Drawings of Scandinavian Plants 103–104

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

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Drawings and descriptions are given for *E. palustre* L. and *E. davuricum* FISCH. ex HORNEM.

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103. **Epilobium palustre** L. 1753

Perennial herb, (5—)15—40(—80) cm high. Stem either simple, or branched in upper part, or in tall specimens richly branched from the base, producing one to several (1—)2—7(—10)-flowered inflorescences. Middle internodes usually 2—6 cm, but in specimens growing in dry places and littoral specimens often more condensed, upper internodes of small specimens usually shorter than the leaves. Stolons epigean, but usually spreading in a moss cover or in other dense vegetation, 2—15(—30) cm long, usually only c. 0.5 mm thick, either white to reddish or green when developed on the surface of earth or vegetation, with small, widely spaced leaves or the green ones rarely with leaves up to 15 mm long, glabrous. Perennating turions formed at the end of the long stolons or on very short ones from the stem base, fleshy, up to 10 mm long and 5 mm broad, with very broad, blunt, scale-like leaves. Short, few-leaved shoots formed in most of those leaf axils not supporting branches or flowers.

Stem terete, near the base usually 1—3 mm thick, with short and inconspicuous ridges below the midrib of leaves, in northern forms rarely also below leaf margins. Subglabrous to moderately hairy, in upper part evenly, in lower part mainly in broad rows below leaf margins, some northern specimens more uniformly hairy throughout. Hairs 0.1—0.3 mm, longer ones curved, short ones patent and at least partly glandular.

Most leaves opposite, only uppermost ones alternate, nonpetiolate or petiole less than 5 mm, bases of lower cauline leaves uniting around the stem but never decurrent. Basal leaves smaller than the cauline ones, spathulate or short-petiolate, obovate to elliptical. Rarely, in plants developing from winter buds, some of the first leaves thick, scale-like. Middle cauline leaves (10—)20—40(—85) mm long, (2—)5—10(—15) mm broad, narrowly to very narrowly ovate or narrowly lanceolate, obtuse or tapering to an obtuse apex or in some tall southern forms acute, subentire or serrate with few, low and broad teeth. Upper leaves shorter, narrower, often more markedly petiolate, usually subentire. Indumentum of leaves like that of the stem, sparse to moderate, denser on upper leaves, usually denser on midribs and margins. Leaves of some coastal ecotypes more densely and uniformly hairy.

Bracts ± large, leafy. Pedicels in bud and early flower nodding, in fruit erect to erecto-patent. Buds ellipsoidal, blunt. Sepals 3—6 mm, connate to 1—2 mm at base, lanceolate to narrowly ovate, obtuse, green but often with reddish mar-


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Fig. 104. *Epilobium davuricum* FISCH. ex HORNEM. — A: Habit, ×1/3. — B: Basal rosette, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

gins, sparsely to moderately hairy, especially towards the base. Petals 5—8.5 (—10) mm, notched to 0.8—2 mm, pinkish-violet to pinkish-white, rarely white. Anthers 0.6—0.8 mm, long filaments 3.5—5.5 mm, short filaments 2—3 mm, usually c. 2/3 as long as the long ones. Style equalling or slightly longer than the long stamens, stigma capitate.

Capsule stalk (5—)15—40(—50) mm.

Fig. 103. *Epilobium palustre* L. — A: Habit, ×1/3. — B: Stolons and winter buds, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaf, ×2.5. — G: Bud, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Styles, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

Capsule (30—)50—60(—75) mm, moderately hairy, denser along the ribs, hairs 0.15—0.4 mm, short ones patent and usually glandular, long ones curved to appressed. Seeds narrowly obovoidal, ± flattened on one side, 1.25—1.8(—2.1) mm long, 0.4—0.55 mm broad, tapering to an obtuse lower end, neck 0.05—0.15(—0.25) mm, surface densely covered with 0.01—0.02 mm long papillae oriented into inconspicuous rows, chalazal hairs 50—60 (—70), 7.5—11 mm long. Flower homogamous.

E. palustre occurs in all sorts of wet places, also in standing or running water, on poor as well as rich soils. It has a circumpolar, temperate to arctic distribution. In Europe it is found as far south as the mountains of the N Mediterranean.

E. palustre is common throughout Scandinavia, occurring up to 1300 m in the southern mountains. It is represented by several very different but intergrading ecotypes in the great variety of biotopes occupied.

Known hybrids: with *E. adenocaulon, alsinifolium, anagallidifolium, collinum, davuricum, glandulosum, hirsutum, hornemanni, lactiflorum, montanum, obscurum, parviflorum, roseum,* and *tetragonum.*

104. **Epilobium davuricum** Fischer ex Hornemann 1819

Perennial herb, (7—)15—30(—40) cm high. Stem either simple, or rarely with one or a few short branches above, thus producing one or rarely a few, 1—5(—7)-flowered inflorescences. Middle and upper internodes usually longer than the leaves. Stolons lacking, dense, short-leaved rosettes developing in the axils of the basal leaves, rarely some of them prolonged up to 3 cm. Shoots in middle leaf axils lacking or rudimentary.

Stem terete, near the base 0.5—1.5 mm thick, usually with weak ridges or lines, in upper and middle part mainly below the midribs of leaves, in basal part also from margins of opposite leaf pairs. Stem sparsely to moderately hairy, either evenly or denser along the ridges, hairs 0.15—0.3 mm, longer ones curved, short ones patent and at least partly glandular.

Basal leaves forming a dense rosette, except in some first-year specimens, lower cauline leaves opposite, middle and upper ones usually alternate, the uppermost one usually odd, all usually with a short but distinct petiole 0—2(—5) mm long. Bases of opposite leaves uniting around the stem but never decurrent. Basal rosette leaves narrowly obovate to elliptical or ovate, 5—15 mm long, glabrous. Middle cauline leaves (5—)10—25(—40) mm long, 1—3 mm broad, lanceolate or narrowly lanceolate to linear, obtuse or tapering to a blunt apex, subentire or with few, often irregular, short teeth. Upper leaves narrower, often shorter and less distinctly petiolate. Indumentum of leaves like that of the stem, though often slightly shorter, sparse, denser on midribs and margins.

Bracts leafy, often placed up to 5(—10) mm up on the pedicel. Pedicels in bud and flower nodding, in fruit erect. Buds broadly ellipsoidal to sphaeroidal, blunt or acutish. Sepals 3—5 mm, connate to 0.9—1.8 mm at base, lanceolate, obtuse, green or often ± reddish, subglabrous or sparsely hairy especially in the basal part, upper margin glandular, slightly fringed, reddish. Petals (3.2—)4—5(—7.5) mm, notched to 0.5—1 mm, white or rarely pinkish-white. Anthers 0.45—0.5 mm, long filaments 2.4—2.8 mm, short filaments 1.4—1.8 mm, usually c. 2/3 as long as the long ones. Style about equalling the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—40) mm. Capsule 30—45(—50) mm, sparsely to moderately hairy, especially on the ribs, hairs 0.1—0.25 mm, like those of the stem. Seeds narrowly obovoidal, ± flattened on one side, 1.3—1.5(—1.7) mm long, 0.5—0.6 mm broad, tapering to an obtuse lower end, neck 0.15—0.3 mm, usually distinctly narrower than the rest of the seed and whitish, surface densely cov-

ered with papillae c. 0.01 mm long in inconspicuous rows, chalazal hairs 60—70, 7.5—11 mm long. Flower homogamous.

E. davuricum is calciphilous, and occurs in different sorts of wet places, especially along streams and on open ground. It has a circumpolar, arctic to subarctic distribution without any great gaps.

In Scandinavia *E. davuricum* occurs mainly in the mountains, up to 1400 m in the south, to 500 m in the north. It is also found scattered in the lowlands of N Finland S to c. 63° N and of Sweden and Norway to c. 60° N.

Known hybrids: with *E. palustre* and *lactiflorum*.

This species and the preceding are no doubt very closely related. They were recently subjected to a detailed investigation in part of their northern range by KYTÖVUORI (1969).

LITERATURE CITED

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Karyotype Analysis and Taxonomic Comments on Irises from SW and C Asia

Mats Gustafsson and Per Wendelbo

GUSTAFSSON, M. & WENDELBO, P. 1975 10 10. Karyotype analysis and taxonomic comments on irises from SW and C Asia. — Bot. Notiser 128: 208—226. Lund. ISSN 0006-8195.

Karyotype analysis has been carried out on 21 taxa of genus *Iris*, originating from SW and C Asia. Chromosome numbers of 10 taxa have not been reported previously, viz. *I. afghanica* 2n=22, *I. heweri* 2n=22, *I. barnumae* ssp. *demawendica* 2n=20, *I. iberica* ssp. *lycotis* 2n=20, *I. pamphylica* 2n=20, *I. aitchisonii* 2n=34, *I. cycloglossa* 2n=28, *I. maracandica* 2n=20, *I. microglossa* 2n=30 and *I. xanthochlora* 2n=14+1 B. The pattern of variation within subgenus *Iris* sect. *Hexapogon* and subgenus *Scorpiris* is discussed. In subgenus *Scorpiris* both morphological and cytological variation is extensive, while variation within sect. *Hexapogon* is comparatively narrow. In species of subgenus *Iris*, sect. *Iris* the karyotypes are relatively symmetrical, while asymmetrical karyotypes are found in sect. *Hexapogon*. One new combination has been made, *I. maracandica* (VVED.) WENDELBO.

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This study mainly comprises karyotype analyses with taxonomic comments on species indigenous to the Irano-Turanian floristic province. Special attention has been paid to variation within subgenus *Iris* sect. *Hexapogon* (BUNGE) BAKER and subgenus *Scorpiris* SPACH (for systematic treatments see FEDTSCHENKO 1935, VVEDENSKY 1963, WENDELBO & MATHEW 1975). Both groups have their centres of evolution in this province. Within *Scorpiris* a pronounced morphological variation is found in Afghanistan—Tadjikistan and the species mostly have very narrow geographical areas of distribution. In Afghanistan there are 17 species, 12 of which are endemic to that country and immediate adjacent parts of surrounding countries. Fourteen species are distributed in Tadjikistan of which 5 are endemic. The section *Hexapogon* is divided into two apparently closely related subsections. Subsect. *Hexapogon* is mainly Central Asiatic and most species are found in NE Afghanistan—Tadjikistan. Subsect. *Oncocyclus* (SIEMSS.) BENTH. has its main area in SW Asia, from Israel—Lebanon to E Turkey and NW Iran. Both subsections show comparatively little variation in morphological characters, but especially in *Oncocyclus* the colour patterns of the perigone are extremely variable. Taxonomically this latter group is confusing and the specific concept varies much between different treatments.

Little information is available as regards the intra- and interspecific cytological variation of Asian irises. Although chro-

mosome numbers of numerous species have been reported (for references see FEDOROV 1969), mostly single individuals representing one or two populations of each species have been investigated, and much of the material has been cultivated in gardens for a long time and their origin uncertain. Detailed karyotype analyses have only been carried out by MITRA (1956), RANDOLPH & MITRA (1961) and WEYMOUTH & CHAUDHARY (1974).

MATERIAL AND METHODS

The investigation has been carried out on material collected in natural habitats, with certain exceptions (cf. *I. fosterana, I. kopet-daghensis* and *I. maracandica*). Bulbs and rhizomes respectively were transplanted to pots and cultivated in the Botanical Gardens of Göteborg, Sweden. Usually only one or a few specimens of each population have been available. Original collections and voucher specimens are preserved at Kew and Göteborg.

Root tips were pretreated in 2 mM 8-hydroxiquinoline, kept in a refrigerator at 3—5°C over a night and then fixed in Carnoy (3:1). The root tips were hydrolyzed in 1 N HCl at 60°C for 10 minutes, stained in Feulgen for about two hours and then treated in a solution of 10 % pectinase before squashing in 45 % acetic acid. The squash technique used was as in ÖSTERGREN & HENEEN (1962).

The karyotypes are based on at least 10 good metaphase plates of each individual. The karyological nomenclature is as suggested by LEVAN et al. (1965). The karyotypes have been arranged in the following manner. The chromosome pairs are referred to four groups according to their r-values: m (r=1.0—1.7), sm (r=1.7—3.0), st (r=3.0—7.0) and t (r > 7.0). Within each group the pairs have been arranged according to size. The satellited pairs have been placed at the end of the group to which they belong. Chromosome pairs which cannot be distinguished from one another by conventional cytological methods have been placed together.

GUSTAFSSON is responsible for the cytological investigation and WENDELBO for the taxonomic treatment.

SUBGENUS IRIS SECT. IRIS

I. imbricata LINDL. 1845

GENERAL DISTRIBUTION. Caucasus, N Iran.

MATERIAL INVESTIGATED. Iran, province of Ghilan, FERGUSON 115.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=24 (Fig. 1). m-chromosomes: One large pair (r=1.2). sm-chromosomes: One large pair (r=2.1) and one small pair (r=2.3). sm—st-chromosomes: Nine pairs successively decreasing in length (r=2.8—6.3).

PREVIOUS REPORTS. 2n=24 (MITRA 1956, RANDOLPH & MITRA 1961). The karyotype is similar to those reported by MITRA and RANDOLPH & MITRA, except that no satellited st-chromosomes have been observed. The material investigated by MITRA originated from the Elburz Mountains of N Iran, that of RANDOLPH & MITRA from the Caucasus.

SUBGENUS IRIS SECT. HEXAPOGON (Bunge ex Alefeld) Baker 1876

Subsect. Hexapogon

I. afghanica WENDELBO 1972

TAXONOMIC COMMENTS. *I. afghanica* is from a morphological point of view related to *I. korolkowii,* and is confined to a small area just south of the area of the latter species.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. Representatives of two populations have been investigated. Population 768 originates from the province of Kataghan, E of Banu, GREY-WILSON/HEWER 768. Population 698 from the same province, east side of the Salang Pass, GREY-WILSON/HEWER 698.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The two populations display a similar karyotype. m-chromosomes: One large pair (r=1.1). st-chromosomes: One large pair (r=6.4). t-chromosomes: Nine pairs showing a continuous decrease in length (r=7.1—12.5).

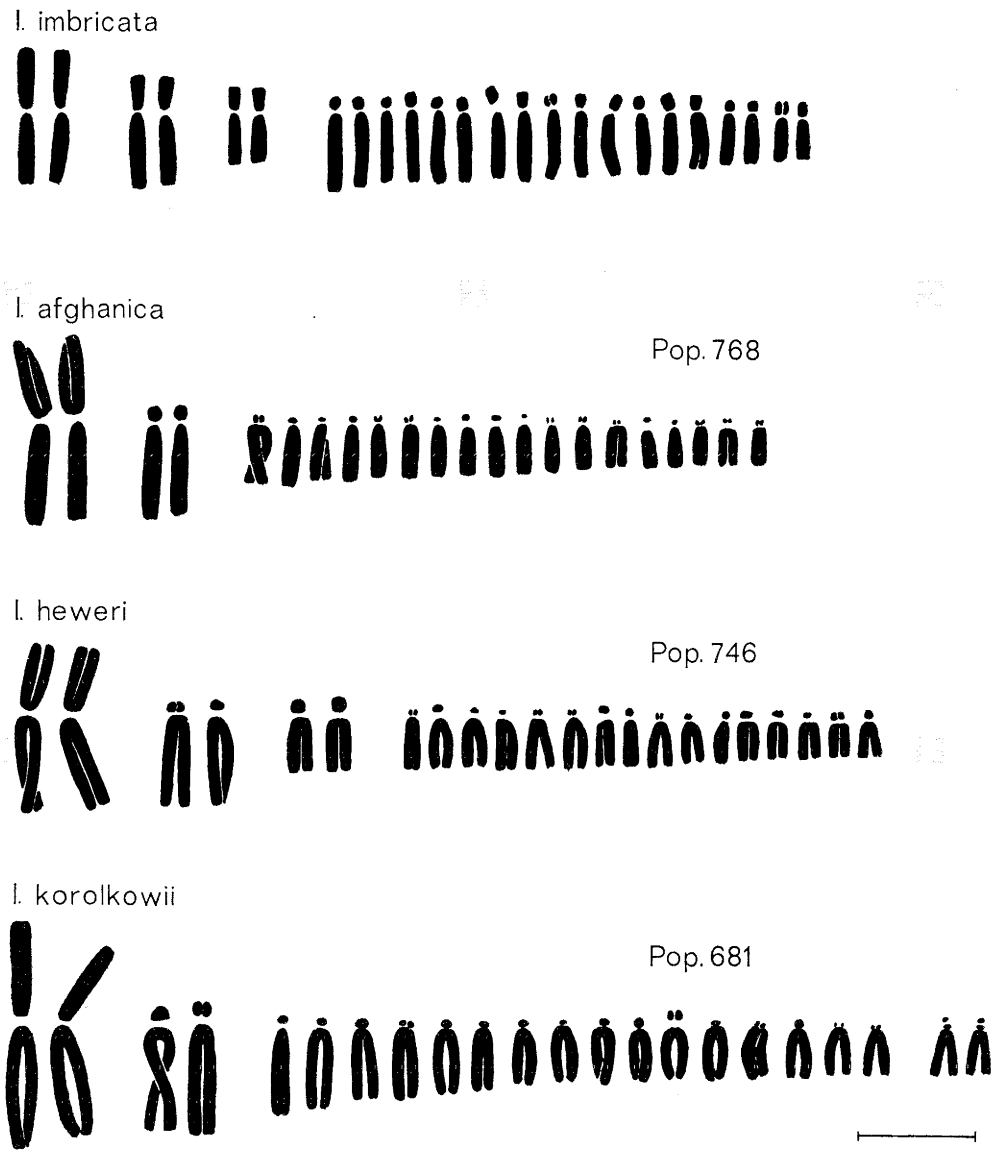

Fig. 1. Karyotypes of *I. imbricata* (2n=24) belonging to sect. *Iris*, and of *I. afghanica*, *I. heweri* and *I. korolkowii* (all having 2n=22) belonging to sect. *Hexapogon* subsect. *Hexapogon*. The scale unit is equal to 5 μ.

I. heweri GREY-WILSON & MATHEW 1974

TAXONOMIC COMMENTS. Morphologically *I. heweri* seems to be most closely related to *I. falcifolia* BUNGE, a species endemic to Soviet Central Asia (cf. FEDTSCHENKO 1935).

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. Representatives of two populations (746 and 757) collected in the province of Kataghan, E of Khinjan, GREY-WILSON/HEWER 746 and 757.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The two populations have a similar karyotype: m-chromosomes: One large pair (r=1.1). st-chromosomes: One large pair (r=6.5) and one small pair (r=3.8). st—t-chromosomes: Eight unidentifiable pairs successively decreasing in length (r=4.3—13.5).

I. korolkowii REGEL 1873

GENERAL DISTRIBUTION. NE Afghanistan to Soviet Central Asia.

MATERIAL INVESTIGATED. Representatives of two populations collected in NE Afghanistan, one (681) in Badakshan, c. 30 km S of Keshm, HEDGE & WENDELBO 9321, the other (918) in Qataghan, FURSE 8207. Population 681 represents the southernmost locality of this comparatively widely distributed species.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=22 (Fig. 1). The karyotypes of the two populations differ somewhat. m-chromosomes: One large pair (r=1.1—1.2). st-chromosomes: One large pair (r=5.7—6.4). st—t-chromosomes: Population 918 has nine unidentifiable pairs (r=6.5—8.6). Population 681 nine pairs (r=5.6—12.0) of which one has a satellite on the short arm.

PREVIOUS REPORTS. 2n=22 (MITRA 1956, ZAKHARYEVA & MAKUSHENKO 1969), 2n=33 (SIMONET 1928, horticultural form), 2n=44 (SIMONET 1928, horticultural form).

The karyotype reported by MITRA corresponds well with those observed by the authors, except that he observed 3 pairs of st-chromosomes with satellites. The origin of the material investigated by MITRA is not known.

Subsect. Oncocyclus (Siemss.) Benth.

I. acutiloba C. A. MEY. ssp. **lineolata** (TRAUTV.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. Caucasus, Iran.

MATERIAL INVESTIGATED. Representatives of two populations from Iran; 659 from Kurdistan, 11 km N of Divandarreh, ARCHIBALD 2170, and 700 from Gorgan, 135 km E of Gonbad-E-Kavus, 1700 m, FURSE 7377. Geographically the two populations are widely separated, population 659 representing the westernmost and 700 the easternmost part of the distributional area.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). Population 659: t-chromosomes: All ten pairs: Four pairs large, of which one pair seems to have a somewhat longer short arm than the other three pairs, and six small pairs about equal in length. Population 700: Differs from the former population in having only three large pairs, and the difference in size of the short arm is not very pronounced. Besides, one of the large chromosomes has a satellite, the others do not.

PREVIOUS REPORT. 2n=20 (ZAKHARYEVA & MAKUSHENKO 1969).

I. barnumae BAKER & FOSTER ssp. **barnumae** f. **urmiensis** (HOOG) MATHEW & WENDELBO 1975.

I. urmiensis HOOG 1900

TAXONOMIC COMMENTS. This form is a yellow variant of *I. barnumae* ssp. *barnumae*.

GENERAL DISTRIBUTION. NW Iran.

MATERIAL INVESTIGATED. Iran, Kurdistan, ARCHIBALD 3188.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). All ten pairs

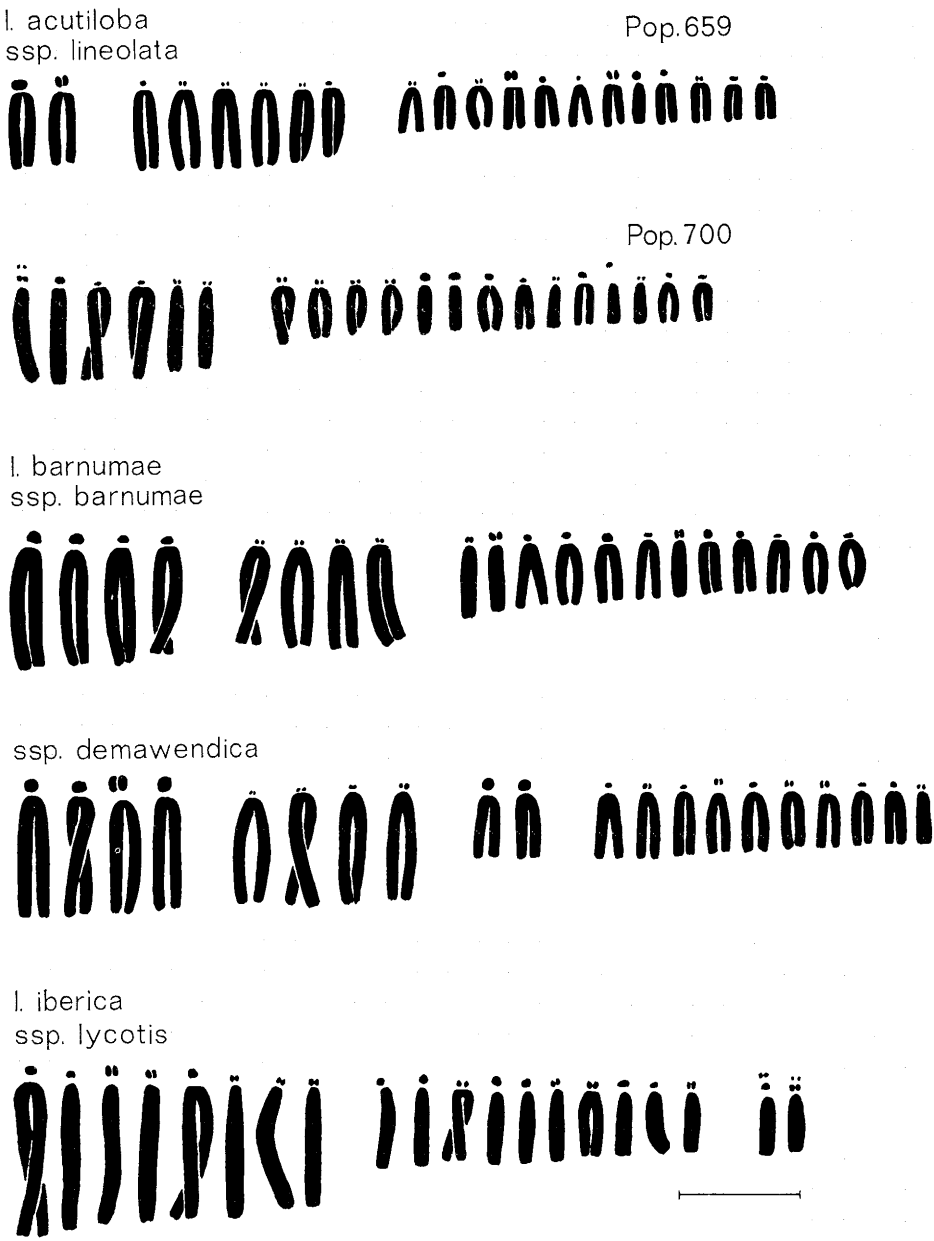

Fig. 2. Karyotypes of four taxa belonging to sect. *Hexapogon* subsect. *Oncocyclus* (all having 2n=20). The scale unit is equal to 5 μ.

