents are well-balanced, and detailed instructions for contributors are given.

It may be asked why such re-planning was necessary so soon after the appearance of "World Pollen Flora". The question answers itself if we consider the evolution of research on pollen and spores. Techniques within electron microscopy and especially scanning electron microscopy (SEM) have given us excellent routine methods for illustrating details of pollen and spores, where formerly they had to be painstakingly drawn. (Optical studies with the light microscope are, however, as important as ever.) Time has suddenly supplied the botanist with tools most suitable for work on this flora. Pollen grains are nothing but developing microspores so that it is natural that spores of cryptogams are now included in the flora. Finally, the flora has of necessity been adapted so that the strained economic resources have been put to effective use by a condensed and uniform treatment of the information.

Each plant group is dealt with in the flora in a separate article with a summary in English. First, the main characteristics of the group concerned are given together with current views on its systematic position. Then comes a comprehensive description of pollen accompanied by SEM and light microscopy illustrations. Features of particular interest, variation in the group, division into pollen types and pollen keys follow, and at the end of the "article" are given up-to-date taxonomic comments based where possible on the new palynological data in the flora. The material investigated is cited in detail (which permits of future revision of determinations), and the references to literature are copious.

Thus each group is placed not in a narrow palynological circle, but within a framework of comparative, all-round discussion, which helps to communicate the results to the systematists.

This is the very positive impression I have received of the first two fascicles.

Fouquieriaceae is still a riddle to taxonomists. There are certain similarities in pollen morphology with, for example, *Cobaea* in the Polemoniaceae, in the vicinity of which it would be natural to place it, were it not for the bitegmic ovules (not otherwise found among sympetalous families that might be considered as possibly related).

Menyanthaceae is usually considered to be closely related to Gentianaceae. Palynologically it is somewhat heterogeneous: the type of pollen found in *Menyanthes* and *Fauria* being similar to that in certain Gentianaceae, whereas the pollen grains of *Nymphoides,* for example, are somewhat different. Thus new problems arise, a fact that must be taken into account where other branches of taxonomical research are concerned.

As stated in the introduction to the flora, it "will hopefully aid scientists in various areas of research such as plant taxonomy, paleobotany, geology, ecology, melittopalynology and aerobiology". There is no doubt that palynology is one of several fields that the taxonomist must use to bring gross systematics in line with modern technical resources.

The "World Pollen and Spore Flora" is thus a very important work, and it is to be hoped that economic support will be secured to ensure its continued publication. It is distributed annually in two fascicles (together approximately 32 pp.) free of charge to subscribers to "Grana", an International Journal of Palynology. It may also be ordered separately for Sw. kr. 50 per annuum.

ROLF DAHLGREN

VALENTINE, D. H. (ed.): Taxonomy, Phytogeography and Evolution. — Academic Press, London & New York 1972. 431 pp. Price £ 7.20.

This book contains the reports of a conference held at the University of Manchester from September 9—11, 1971, by the Linnaean Society of London, the Botanical Society of the British Isles and the International Organisation of Plant Biosystematists.

The purpose of the conference was to deal mainly with how the results of biosystematic and other intricate taxonomic research can be put to use in phytogeographic practice. At the same time the value of planning such investigations on the basis of phytogeographic and geological data and hypotheses was demonstrated.

The problems of endemism, especially insular and mountain endemism, took up a great deal of the conference. In this part in particular there appears to be a rising interest on the part of phytogeographers to look for experimental and other biosystematic evidence about groups of endemics and taxa with disjunct distributions. European mountain endemism, as one of the main keys to the history of European alpine and montane floras, is handled by C. FAVARGER. Similar problems in relation to African mountains are discussed by J. K. MORTON. MORTON's paper ends with the conclusion that the origin of W African mountain floras must be understood as a combination of climatic changes and long-distance dispersal. Island endemism is discussed by W. GREUTER and A. STRID for European islands, for the Canary Islands by D. BRAMWELL and for the Caribbean Islands by B. MORLEY. In many of the contributions the role of insular and mountain isolation as a driving force within plant evolution is stressed. It is therefore astonishing to find in GREUTER's paper the theory that subsequent to isolation practically all differentiation ends up in a state of "non-evolution", so that only the remnants of a preexisting diversity remain.