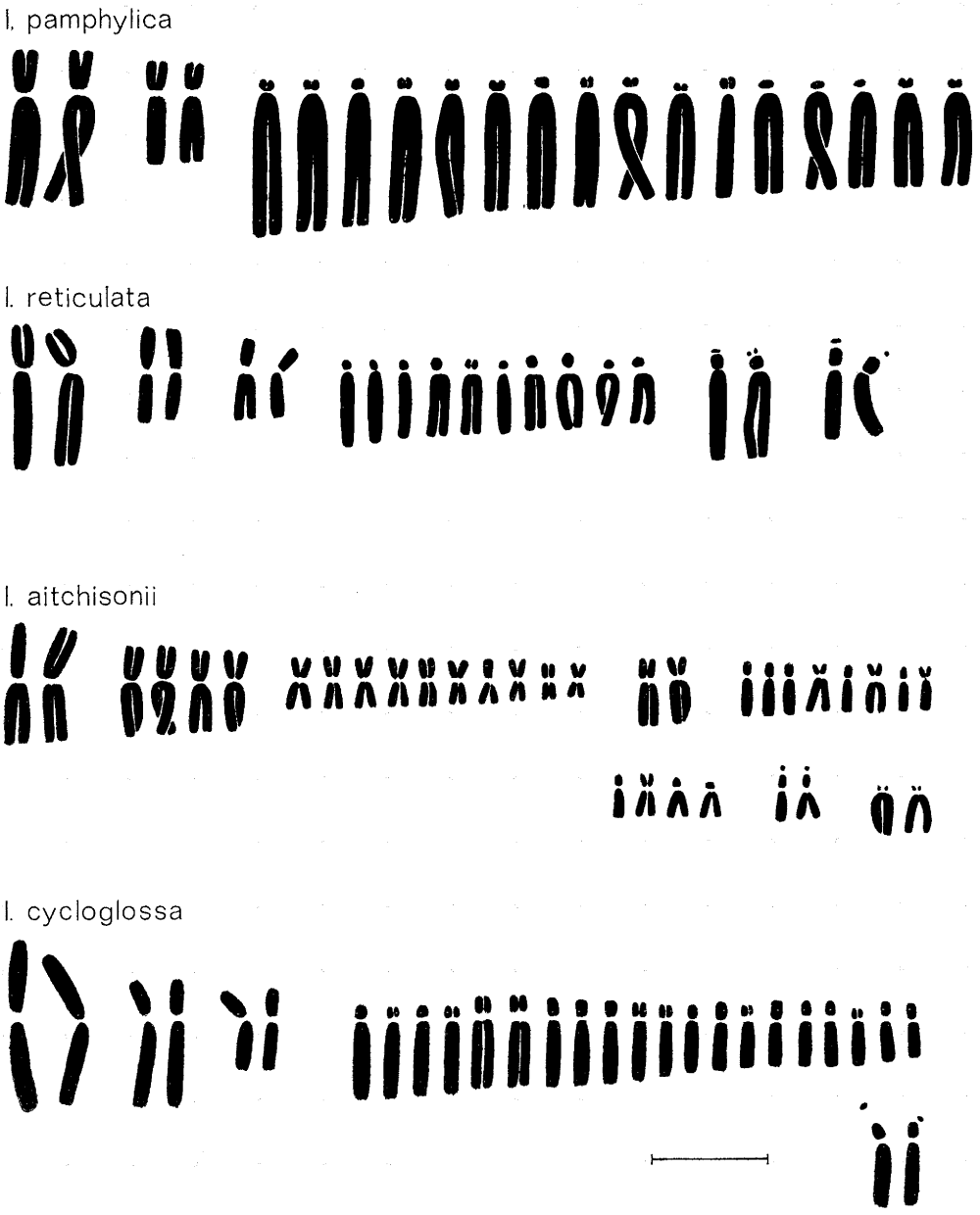

Fig. 3. Karyotypes of *I. pamphylica* (2n=20), *I. reticulata* (2n=20) both belonging to subgenus *Hermodactyloides*, and of *I. aitchisonii* (2n=34) and *I. cycloglossa* (2n=28) belonging to subgenus *Scorpiris*. The scale unit is equal to 5 μ.

are t (r > 7.1), four pairs large, of which two seem to have a somewhat larger short arm than the other two, and six small pairs successively decreasing in length.

PREVIOUS REPORTS. 2n=20 (SIMONET 1932, 1934).

I. barnumae BAKER & FOSTER ssp. **demawendica** (BORNM.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. N Iran.

MATERIAL INVESTIGATED. Elburz Mts, Dizin, 9000 feet. The material was obtained from Kew in 1972.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). st-chromosomes: One small pair (r=3.9). t-chromosomes: Nine pairs, four pairs large of which two pairs have a somewhat larger short arm than the other two, and five small pairs.

I. iberica HOFFM. ssp. **lycotis** (WORON.) TAKHT. in TAKHT. & FEDOR. 1972

GENERAL DISTRIBUTION. Armenia, NE Iraq, W Iran.

MATERIAL INVESTIGATED. Iran, Bakhtiary, 25 km NW of Shahr Kord, 2700—3000 m, FURSE 1446. The material represents the southernmost part of the distributional area.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 2). All ten pairs are t, four pairs large and unidentifiable, six pairs small of which one pair has a satellite on the short arm.

SUBGENUS HERMODACTYLOIDES Spach

I. pamphylica HEDGE 1961

TAXONOMIC COMMENTS. This species is probably most closely related to *I. reticulata* M. B.

GENERAL DISTRIBUTION. Central parts of South Turkey.

MATERIAL INVESTIGATED. Turkey, Isparta, Sübeüler, Kesmeköy, Ahmel UNZOGEN 207.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 3). sm-chromosomes: One large pair (r=2.5) and one small pair (r=2.5). t-chromosomes: Eight pairs (r > 10) successively decreasing in length.

I. reticulata M. B. 1808

TAXONOMIC COMMENTS. The material investigated represents a typical dark violet *I. reticulata*. As the occurrence in Afghanistan is far outside the general area of distribution of this species there is reason to believe that the material represents an escape.

GENERAL DISTRIBUTION. E Turkey, Transcaucasus, N and W Iran, NE Iraq.

MATERIAL INVESTIGATED. Afghanistan, Kabul in Paghman, FREITAG s.n.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 3). m-chromosomes: One small pair (r=1.2). sm-chromosomes: One large pair (r=2.3) and one small pair (r=1.8). st-chromosomes: Two large pairs with satellites (r=6.3 and 3.8 respectively), and five pairs successively decreasing in length (r=3.8—6.9).

PREVIOUS REPORTS. 2n=20 (DELONE 1928, SIMONET 1928). The karyotype is similar to that drawn by DELONE. In 1959 MITRA & RANDOLPH reported the chromosome numbers 2n=18 for *I. reticulata* "Violet" and 2n=20 for *I. reticulata* "Clarette", both the varieties originating from the firm van Tubergen, Holland. However, this material was obviously of hybrid origin and must be left out of account.

SUBGENUS SCORPIRIS Spach

Juno TRATT. ex ROEM. & SCHULT.
Iris sect. *Juno* (TRATT.) BENTH.
Iris subgenus *Juno* (TRATT.) BAKER.

In his treatment of *Iris,* RODIONENKO (1961) considered this group to be a genus of its own (*Juno*) and most recent reports from Soviet botanists seem to follow him.

I. aitchisonii (BAKER) BOISS. 1882

TAXONOMIC COMMENTS. *I. aitchisonii* may be related to *I. cycloglossa* WENDELBO because of its elongated stem and the winged claw of the outer perigone segments, but the relationship is not very obvious.

GENERAL DISTRIBUTION. W Pakistan to extreme E Afghanistan.

MATERIAL INVESTIGATED. Representatives of one population originating from W Pakistan collected by Dr E. NASIR, Rawalpindi.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=34 (Fig. 3). m-chromosomes: One large pair (r=1.1), two medium-sized pairs (r=1.6) and five small unidentifiable pairs (r=1.1—1.4). sm—st-chromosomes: Seven pairs successively decreasing in length (r=2.4—3.5), and one pair with a satellite on the short arm. t-chromosomes: One small pair (r=11).

I. cycloglossa WENDELBO 1958

TAXONOMIC COMMENTS. This species occupies a somewhat isolated position taxonomically. According to WENDELBO & MATHEW (1975), several characters may be taken as primitive in this otherwise advanced group of *Iris,* and it may therefore be considered the most primitive species of the subgenus.

GENERAL DISTRIBUTION. Endemic to the province of Herat of W Afghanistan.

MATERIAL INVESTIGATED. Near the top of Kotal-e Mir Ali, 1680 m, HEDGE, WENDELBO & EKBERG 7727.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=28 (Fig. 3). m-chromosomes: One large pair (r=1.2). sm-chromosomes: One large (r=2.5) and one medium-sized pair (r=2.0). sm—t-chromosomes: Ten pairs successively decreasing in length (r=2.2—8.0), and one pair of st-chromosomes with a satellite on the short arm.

I. drepanophylla AITCH. & BAKER

TAXONOMIC COMMENTS. *I. drepanophylla* is closely related to *I. kopetdaghensis* (VVED.) WENDELBO & MATHEW and to *I. xanthochlora* WENDELBO.

GENERAL DISTRIBUTION. E Iran, Turkmenistan, Afghanistan.

MATERIAL INVESTIGATED. Representatives of one population from W Afghanistan, the province of Herat, 25.5 miles S of Herat. GREY-WILSON/HEWER 477.

CHROMOSOME NUMBER AND KARYOTYPE. A great number of metaphase plates, derived from several root tips, have been investigated and all have 2n=19 (Fig. 4). m-chromosomes: One large chromosome (r=1.3) apparently without any homologue, and four chromosomes successively decreasing in length (r=1.5, 1.6, 1.6. and 1.1 respectively). st-chromosomes: Five pairs successively decreasing in length (r=3.7—6.9), and one pair of st-chromosomes with a satellite on the short arm (r=4.0). t-chromosomes: One pair (r=8.5).

PREVIOUS REPORT. 2n=20 (BOCHANTSEVA 1966).

I. fosterana AITCH. & BAKER 1888

TAXONOMIC COMMENTS. This species occupies an isolated position and there is no obvious relationship to any other species.

GENERAL DISTRIBUTION. NE Iran, Turkmenistan and W Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Ashkhabad in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=18 (Fig. 4). m-chromosomes: Five unidentifiable pairs successively decreasing in size (r=1.1—1.3). st-chromosomes: Three pairs (r=4.3—5.5) and one pair with a satellite on the short arm (r=5.0).

PREVIOUS REPORT. 2n=18 (ZAKHARYEVA & MAKUSHENKO 1969).

I. kopetdaghensis (VVED.) MATHEW & WENDELBO 1975

GENERAL DISTRIBUTION. NE Iran, Turkmenistan and Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Ashkhabad in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=18 (Fig. 4). m-chromosomes: One large pair with satellite on the shortest arm (r=1.1), one medium-sized pair (r=1.2), and three small unidentifiable pairs (r=1.3—1.6). st-chromosomes: Three unidentifiable pairs (r=4.2—5.3), and one pair with a satellite on the short arm (r=3.1).

PREVIOUS REPORTS. 2n=18 (BOCHANTSEVA 1966), 2n=24 (ZAKHARYEVA & MAKUSHENKO 1969).

I. maracandica (VVED.) WENDELBO, comb. nov.

Basionym: *Juno maracandica* VVED. 1963, p. 426.

TAXONOMIC COMMENTS. This species seems to be most closely related to *I. orchioides* CARR., *I. pseudocaucasica* GROSSH. and *I. caucasica* HOFFM.

GENERAL DISTRIBUTION. Tadjikistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Tashkent in 1962.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 4). m-chromosomes: One large pair (r=1.1), and three small pairs successively decreasing in length (r=1.1—1.4). sm-chromosomes: One large pair (r=2.7) and one small pair (r=2.0). st-chromosomes: One small pair (r=5.3), and two pairs with satellites on the short arm, of which one pair is large (r=5.4) and one small (r=5.0). t-chromosomes: One large pair (r=8.0).

I. microglossa WENDELBO 1958

TAXONOMIC COMMENTS. *I. microglossa* belongs to the species which have non-arillate seeds and a winged claw to the outer perigone segments (cf. p. 222). It is, however, a very characteristic plant which cannot directly be related to any of the other species of this group.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. The province of Kataghan, the north side of the Salang Pass, c. 2000 m, EKBERG & WENDELBO. The same locality as HEDGE, WENDELBO & EKBERG 7560.

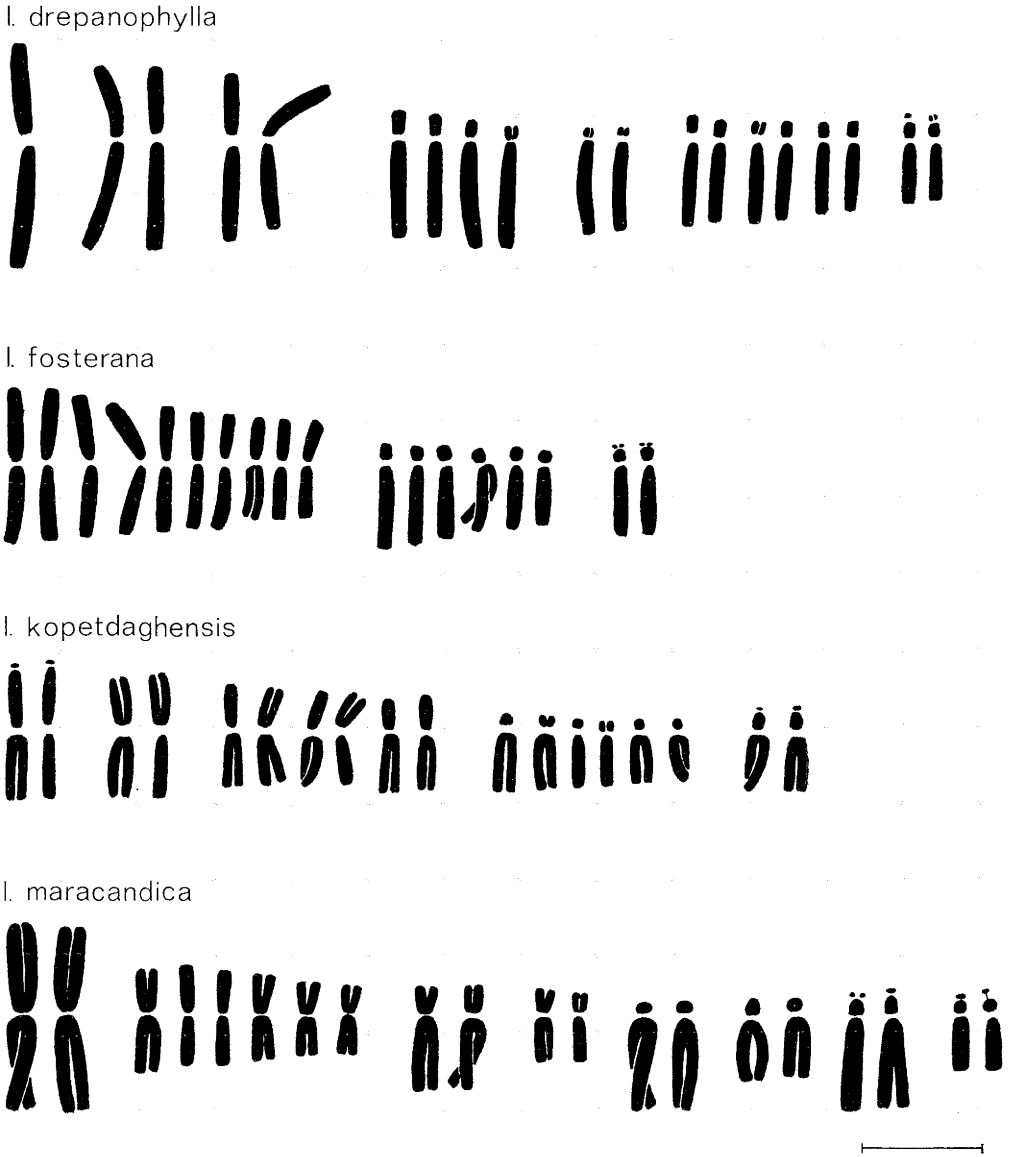

Fig. 4. Karyotypes of four species of subgenus *Scorpiris*, *I. drepanophylla* (2n=19), *I. fosterana* (2n=18), *I. kopetdaghensis* (2n=18) and *I. maracandica* (2n=20). The scale unit is equal to 5 μ.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=30 (Fig. 5). m-chromosomes: One large pair (r=1.5), and six pairs of small chromosomes about equal in length (r=1.1—1.3). sm—st-chromosomes: Eight pairs successively decreasing in length (r=2.8—6.5).

I. persica L. 1753

TAXONOMIC COMMENTS. *I. persica* is a very variable species, with a relatively large area of distribution, and both the taxonomy and nomenclature are rather confused. The material investigated belongs to the taxon described as *I. stenophylla* HAUSSKN. & SIEHE ex BAKER 1900.

GENERAL DISTRIBUTION. Turkey to N Iraq, Syria.

MATERIAL INVESTIGATED. S Turkey, W of Konya, RUNEMARK & WENDELBO 98 B.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=24 (Fig. 5). m-chromosomes: One large pair (r=1.6) and one medium-sized pair (r=1.1). sm—st-chromosomes: Ten pairs (r=2.3—6.9) of which two pairs are large, five pairs medium-sized and three pairs small.

PREVIOUS REPORTS. 2n=26 (SIMONET 1932, 1934, RANDOLPH 1934).

I. rosenbachiana REGEL 1884

TAXONOMIC COMMENTS. *I. rosenbachiana* is probably conspecific with *Juno nicolai* VVED. For further information see discussion in WENDELBO & MATHEW 1975.

GENERAL DISTRIBUTION. The U.S.S.R., Tadjikistan to NE Afghanistan.

MATERIAL INVESTIGATED. Seeds obtained from the Botanical Gardens of Tashkent in 1968. Determination controlled on flowering individuals in Göteborg.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=20 (Fig. 5). m-chromosomes: One large pair (r=1.5), one medium-sized pair (r=1.3), and one small pair (r=1.2). sm-chromosomes: Six unidentifiable pairs (r=1.7—2.2), and one large pair with a satellite on the short arm (r=2.4).

PREVIOUS REPORT. 2n=22 was determined for *Juno nicolai* VVED. by ZAKHARYEVA & MAKUSHENKO 1969.

I. xanthochlora WENDELBO 1969

TAXONOMIC COMMENTS. This species is closely related to *I. drepanophylla* and *I. kopetdaghensis*. It is confined to a small area just to the east of the distributional area of *I. kopetdaghensis*.

GENERAL DISTRIBUTION. Endemic to NE Afghanistan.

MATERIAL INVESTIGATED. The province of Kataghan, the north side of the Salang Pass, 2600 m, EKBERG & WENDELBO, the same locality as pressed material HEDGE, WENDELBO & EKBERG 8568.

CHROMOSOME NUMBER AND KARYOTYPE. 2n=14 + 1B (Fig. 5). m-chromosomes: One large pair with a satellite on the short arm (r=1.5). m—sm-chromosomes: Four pairs successively decreasing in length (r=1.2—2.1). st-chromosomes: One pair with a small satellite and another pair with a minute satellite on the short arm (r=5.5 and 4.8 respectively). B-chromosome: 1.

DISCUSSION

Variation Within Subsect. Hexapogon

The species of this subsection are characterized by having 2 rarely 3 flowers, with falls and usually standards bearded by unicellular hairs, and by arillate seeds. Despite this rather strict morphological definition of the subsection the number of species included varies with different authors. Particularly, the taxonomic position of *I. humilis* GEORGI (=*I. flavissima* PALL., and *I. arenaria* WALDST. & KIT.), *I. falcifolia* BUNGE and *I. longiscapa* LEDEB. has been a matter for discussion. According to FEDTSCHENKO (1935) these species belong to sect. *Pogoniris* BAKER

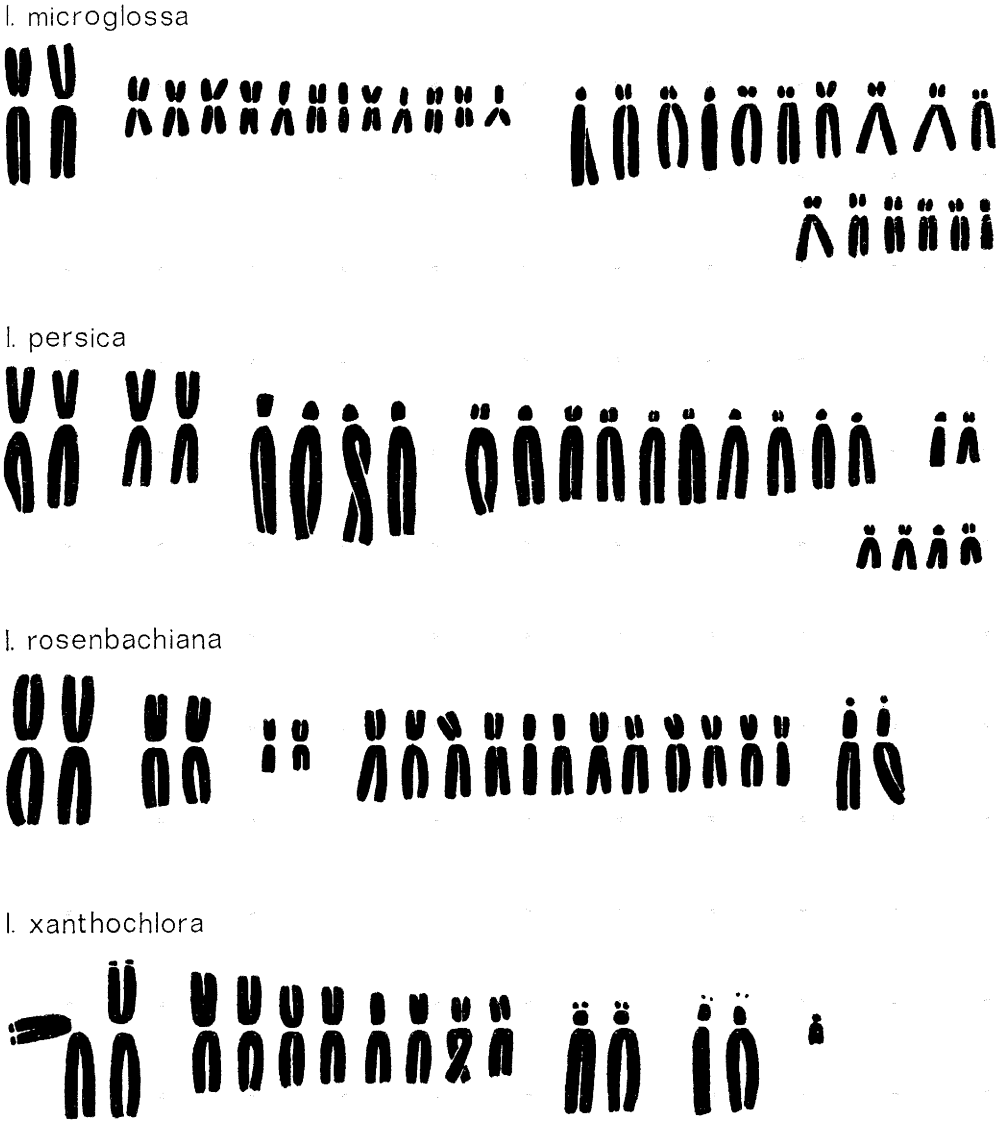

Fig. 5. Karyotypes of four species of subgenus *Scorpiris*, *I. microglossa* (2n=30), *I. persica* (2n=24), *I. rosenbachiana* (2n=20) and *I. xanthochlora* (2n=14+1 B). The scale unit is equal to 5 μ.

(now sect. *Iris*), but according to LAWRENCE (1953) they belong to subsect. *Hexapogon*.

The chromosomal differentiation is summarized in Table 1. *I. afghanica, I. heweri* and *I. korolkowii* seem to be closely related, they are all diploid (2n=22) and the chromosome complement comprises one pair of m-chromosomes, one pair of large st-chromosomes and nine pairs of st—t-

Table 1. A summary of karyotypes of species within sect. *Hexapogon* subsect. *Hexapogon*. Nomenclature of centromere position see p. 209; sat and non sat indicate chromosomes with and without satellites respectively.

Species	Number and type of chromosomes				2n	Author	Origin
	m	sm	st—t				
			non sat	sat			
I. afghanica WENDELBO	2	—	20	—	22	GUSTAFSSON & WENDELBO	Afghanistan
I. heweri GREY-WILSON & MATHEW	2	—	20	—	22	"	"
I. korolkowii REGEL	2	—	14	6	22	MITRA 1956	Unknown cultivated
I. korolkowii REGEL	2	—	18	2	22	GUSTAFSSON & WENDELBO	Afghanistan
I. korolkowii REGEL	2	—	20	—	22	"	"
I. hoogiana DYKES	4	—	34	6	44	MITRA 1956	Unknown cultivated
I. stolonifera MAXIM.	4	—	38	2	44	"	"
I. longiscapa LEDEB.	—	2	16	—	18	RANDOLPH & MITRA 1961	Turkmenistan

chromosomes. However, intra- as well as interspecific differences exist, although they are of a low magnitude. In *I. heweri* one pair of st-chromosomes has a relatively long short arm not observed in the other species. In *I. korolkowii* the number of pairs of satellited st-chromosomes varies from none to three. The two pairs of marker chromosomes seem to be similar in all the species (Fig. 6), except for population 918 of *I. korolkowii*. In this population structural changes have occurred in the m-chromosomes as well as in the st-chromosomes. Possibly a translocation is involved, but information from meiosis is needed before any conclusions can be drawn. The tetraploid species (2n=44) *I. hoogiana* DYKES and *I. stolonifera* MAXIM. show a close affinity to the other three species. The different types of chromosomes observed in *I. afghanica, I. heweri* and *I. korolkowii* seem to occur in quadruplicate (MITRA 1956). *I. hoogiana* only differs from *I. stolonifera* in having one pair of satellited m-chromosomes.

The karyotype of *I. humilis* differs from the previous species in having one small pair of m-chromosomes and two pairs of sm-chromosomes. This karyotype shows a close similarity to those observed within sect. *Iris*. Although some morphological traits, for instance arillate seeds, indicate affinity to species of subsect. *Hexapogon, I. humilis* and allied taxa are probably better accommodated in sect. *Iris*.

The karyotype and chromosome number of *I. longiscapa* deviate from the other species. It has 2n=18 and one small pair of sm-chromosomes and eight pairs of st—t-chromosomes (RANDOLPH & MITRA 1961).

The appearance of the karyotypes indicates that *I. afghanica, I. heweri, I. korolkowii, I. hoogiana* and *I. stolonifera* form a fairly uniform group distinguished from *I. longiscapa*. This difference is supported by other diversities, for instance

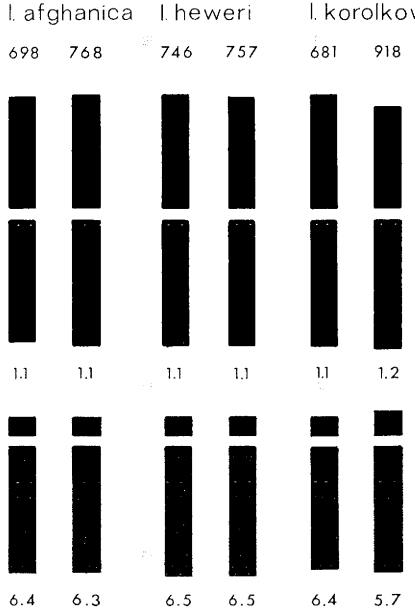

Fig. 6. Variation in two marker chromosomes in *I. afghanica* (populations 698 and 768), *I. heweri* (populations 746 and 757) and *I. korolkowii* (populations 681 and 918). The figures indicate r-values.

in habitat. *I. longiscapa* and the closely related *I. falcifolia* (not yet cytologically investigated) inhabit arid biotopes such as clayey deserts, rocks and sandy places. The other species grow at higher altitudes under less arid conditions. Despite these differences *I. longiscapa* and *I. falcifolia* probably belong to subsect. *Hexapogon*, but further information on morphological variation and cytology is highly desirable.

Variation Within Subsect. Oncocyclus

The number of species varies between 20 and 35 according to the author. The distinguishing characteristics of some of the species are insignificant and do not extend beyond differences in the colouration of the perigone segments. There are two main centra of evolution, one in Transcaucasus—NW Iran and one in Lebanon, Syria— SE Turkey.

The chromosome number of about 31 taxa has hitherto been determined (for references see FEDOROV 1969, and WEYMOUTH & CHAUDHARY 1974). All taxa have 2n=20 except *I. lupina* FOSTER (probably conspecific with *I. sari* SCHOTT in BAKER), which has the deviating number 2n=21 (SIMONET 1934). In all the species the chromosome complement seems to be exclusively represented by st—t-chromosomes. Four chromosome pairs are usually large, the other six medium-sized to small. The only deviation is population 700 of *I. acutiloba* ssp. *lineolata*, which has three large pairs instead of four. The number of pairs with a satellite varies from none to three and heterozygosity for satellites is known in some taxa, for instance in *I. susiana* L., *I. lortetii* BARB. (MITRA 1956) and in *I. acutiloba*. Very little is known about the degree of intraspecific variation as usually only a few individuals of single populations have been investigated. However, differences exist at least in *I. acutiloba* ssp. *lineolata*. In contradiction to WEYMOUTH & CHAUDHARY the present authors consider the interspecific differences to be small. It is necessary to investigate meiosis in artificially produced hybrids before any conclusions concerning relationships can be drawn.

Variation Within Subgenus Scorpiris

Scorpiris is distinguished from all other *Iris* groups in having the combination of bulb and canaliculate leaves. The pattern of morphological variation within *Scorpiris* is rather complicated and most of the species described are endemic to very small areas. The variation is most pronounced in characters such as development of stem, shape of outer and inner perigone segments, form of stylar branches, colour of flower and presence or

absence of aril on the seeds. At present the phylogenetic relationship is not quite clear, but three sections have been distinguished.

Sect. *Juno* is characterized by a bulb consisting of storage leaves, non-tuberculate pollen grains and non-arillate seeds. It comprises about 27 species distributed in SW and C Asia except the Mediterranean parts. To this section belong *I. aitchisonii, I. cycloglossa, I. fosterana, I. maracandica, I. microglossa* and *I. persica.*

Sect. *Physocaulon* (RODION.) MATHEW & WENDELBO is characterized by a bulb consisting of a swollen and persistent stem base and with few storage leaves only, non-tuberculate pollen grains and arillate seeds. It comprises about 11 species distributed in the central parts of Asia, for example *I. drepanophylla, I. kopetdaghensis, I. rosenbachiana* and *I. xanthochlora.*

Sect. *Acanthospora* RODION. (under the genus *Juno*). The bulb consists of storage leaves, pollen grains are tuberculate and it has non-arillate seeds. It comprises two species only, *I. planifolia* (MILLER) FIORI & PAOL. (syn. *I. alata* POIR.) and *I. palestina* BOISS. which are both Mediterranean in distribution. It is uncertain as to whether they deserve a section of their own or not.

The chromosome numbers of the species investigated within the different sections are summarized in Table 2. In sect. *Juno* 18 species have so far been investigated and the chromosome number varies considerably from 2n=18 (*I. caucasica* and *I. fosterana*) to 2n=50 (*I. albomarginata*). However about one half of the species have the chromosome number 2n=22. The aneuploid number 2n=21 has been observed within *I. willmottiana* M. FOSTER (SIMONET 1952). Intraspecific variation has been recorded within *I. caucasica* (2n=18, SIMONET 1932; 2n=22, BOCHANTSEVA 1966), within *I. orchioides* (2n=22, SIMONET 1930; RANDOLPH & MITRA 1956; 2n=30, BOCHANTSEVA 1966) and within *I. persica* (2n=24, present authors; 2n=26, SIMONET 1932; RANDOLPH 1934). In sect. *Physocaulon* the chromosome number of 4 species out of 11 has been determined and varies between 2n=14 (*I. xanthochlora*) and 2n=24 (*I. kopetdaghensis*). An aneuploid chromosome number has been observed in *I. drepanophylla* (2n=19; present authors). Intraspecific variation has been recorded within *I. kopetdaghensis* (2n=18, BOCHANTSEVA 1966; present authors; 2n=24, ZAKHARYEVA & MAKUSHENKO 1969) and in *I. rosenbachiana* (2n=20, present authors; 2n=22, ZAKHARYEVA & MAKUSHENKO 1969). In sect. *Acanthospora* the only species investigated, *I. planifolia,* has 2n=24 (SIMONET 1932). Thus, sections *Juno* and *Physocaulon* at least show a considerable variation in chromosome number, apparently without any relationship to the morphological variation.

The karyotypes, which are summarized in Table 3, show a similar pattern of variation. There seems to be little or no correlation between appearance of karyotype and morphological similarity. The karyotype of *I. rosenbachiana* most closely resembles that of *I. aitchisonii,* although the chromosome numbers differ and there are small differences in the karyotypes, but they represent different sections. The karyotype of *I. fosterana* most closely resembles that of *I. kopetdaghensis,* but they, too, belong to different sections. *I. kopetdaghensis* is undoubtedly related to *I. xanthochlora.* The karyotypes are similar, but the chromosome numbers differ.

Hybridization is reported to occur in sect. *Juno,* mainly between species with the same chromosome number (*I. narbuti* × *orchioides, I. narbuti* × *subdecolorata, I. bucharica* × *vicaria,* all having 2n=22, cf. FEDTSCHENKO 1935), but also between species with differing chromosome numbers (*I. narbuti,* 2n=22 × *maracandica,* 2n=20). Moreover, vegetatively vigorous plants of hybrid origin have been used for ornamental purposes, for example *I. warlsind* (*I. sindjarensis* × *warleyensis*) produced by the firm van Tubergen, Holland.

Table 2. Distribution of chromosome numbers in three sections of subgenus *Scorpiris*. a indicates the number of populations investigated and b the number of species investigated. Intraspecific variation has been observed in three species of sect. *Juno* and in two species of sect. *Physocaulon*, see page 222.

Section	2n												a	b
	14	18	19	20	21	22	24	26	28	30	34	50		
Juno	—	2	—	1	1	10	2	1	1	1	1	1	21	18
Physocaulon ...	1	1	1	1	—	1	1	—	—	—	—	—	6	4
Acanthospora ..	—	—	—	—	—	—	1	—	—	—	—	—	1	1

Obviously, the interspecific cytological differentiation as regards chromosome number and karyotype is not sufficiently large to prevent hybridization and the establishment of hybrid derivatives. Vegetative propagation of bulbs probably makes it possible for hybrids and plants with aneuploid chromosome numbers to become established in natural habitats.

The great morphological and cytological variation and differentiation within subgenus *Scorpiris* indicates that this group is in an active stage of evolution.

Chromosome Evolution Within the Genus Iris

The pattern of morphological variation seems to be similar in *Scorpiris, Hexapogon* and *Oncocyclus,* i.e. there is strong local differentiation. By contrast, the pattern of cytological variation differs entirely in *Scorpiris* and *Oncocyclus. Scorpiris* shows a wide variation in chromosome number and in the appearance of the karyotypes. All the species in subsect. *Oncocyclus* have the same chromosome number (2n=20) and the karyotypes of

Table 3. Karyotype differentiation within subgenus *Scorpiris*. The number of pairs belonging to each group is not noted, as transitions from m to sm, and sm to st-chromosomes are present. Nomenclature of centromere position see p. 209. sat and non sat indicate chromosomes with and without satellites respectively. The lengths of the chromosomes are abbreviated as follows: la=large, me=medium-sized, sm-small.

Species	Number and type of chromosome									
	2n	m			sm		st		t	
		non sat		sat	non sat	sat	non sat	sat	non sat	
		la	me—sm	la	la—sm	la—sm	la—sm	la—sm	la—sm	
I. aitchisonii	34	+	+	—	+	+	+	—	+	
I. cycloglossa	28	+	—	—	+	—	+	+	+	
I. drepanophylla	19	+	—	—	—	—	+	+	+	
I. fosterana	18	+	+	—	—	—	+	+	—	
I. kopetdaghensis	18	—	+	+	—	—	+	+	—	
I. maracandica	20	+	+	—	+	—	+	+	+	
I. microglossa	30	+	+	—	+	—	+	—	—	
I. persica	24	+	+	—	+	—	+	—	—	
I. rosenbachiana	20	+	+	—	+	+	—	—	—	
I. xanthochlora	14+1B	—	+	+	+	—	—	+	—	

species from the Middle East and Asia respectively seem to be similar. In subsect. *Hexapogon* the variation is approximately intermediate, a certain amount of variation is obvious in the chromosome number as well as in the karyotype, but it is not at all as pronounced as in *Scorpiris*.

Karyotypes of species of *Scorpiris* differ from those of species of *Hexapogon* and *Oncocyclus*. In all species of *Scorpiris* there is one pair of large m-chromosomes while the number of sm and st-chromosomes varies. Telocentric chromosomes seem to be rare in this group. All species of *Hexapogon*, except *I. longiscapa*, have one or two pairs of large m-chromosomes and of large st-chromosomes. In *Oncocyclus* all ten pairs are st—t-chromosomes, m—sm-chromosomes have not been observed at all. It is rather remarkable that this asymmetrical karyotype is found in all *Oncocyclus* species, as complements with a high proportion of stable t-chromosomes are rare in higher plants. The most extreme karyotypes in this respect have been observed in *Welwitschia mirabilis* (KHOSHOO & AHUJA 1963) and in *Tradescantia micrantha* (JONES & COLDEN 1968) where all the chromosomes are telocentric. In addition, a large proportion of st—t-chromosomes has been found in the genera *Ginkgo* (LEE 1954), *Podocarpus* (HAIR & BEUZENBERG 1958), *Tripogandra* (JONES & COLDEN 1968) and *Goniolimon* (RUNEMARK 1974). Telocentric chromosomes may arise in two ways, by misdivision in the centromeric region of biarmed chromosomes, or by structural changes such as shifts, pericentric inversions and translocations. In subsect. *Oncocyclus* it seems less probable that the t-chromosomes have arisen by centromeric misdivision as at least five must have occurred. Moreover, the successive transition from st to t-chromosomes in *Oncocyclus* and the presence of such chromosomes in other *Iris*-groups indicate that they have arisen by some types of chromosomal rearrangements.

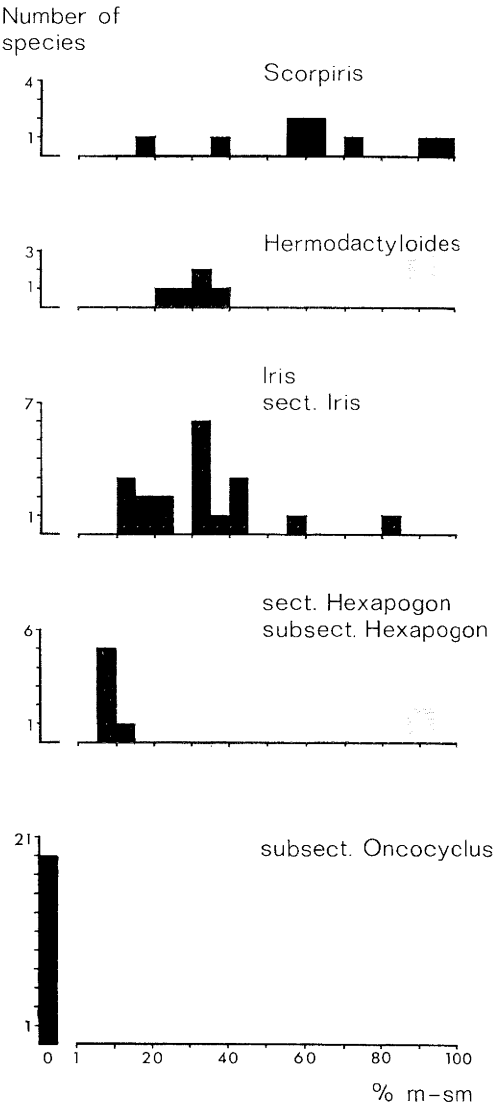

Fig. 7. The relative proportion of m—sm-chromosomes in species of subgenera *Scorpiris*, *Hermodactyloides* and *Iris*.

The relationship between plant phylogeny and symmetrical-asymmetrical karyotypes has been extensively discussed. It is generally considered that asymmetrical karyotypes have evolved from sym-

metrical ones (for references see SWANSON 1965, STEBBINS 1971), but reversals of this trend may occur (see JONES 1970). The relative proportion of m and sm-chromosomes in species of *Iris* subgenera *Scorpiris, Hermodactyloides* and *Iris* is summarized in Fig. 7. In *Scorpiris* the proportion of m—sm-chromosomes varies between 15 and 100 %, and in *Hermodactyloides* from 20 to 40 %. In subgenus *Iris* the frequency varies with the group. Species of sect. *Iris* show a variation from 10 to 85 %, subsect. *Hexapogon* from 5 to 15 %, and in subsect. *Oncocyclus* no m—sm-chromosomes are present at all. Thus *Iris* species belonging to sect. *Iris,* like those of *Scorpiris* and *Hermodactyloides,* show a more or less symmetrical karyotype, while the asymmetrical karyotype is most pronounced in subsect. *Oncocyclus.* In *Iris,* a too limited amount of information is available for certain conclusions concerning the direction of chromosome evolution. But species of subsect. *Oncocyclus* show some advanced morphological features in addition to the asymmetrical karyotype, for instance reduced number of flowers and arillate seeds.

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A Study of Cachrys Populations in Israel and Its Application to Generic Delimitation

Ilana Herrnstadt and Chaia C. Heyn

HERRNSTADT, I. & HEYN, C. C. 1975 10 10. A study of Cachrys populations in Israel and its application to generic delimitation. — Bot. Notiser 128: 227—234. Lund. ISSN 0006-8195.

Sixteen local populations referred to either *Cachrys* L. or *Prangos* LINDL. (Umbelliferae) were studied in their natural habitats. In seven of these, 2n=66 (or n=33) was found. The characters examined included the suberization and wing development of fruit and other fruit and leaf characters. As a rule considerable intra- and interpopulational variation occurs in the majority of the characters including those used for generic delimitation. A study of fruit ontogenesis showed that the relative extent of suberized tissue and wing development may undergo considerable change during the maturation of the fruit. No correlation was found between any trend in fruit variation and the variation of leaf lobes. It is proposed to accept the pattern of continuous variation as being sufficient proof for including *Cachrys* L. and *Prangos* LINDL. in a single genus, and the plants from the populations investigated in a single species. For nomenclatural reasons this species must be called *Cachrys ferulacea* (L.) CALEST.

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The problematic status of *Cachrys* L. and *Prangos* LINDL. (Umbelliferae) has been previously discussed by us (HERRNSTADT & HEYN 1974). Though several authors, including the present ones, consider that the above genera comprise a single genus, no detailed reason for this has so far been published.

This study is an attempt to approach the problem of the generic delimitation of *Cachrys* and *Prangos* by examining populations of plants described as belonging to one of the genera in Israel.

The extent of the confusion prevailing between *Cachrys* and *Prangos* is reflected in the names of the species recorded from the region investigated: BOISSIER (1872) described *Cachrys goniocarpa* from "circa Asdod (=Ashdod) et Ramlah (=Ramla)". POST (1932) also recorded the same species from Mt Carmel, Sharon, Esdraelon (=Yizre'el Valley) and Safad, *Prangos asperula* from Gaza, the Galilee and Jerusalem and *P. asperula* var. *leiopetala* (POST 1896) from Gaza. As the diagnostic characters for these three taxa he used the degree of the development of ridges on the fruit and the pubescence of petal surface. RECHINGER (1952) also records *C. goniocarpa* and adds two varieties to *P. asperula*: var. *stenoptera* BOISS. (Distr. Safed, Safad, Zefat — all refer to the same locality in different transcriptions) and var. *judaica* SAM. (from the Judean Mts — "el Kubab"). The characters used to define these taxa are again the extent of ridge development as well as the length and breadth of fruit (as compared with the length of pedicels). MOUTERDE (1953) added *C. goniocarpa* var. *asperifolia* as growing in the region concerned (having scabrid leaves in contrast with the smooth-leaved typical variety). ZOHARY (1972),

Table 1. *Cachrys* populations studied.

	Population number and locality	Organs investigated: Leaves	Organs investigated: Fruit
	N Negev		
1	10 km W of Arad ..	+	+
2	Lahav (single plant)		+
3	Shoval (single plant)	+	
4	Qiryat Gat	+	+
	Shefela		
5	6 km N of Mashmia	+	+
6	Bet Hashmonai		+
7	Gilboa, N slopes	+	+
8	Lower Galilee, Migdal Ha'Emeq	+	+
9	Belvoir	+	+
10	Yizre'el Valley, Daverat	+	+
	Lower Galilee		
11	Kafr Kanna	+	+
12	Biq'at Bet Netofa ...	+	+
13	Golan Heights, Mevo Hamma	+	+
	Upper Galilee		
14	btw. Rosh Pinna & Zefat	+	+
15	Meron Junction	+	+
16	Har Almon		+

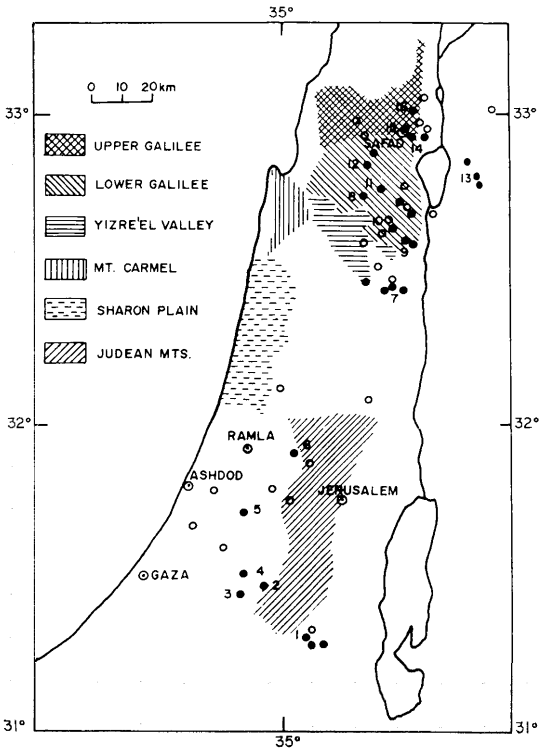


Fig. 1. Distribution of *Cachrys ferulacea* in Israel. Previous records from literature: regions — differentially shaded; localities — named. Dots represent single plants or populations investigated in this study (numbers correspond to those in Table 1); circles represent herbarium specimens.

who considers *Prangos* and *Cachrys* a single genus, records the following taxa: *P. asperula* as a very rare plant of the S Judean Desert and *P. goniocarpa* with a rare typical variety and the more widespread var. *stenoptera* with narrowly winged fruits. (See Fig. 1 for the above localities.)

MATERIAL AND METHODS

Plants of "*Cachrys*" and "*Prangos*" are fairly widespread in Israel and usually grow in small populations, at 150—500(— 800) m above sea level on diverse soils. They are tumble-weeds of fallow fields occurring mostly along the border of the Mediterranean and Irano-Turanian regions.

Sixteen populations were studied in their natural habitats (cf. Table 1 and Fig. 1). In each population about 5—15 plants were examined in the field; additional material was collected for documentation and further studies. Special attention was paid to individual plants with characters deviating from the normal. Most localities were visited twice a year, once in the early spring for a study of vegetative parts and flowers and again in summer for a study of fruits. As far as possible the same individuals were examined within each population for 3 consecutive years (1968—1971).

The following characters were investigated: size and shape of fruit (length/breadth), development of suberized mesocarp, fruit surface (obsoletely ribbed, distinctly ridged or

Fig. 2. Inter- and intrapopulational variation in fruit shape of *Cachrys ferulacea*; fruits in horizontal rows are from one population (numbers correspond to those in Table 1).

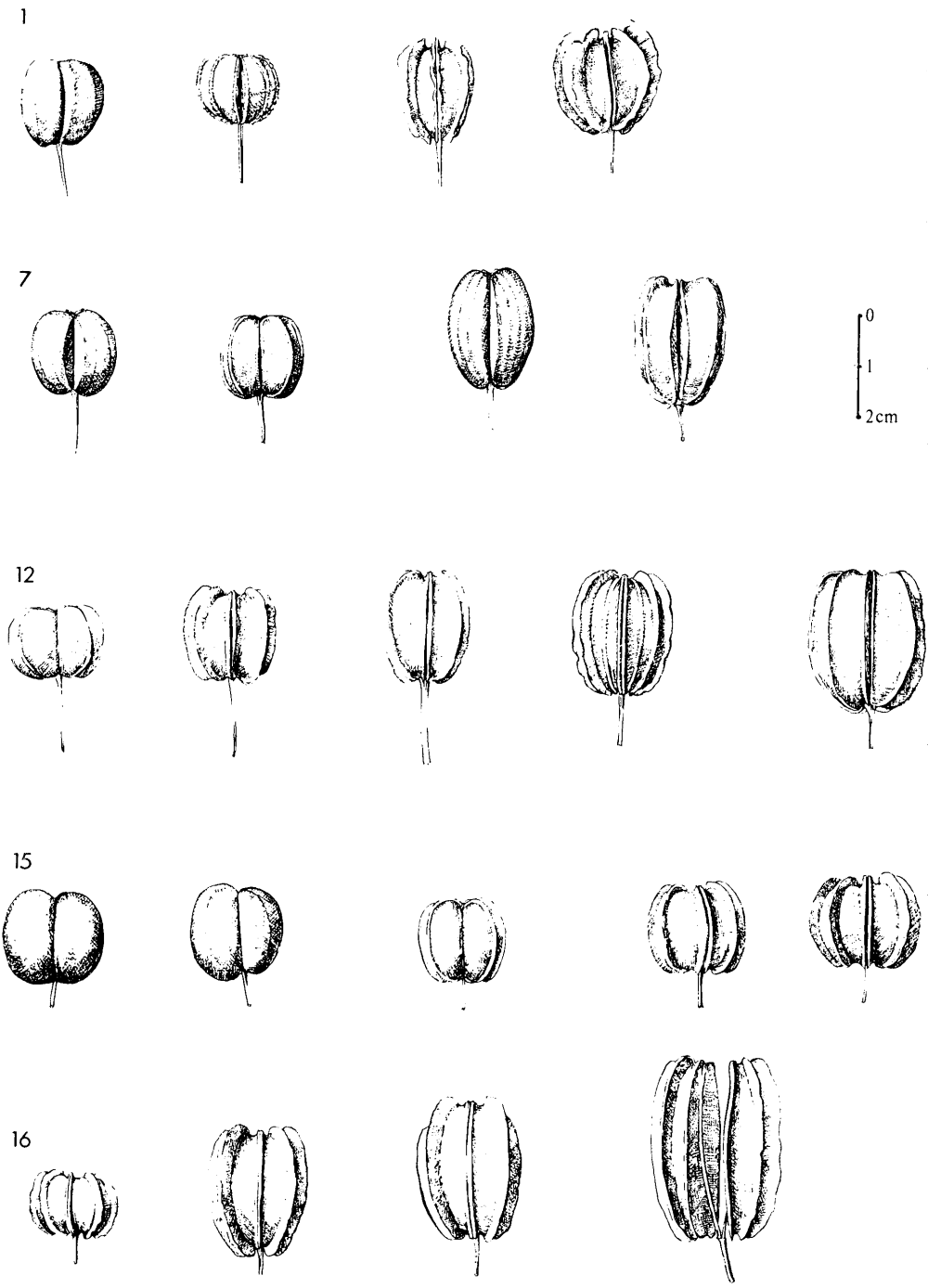


Fig. 2.

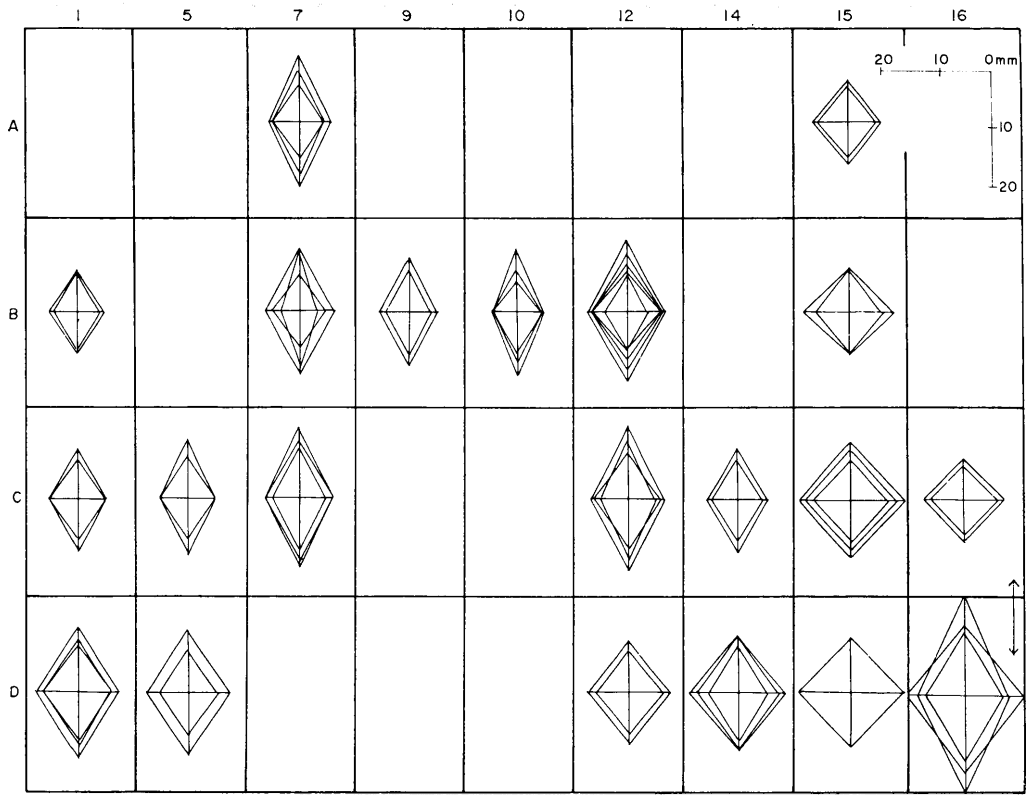


Fig. 3. Diagrammatic representation of inter- and intrapopulational variation in fruit shape of *Cachrys ferulacea*. Each vertical row represents one population (numbers as in Table 1); each horizontal row shows the extent of wing development. (A: Fruit smooth. B: With prominent ridges. C: With wings up to 1.5 mm wide. D: With wings 2—4 mm wide.) — In each square one to several fruits are represented by rhombs (horizontal diagonal shows width, vertical shows length).

winged), the length of the fruit in relation to the length of the pedicel; the size and indumentum of terminal leaf lobes.