The special problems of differentiation in floras wholly or partly derived as a result of long-distance dispersal are discussed for Hawaiian taxa by G. W. GILLET, for New Zealand by P. H. RAVEN. These two contributions have been placed in different sections, which partly disguises the similarity of the results reported in them. In both cases there are indications that groups retaining interfertility between differentiating taxa are favoured in such situations.

The complex of disjunct distributions are discussed for different areas by H. HARA, J. KORNAS, D. F. CUTLER, O. T. SOLBRIG, T. W. BÖCHER and D. M. MOORE. In MOORE's paper in particular the necessity for a closer study of each individual case is stressed, concerning both the actual biological relations of the disjunct parts and the dispersal capacity etc. Our increasing knowledge of details of continental drift and other paleogeographical phenomena has also been included in the discussions and tends to reduce the amount of pure speculation that has formerly always burdened phytogeography.

Among the several articles on more general problems the introductory paper by G. L. STEBBINS should be mentioned. STEBBINS rules out the old theories that mesic tropical habitats were the centre of origin and differentiation for the angiosperms. He shows that many groups display greatest diversity and probably originated in semi-arid habitats. His projection backwards of these conclusions to indicate the whereabouts of the first stages of angiosperm evolution is more speculative and will no doubt give rise to further discussion.

In this review it has only been possible to refer to some of the many interesting articles in the book. As this book is well disposed and centres on problems, it is of greater common interest than most conference papers. Through its broad exposure of new lines of thought as well as in working methods, it gives a positive picture of the future of taxonomic phytogeography.

SVEN SNOGERUP

KULLENBERG, B. & STENHAGEN, E. (eds.): The Ecological Station of Uppsala University on Öland 1963—1973. — Zoon. A Journal of Zoology, Suppl. 1. Uppsala 1973. 150 pp.

Uppsala University's Ecological Station is located on Öland, a long, low island situated in the southern Baltic near the east coast of Sweden. Due to the special climatic and edaphic conditions prevailing on the island the flora and fauna are richly varied and comprise many species, despite the relatively small size of the island. In particular the vegetation on the Great Alvar is more or less unique and there are many plants, southeastern as well as more or less arctic-alpine, displaying great disjunction. These elements of Öland's flora are considered to be relicts of floras from the arctic and warmer periods of Late Pleistocene and Holocene times. The great variety of species makes Öland well suited to the purpose of biological research.

This volume presents work that has been carried out at the Ecological Station during a ten-year period, 1963—1973. The research programme is mainly concerned with four major projects: (1) The biological function and chemical structure of natural odorous compounds. The entomologist B. KULLENBERG is one of the pioneers in the study of the pollination ecology of *Ophrys* L. (Orchidaceae). (2) Bioclimatology of insects. (3) External parasites of the hedgehog. (4) Terrestrial phytoecology with reference to the peculiar vegetation of Öland: the relatively luxuriant deciduous forest types and the Alvar vegetation. There are studies of past and present changes in deciduous forest vegetation, and the influence of grazing by sheep on the vegetation on the limestone heath.

For the botanical taxonomist it is worth while knowing the existence of the Ecological Station on Öland. Scientists working on material from Öland have the opportunity of visiting the Ecological Station for short-term stays in order to carry out field studies or collect material.

Botanists intending to visit Öland for scientific purposes are recommended to write in advance to Uppsala Universitets ekologiska station, Ölands Skogsby, S-380 60 Färjestaden, Sweden.

Björn Widén

Ferry, B. W., Baddeley, M. S., and Hawksworth, D. L. (eds.): Air Pollution and Lichens. — University of London. The Athlone Press. London 1973. 389 pp. Many figures, tables and maps in the text. Price £ 6.25 (cloth).