Chromosomes were studied in seven populations. In four, mitotic metaphase was investigated in roots of seedlings pre-treated with paradichlorobenzene; squashes were made in 2 % aceto-orcein. In three populations meiosis in PMCs was studied in 2 % aceto carmine smears.

RESULTS

FRUIT. Many of the characters examined were found to be extremely variable within populations and between populations (Figs. 2 and 3).

In general populations differ greatly from one another in the size, shape and ridge development of the fruit. Also, whereas some populations are homogeneous in fruit shape (populations 7, 9, 10, 15), length (5, 9, 14, 15), ridge development (5, 9, 10, 14, 16) and suberization (5, 9, 10, 11, 14), others show remarkable heterogeneity of shape (1, 5, 12, 14, 16), length (1, 7, 10, 12, 16), ridge development (1, 7, 12, 15) and suberization (1, 7, 12, 15, 16).

Table 2. Range of variability of fruits in single plants. Each population is represented by one plant (as a rule the more variable plants were chosen in field studies). All measurements in mm.

Population number	Fruit length	Fruit, length/width ratio of extreme values	Width of ridges of fruit
1	15—22	1.8—2.1	0.25—1.5
2	10.5—17	1.1—1.6	0.25—0.75
4	10—16.5	1.2—1.4	0—0.25
6	11.5—21	1.6—1.9	0.25—0.75
7	16—25.5	2.0—2.3	0—0.75
8	(12) 16—21	1.5—1.6 (1.7)	0.25
9	15—25	1.6—2.6	0
10	14.5—19	1.8—2.2	0—0.25
11	12.5—23	1.2—1.4	0—0.5
12	13—19	1.2—2.0	0.25—0.5
13	17—22	1.6—1.8	0.5—1
14	13—20.5	1.3—1.5	0.25—1
15	11.5—19	1.2—1.5	0
15	12—25	1.1—1.4	0.75—2
16	20—36	1.9—2.1	0.5—2

The variation in fruit shape in single plants was studied in each population (usually over 100 fruits per plant). The characters measured were length, breadth and ridge development. Fruits of single plants show considerable variation in all characters mentioned and may represent the range of variability existing in the population as a whole (Table 2).

The relative amount of suberized tissue and the size of ridges or wings (=ridges over 1 mm wide) as compared with the whole fruit may gradually change during fruit ontogenesis and may reach a different degree of development in mature fruit (Fig. 4 A—C). Sometimes wings of the young fruit are somewhat undulate, straightening later (this may be the source of the records of *C. asperula* Boiss. from Israel).

The ratio fruit/peduncle was as a rule found to be most inconstant and therefore an unreliable character.

LEAVES. The size of leaves, of leaf segments and lobes is variable within and between populations. Some examples of the variation of leaf segments and lobes may be seen in Fig. 5. Fig. 6 is a diagrammatic representation of the length and width of leaf lobes of some plants within each of the populations studied.

Scabridity of leaves and other parts (assessed by the number of papillae per square unit) was found to be fairly constant within each population but varied greatly between populations.

CHROMOSOMES. The same chromosome number was found in seven populations examined: 2n=66 (populations 6, 10, 12, 16) (Fig. 4 D); n=33 (populations 9, 14, 15). Karyotypes seem to be identical according to a preliminary study.

CONCLUSIONS AND DISCUSSION

The characters studied by us are mainly those used for defining the genera *Cachrys* and *Prangos*, i. e., in the former, wingless strongly suberized fruit, in the latter, winged and only slightly suberized fruit. However, these characters were found to exhibit a wide range of variability in and between populations and no correlation between this variability and the variation

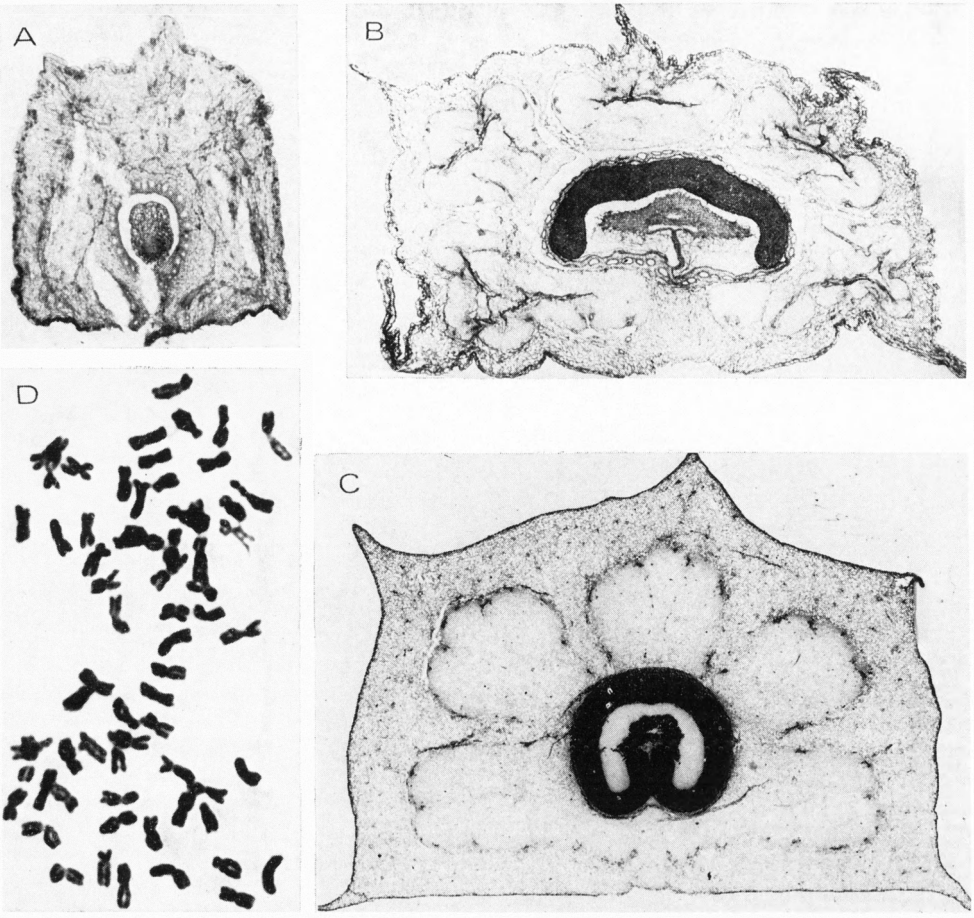
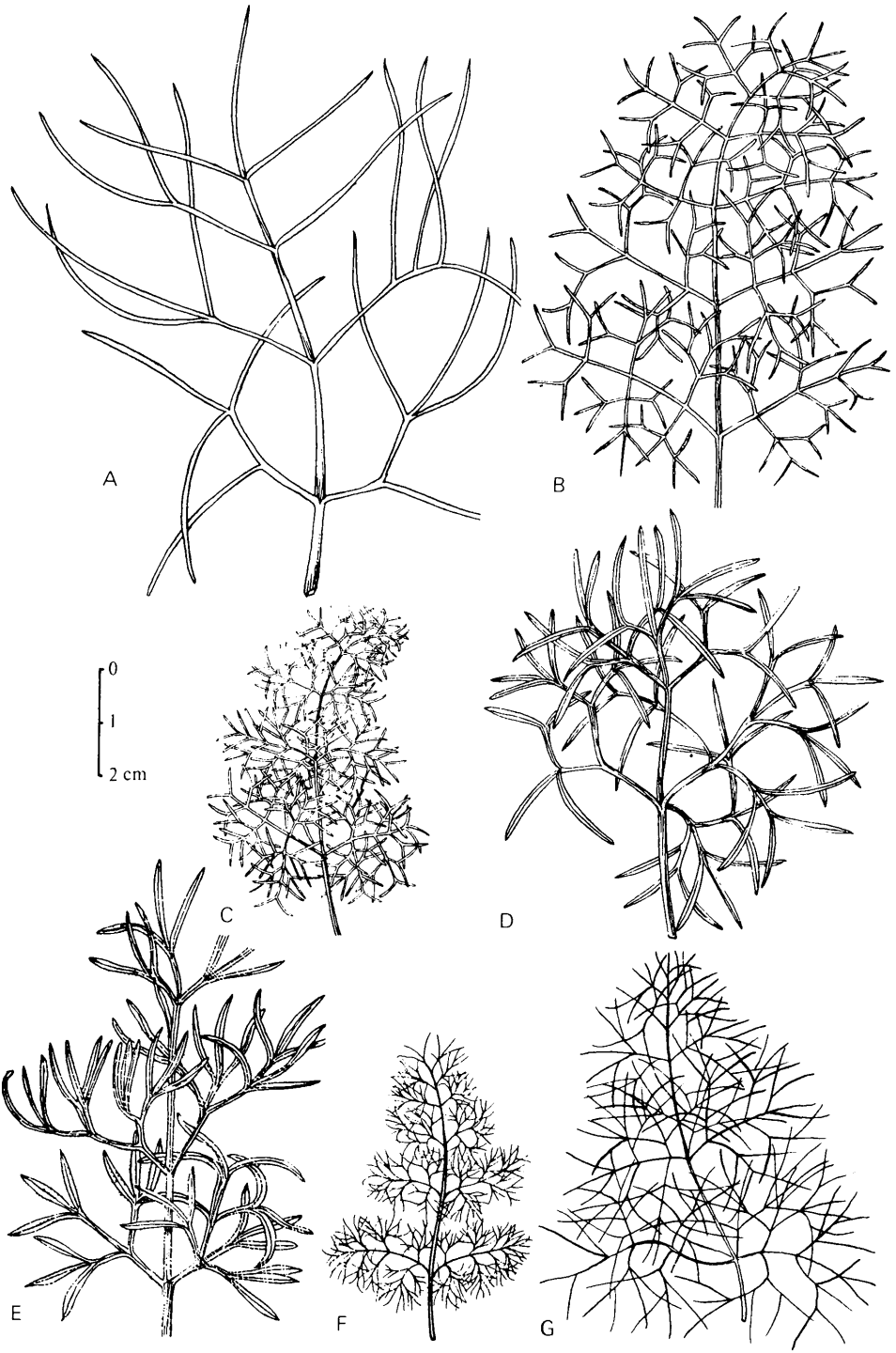


Fig. 4. A—C: Fruit ontogenesis in *Cachrys ferulacea* (cross-sections of one mericarp). A: × 19. B: × 9.5. C: × 7.5. — D: Chromosomes of metaphase plate in root tip mitosis. ca. × 1350. — A—C: population 5. D: population 10; numbers correspond to those in Table 1.

in length and breadth of leaf lobes could be observed. The fruit characters studied intergrade, they occur in diverse combinations within single populations and vary to some extent even between individual fruits of single plants. Therefore it does not seem reasonable to separate the two genera on the basis of these characters and because of priority the thus extended genus must be named *Cachrys* L. (cf. GRUENBERG-FERTIG et al. 1973).

Even more, because of the continuous variation in characters it seems that all plants examined must be regarded as part

Fig. 5. *Cachrys ferulacea*. Inter- and intrapopulational variation in leaf segments and lobes. — A, B: Population 7; C, D: Population 9; E, F: Population 1; G: Population 12. Numbers correspond to those in Table 1.


A
B
0
1
2 cm
C
D
E
F
G

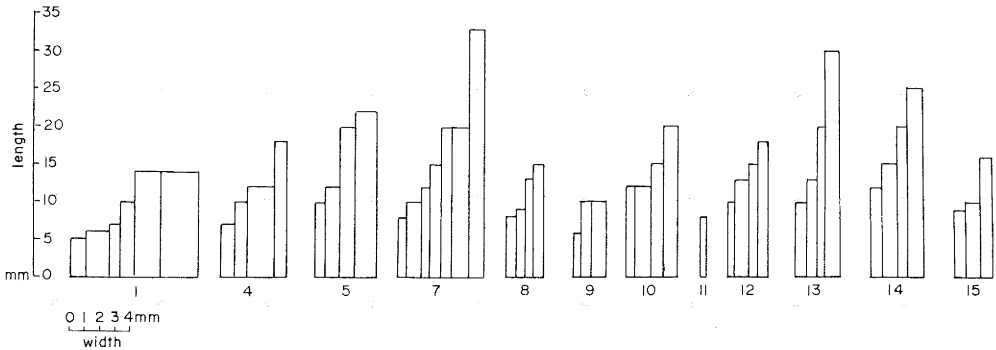


Fig. 6. *Cachrys ferulacea.* Diagrammatic representation of the variation in size of leaf lobes in and between populations; each column represents the longest terminal leaf lobe of one plant (population numbers correspond to those in Table 1).

of one species with a wide range of variation. (Such variation might be explained to some extent by the hexaploid level of the plants.) The earliest name available for this taxon is *C. ferulacea* (L.) CALEST. This species has a wide range of distribution — from Italy eastwards to Iran, Armenia and the Caucasus and throughout the eastern Mediterranean. All other species of "*Cachrys*" and "*Prangos*" previously recorded from Israel are to be referred to *C. ferulacea* and to be considered synonymous with it.

ACKNOWLEDGEMENTS

Thanks are due to Mrs E. HUBER for the drawings and to Mrs R. FRENKEL for the map and the diagrams.

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Asystasia laticapsula (Acanthaceae), a Widely Used but Previously Invalid Name

Per-Olof Karlström

KARLSTRÖM, P.-O. 1975 10 10. Asystasia laticapsula (Acanthaceae), a widely used but previously invalid name. — Bot. Notiser 128: 235—238. Lund. ISSN 0006-8195.

Asystasia laticapsula is described from tropical East Africa. The somatic chromosome number found is 2n=26.

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Asystasia laticapsula C. B. CL. ex KARLSTRÖM, sp. nov.

Herba perennis, usque ad 40 cm alta, basi decumbens, partes floriferae erectae. Planta omnis pilis multicellulosis uniseriatis praedita. *Folia* oblonga, pilosa, pili plerumque 8—10-cellulis praediti; lamina 3—7 cm longa, 1—2 cm lata, apice obtusa—subacuta, basi attenuata; petioli usque ad 3 mm longi, plerumque circiter 2 mm longi. *Inflorescentiae* axillares, racemosis instructae, usque ad 20 cm longae (pedunculo incluso), plerumque 6—8-floribus ornatae; bracteae minutae, lineares, usque ad 3 mm longae; pedicelli circiter 2 mm longi, ad basin bracteolis linearibus, circiter 2 mm longis, praediti. *Calyx* 5-partitus, pilis uniseriatis, cellulosis (4 cellulae) obtectus; segmenta calycis linearia, 8—13 mm longa, 1 mm lata. *Corolla* alba, lobus inferior prope faucem maculis violaceis ornatus; tubus circiter 15 mm longus, ad basin 2—3 mm latus, ad faucem gradatim dilatatus usque ad circiter 5 mm. *Stamina* 4; filamenta basi per paria usque 0,5 mm connata, breviora 4 mm longa, altiora 5 mm longa; antherae 3 mm longae. Granulae pollinis 3 poris instructae, 50—53 µm × 30—32 µm. *Ovarium* pilis uniseriatis obtectum; basis styli aeque pilosa. *Capsula* circiter 2 cm longa, pilis multicellulosis uniseriatis et pilis glandulosis instructa. *Semina* 4, 3—4 mm diametro, compressa, rugosa.

Perennial herb up to 40 cm high, decumbent at base, flowering parts erect. The whole plant covered with many-celled, uniseriate hairs. Leaves oblong with generally 8—10-celled, uniseriate hairs; laminae 3—7 cm long, 1—2 cm wide, obtuse to subacute at apex, narrowed at base into the very short petiole (Fig. 2 D); petioles up to 3 mm long, usually about 2 mm. Cystoliths common in stems and leaves, solitary, rounded or somewhat elongated, blunt at both ends. Inflorescences axillary, racemose, loose, up to 20 cm long (the lower flowerless part included), mostly 6—8-flowered; lower flowers remote. Bracts minute, linear, up to 3 mm long (Fig. 2 B). Pedicels about 2 mm long, with two linear bractlets about 2 mm long, near the base. Calyx divided to the base, segments 5, linear, 8—13 mm long, 1 mm wide, covered with 4-celled, uniseriate hairs (Fig. 2 B). Corolla white, lower lip with violet markings near the throat (Fig. 1 A, B); tube about 15 mm long, 2—3 mm wide near the base, expanding to about 5 mm at the throat. Stamens 4; filaments basally united in pairs (Fig. 2 E), shorter ones 4 mm long, longer ones 5 mm long; anthers 3 mm long. Pollen grains 3-porate, prolate, 50—53 µm×30—32 µm. Style base and ovary covered with uniseriate hairs (Fig. 2 C); ovary 2-celled with 2 ovules in each cell. Capsule 4-seeded, about 2 cm long (Fig. 2 F), with many-celled, uniseriate hairs and stalked glandular hairs. Seeds 3—4 mm in diameter, compressed, rugose (Fig. 2 G).

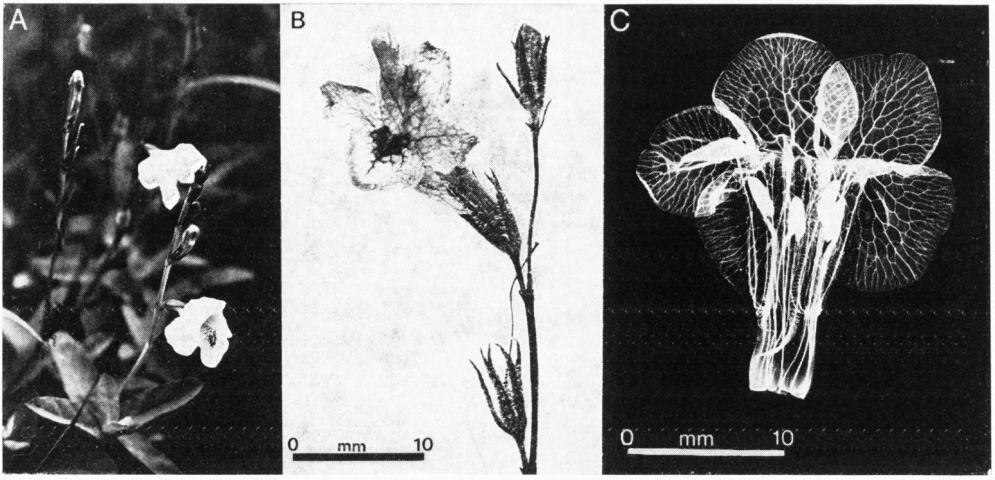

Fig. 1. *Asystasia laticapsula*. — A: Flowering specimen. Photo: P.-O. KARLSTRÖM, Ruiru, 16 km NE Nairobi 13.V. 1971. — B: Part of inflorescence (BALLY 356 a). Photo: D. NILSSON. — C: Corolla, showing the attachment of the stamens (KARLSTRÖM 371). Photo: D. NILSSON.

CHROMOSOME NUMBER. 2n=26. Counts were made in six cells, all from one plant.

TYPE COLLECTION. Kenya, "British East Africa", near Nairobi 1903 A. WHYTE s.n. (K; two sheets, one of which is the holotype).

FURTHER COLLECTIONS STUDIED. Kenya. ARCHER 204 (K), BALLY 356 a (K), BOGDAN 838 (K), ELLIOTT s.n. (K, mounted on the same sheet as one of WHYTE's specimens), GILLET 18108 (K), HINDORF 823 (K), KARLSTRÖM 306, 352, 356, 371 (GB), NAPIER 426 (K), NAPPER & ABDALLAH 1896 (K), STRID 4029 (GB), VERDCOURT 506 (K), VERDCOURT & POLHILL 3163 (K).

Asystasia laticapsula is a commonly used name for a species from tropical East Africa characterized among other things by oblong, hairy leaves, white corolla, and the lower lip of the corolla with violet markings near the throat. The specific epithet originates from a specimen collected by ALEXANDER WHYTE near Nairobi in 1903 and labelled "Asystasia laticapsula sp. nov. C. B. Cl. ms 17 Aug. 1901". (The date is probably incorrect, since another specimen collected by WHYTE near Nairobi in 1903 is labelled "Asystasia laticapsula sp. nov. C. B. Cl. ms 17 Aug. 1905".) The label bears the annotation "Close to A. coromandeliana Nees. Capsule broader, more hairy. Corolla smaller. Leaves more oblong and hairy". In a recently published flora of upland Kenya (AGNEW 1974) the species described above is included, and there is also a drawing of the species. The species is cited as "*Asystasia laticapsula* C. B. CL.". However CLARKE never published a description of the species. In order not to cause confusion I have chosen to use the specific epithet *laticapsula* since many botanists do so for the species described above.

All specimens studied originate from Kenya. According to Dr R. WINGFIELD, the university of Dar es Salaam, Tanzania, who is working on the "*Asystasia gangetica*" group in East Africa, *A. laticapsula* probably occurs throughout Tanzania above 550 m and probably in all surrounding countries (pers. comm.).

Fig. 2. *Asystasia laticapsula.* — A: Specimen grown under greenhouse conditions and taken from the same population as the specimen in Fig. 2 D. — B: Detail of inflorescence showing calyx, bracts and bractlets (KARLSTRÖM 356). — C: Gynoecium with hairy style base and ovary (KARLSTRÖM 371). — D: Specimen collected in the field in Kenya (KARLSTRÖM 371). — E: Corolla opened (corolla from the same specimen as in Fig. 2 A). — F: Ripe capsule (KARLSTRÖM 352). — G: Seed (KARLSTRÖM 352).

Specimens were collected by me in different grassland localities in Kenya during the period Dec. 1970—Jan. 1971 and in May 1971. The cuttings collected were grown at the Department of Systematic Botany, University of Göteborg. Compared with the collected specimens, these plants often had leaves that were more markedly oblong, had longer and wider laminae and longer petioles (Fig. 2 A). This is probably due to the favourable conditions in the greenhouse.

Cystoliths are common in the stems and leaves of *A. laticapsula*. They are solitary, rounded or somewhat elongated, blunt at both ends. This is in agreement with HOBEIN (1884), who studied the cystoliths in several species of the Acanthaceae, including some species of *Asystasia*.

Asystasia incl. *A. laticapsula* has been studied embryologically by KARLSTRÖM (1974).

ACKNOWLEDGEMENTS

I am much indebted to Professor GUNNAR HARLING for the critical reading of the manuscript and to Dr UNO ELIASSON for fruitful discussions on taxonomy and terminology. The Latin diagnosis was written by Dr EMIN TENGSTRÖM. I greatly appreciate his kindness and help.

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Cytological Studies in the Macaronesian Genus Argyranthemum (Compositae: Anthemideae)

Christopher John Humphries

HUMPHRIES, C. J. 1975 10 10. Cytological studies in the Macaronesian genus Argyranthemum (Compositae: Anthemideae). — Bot. Notiser 128: 239—255. Lund. ISSN 0006-8195.

Seventeen species of *Argyranthemum* WEBB ex SCHULTZ BIP. from the Canary Islands and the Salvage Islands have been investigated cytologically. All taxa are diploid (x=9), except for a cultivated population of the natural hybrid *A. frutescens* (L. FIL.) SCHULTZ BIP. × *A. coronopifolium* (WILLD.) WEBB ex SCHULTZ BIP., which has a range of chromosome numbers between the diploid and tetraploid levels. Chromosome counts have been determined in 72 populations.

A general survey of chromosome morphology at mitosis is presented. Twenty-eight populations representing 12 species have been studied in detail and variation in two pairs of marker chromosomes is given. Differences are in no way correlated with recognised taxa but do vary significantly between populations. Details of pairing behaviour at meiosis are also given and chiasma frequency variation is discussed in the light of its adaptive significance.

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Since 1969 the author has been studying relationships in *Argyranthemum* WEBB ex SCHULTZ BIP., a woody perennial genus allied to *Chrysanthemum* L. s.str., endemic to the Macaronesian archipelagos of Madeira, the Salvage Islands and the Canary Islands.

The purpose of the work is partly to provide a taxonomic revision of the genus (HUMPHRIES 1973, 1975 in press), but principally to study problems of variation and evolution at the population level in one of the largest Macaronesian endemic genera. For this type of investigation, chromosome studies and crossing experiments have provided a wealth of valuable information for interpretation of the evolutionary situation in *Argyranthemum*.

This publication is the first of two papers on problems of adaptation in *Argyranthemum* and part of a wider study on the systematics of the Compositae: Anthemideae. In the present paper a general survey of chromosome number, chromosome morphology at mitosis, and pairing behaviour at meiosis in cultivated and natural populations of seventeen species of *Argyranthemum* will be given.

MATERIAL

The genus *Argyranthemum* consists of twenty-two allopatric species appearing in all of the principal vegetation zones of the northern Macaronesian archipelagos, except the Azores (HUMPHRIES 1973, 1975 in press). Apart from two relatively widespread species, *A. frutescens,* a polymorphic coastal and lowland species found on the islands of Tenerife, Gran Canaria and Gomera and *A. adauctum* (LINK) C. J. HUMPHRIES an upland species found in the pine forests and highlands of Gran Canaria, Tenerife and Hierro, the remaining species occur as distinct, isolated population groups on individual islands. The taxonomy and nomenclature follows that of HUMPHRIES (1975 in press).

The cultivated material was raised primarily from seed collected in the Canary Islands by Dr D. BRAMWELL and myself during the spring of 1971. Seed was also provided by Dr D. BRAMWELL, the late Dr E. R. SVENTENIUS, Mr G. KUNKEL and Miss LIV BORGEN from collections made by them during 1969, 1970 and 1971. Chromosome numbers have been determined in all populations and marker chromosomes from at least one or two populations of each taxon have been examined in detail. Pairing behaviour at meiosis has been studied in buds fixed in the field during 1971.

PREPARATORY TECHNIQUES

Mitotic preparations were made from root-tips of 3—12-month-old plants using monobromonaphtalene for pre-treatment, Feulgen and acetic orcein as stains. Meiotic preparations were stained with acetic orcein without prior fixation. Slides were made permanent by using the 'Arcton' (CF_2Cl_2) gas method.

CHROMOSOME MEASUREMENTS

For karyotype studies 10 good mitotic preparations showing about the same degree of chromosome contraction were selected from each plant. Usually 4—5 plants were studied in any one population. Drawings were made with the aid of a Zeiss camera lucida at a magnification of × 1600. Measurements were taken from the drawings, and the diagrams in Fig. 1 represent the karyotypes examined in detail. Photographs in Figs. 2 and 3 were taken on a Zeiss photomicroscope. The populations studied were all from Canary Islands taxa, apart from one sample of *Argyranthemum thalassophilum* from the Salvage Islands. No data for Maderian plants are available.

The definition of chromosome type is based upon the scheme devised by LEVAN et al. (1965), whereby the centromeric position is determined by calculating the r-index.

To show variation between populations, the ordinary r-index (long arm/short arm) and the l-index (haploid complement/length of the chromosome) were calculated for two marker chromosomes. The chromosomes with satellites (SAT-chromosomes) numbers 13, 14, 15 and 16 (Fig. 1) were easily identified and used for statistical calculations. The length of the satellite, but not of its connecting thread was added to the length of the short arm.

SOURCES OF ERROR IN THE DETERMINATION OF ARM RATIOS

During the preparation of root tip squashes for comparative studies at mitosis there are many occasions when artifacts may occur both mechanically and through the influence of chemical treatments (SYBENGA 1959, BOTHMER 1970, BENTZER et al. 1971), notably in the use of pre-treatment drugs for chromosome contraction. Mechanical difficulties usually arise from uneven squashing, causing stretching or constrictions of chromosome segments and poor separation of chromosomes causing overlapping, twisting and apparent shortening by vertical rises within the cell (LEWITSKY 1931, SYBENGA 1959, SIMAK 1962, BOTHMER 1970).

There are several reports on information regarding chemically induced contraction during the course of mitosis. SASAKI (1961) observed that long mammalian chromosomes for example, varied more in relative length than short ones under colchicine pre-treatments and thus had a distinct tendency for centralisation of the centromere in highly differentiated karyotypes. In groups with symmetrical karyotypes, such as *Argyranthemum* this effect is likely to be small and can be disregarded (BOTHMER 1970). BENTZER et al. (1971) indicated that the same applies with long chromosome arms versus short ones. SYBENGA (1959), working on the cereal grass *Secale,* observed that similar effects were achieved with a variety of different pre-treatments including 8-hydroxyquinoline and monobromonaphthalene.

In *Argyranthemum* identification of individual chromosomes is the worst problem so far encountered. In m-chromosomes with low r-values and no secondary constriction confusion between non-homologous arms and reversal of homologous chromosomes is unavoidable when the significant difference between overall arm lengths is less than 12—20 % (SIMAK 1962, MATERN & SIMAK 1968, BOTHMER 1970).

Table 1. Chromosome number reports in *Argyranthemum*.

Species	Present determinations		References for previous determinations
	Somatic 2n=18	Gametic n=9	
frutescens			
subsp. *frutescens*	×	×	Shimotomai 1937, Dowrick 1952, Tahara 1915, Harling 1951, Larsen 1960, Bramwell et al. 1971
subsp. *succulentum* ..		×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
subsp. *gracilescens* ..	×	×	Borgen 1969, Bramwell et al. 1971
subsp. *parviflorum* ..	×	×	Larsen 1960
subsp. *foeniculaceum* .	×	×	Larsen 1960
subsp. *canariae*	×	×	
subsp. *pumilum*		×	
haouarytheum	×	×	Harling 1951, Bramwell et al. 1971
foeniculaceum	×	×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
gracile	×	×	Harling 1951, Larsen 1960, Borgen 1969
tenerifae	×	×	Harling 1951, Linder & Lambert 1965 Larsen 1958, 1960, Borgen 1969, 1970, Bramwell et al. 1971
maderense	×	×	Larsen 1958, 1960, Borgen 1970
winteri		×	
lidii		×	
thalassophilum	×	×	
callichrysum	×	×	Bramwell et al. 1971, Borgen 1974
coronopifolium	×	×	Larsen 1960, Bramwell et al. 1971
broussonetii			
subsp. *broussonetii* ..	×	×	Larsen 1958, 1960, Borgen 1970
hierrense	×	×	
webbii		×	
filifolium	×	×	Shimotomai 1937, Dowrick 1952, Borgen 1970
escarrei		×	
adauctum			
subsp. *canariense* ...	×	×	Larsen 1960, Borgen 1969, Bramwell et al. 1971
subsp. *gracile*	×	×	Larsen 1960
subsp. *jacobaeifolium*		×	Borgen 1970
subsp. *dugourii*		×	
subsp. *adauctum*		×	Larsen 1960
subsp. *erythrocarpon* .		×	

In *Argyranthemum* virtually the whole karyotype consists of m-chromosomes (with r-values around 1) and the total complement has less than a 20 % difference between the largest and smallest chromosomes at any stage during contraction. Closer study of the whole karyotype is therefore impossible and detailed arm-ratio analysis has been restricted to the two pairs of chromosomes with secondary constrictions (Fig. 1; nos. 13—14, 15—16), the only ones to be positively identified in any preparation without fear of misidentification or reversal. Idiogram analysis to compare different taxa has not been carried out due to the difficulties outlined above, but samples of each examined species are presented to give an idea of the variation throughout the genus.

RESULTS

Chromosome Numbers

All species of *Argyranthemum* hitherto investigated from natural populations are diploid, with a basic number of x=9 and a somatic chromosome number of 2n=18 (TAHARA 1915, HARLING 1951, LARSEN 1958, 1960, BORGEN 1969, 1970, 1974). Table 1 shows the chromosome numbers determined by previous authors and the new counts resulting from this study.

During the course of this work new counts have been made for 6 species, 2 subspecies of *A. frutescens,* and 2 subspecies of *A. adauctum* and confirmed at least once in 10 of the remaining 16 species.

Sterile triploids have been reported for garden populations of *A. frutescens* (TAHARA 1915, DOWRICK 1952), a plant commonly known as the 'Paris Marguerite'. In the present study diploids have been found in all field population samples, but in F_2 and later generations cultivated from seed collected from a single population occurring in the wild of the hybrid between *A. coronopifolium* and *A. frutescens* subsp. *frutescens.* In this, the only example of natural interspecific hybridisation within the genus, plants with somatic numbers ranging from 18 to 36 were detected (HUMPHRIES 1973). It seems possible that disturbances during meiosis have given rise to unbalanced gametes in the hybrid plants, in turn giving rise to aneuploids, triploids and tetraploids. Moreover, individuals normally having 18 chromosomes in the complement have numbers of 19, 24, 27, 35, 36, and 37 in some root-tip cells. The triploid is shown in Fig. 2 A.

Chromosome Morphology

In *Argyranthemum* there is little apparent structural differentiation of the karyotype between the various species. The chromosomes are more or less symmetrically metacentric (m) or submetacentric (sm) (Fig. 1, 2 B, C). There is a small but continuous transition from the largest to the smallest chromosomes, and there are no chromosomes conspicuously larger or smaller than the others. In most cases the only chromosomes that can be identified with certainty are the SAT-pairs 13—14, 15—16 (Fig. 1). One exception is a pair of subterminal (st) chromosomes detected in *A. hierrense* (Fig. 1 N).

Most previous cytological reports of chromosome morphology in the Canary Islands species have mentioned the ocurrence of none, or only one pair of satellite chromosomes (DOWRICK 1952, LARSEN 1958, 1960, BORGEN 1969, 1970, 1974). This is not borne out by my results. Only the Salvage Islands species *A. thalassophilum,* reported here for the first time (Fig. 1 K), has been seen to have one pair of satellite chromosomes and in all other species two pairs are present.

The short arm and satellites of the non-homologous chromosome-pairs (13—14, 15—16) can usually be separated from one another as the long arm is consistently longer in chromosomes 13—14. Thus, a much higher r-value is obtained. In both pairs of chromosomes with secondary constrictions the satellites consist of a small distal body connected to the short arm by a thin thread. In chromosomes 15—16 the satellite is sometimes larger than the non-homologous satellites of chromosomes 13—14 and in good preparations of early metaphase with little contraction in the connecting thread, an interstitial body comparable to the 'tandem satellites' described by JONES & JOPLING (1972) can be seen (Fig. 2 B).

Chromosome Variation

To investigate the possibility of interpopulational chromosomal differences, 28 populations belonging to 12 different species were examined in respect of the r-index and l-index for the chromosome pair 15—16. Similar data were also obtained for the chromosome pair 13—14 in 21 populations of 6 different species.

Fig. 1. Karyotypes from root-tip mitoses in different species of *Argyranthemum*. — A: *A. frutescens* subsp. *frutescens* (70247). — B: *A. frutescens* subsp. *gracilescens* (71020). — C: *A. frutescens* subsp. *parviflorum* (71012). — D: *A. frutescens* subsp. *canariae* (71039). — E: *A. frutescens* subsp. *foeniculaceum* (71022). — F: *A. haouarytheum* (70266). — G: *A. foeniculaceum* (70036). — H: *A. gracile* (70227). — I: *A. maderense* (70076). — J: *A. callichrysum* (70284). — K: *A. thalassophilum* (71010). — L: *A. broussonetii* subsp. *broussonetii* (71030). — M: *A. coronopifolium* (70236). — N: *A. hierrense* (71006). — O: *A. filifolium* (71008). — P: *A. adauctum* subsp. *canariense* (71039). — Scale 10 µ.

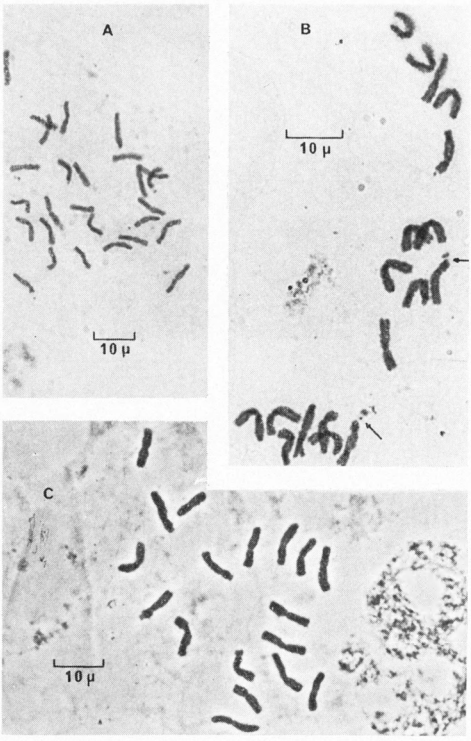

Fig. 2. Metaphases of root-tip mitoses in *Argyranthemum*. — A: Cultivated triploid progeny of the natural hybrid *A. frutescens*× *A. coronopifolium* (population 70237). — B: *A. frutescens* subsp. *frutescens* (population 70247). — C: *A. frutescens* subsp. *gracilescens* (population 71020). — Arrows refer to "tandem satellites" (see p. 242).

The data are presented in Table 2 and the t-values obtained by comparing mean values and standard deviations for homologous chromosomes measurements are presented in Figs. 3—6. In many cases it appears that the differences are statistically significant, from which several conclusions can be drawn:

1. There is a wider and more independent range of variation in the chromosome pair 15—16 for both the relative arm-length (r-index) and relative chromosome-length (l-index) than in chromosomes 13—14.

2. Variation in relative arm-length is greater than in relative chromosome-length for the same chromosome.

3. Populations 71013, 70223, 71021, 71039, 70224, 71030, 70238, 70240, 70236 and 70219 appear to be the most distinctive populations.

4. There tends to be greater variation between populations of different species than between populations of the same species. Thus, the ten populations of *A. frutescens* show fewer significant differences, than for example occur between the other populations listed in Figs. 3—6, which belong to different species.

Meiosis

Diakinesis and metaphase I were studied in 51 populations belonging to 15 species of Canary Islands *Argyranthemum*. The haploid number was invariably n=9 and several new counts confirming this chromosome number have been determined in the following taxa: *A. frutescens* subsp. *canariae*, *A. adauctum* subsp. *dugourii* and subsp. *erythrocarpon*, *A. winteri*, *A. lidii*, *A. hierrense*, *A. webbii* and *A. escarrei* (Table 1).

In most populations chromosome pairing is normal, with 9 bivalents being formed (Table 3). The chiasma position can be terminal, subterminal or median (Fig. 7 A, C).

Variation in Chiasma Frequency

There is good reason to suppose that adjustments in chiasma frequency at meiosis may have a direct adaptive significance (Rees & Ahmad 1963, Jones & Rees 1966, Crowley 1969, Rees & Dale 1974) as there is a strong correlation between chiasma position and genetic recombination (Darlington 1939). One expects, therefore, to find variation in chiasma frequency within and between populations of the same and different species exposed to different kinds of selection in different habitats as recombination

Table 2. r-index (relative arm length) and l-index (relative chromosome length) values for the homologous chromosome pairs 13—14 and 15—16 in twelve species of *Argyranthemum*. Means ± standard deviations.

Population number	Species	Chrom. 13—14		Chrom. 15—16	
		r-index	l-index	r-index	l-index
	frutescens				
70247	subsp. *frutescens*	2.46±0.54	9.4 ±0.95	1.98±0.5	9.98±0.2
70282	„	2.40±0.3	8.6 ±1.2	2.4 ±0.5	10.2 ±0.6
71013	„	2.78±0.5	8.85±0.86	2.6 ±0.57	9.95±0.4
70223	„	2.96±0.57	9.76±0.6	2.68±0.59	9.9 ±1.1
71031	subsp. *gracilescens*	3.36±0.95	8.92±0.89	2.29±0.67	9.48±0.96
71020	„	2.5 ±0.70	9.4 ±0.67	1.86±0.2	9.7 ±1.1
71021	„	2.75±0.3	9.1 ±0.28	2.74±0.2	10.2 ±0.1
71012	subsp. *parviflorum*	2.26±0.15	9.56±0.58	1.9 ±0.4	10.6 ±1.2
71022	subsp. *foeniculaceum* ...	2.74±0.38	8.78±1.26	2.26±0.28	10.46±0.9
71039	subsp. *canariae*	3.29±0.78	9.96±2.26	2.3 ±0.2	9.86±1.78
70266	*haouarytheum*	2.96±0.54	9.02±1.14	2.12±0.67	10.5 ±1.25
70267	„	2.74±0.6	8.66±1.3	1.64±0.39	10.84±0.74
70228	„	2.32±0.68	9.55±0.6	2.09±0.5	10.2 ±1.29
70036	*foeniculaceum*	—	—	1.72±0.59	8.95±0.87
70227	*gracile*	—	—	7.74±0.4	8.98±1.22
70076	*maderense*	—	—	1.8 ±0.38	8.3 ±0.58
71010	*thalassophilum*	—	—	2.4 ±0.7	8.95±1.57
70240	*callichrysum*	2.18±0.54	9.46±1.35	2.28±0.38	8.82±0.87
70284	„	2.19±0.66	9.67±1.3	2.55±0.58	9.28±1.13
70236	*coronopifolium*	2.5 ±0.7	9.82±1.8	2.46±0.85	9.14±0.7
70219	„	2.1 ±0.27	9.85±0.84	2.11±0.4	8.13±0.5
	broussonetii				
71030	subsp. *broussonetii*	2.63±0.69	10.0 ±1.1	3.05±0.4	9.58±0.54
70238	„	3.04±0.75	9.95±1.8	3.68±0.88	8.3 ±1.04
71042	„	2.18±0.79	10.24±1.5	1.85±0.4	8.95±1.25
71005	*hierrense*	—	—	1.57±0.36	9.17±1.57
71006	„	—	—	2.0 ±0.7	8.85±0.33
71008	*filifolium*	—	—	1.7 ±0.17	9.23±0.32
	adauctum				
70224	subsp. *canariense*	2.0 ±0.1	8.3 ±0.1	2.4 ±0.1	8.3 ±0.1

at meiosis in outbreeders is a major source of heritable variation. The survey has shown that indeed significant differences can be found and Table 3 gives a list of the chiasma frequencies for the populations studied in *Argyranthemum*. The results indicate that there is a wider range of chiasma frequencies for populations of widespread variable species (e.g. *A. frutescens* and *A. adauctum)* than for distinctive, less variable 'narrow' endemics of restricted distributions (e.g. *A. filifolium, A. lidii* and *A. escarrei*).

In virtually every plant in which meiosis was studied in detail the pollen mother cells showed a regular formation of bivalents at prophase and metaphase I. However, a single interchange has been detected in two populations of *Argyranthemum* (Table 3). Quadrivalents occur in 25 % of cells examined in plants from a large population of *A. frutescens* subsp. *frutescens* collected at Santa Ursula on Tenerife (Fig. 7 B) and a similar percentage of interchange heterozygotes was found in a large population of *A. adauctum*

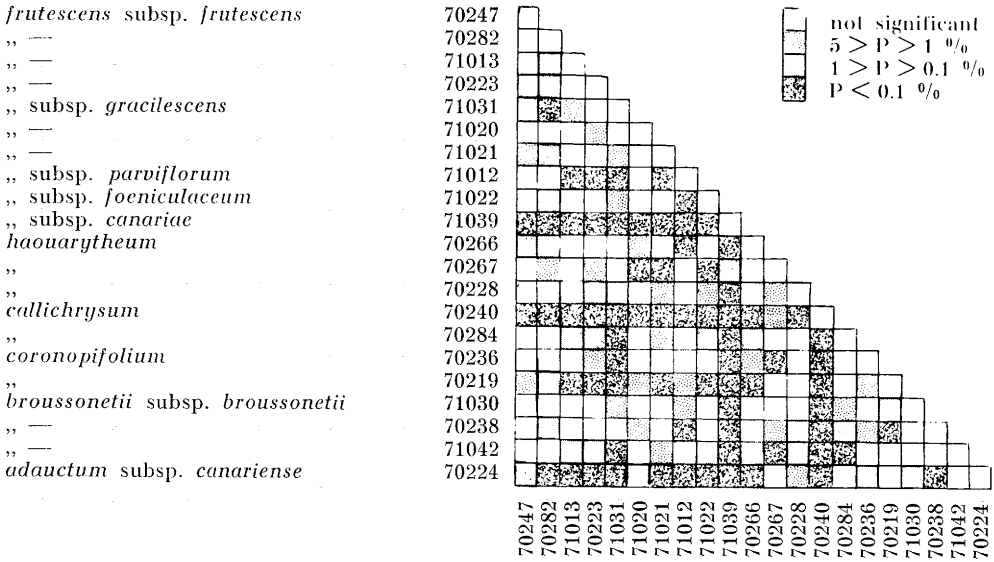

Fig. 3. Significant t-values obtained by comparing arm indices (r-index) for chromosomes no. 13—14 in 21 populations from 6 species of *Argyranthemum*.

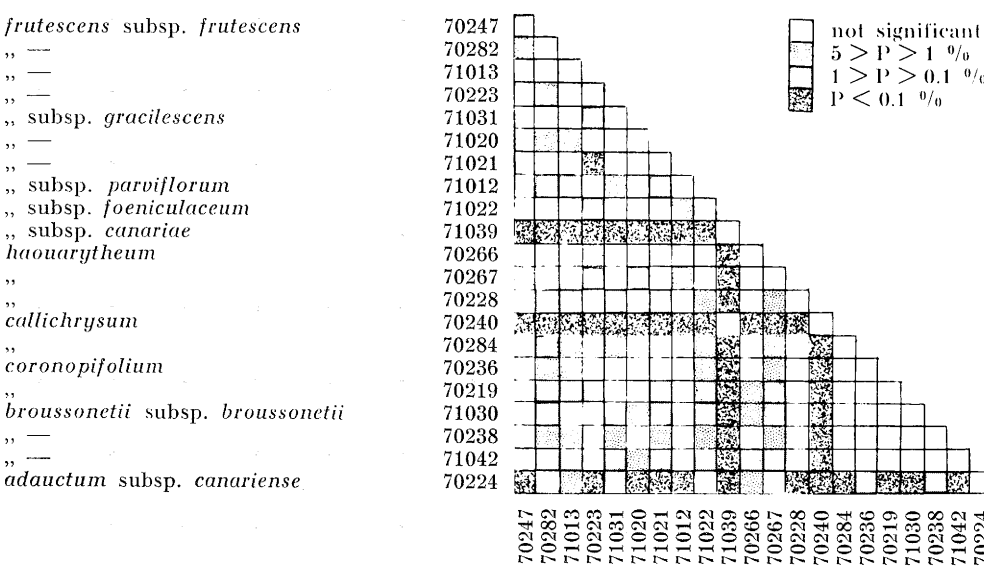

Fig. 4. Significant t-values obtained by comparing length indices (l-index) for chromosomes no. 13—14 in 21 populations from 6 species of *Argyranthemum*.

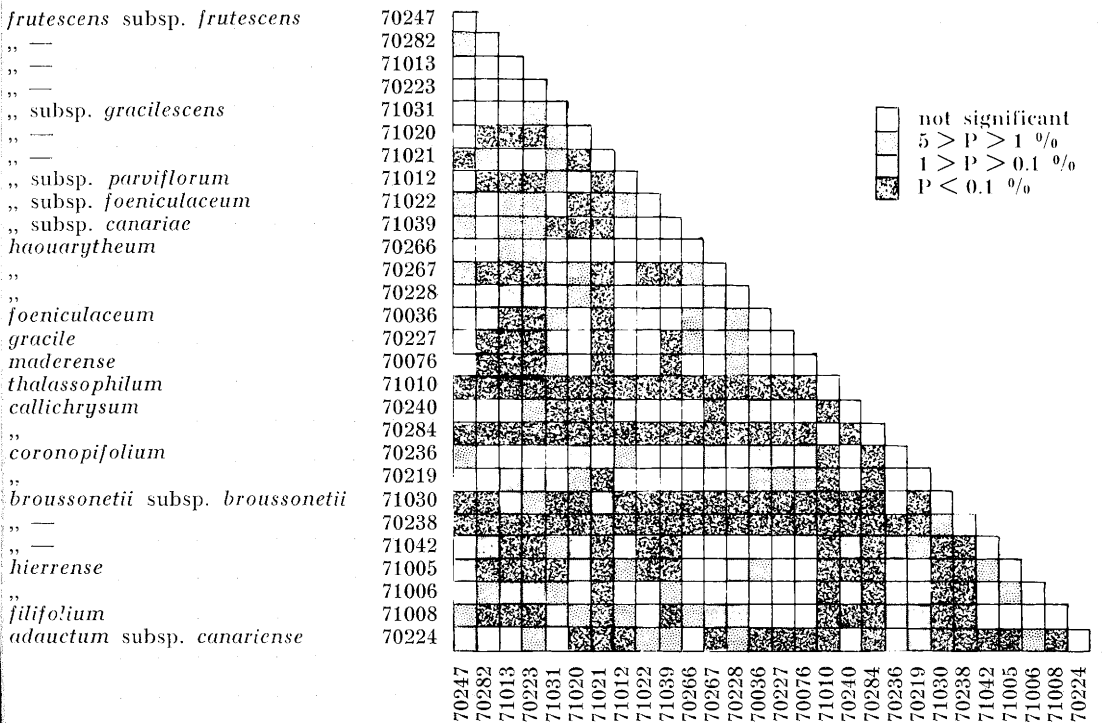

Fig. 5. Significant t-values obtained by comparing arm indices (r-index) for chromosomes 15—16 in 28 populations from 12 species of *Argyranthemum*.

subsp. *canariense* collected at Rincon de Teneguida on Gran Canaria. In both cases, the cells with quadrivalents had a reduced chiasma frequency but there was little overall effect on the recombination index (haploid chromosome number/number of chiasmata) for the whole population.

DISCUSSION

Chromosome Numbers

About 400 out of the approximate estimate of 1400 species of the Anthemideae are known cytologically with respect to chromosome numbers (Table 4). The basic number is invariably x=9 and variations from the diploid 2n=18 are known mostly in polyploid series and occasional aneuploids. There is a wide range of polyploid numbers in the tribal complex from the 2x (2n=18) to the 22x (2n=198) levels (DOWRICK 1952), the specific frequencies of which are shown in Table 4.

Although the Anthemideae are widely distributed throughout the temperate northern hemisphere and South Africa with few taxa outside these areas polyploid variation is restricted to two or three genera and closely associated with particular eco-geographical conditions and regional diversity. Undoubtedly, the widest range of variation is found in the genus *Leucanthemum*, with a centre of distribution in the central and southern European mountains and the western Mediterranean mountains of Morocco. In North Africa all members of the genus appear to be

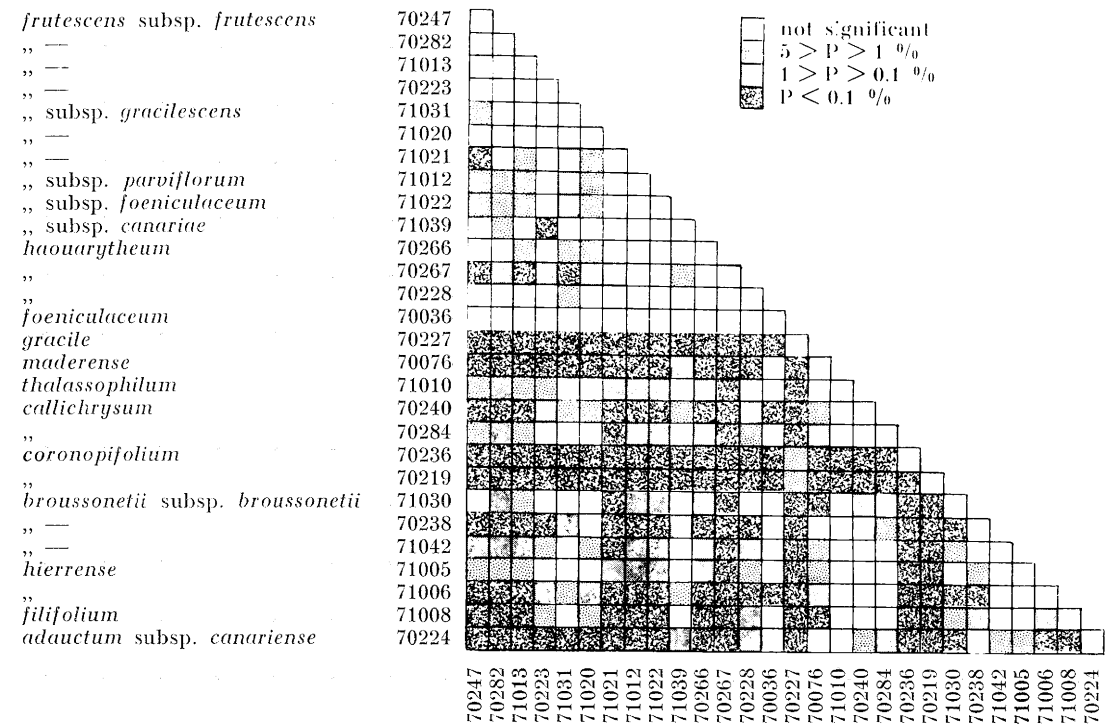

Fig. 6. Significant t-values obtained by comparing length indices (l-index) for chromosomes 15—16 in 28 populations from 12 species of *Argyranthemum*.

diploid but in Europe species exhibit a wide range of numbers between the diploid (2n=18) and decaploid (2n=90) levels (Baksay 1956, 1957, Böcher & Larsen 1957, Favarger 1959, Favarger & Villard 1965, Polatschek 1966, Villard 1970, Papeš 1972). The polyploid endemic species of *Dendranthema* of eastern China and Japan are also well known cytologically. In this region about 30 species have been examined and shown to have a range of ploidy levels between the diploid (2n=18) and the dodecaploid (2n=108) (Shimotomai 1932, 1933, 1937 a, b, 1938, Shimotomai & Takemoto 1939, Shimotomai et al. 1956, 1957, 1958, 1960, Tanaka 1959 a, b, c, Shimuzu 1962). Few high chromosome counts exist for genera in other areas of Anthemidean diversity and available reports seem to indicate that most taxa are either diploid (2n=18) or tetraploid (2n=36) (see Bolkovskikh et al. 1969, Moore 1973). In Macaronesia all taxa of the Chrysantheminae so far examined are diploid, apart from a single tetraploid population of *Tanacetum ptarmiciaeflorum* reported from Gran Canaria by Larsen (1960).