For more than a century the sensitivity of lichens to air pollution has been acknowledged. In a classical study of the lichen flora of the Luxembourg Garden in Paris, Nylander (1866) states: "La plupart des lichens semblent fuir les villes, et ceux qu'on y rencontre n'y arrivent souvent qu'à un développement incomplet, à un état sorédifère ou tout à fait stérile". The literature on these problems is exceedingly rich; especially during the past few decades a great deal has been published. In his paper on "The Nature of Stockholm", Sernander (1926) develops the concepts "lichen desert" (for the central part of the city which is quite devoid of lichens), "struggle zone" (more or less in the suburbs, where most lichens are poorly developed or damaged) and "normal zone" (beyond the limits of air pollution effects).

Many similar investigations have been carried out during the past fifty years, mainly in urban and industrial areas in Europe and North America. Information from other geographical regions shows the same trend. It is clear that the negative effect of air pollution on lichen vegetation is a universal phenomenon.

The present volume is an excellent introduction to these problems and a comprehensive and up-to-date survey of the various kinds of research carried out in this field. Its publication was initiated at the First International Mycological Congress held at Exeter, England, in September, 1971. Several articles have their origin in papers read by their authors at this conference.

According to current opinion, the cause of the harmful effects of polluted air on lichens and other organisms is sulphur dioxide and its derivatives, not "smoke" in general as was believed earlier. The production, dispersal and fate of SO_2 is treated in an introductory chapter by P. J. W. Saunders and C. M. Wood. "The effect of airborne fluorides" is discussed by O. L. Gilbert, and "The effects of other air pollutants" (radiation effects, fertilizers, smoke etc.) by P. W. James. T. H. Nash has written a useful chapter on "The effect of air pollution on other plants, particularly vascular plants" including a survey of the very rich literature in this field. "The drought hypothesis", i.e. a theory developed by the late Dr. J. Rydzak (Poland) who considered the lowering of humidity, not "toxic gases" to be the main factor limiting the lichen vegetation of urban areas, is scrutinized critically by B. J. Collins.

The classical approach to studies of the effects of air pollutants on lichens has been to map the present distribution of certain lichen species in urban areas, often in comparison with their frequency in the past century, where such data are available. Several articles (by D. L. Hawksworth, F. Rose, J. Laundon et al.) deal with the past and present distribution of lichens in more or less polluted districts of Great Britain.

Although it is certain that sulphur dioxide is the essential factor in affecting lichen growth and distribution, the physiological and biochemical pathways in these changes are still imperfectly known. The physiological aspects, especially photosynthesis and respiration, of the decline of lichens in polluted areas are treated by L. C. Pearson, J. F. Farrar, M. S. Baddeley, B. W. Ferry et al. An important part of this process seems to be the destruction (reduction) of chlorophyll A.

The Swedish reader will notice mention of our Government's efforts to reduce sulphur dioxide levels in urban areas through the prohibition of petrol and other oil products containing a high percentage of sulphur. Unfortunately, the results of these efforts have been delayed, as, for economic reasons, the use of these dangerous oils has been temporarily permitted again during the present oil crisis.

OVE ALMBORN

IN MEMORIAM

Stenbergs, 1967

Gustaf VI Adolf 1882—1973

GUSTAF VI ADOLF, King of Sweden, passed away on September 15th, 1973 at the age of ninety-one. He became an honorary member of the Lund Botanical Society in 1898 and its Patron in 1950.

Most of us are acquainted with the late King GUSTAF ADOLF's interest in archaeology and the fine art, in connection with which he partook personally in field work as well as acting as a collector and donor. His interest in botany is almost equally well known and began at a very early stage. In particular, applied botany attracted him. During the very last summer of his life he took an active part in practical horticulture, continuing to show the ardent devotion and energy that was so typical of him.

The Lund Botanical Society owes its former honorary member and Patron a great debt of gratitude. *Requiescat in pace.*

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