Chromosome Morphology

There have been numerous well documented examples of karyotype evolution (Babcock 1947, Lewitsky 1931, Smith 1964, Stebbins 1950). Stebbins (1971) showed that it is often quite possible to determine the morphological sequence of karyotype evolution by using the following

Table 3. Chiasma frequencies, mean number of chiasmata ($\bar{x}$), recombination indices (R. I.), and pairing configurations of chromosomes at diakinesis and metaphase I in field collections of 15 species of *Argyranthemum*. — N: number of cells studied.

Population	Species	Per cent chiasmata						$\bar{x}$	R.I.	Configuration	N
		14	15	16	17	18	19				
	frutescens										
3461	subsp. *frutescens*	—	—	—	10	90	—	17.9	1.99	9II	195
3275	„	—	12	—	24	64	—	17.5	1.94	9II	300
3282	„	—	—	—	25	75	—	17.9	1.99	9II	119
70282	„	—	—	40	15	15	30	20.1	2.24	9II (75 %) 1IV+7II (25 %)	700
DB320	„	—	—	—	—	50	50	18.5	2.08	9II	50
70223	„	—	—	—	20	60	—	18.2	2.03	9II	76
3376	subsp. *succulentum* ..	—	—	—	85	15	—	17.9	1.99	9II	80
70227	subsp. *gracilescens* ..	—	—	50	20	30	—	16.8	1.66	9II	142
70265	„	—	—	20	20	10	50	18.0	2.00	9II	225
3179	„	—	—	—	15	85	—	17.9	1.99	9II	133
3208	„	—	—	—	—	100	—	18.0	2.00	9II	175
3360	subsp. *parviflorum* ..	—	—	—	45	55	—	17.5	1.94	9II	40
3363	„	—	—	—	80	20	—	17.3	1.92	9II	138
3348	subsp. *foeniculaceum*	—	—	—	33	67	—	17.8	1.98	9II	150
3352	„	—	—	10	45	45	—	17.4	1.93	9II	124
3001	subsp. *canariae*	—	—	—	85	15	—	17.9	1.99	9II	254
3002	„	—	—	—	—	100	—	18.0	2.00	9II	250
3417	*haouarytheum*	—	—	—	25	75	—	17.9	1.99	9II	170
3429	„	—	—	—	15	75	10	18.0	2.00	9II	166
70036	*foeniculaceum*	—	—	30	40	30	—	17.0	1.88	9II	355
3262	„	—	—	—	—	100	—	18.0	2.00	9II	125
71017	„	—	—	—	—	100	—	18.0	2.00	9II	107
3252	*gracile*	—	—	—	15	85	—	17.9	1.99	9II	195
3260	„	—	—	10	—	90	—	17.9	1.99	9II	70
DB265	*tenerifae*	—	—	—	10	75	15	18.1	2.01	9II	65
71019	*winteri*	—	—	—	—	100	—	18.0	2.00	9II	13
3152	*lidii*	—	—	—	—	100	—	18.0	2.00	9II	23
70240	*callichrysum*	15	—	15	40	30	—	16.7	1.63	9II	44
70236	*coronopifolium*	—	—	—	—	100	—	18.0	2.00	9II	32
3382	*broussonetii*	—	—	—	10	90	—	17.9	1.99	9II	230
3364	„	—	—	—	40	60	—	17.6	1.95	9II	20
3323	*hierrense*	—	—	—	60	40	—	17.4	1.93	9II	12
3409	*webbii*	—	—	—	—	100	—	18.0	2.00	9II	72
3060	*filifolium*	—	—	—	40	60	—	17.6	1.95	9II	90
3081	„	—	—	—	—	100	—	18.0	2.00	9II	45
3077	*escarrei*	—	—	—	—	100	—	18.0	2.00	9II	45
	adauctum										
70224	subsp. *canariense* ...	20	40	30	10	—	—	15.3	1.70	9II	133
3007	„	8.5	58	25	8.5	—	—	14.8	1.60	9II	140
3008	„	—	—	—	30	70	—	17.6	1.95	9II	30
3009	„	—	10	20	40	20	10	17.0	1.88	9II (77 %) 1IV+7II (23 %)	165
3013	subsp. *gracile*	—	—	—	10	80	10	17.6	1.95	9II	112
3012	„	—	—	—	30	70	—	17.6	1.95	9II	64
3014	„	—	—	—	12.5	77.5	10	18.0	2.00	9II	340
3034	„	—	—	—	—	100	—	18.0	2.00	9II	25
3046	„	—	—	—	—	100	—	18.0	2.00	9II	34
3110	„	—	—	—	30	70	—	17.5	1.94	9II	24
3111	subsp. *jacobaeifolium*	—	—	—	10	90	—	17.9	1.99	9II	17
3386	subsp. *dugourii*	—	—	—	—	100	—	18.0	2.00	9II	90
3186	subsp. *adauctum*	—	—	5	30	60	5	17.6	1.95	9II	42
3190	„	—	—	—	25	75	—	17.7	1.96	9II	18
3309	subsp. *erythrocarpon*	—	—	—	10	90	—	17.9	1.99	9II	20

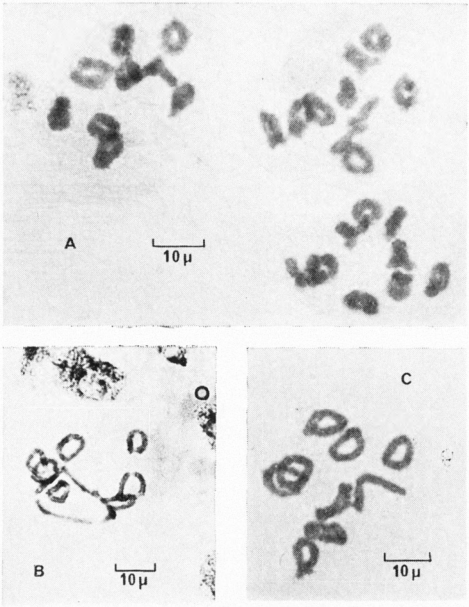

Fig. 7. A: Meiotic metaphase bivalents in *Argyranthemum tenerifae* (population DB265), showing variation in chiasma position. — B: A single terminal reciprocal translocation in chromosomes of *Argyranthemum frutescens* subsp. *frutescens* (population 70282). — C: Metaphase bivalents in *Argyranthemum filifolium* (population 3060).

criteria: (a) differences in the absolute size of chromosomes; (b) differences in centromere position (symmetry v. asymmetry); (c) differences in relative chromosome size; (d) differences in the basic number; and (e) differences in the number and position of satellites. In many plant groups, however, where there are only slight changes in the appearance of chromosomes, the significance of cytological differentiation can be very difficult to assess directly from morphological observation (Bothmer 1970, Jones 1970, Jones & Jopling 1972, Morley 1972).

The chromosomal variation in *Argyranthemum*, for example, has been shown to be due to slight differences in chromosome size and centromeric position. However, there is no discernible morphological sequence which can be interpreted as an evolutionary sequence, from one species to the next. Minute differences do occur but they may be of the same magnitude between different populations within a species as between different species in the genus. Thus, in a genus in which all taxa have a basically similar karyotype, adaptive gene sequences are presumably brought about by genic or slight structural cytological changes. These may be affected mechanically by erosion at the tips of chromosome arms (*A. hierrense*), by loss of satellites (*A. thalassophilum*), or by the translocation of small terminal segments which can only be detected at meiosis (*A. canariense* and *A. frutescens*). These processes may become rapidly fixed in a population by an outcrossing breeding system. Populations of *Argyranthemum* are normally strongly ecologically isolated from one another and hybrids between them rarely become established (Humphries 1973). There are always some phenotypic differences between adjacent populations which can be interpreted as the direct result of minute structural or genic changes.

Significant statistical differences in the karyotype between populations do tend

Table 4. Frequency of different chromosome numbers within the Anthemideae. Compiled from Bolkovskikh et al. 1969 and Moore 1973.

2n	18	27	36	54	72	90	108	198	Intraspecific polyploids	Aneuploids
No. of species	252	5	75	28	8	6	1	1	65	36

to be greater for populations of different species than for populations of the same species. However, it must be pointed out that such differences are not always necessarily significant cytologically. Normally there is no well defined specific variation which can be detected at mitosis except perhaps for *A. hierrense,* which has a single pair of subterminal (st) chromosomes, and *A. thalassophilum* which has only one pair of satellite (SAT) chromosomes.

Meiosis and the Breeding System

Studies of pairing behaviour at meiosis in natural populations of different species of *Argyranthemum* indicates that there is some genetic and cytological control of population variability. The principle effect of significant differences in chiasma frequency and hence adjustments in the degree of recombination is the regulation of extent and flow of variability within populations. DARLINGTON (1939) and MATHER (1943) postulated on theoretical grounds that a restriction of recombination to reduce variability, i.e. a low chiasma frequency, would be desirable for survival among short-lived ephemeral and annual plants. However, recently the totally opposite situation has been suggested for the agriculturally important grasses *Lolium, Festuca* and *Secale.* Investigations on these grasses by REES & AHMAD (1963), SUN & REES (1964), JONES & REES (1966), CROWLEY (1969) and REES & DALE (1974) have shown that a low chiasma frequency can be correlated with the perennial habit, and a high chiasma frequency predominates in annual populations. REES & AHMAD (1963) and CROWLEY (1969) suggest that the high chiasma frequencies in short-lived populations may compensate for reduced variability, although recently REES & DALE (1974), working on the assumption that chiasma frequencies are heritable in populations of different origins, argue that high chiasma frequencies are not the result of low genetic variability but are instead the cause of it. All species of *Argyranthemum* are perennial with some individuals known to survive to the age of ten or fifteen years (HUMPHRIES 1973) and so the observed variations in chiasma frequency cannot be explained in terms of an adaptation correlated with longevity. Species represented by a few populations and individuals with low overall variability (HUMPHRIES 1973), such as the Gran Canarian endemics *A. filifolium* and *A. lidii,* have an overall relatively high chiasma frequency when compared with more widespread taxa. Variable species such as *A. adauctum* and *A. frutescens,* both found in a number of different ecological conditions on three of the western Canary Islands, have much lower observed chiasma frequencies. The high chiasma frequency of the specialised endemic is presumably best explained as a compensatory device for depleted variability and in the more variable taxa as a conservation maintenance system preserving well adapted genotypes. Indeed the presence of a single translocation in the chromosomes of just two populations of *A. frutescens* and *A. adauctum* underlines the adaptive value of complex heterozygosity for survival in the Chrysantheminae (RANA & JAIN 1965, PARIA & PRADHAM 1972).

An added complication to this interpretation stems from the nature of the breeding system. Although all species of *Argyranthemum* so far examined show obvious characteristics for outbreeding, with heterogamous radiate capitula, exhibiting centripetalous floral maturation, they can also be self-compatible (HUMPHRIES 1973). Individuals can be found in most of the vegetation zones of the Macaronesian islands and it is highly likely that in pioneer situations self-fertilization will be the principal breeding system, rather than the exception. One would expect therefore in these situations for an increase in chiasma frequency as a response to increased homozygosity in the inbreeding plants. In conclusion it must be said that

there must be many factors which can effect the variability of populations and the ways in which they respond to different selective pressures. However, despite the lack of critical quantitative data on the precise modes of genetic flexibility and variability in *Argyranthemum,* it seems that variation in chiasma frequency is an effective method of controlling genetic and hence phenotypic expression in a diploid genus with species of a similar genomic constitution.

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APPENDIX

List of material investigated

Collecting data for population samples are as follows, and unless otherwise specified, collecting and cultivation numbers are those of HUMPHRIES and BRAMWELL, collected jointly in 1971.

Argyranthemum frutescens (L. FIL.) SCHULTZ BIP. subsp. *frutescens*: 70223, Tenerife, Teno, 1969, BRAMWELL; 70247, 70282, 71013, Tenerife, Santa Cruz, 1969, BRAMWELL; DB320, Tenerife, Casas de Teno Bajo, 25 m, 25.10. 1968, BRAMWELL; 3275, same locality, 5.4. 1971; 3282, Tenerife, El Fraile, 50 m, 5.4. 1971; 3461 Igueste de San Andrés, 200 m, 18.4. 1971.

A. frutescens subsp. *succulentum* C. J. HUMPHRIES: 3376, Tenerife, Playa del Roque, Taganana, 20 m, 9.4. 1971.

A. frutescens subsp. *gracilescens* (CHRIST.) C. J. HUMPHRIES: 71031 & 3178, Tenerife, between Sobradillo & Bco. Grande, 2.4. 1971; 70227 & 70265, Tenerife, Candelaria, 4.11. 1968, BRAMWELL; 3208, Tenerife, Bco. de Tamadaya, 600 m, 3.4. 1971.

A. frutescens subsp. *foeniculaceum* PITARD & PROUST: 71022 & 3348, Gomera, Bco. de Vallehermoso nr. El Puerto, 6.4. 1971; 3352, Gomera, 3 km W of Agulo nr. Las Rosas 500 m, 3.4. 1971.

A. frutescens subsp. *canariae* (CHRIST.) C. J. HUMPHRIES: 71039, Gran Canaria, nr. Banaderos, 15.3. 1970, BORGEN; 3001, Gran Canaria, San Felipé, 50 m, 17.3. 1971; 3002, same locality, 200 m, 17.3. 1971.

A. frutescens subsp. *pumilum* C. J. HUMPHRIES: 3155, 3169, Gran Canaria, Bco. Laya del Risco, 23.3. 1971.

A. haouarytheum C. J. HUMPHRIES & D. BRAMWELL: 70228, La Palma, La Cumbrecita, 9.6. 1969, BRAMWELL; 70266, La Palma, Pinar de Fuencaliente, 50 m, 9.6. 1969, BRAMWELL; 70267 & 3429, La Palma, Casa de Cumbrecita, 15.4. 1971; 3414, La Palma Heliño, between Fuencaliente and Los Llanos, 15.4. 1971, BRAMWELL; 3417, La Palma, Roque de Teneguia, 150 m, 15.4. 1971.

A. foeniculaceum (WILLD.) WEBB ex SCHULTZ BIP.: 70036, Tenerife, SVENTENIUS; DB390, Tenerife, Hoya de Malpais, 450 m, 1969, BRAMWELL; 71017, Tenerife, 1971, cult. ex Tafira Botanic Garden; 3262, Tenerife, El Retamar, 4.4 1971; 3469, Tenerife, Bco. del Masca, 19.4. 1971.

A. gracile SCHULTZ BIP.: 70227, Tenerife, Adeje, 11. 1968, BRAMWELL; 70288, Tenerife, Guimar, ex Jardin de Acclimatacion; 3252, Tenerife, Valle Seco, 600 m, 4.4. 1971; 3260, Tenerife, Tamaimo, Riscos de Malpais, 4.4. 1971.

A. tenerifae C. J. HUMPHRIES: DB265, Tenerife, Las Cañadas, El Portillo, 2000 m, 1969, BRAMWELL.

A. maderense (D. DON) C. J. HUMPHRIES: 70076, Lanzarote, Famara, 1969, BORGEN; DB1655, same locality, 300 m, 15.5. 1969, BRAMWELL.

A. winteri (SVENT.) C. J. HUMPHRIES: 71019, Fuerteventura, Handia (typus leg. SVENTENIUS) 1971, coll. ex Tafira Botanic Garden.

A. lidii C. J. HUMPHRIES: 3152, Gran Canaria, Anden verde between Agaëte and San Nicolas, 600 m, (typus).

A. thalassophilum (SVENT.) C. J. HUMPHRIES: 71010, Salvage Islands, Pico Grande, (SVENTENIUS) coll. ex Tafira Botanic Garden.

A. callichrysum (SVENT.) C. J. HUMPHRIES: 70240, Gomera, between Agando & Iguelero, 27.7. 1969, BRAMWELL; 70284, Gomera, Valle Exito, Cañada de Horchilla, Iguelero, SVENTENIUS.

A. coronopifolium (WILLD.) C. J. HUMPHRIES: 70219 and 70236, Tenerife, Buenavista, El Fraile, 6. 1969, BRAMWELL.

A. broussonetii (PERS.) C. J. HUMPHRIES subsp. *broussonetii:* 70238, Tenerife, Cumbre de Taganana, El Bailedero, 21.5. 1969, BRAMWELL; 71030 & 3382, Roque del Agua, 9.4. 1971; 71042, Tenerife, Monte Mercedes, 450 m, 24.3. 1970, BORGEN; 3364, Tenerife, Azano, 9.4. 1971.

A. hierrense C. J. HUMPHRIES: 71005, Hierro, Cuesta de Sabinosa, 150 m, 8.4. 1971; 71006, Hierro, Roques de Salmar, 9.4. 1971; 3323, Hierro, NW of Sabinosa, 9.4. 1971.

A. webbii SCHULTZ BIP.: 3409, La Palma, Bco. del Agua, 14.4. 1971.

A. filifolium (SCHULTZ BIP.) C. J. HUMPHRIES: 71008 & 3060, Gran Canaria, Arguiniguin, 250 m 21.3. 1971; 3081, Gran Canaria, 7 km N of Mogan, 21.3. 1971.

A. escarrei (SVENT.) C. J. HUMPHRIES: 3077, Gran Canaria, Bco. de Tasarte, 600 m, 21.3. 1971.

A. adauctum (LINK) C. J. HUMPHRIES subsp. *adauctum*: 3186, Tenerife, Mirador Ortuno 2.4. 1971; 3190, Tenerife Los Raices, Monte De Esperanza, 2.4. 1971.

A. adauctum subsp. *canariense* (SCHULTZ BIP.) C. J. HUMPHRIES: 70224, Gran Canaria, Lentiscal, 400 m, KUNKEL; 3008, Gran Canaria, 2 km S of San Mateo, 650 m, 17.3. 1971; 3009, Gran Canaria Rincon de Tenteniguada, 600 m, 19.3. 1971.

A. adauctum subsp. *gracile* (SCHULTZ BIP.) C. J. HUMPHRIES: 3012, Gran Canaria, Temisas, 900 m, 19.3. 1971; 3013, Gran Canaria, 1 km S of Santa Lucia de Tirajana, 19.3. 1971; 3014, Gran Canaria, San Bartolomé, 750—800 m, 19.3. 1971; 3034, Gran Canaria, 3 km N of Paso de la Plata, 19.3. 1971; 3046, Gran Canaria, below Fataga, 200 m, 21.3.

1971; 3110, Gran Canaria, Pinos de Tamadaba, 25.3. 1971.

A. adauctum subsp. *jacobaeifolium* (SCHULTZ BIP.) C. J. HUMPHRIES; 3111, Gran Canaria, 1350 m, Pine forest, 25.3. 1971.

A. adauctum subsp. *dugourii* (BOLLE) C. J. HUMPHRIES: 3386, Tenerife, El Retamar, 2300 m, 10.4. 1971.

A. adauctum subsp. *erythrocarpon* (SVENT.) C. J. HUMPHRIES: 3309, Hierro, La Frontera, 850 m, 7.3. 1971.

On the Size and Microstructure of Pollen Grains of Quercus robur and Q. petraea (Fagaceae)

Ulf Olsson

OLSSON, U. 1975 10 10. On the size and microstructure of pollen grains of Quercus robur and Q. petraea (Fagaceae). — Bot. Notiser 128: 256—264. Lund. ISSN 0006-8195.

The tricolpate pollen grains of *Q. petraea* and *Q. robur* are very similar in the structure of the exine and intine. All types described are to be found within all the species. The pollen dimensions (P, E) of polar and equatorial axes are greater in *Q. petraea* than in *Q. robur* but intraspecific variation is greater than interspecific. A wide or skewed distribution of the values of E sometimes exceeding the extremes of either species is indicative of the hybrid nature of an oak. This is also shown to be valid for two oaks with aberrant leaves (*Q. petraea* ×*robur* nm. *mespilifolia*).

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INTRODUCTION

Quercus petraea (MATTUSCHKA) LIEBL. and *Q. robur* L., subgenus *Lepidobalanus* (ENDL.) OERSTED have a wide distribution in Europe. The optimum ecological demands as regards habitat differ with the species (FRIES 1865, WEIMARCK 1947 a). However, the sessile and pedunculate oaks do exist as sympatric species resulting in hybrids and introgressive populations (COUSENS 1962, 1963, 1965; CARLISLE & BROWN 1965). This is also confirmed by the author, who has examined the population structure of oak woods in southern Sweden (OLSSON 1975 a).

The object of this investigation is to compare variation in pollen morphology in *Q. petraea* and *Q. robur* as well as in oaks which are presumed to be the spontaneous hybrid progeny of these species. In addition the characteristics of pollen grains of two oaks with aberrant leaf forms are noted (cf. OLSSON 1975 b).

The pollen morphology of *Q. petraea* and *Q. robur* has been described by ČERNJAVSKY (1935), ERDTMAN (1943), ERDTMAN et al. (1961), VAN CAMPO & ELHAI (1956), MONOSZON (1954, 1962) and PRAGLOWSKY (1962) who all used conventional light microscopy. VAN DER SPOEL-WALVIUS (1963) presents a description based on phase contrast microscopy. The *Quercus* species studied by him are subdivided into two groups on the basis of their pollen morphology. Thus *Q. petraea, Q. robur* and *Q. pubescens* WILLD. constitute one type according to the taxonomic subdivision made by SCHWARZ (1936—1939). This is also confirmed by SMIT (1973) in a scanning electron microscopic study of *Quercus* pollen grains. He combines six species to form a *robur* — *petraea* group but makes no attempt to subdivide this group further. PILCHER (1968) states "that the variation seen in the pollen of a single tree is so great that the differentiation of the two species in fossil material seems to be impossible". In another scanning electron microscopic examination of recent pollen grains DUPONT & DUPONT (1972) confirm this statement and note moreover the greater variability of *Q. robur* grains.

According to the present study of the exine and intine structures all types observed are to be found in *both* species. There is a statistically significant difference between the species as regards the length of the polar and equatorial pollen axes: the grains of the sessile oak are on the average larger, but the intraspecific variation may be the same as or greater than the interspecific one. Yet the distribution of these characters is of great value in detecting introgressive individuals. In a previous experimental study of *Linaria vulgaris* (L.) MILLER and *L. repens* (L.) MILLER the author has shown that, after repeated crossings, plants of the first filial generations in particular have a frequency distribution of biometric pollen values (P, E, P/E) which is markedly divergent from what is normal for either of the parent species (OLSSON 1975 c). The results of corresponding analyses of oak pollen support the assumed occurrence of hybrid individuals. These are presumed to be introgressives on the results of other morphological studies (OLSSON 1975 a).

MATERIAL AND METHODS

Light microscopy (LM) and scanning electron microscopy (SEM) have been used to study pollen grains of *Q. robur* and *Q. petraea* from localities in Bohuslän and Skåne in southern Sweden. Apart from pollen grains of the oaks mentioned the pollen types of two oaks with subentire leaves (*Q. petraea*× *robur* nm. *mespilifolia* (WALLR.) WEIM.) are described (vouchers, see Appendix).

Preparation Techniques

LM

The slides have been prepared by the Palynological Laboratory, Solna, Sweden and by the author following the method of acetolysis introduced by ERDTMAN (1960).

SEM

The instrument used was a Cambridge Stereoscan Mark II microscope (30 kV accelerating voltage; the specimen stage placed at 30—45° to the beam; Department of Zoology, University of Lund). The pollen grains were mounted on wax-coated (OLSSON 1975 c) specimen stubs, subsequently shadowed with gold/palladium (40/60). A couple of these preparations of pollen grains from the oak species concerned were treated with short beams of ruby laser radiation in order to get ruptured grains for the study of inner structures. This technique is described in a separate paper (OLSSON 1975 d).

RESULTS

Quercus petraea (MATTUSCHKA) LIEBL.

Pollen grains radially symmetrical, isopolar, 3-colpate, spheroidal-subprolate, 28×27 µ (cf. Table 1, $\bar{x}$ /P/, $\bar{x}$ /E/). Amb rounded triangular. Colpi rather narrow. Apocolpium about 9 µ. Exine 1.6—1.9 µ thick, stratification usually verrucose. Verruca often have microverrucae (Fig. 2 A, E). Other types may be found, such as semipsilate-pitted (Fig. 2 I a) or more or less verrucose-ornate (Fig. 2 I b, M). Inner side of intine striate-reticulate (Figs. 3, 4).

Quercus robur L.

Pollen grains radially symmetrical, isopolar, 3-colpate, spheroidal-subprolate, 27×26 µ (cf. Table 1). Exine, amb, colpi and apocolpium as in *Q. petraea*. However, of the verrucae types observed (Fig. 1 A, E, I, M), semipsilate-pitted areas with microverrucae between groups of larger verrucose processes are a more usual type of exine structure than that found in *Q. petraea*. Intine structure as in *Q. petraea* (illustrated in OLSSON 1975 d).

Introgressives

Structural and sculptural elements as in the parent species. The relative frequency distribution of different stratification types has not been considered. However, a comparison of P, E and P/E for the species and their spontaneous hybrid offspring is presented below.

Biometry

Survey of pollen samples from *Q. petraea, Q. robur,* their introgressives and

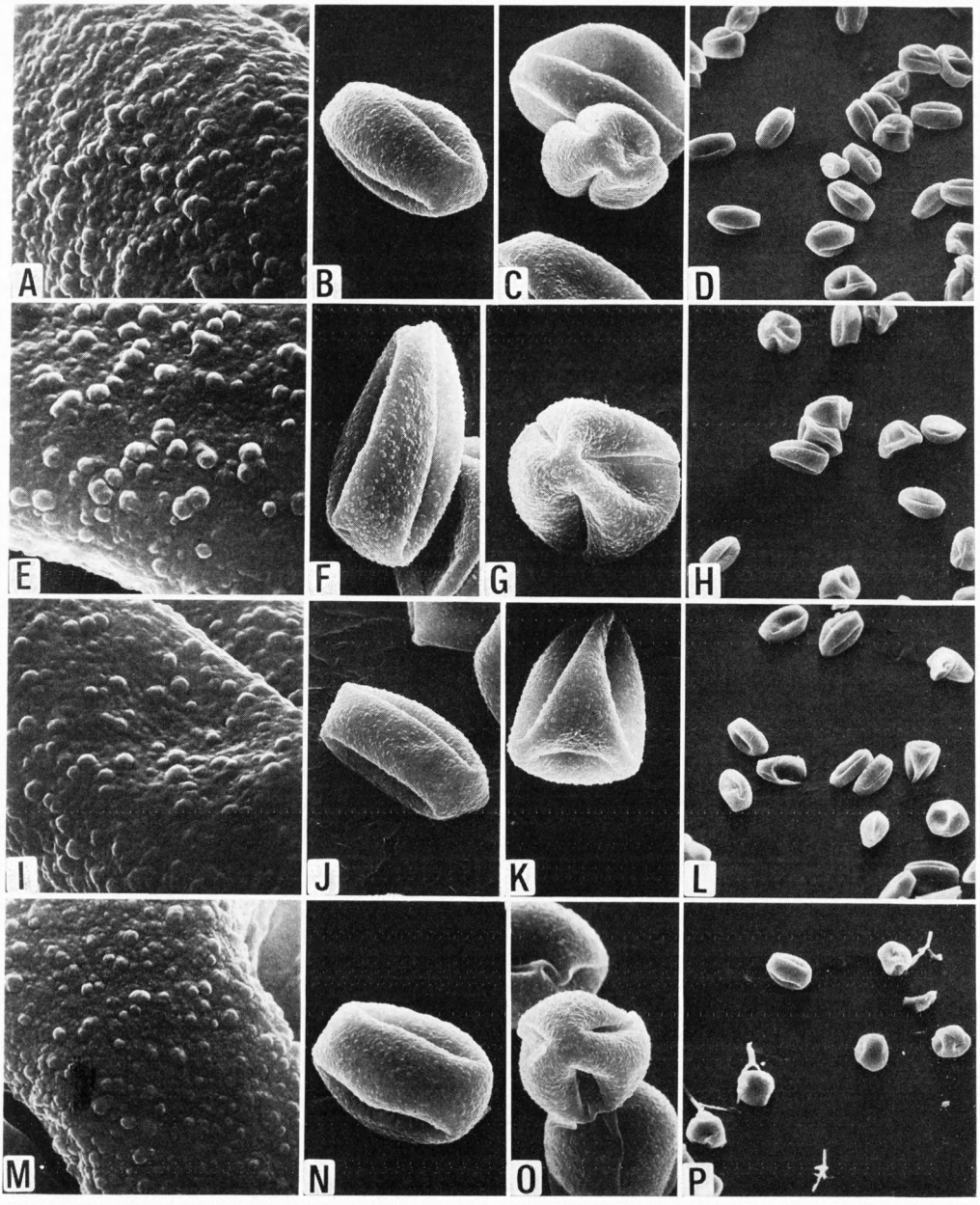

Fig. 1. *Quercus robur*. SE micrographs of pollen grains. — B, F, J, N: Lateral view of pollen grains showing the mesocolpium area (x 2,400). — A, E, I, M: Details of mesocolpium area, representative of the entire exine, showing the unevenly distributed verrucae of varying shapes. Between the groups of verrucae one can find areas of a semipsilate nature with very small processes and perforations (E, I), (x 12,000). — C, G, K, O: Pollen grains in polar view. Because of shrinkage the actual shape of the colpi is difficult to interpret (x 2,400). — D, H, L, P: Surveys of pollen grains from four oaks (x 600).

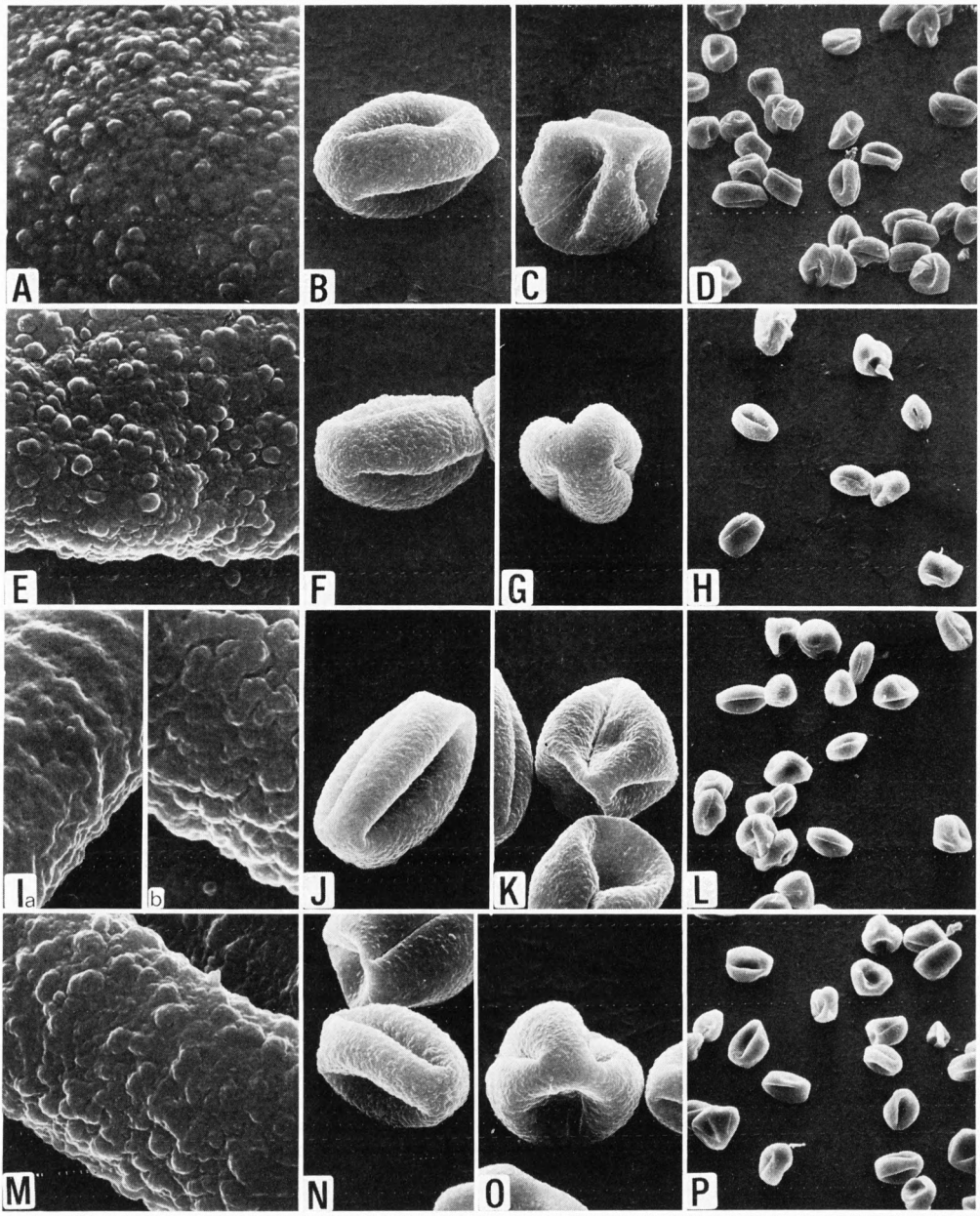

Fig. 2. *Quercus petraea.* SE micrographs of pollen grains. — B, F, J, N: Lateral view of pollen grains showing the mesocolpium area (x 2,400). — A, E, I a and b, M: Details of the mesocolpium area. Apart from the most representative types of verrucae in A and E one can find exine sculpturing as in I b and M showing verrucae interlacing to form winding ridges. Note the almost psilate surface of I a (x 12,000). — C, G, K, O: Pollen grains in polar view (x 2,400). — D, H, L, P: Surveys of pollen grains from four oaks (x 600).

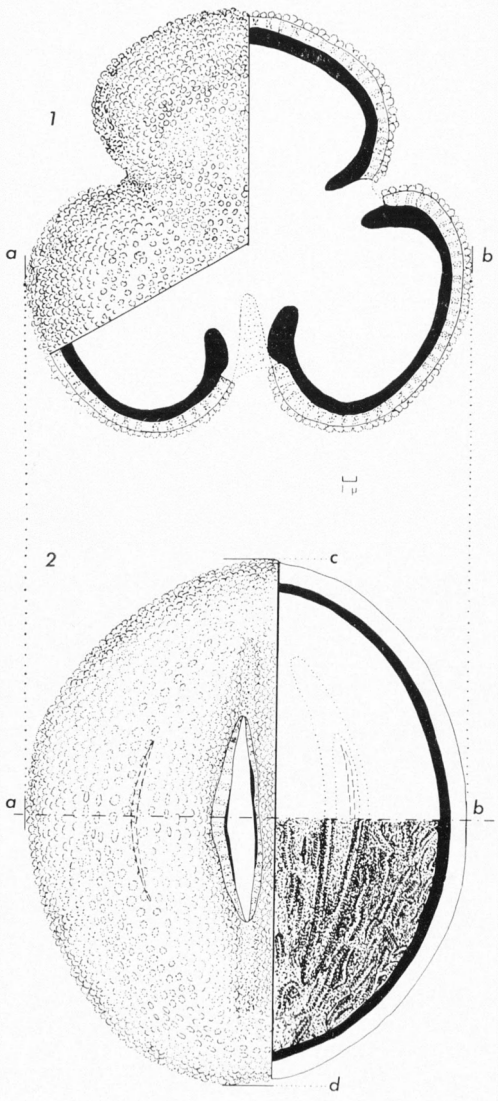

Fig. 3. *Quercus petraea* and *Q. robur*. — Palynogram showing the arrangement and shape of colpi of the tricolpate pollen grain. The structure of the inner surface of the intine is also shown. The cross-section a—b in polar view (1) coincides with the equator of the lateral view (2). The actual shape of the verrucae is not shown.

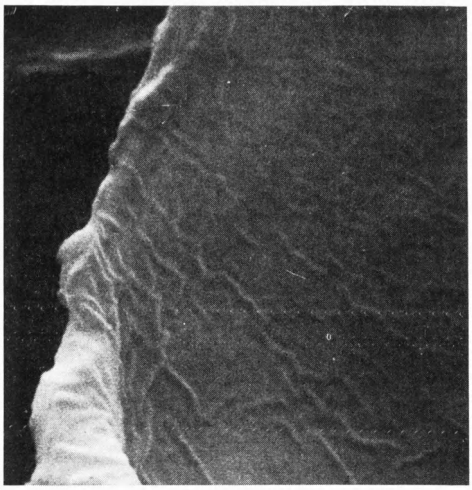

Fig. 4. *Quercus petraea*. — Pollen grain fractured by ruby laser beams. SE micrograph of the inner surface of the intine showing striate-reticulate ornamentation (x 12,000).

two trees with aberrant leaf forms have been the subject of a biometric analysis of the frequency distribution of the values of the length of the polar axis (P), the equatorial axis (E) and their quotient (P/E). Samples of each species were chosen from trees with high male fertility (i.e. as a rule > 90 % stainable pollen) from populations which have been found to be representative for the species. In the same way introgressives have been taken from oak populations which are composed of many hybrid individuals (Olsson 1975 a).

The differences in mean values of E and P observed between the species are statistically significant (Table 1). The cumulative distribution curves of Fig. 5 show the overlapping range of values (E) of both species compared. Obviously, although the differences in mean values between the species are statistically significant, these data cannot be used for taxonomical conclusions at species level.

Corresponding pollen data for a sample of oaks from an introgressive population exhibit skewed or bi- to polymodal distri-

Table 1. *Quercus petraea, Q. robur* and their spontaneous introgressives including *Q. petraea*×*robur* nm. *mespilifolia*. — Pollen biometry; statistical data. — E: Length of equatorial axis (μ). — P: Length of polar axis (μ). — n: Number of pollen grains. — $\bar{x}$: Mean value. — $\bar{x}_d$: Difference between mean values. — SD: Standard deviation. — P. Levels of significance in per cent. — The representatives of nm. *mespilifolia* have the voucher nos 480101 (Gullarp) and 480201 (Högsma).

	Character	Taxon	n	$\bar{x}$	SD	$\bar{x}_d$	P (%)
Quercus petraea (Qp) ..... and *Q. robur* (Qr) with ⩾ 90 per cent stainable pollen	E	Qp	250	27.26	2.72	1.37	P < 0.1
		Qr	350	25.89	2.45		
	P	Qp	200	28.41	2.31	1.64	P < 0.1
		Qr	200	26.77	2.73		
	P/E	Qp	200	1.08	0.11	0.04	0.1 < P < 1
		Qr	200	1.11	0.13		

	Character	Voucher	n	$\bar{x}$	SD	Stainable pollen (%)
Introgressives	E	480101	50	28.89	2.58	94
		480201	50	31.67	2.54	92
		QX01	50	23.62	5.41	24
		QX05	50	26.94	3.59	48
		QX09	50	26.30	3.76	64
	P	480101	50	34.16	2.09	
		480201	50	40.36	3.09	
		QX01	50	29.18	3.65	
		QX05	50	28.11	2.84	
		QX09	50	30.21	2.83	
	P/E	480101	50	1.19	0.12	
		480201	50	1.31	0.14	
		QX01	50	1.30	0.27	
		QX05	50	1.07	0.12	
		QX09	50	1.17	0.17	

bution curves (not illustrated). The wide distribution is also reflected in the high values for standard deviation or quartile deviation (Tables 1, 2). This indicates the hybrid nature of the individual in question. Indeed the occurrence of a wide amplitude of, for example, pollen diameter (E) better indicates the hybrid nature of a plant than does a low percentage of stainable pollen grains alone (cf. OLSSON 1975 c).

The aberrant oaks examined from northern Skåne (Högsma, Gullarp) have previously been studied by SYLVÉN (1934), WEIMARCK (1947 b) and others, who stressed the problems in connection with the origin of these oaks with subentire leaves. In another paper (OLSSON 1975 b) the author has shown that the oaks may be the hybrid offspring of *Q. petraea* and *Q. robur,* as WEIMARCK (1947 b) also concluded.

Both representatives of "mespilifolia" oaks have markedly large pollen grains, in the Högsma oak even larger than in *Q.*

Table 2. *Quercus petraea, Q. robur* and introgressives including *Q. petraea×robur* nm. *mespilifolia.* — Pollen data, viz. male fertility as percentage of stainable pollen grains, quartile deviation of pollen diameter (μ) (equatorial axis, E; n=50), and number of leaf and fruit characters indicating hybrid or introgressive nature.

Taxon	Voucher	Per cent stainable pollen	Quartile deviation of E	Number of intermediate characters
Quercus robur	QO13	96	0.96	0
	QO09	96	1.13	0
	QO01	95	1.32	0
	QO12	95	1.36	0
	QO08	94	1.56	0
	QO15	93	1.24	0
	QN15	90	1.49	0
	QO04	55	1.16	(1)
	QO02	48	2.26	0
Introgressives	QX01	24	2.41	3
	QX05	48	2.02	1
	QX09	64	2.31	1
	QY11	59	2.03	1
	QY22	57	2.69	2
Q. petraea×robur nm. *mespilifolia*	480101	94	1.90	1
	480201	92	1.46	2
Q. petraea	QB07	71	1.78	0
	QA02	81	2.35	(1)
	QB10	91	2.20	0
	QB18	91	2.20	0
	QB19	94	2.07	0
	QA08	96	1.58	0
	QB11	99	1.05	0

petraea (Fig. 5). This is indicative of the hybrid nature of these oaks and thus supports the previous results.

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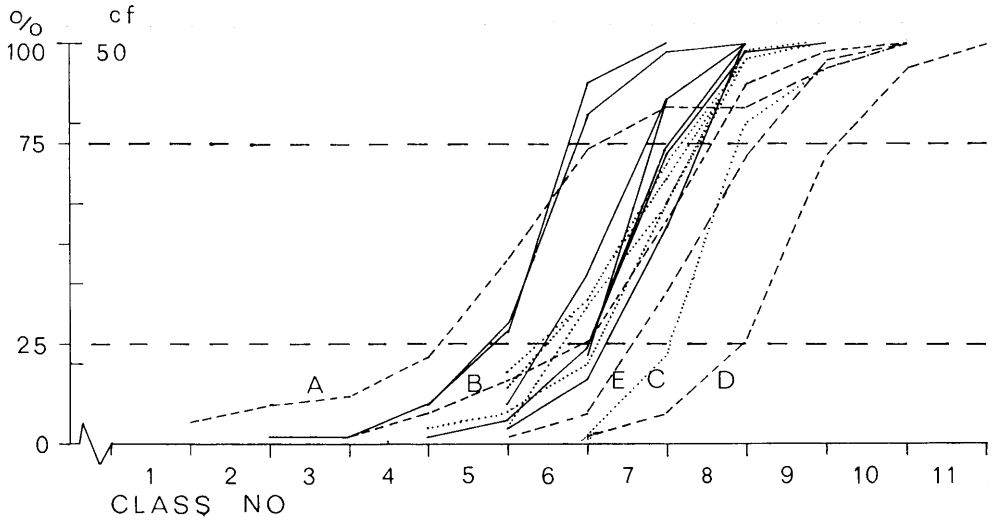

Fig. 5. *Quercus petraea*, *Q. robur* and their spontaneous introgressives including *Q. petraea* ×*robur* nm. *mespilifolia*. — Cumulative distribution curves of pollen data (E, equatorial axis) of pollen samples from single trees. Heavy lines=*Q. robur*. Dots=*Q. petraea*. Broken lines=Introgressives. All representatives of the species have a percentage of stainable pollen grains exceeding 90 %. C represents a sessile oak with especially high pollen stainability (99 %). The material is divided into eleven classes. The class width is 2.44 µ. The lower limit of class no. 1 is 10.98 µ. — A. Introgressive oak (QX01). — B. Ditto (QX05). — C. (QB11, see above). — D. *Q. petraea*×*robur* nm. *mespilifolia* (Högsma). — E. Ditto (Gullarp).

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APPENDIX

Code to collections of natural oak populations used in this investigation.

Q. petraea. QA02, QA08: Hjärsås (Skåne); QB07, QB10, QB11, QB18, QB19: Sundsvik (Bohuslän).

Q. robur. QO01, QO02, QO04, QO08, QO09, QO12, QO13, QO15: Veberöd (Skåne); QN15: Hemlinge, Glimåkra (Skåne).

Hybrid populations. Introgressives: QX01, QX05, QX09: Tjurkö (Blekinge); QY11, QY22: Verkö (Blekinge). The *mespilifolia* types: 480101: Gullarp, Osby (Skåne); 480201: Högsma (Skåne).

Oaks With Subentire Leaves from Skåne, Sweden. A New Critical Attempt to Explain Their Origin

Ulf Olsson

OLSSON, U. 1975 00 00. Oaks with subentire leaves from Skåne, Sweden. A new critical attempt to explain their origin. — Bot. Notiser 128: 265—274. Lund. ISSN 0006-8195.

Of the known occurrences of oaks with entire or subentire leaves belonging to the form series between *Quercus petraea* (MATTUSCHKA) LIEBL. and *Q. robur* L., two trees from northern Skåne have been studied in detail. The results of morphological investigations of these oaks compared with corresponding investigations of *Q. petraea* and *Q. robur* afford a certain amount of evidence that these oaks with subentire leaves are hybrids between *Q. petraea* and *Q. robur*.

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INTRODUCTION

In Scandinavia, oaks with entire leaves, described as forms of *Q. petraea* or *Q. robur*, have been observed exclusively in Sweden (WEIMARCK 1947). In the remaining parts of Europe many forms or varieties have been described, some of which are discussed below.

Two oaks with aberrant leaf forms at Högsma and Gullarp in NE Skåne (Sweden) have been studied over a period of years. Morphological variation, observations on fruit-setting and percentage stainable pollen are presented and compared with corresponding observations on *Q. petraea* and *Q. robur* in their Swedish range.

The "Högsma" oak was discovered in 1868 and then named *Q. sessiliflora* var. *subintegrifolia* (PERSSON 1885). The "Gullarp" oak is younger. On account of its entire leaves this oak was protected in 1943 (GERTZ 1944). The Högsma oak is also protected. Both oaks have long been interpreted as forms of *Q. petraea* (HYLANDER 1941; GERTZ 1945). HYLANDER distinguishes two types with subentire leaves: *Q. petraea* f. *mespilifolia* (WALLR.) SCHWARZ and *Q. petraea* f. *subintegrifolia* (J. PERS.) HYL. The Högsma oak is the type tree of the latter form. The Gullarp oak may also belong to this form. WEIMARCK (1947) combines the oaks with subentire leaves into one hybrid form, *Q. petraea*×*robur* f. *mespilifolia* (WALLR.) WEIM., later called *Q. petraea*×*robur* nm. *mespilifolia* (WEIMARCK 1963). This view (WEIMARCK) is in part supported by the results of this investigation.

RESULTS

Plant Habit

The general morphology of sessile and pedunculate oaks has been summarized earlier (OLSSON 1974, 1975 a). The original shoot type of oaks is a monopodium. The tendency to drop annual shoots or larger twigs in the autumn (especially by *Q. robur*) may modify the shape of the crown so that it resembles that of a tree with sympodial branching (JONES 1959). In addition the Högsma oak is characterized by a bunched crown. The Gullarp oak resembles *petraea* in crown habit.

Table 1. *Quercus petraea×robur* nm. *mespilifolia*. Some morphological data.

Character	Oak at Högsma	Oak at Gullarp
Petiole length	22.7 ±0.7 mm	15.3 ±0.5
Peduncle length to first bract	7.7 ±0.6 mm	2.3 ±0.3
Width to length ratio of acorn	1.27 ±0.03	1.36 ±0.03

Special crown forms such as those found in pendulous and fastigiate oaks are inherited in a simple Mendelian manner (OPPERMANN 1932, PYATNITSKII 1947). The almost "corymbous" crown of the Högsma oak may be a heritable oak form. About three per cent of the trees of *Q. robur* examined have corymbous crowns. None of these oaks, however, has subentire leaves.

Buds

Buds are more or less like those of *Q. robur*. Terminal and lateral buds of fruiting shoots of these trees resemble "typical" buds of *Q. robur* and *Q. petraea* (Fig. 4). The buds illustrated from specific individuals are regarded as representative as they agree with earlier results of morphological analyses of *petraea*- and *robur*- oaks (OLSSON 1974, 1975 a). There is no pronounced difference between these buds, indeed, the bud characters are very variable. One can find *Q. petraea* trees with large acute buds.

Leaves

The Högsma oak tends to have leaves that are more elliptical than in the other taxa. However, leaf shape cannot be used as a distinguishing character in the taxonomic analysis. The leaf bases are cuneate of *petraea*-type. In the case of lobed leaves that can appear on epicormics, the leaves look like true *Q. petraea* leaves, except that the lobes are acute or almost acuminate. New foliage consisting of lobed leaves was seen in 1969 on the Gullarp oak after the foliage had been completely destroyed by caterpillars (Figs. 2 B, 3 A—C).

The length of the petiole is a good distinguishing character. In *Q. petraea* the petiole is about twice as long as in *Q. robur*. The petioles of the Högsma oak are extremely long, longer than those of the Gullarp oak which exceed those of *Q. petraea*.

Flowers and Fruiting

The Gullarp oak resembles *Q. petraea* in flower and fruit characters. The Högsma oak usually has longer catkins, but one can find almost "sessile" and very long catkins side by side on the same shoot (Fig. 5 A). The acorns of both subentire-leaved oaks resemble the fruits of sessile oaks, but the acorns of the Gullarp oak in all samples hitherto obtained have constricted tops, indicating non-maturity (Figs. 5 C, 7).

Male Fertility and Fruit-Setting

The Högsma oak has about 92 per cent stainable pollen, the Gullarp oak 94 per cent, but this alone is not indicative of hybridity. Both oaks, however, have on the average larger pollen grains than the putative parent species (see OLSSON

Fig. 1. *Quercus petraea×robur* nm. *mespilifolia*. The Högsma oak. — A. Fruiting shoot. — B. Flowering shoot. — C. Detail of male catkin; b bract of male flower. — D. Clustered female inflorescences.

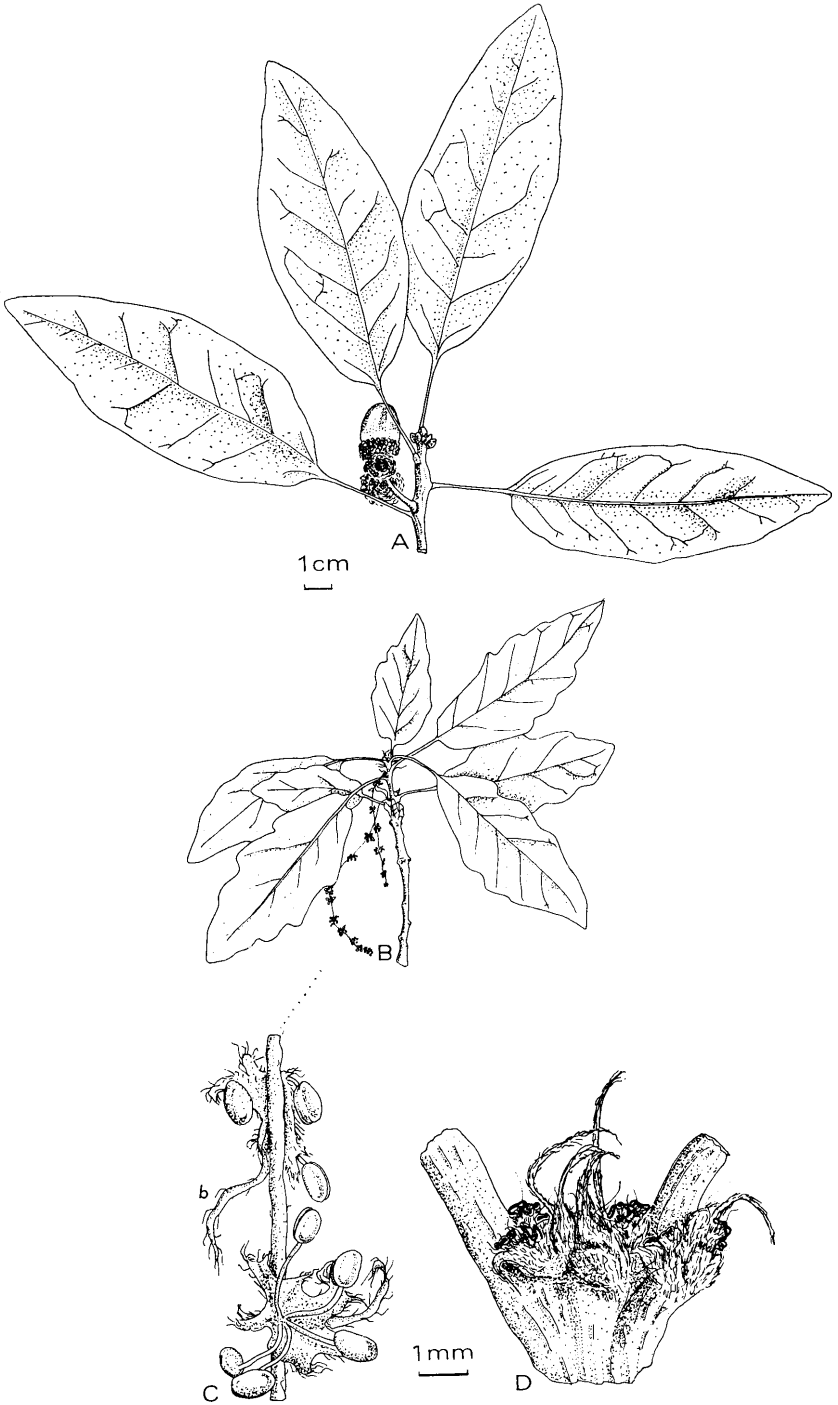
A
1cm
B
b
C
1mm
D

Fig. 2. *Quercus petraea*×*robur* nm. *mespilifolia*. The Gullarp oak. — A. Fruiting shoot. — B. Epicormic shoot. — C. Flowering shoot. — D. Detail of male catkin; b bract of male flower. — E. Female catkin.

1975 b) where the variation in size and microstructure is reported. Cryptic structural hybridity may be the cause of the unexpectedly high percentage of stainable pollen (OLSSON 1975 a). The acorn growth of the oaks in Skåne in 1971 was very good. Even young trees bore fruit, which is unusual. Both the Högsma oak and the Gullarp oak also yielded acorns which have been described earlier. Yet the fruit-setting in these trees was very low compared with "normal" oaks in the same localities. This may be a good indication of the hybrid origin of these oaks with subentire leaf margins.

Progeny of the Högsma Oak

Twenty acorns from the Högsma oak and Gullarp oak respectively collected in 1971 were put into pots in the greenhouse in Lund (March 1972). At the same time the same number of acorns from typical *Q. petraea* and *Q. robur* were also sown. The seedlings of *Q. robur* (19 in number) and of *Q. petraea* (13) had normally lobed leaves. Three acorns only of the Högsma oak germinated, but in all seedlings the leaf margins were more or less entire. None of "Gullarp" acorns germinated. The persistent character of almost non-lobular leaves of the few seedlings from the Högsma oak may indicate that this leaf form is hereditary.

Some of the younger oaks in the vicinity of the Högsma oak may be the progeny of this oak. They have divergent leaf shapes. In one case the leaves are very little lobed (Fig. 6 B).

CONCLUSIONS AND DISCUSSION

The morphological analysis of the oaks with subentire leaves (Högsma, Gullarp)

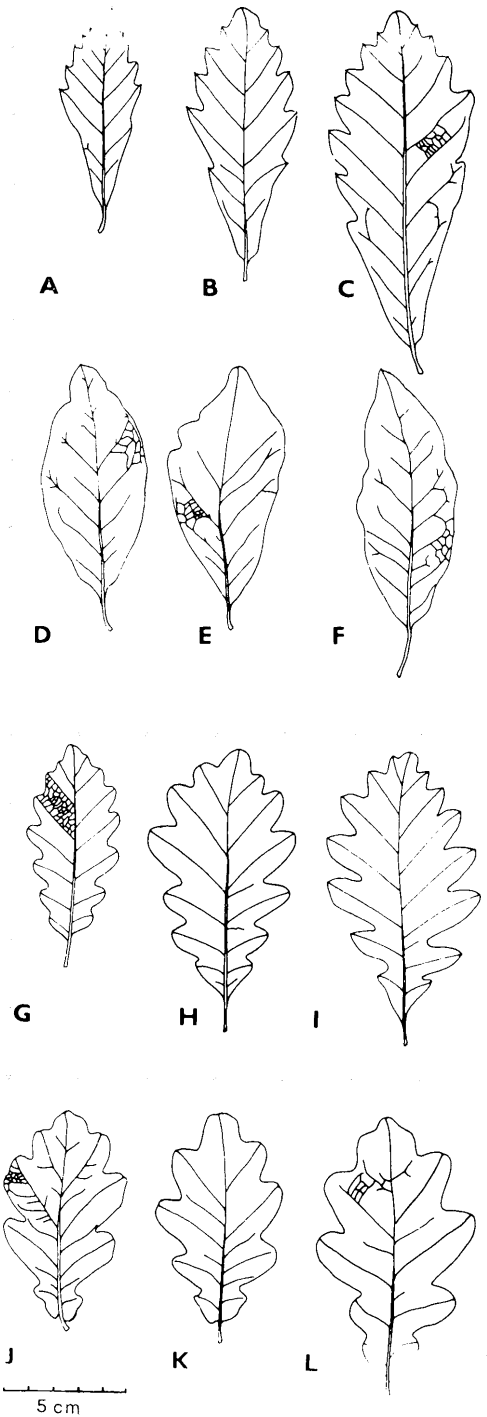

Fig. 3. Leaf types of oaks with subentire leaves (A—F) compared with typical leaves of *Quercus petraea* (G—I) and *Q. robur* (J—L). A—C show leaves from epicormics of the Gullarp oak.

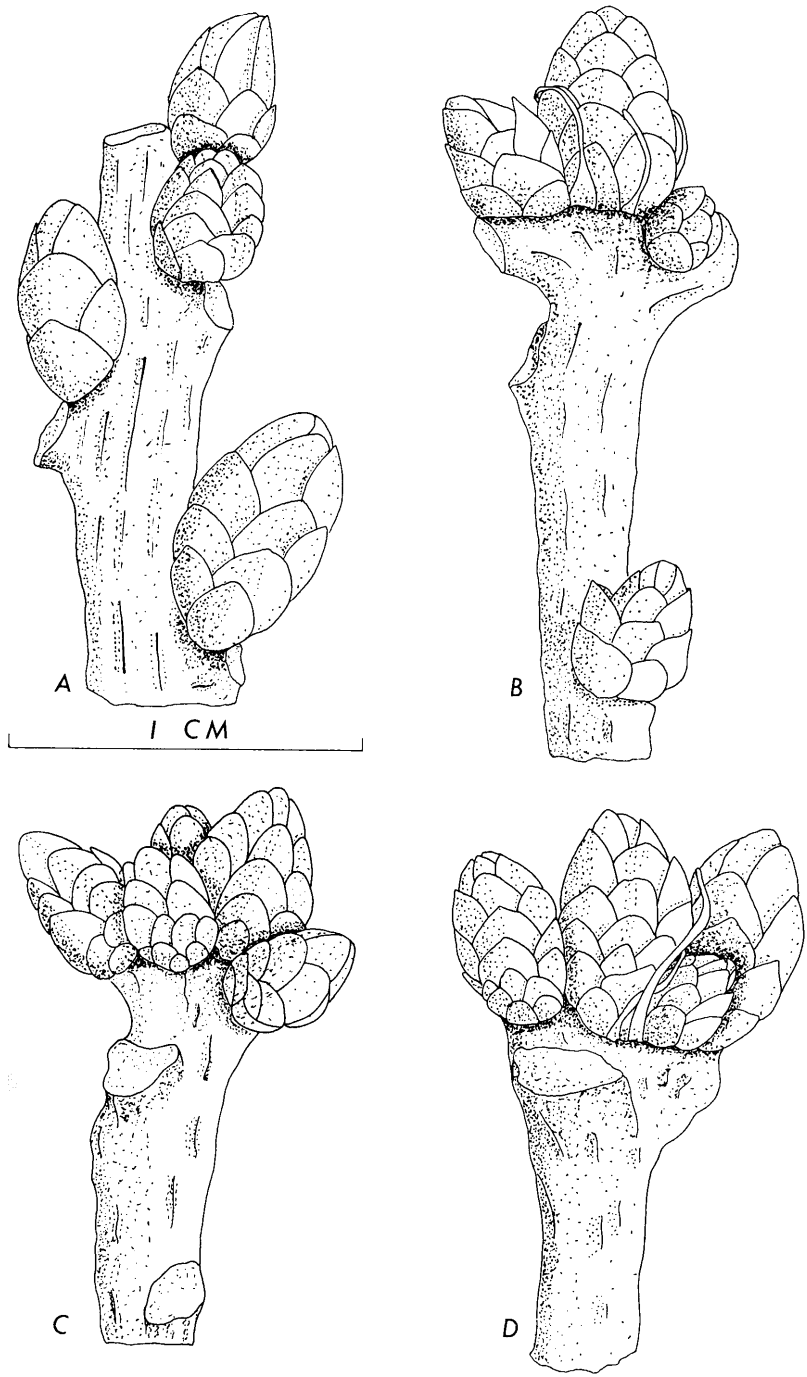

Fig. 4. Terminal buds of fruiting twigs (October) from oaks regarded as representative. — A. *Quercus robur*. — B. *Q. petraea*. — C. The Högsma oak. — D. The Gullarp oak.

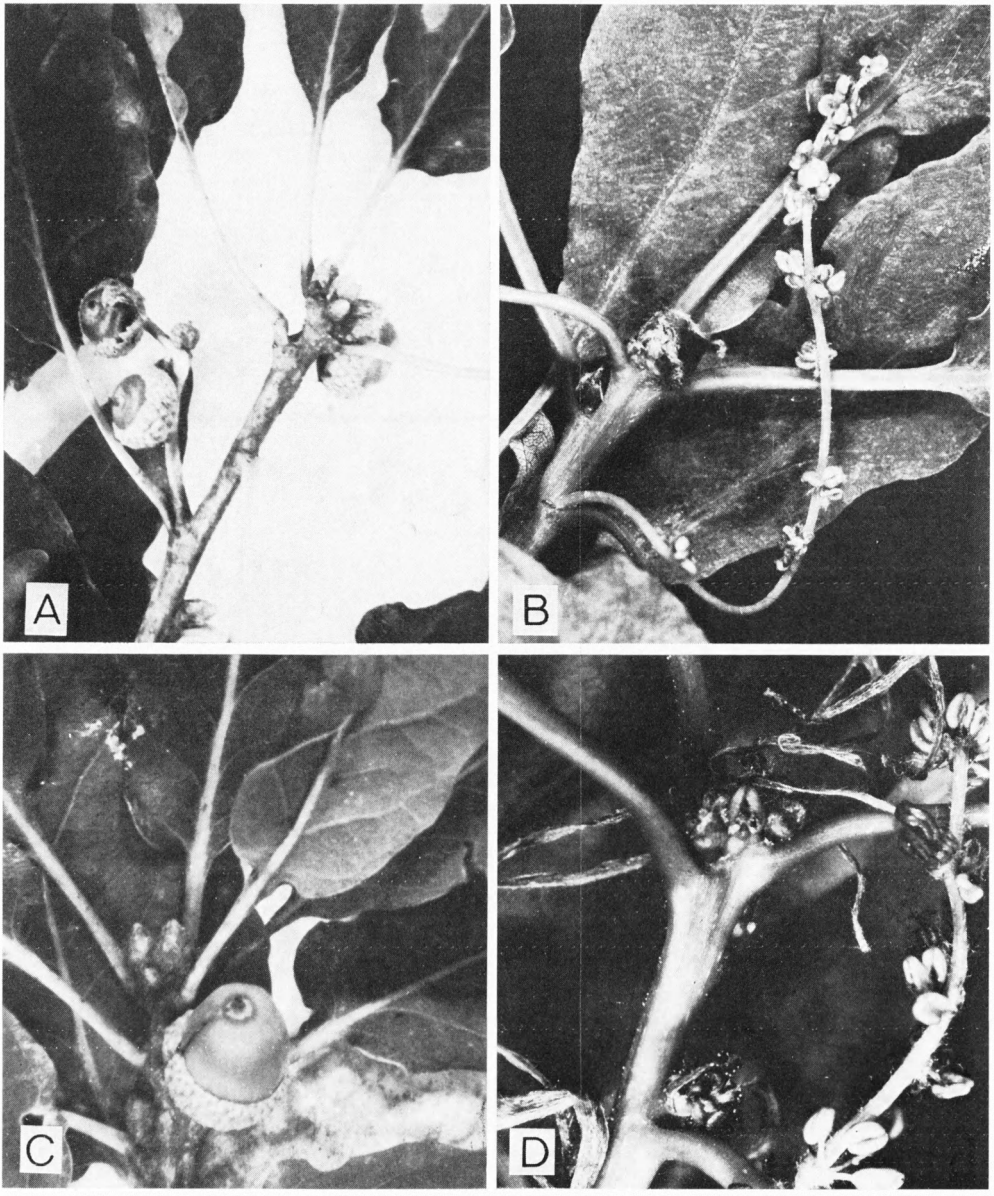

Fig. 5. Fruiting and flowering shoots from the Högsma oak (A, B) and the Gullarp oak (C, D). Note the varying length of the female peduncles on the same shoot and the small undeveloped acorns in A (Högsma). The acorns from the Gullarp oak (C) are usually small and conical with a somewhat constricted zone near the top and a lateral "suture" of ectocarpous folds. In D is shown the sessile female inflorescence. — A (×0.6), B (×2), C (×1.5), D (×3).

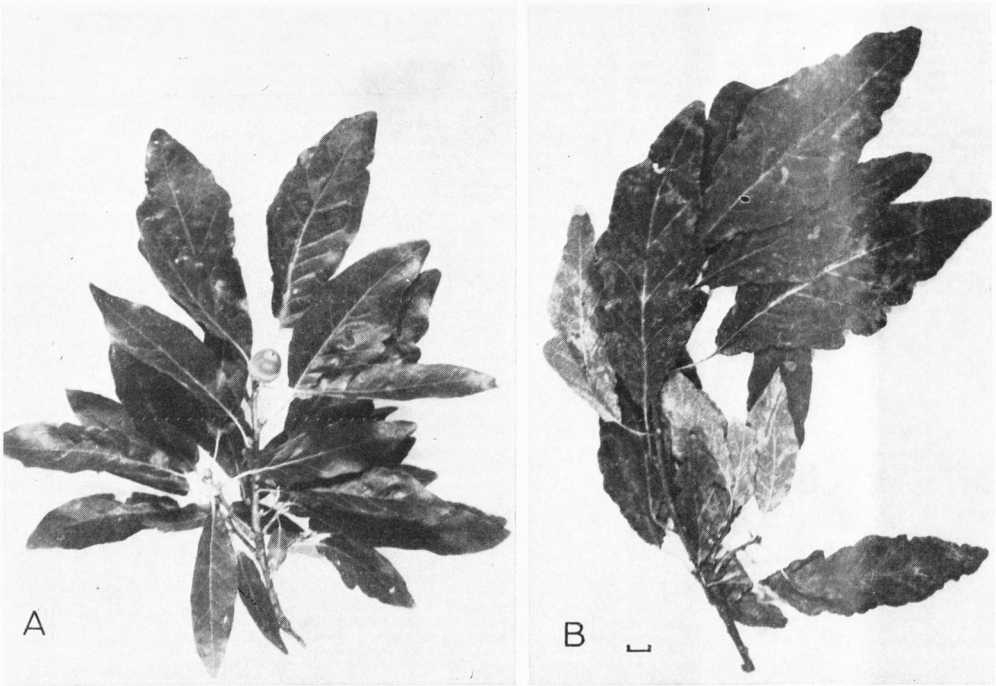

Fig. 6. A twig from the Högsma oak (A) compared with another twig (B) from an oak c. 6 m high, in the vicinity of the Högsma oak. The leaves are rounded-acute at the top and base and have very few lobes. The tree may be a spontaneous progeny of the Högsma oak. Collected 1971. — A (×0.3), B (scale=1 cm).

does not give a clear indication of hybrid origin. This is true of the leaf characters in particular. Precautions must be taken in comparing the leaf characters of the Högsma and Gullarp oaks and the oak species investigated, as the possibility cannot be excluded that a pleiotropic effect at the leaf primordium stage can also have been the cause of other changes as well as that of entire leaf margins. Moreover an exceptional leaf shape with almost no lobes does not permit of an adequate comparison between spontaneous hybrids and parental species with regard to certain characters such as leaf outline, lobation and venation which will make it difficult to use some indices for comparison.

Some *Q. petraea*×*robur* probably represent crosses between the primary hybrid and one of its parents. GESCHWIND (1876), PYATNITSKII (1939) and DENGLER (1941) have shown that the primary hybrid between *Q. robur* and *Q. petraea* displays hybrid vigour expressed, for instance, in an abundance of new shoots with large leaves. GESCHWIND's crossings of *Q. robur* (male) and *Q. petraea* (female) produced a hybrid which had entire leaves. He writes: . . . "Das Blatt, grösser als das von Q. sessiliflora Sm., aber kleiner als das von Q. pedunculata, zeigt die Unregelmässigkeit der Form von letzterer Species, ist l a n g g e s t i e l t, ganzrandig, am Rande wellenförmig, sonst ei-lanzettförmig, kahl, entbehrt der characteristischen Einbuchtungen des Eichenblattes gänzlich und ähnelt oft mehr jenem von Castanea vesca, Gärtn.". Furthermore he

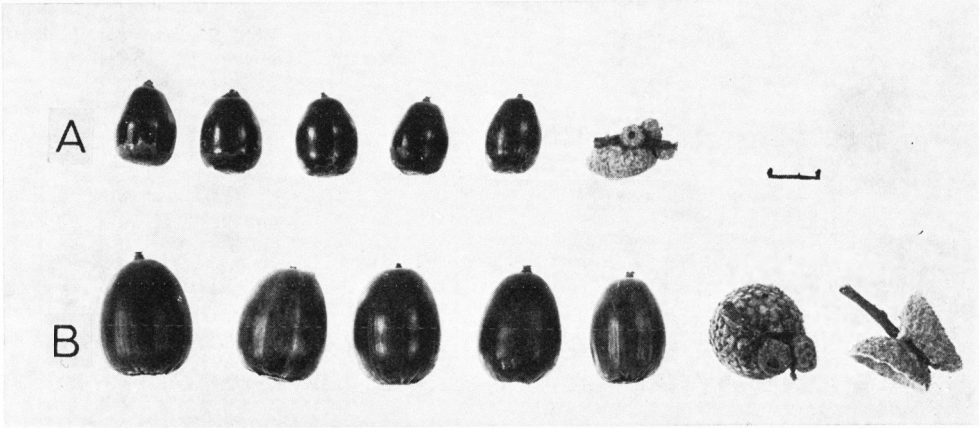

Fig. 7. A series of acorns with catkins from the Gullarp oak (A) and the Högsma oak (B) showing relative size and shape. — Scale=1 cm.

states that the male flowers have well-developed pollen and that the female catkins are short and have fewer flowers than those of *Q. petraea*. He obtained four hybrids, all with different types of leaves. This is important and may indicate that the parent trees were not truly specific but heterozygous and possibly introgressive. It is remarkable how well the description of one of the artifically produced hybrids agrees with the Högsma and Gullarp oaks regarding leaf characters, pollen and fruit-setting.

The strongest indications of hybridity (*Q. robur*×*Q. petraea*) in the Högsma oak are the relatively low frequency of flowers and normal acorns, and in the Gullarp oak there is a low frequency of flowering with presumably no normal acorns. In spite of insufficient indications of hybridity in parts of the investigation there is still reason to believe that the Högsma oak and the Gullarp oak are crossing products of *Q. petraea* and *Q. robur*.

TAXONOMY

In the early 1800's entire- and subentire-leaved oaks from different parts of Europe were described. The first oaks observed were given the rank of species: (1) *Q. sublobata* KIT. (see SCHULTES 1814 p. 619, KITAIBEL 1863 p. 355); (2) *Q. mespilifolia* WALLROTH 1822; (3) *Q. louettei* PETZOLD & KIRCHNER 1864 p. 531. Many botanists and authors of floras have called attention to these aberrant oaks. However, the taxonomic interpretation of the oaks has changed. Most later writers are inclined to describe the entire-leaved type as a forma or varietas of *Q. petraea* (MATTUSCHKA) LIEBL. (syn. *Q. sessiliflora* SALISB., *Q. sessilis* EHRH.): (4) *Q. sessiliflora* SALISB. var. *subintegrifolia* J. PERSSON 1885; (5) *Q. sessilis* EHRH. var. *schidlayana* DOMIN 1937.

The author confirms the opinion of WEIMARCK (1947, 1963) that the subentire-leaved oaks at Högsma and Gullarp may belong to the hybrid *Q. petraea*×*robur*. The correct name will be *Q. petraea* (MATTUSCHKA) LIEBL. ×*robur* L. nm. *mespilifolia* (WALLR.) WEIM. 1963. (syn. *Q. sessiliflora* SALISB. var. *subintegrifolia* J. PERS. — the Högsma oak; *Q. petraea*× *robur* f. *mespilifolia* (WALLR.) WEIM. 1947. — the Högsma and Gullarp oaks; Other names than these synonyms (cf.

1—5 above) are assigned to entire-leaved oaks, but do not apply to the trees at Högsma and Gullarp.)

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Botanical Literature

AHMADJIAN, V. and HALE, M. E. (eds.): The Lichens. — Academic Press, New York and London, 1973. XIV+697 pp., 62 plates, 296 figures. Price £ 19.50 (cloth).

The present volume is a comprehensive and up-to-date survey of various fields within lichenology. It is a companion to the five-volume treatise "The Fungi" edited by G. C. AINSWORTH, F. K. SPARROW and A. S. SUSSMAN and published by Academic Press between 1965 and 1973. The high standard of the print and of the illustrations known from the latter work is also met with in "The Lichens". Most figures are original or reproduced from recent literature. This should be noted as a decided improvement as some similar works issued in the 1960's have borrowed illustrations from SCHWENDENER, BORNET and other 19th century lichenologists.

"The Lichens" is a multi-authored treatise produced by no less than 23 authors from various parts of the world. Hence it is self-evident that the way of presenting the material differs fairly widely from one chapter to another. In some cases we meet with detailed surveys including several previously unpublished data. Other chapters are rather brief summaries, but the mostly comprehensive lists of references will facilitate the reader's further studies.

The volume is organized into 5 major parts, viz. "Structure and Development", "Physiology of the Intact Thallus", "Environmental Response and Effects", "Secondary Metabolic Products" and "Symbiont Interactions".

The introductory chapter "Anatomy, Morphology, and Development" by H. M. JAHNS is a most valuable account illustrated with excellent figures mainly taken from HENSSEN and JAHNS, "Lichenes" (cf. review below). M. A. LETRUIT-GALINOU gives useful information, often from recent research, on "Sexual Reproduction". It is evident, however, that several problems, for example the fertilization of the ascogone by spermatia and role of the apogamy, are still under discussion. Brief chapters on "Systematic Evaluation of Morphological Characters" and "Lichen Propagules" are presented by J. POELT and F. BRIAN PYATT respectively. An informative and critical chapter on "Fine Structure" by E. PEVELING has been illustrated with electron micrographs and SEM photographs of very high quality.

Part II deals with "Physiology of the Intact Thallus" including chapters on "Absorption and Accumulation of Mineral Elements and Radioactive Nucleides" (Y. TUOMINEN and T. JAAKOLA), "Pedogenetic Significance of the Lichens" (J. K. SYERS and I. K. ISKANDAR), "Photosynthesis and Carbohydrate Movement" (D. H. S. RICHARDSON) and "Nitrogen Metabolism" (J. W. MILLBANK and K. A. KERSHAW).

Part III "Environmental Response and Effects" discusses "Response to Extreme Environments" (L. KAPPEN), "Water Relations" (O. B. BLUM), "Substrate Ecology" (I. M. BRODO), "Lichens and Air Pollution" (O. L. GILBERT) and "Growth" (M. E. HALE).

Some aspects of "Secondary Metabolic Products" are treated in Part IV, viz. "Nature of Lichen Substances" (S. HUNECK), "Biosynthesis of Lichen Substances" (K. MOSBACH) and "Antibiotics in Lichens" (K. O. VARTIA).

Part V is concerned with "Symbiont Interactions". V. AHMADJIAN gives a very brief survey of his research on "Resynthesis of Lichens". "Evolutionary Aspects of Symbiosis" are presented in a somewhat philosophical article by G. D. SCOTT.

For reasons difficult to understand three concluding chapters have been entitled "Appendices", viz. "Classification" (J.

POELT), "Identification and Isolation of Lichen Substances" (J. SANTESSON) and "Methods of Isolating and Culturing Lichen Symbionts and Thalli" (V. AHMADJIAN). POELT briefly discusses previous lichen systems and outlines, in a very fragmentary manner, a new system "based partly on my own preliminary studies of ascus structure". He rightly emphasizes the difficulties in integrating the lichenized fungi in any accepted fungal system. "Lichen systematists have hardly ever been really familiar with the corresponding fungal groups, and mycologists have had enough difficulties with their own groups without bringing in the lichenized fungi."

The "complete authoritative coverage" of lichenology stated on the cover of this book is somewhat of an exaggeration. Certain topics are not treated at all, for example lichen sociology and geographical distribution and there are others that could have been dealt with in greater detail. Nevertheless, "The Lichens" is a mine of information both for the student and the advanced lichenologist.

OVE ALMBORN

HENSSEN, A. and JAHNS, H. M.: Lichenes. Eine Einführung in die Flechtenkunde. — Georg Thieme Verlag, Stuttgart, 1974. XII+467 pp., 142 figures, 8 plates. Price DM. 19.80 (flexible paper cover).

The notable new interest in lichens during the last two decades has resulted in several floras, monographs and handbooks covering more or less wide fields of "general lichenology". As nearly forty years have elapsed since such a textbook was issued in the German language, the present work by Dr AINO HENSSEN (Marburg) and Dr HANS M. JAHNS (Groningen, now Frankfurt am Main) is especially welcome.

The authors have modestly called their book "An Introduction to Lichenology". They have, however, admirably succeeded in condensing a surprising number of facts into a comprehensive volume no bigger than a pocket book, and at a very reasonable price.

A brief introductory survey of the history of lichenology is followed by far more elaborate chapters on the morphology of the lichens, especially the organs of reproduction. These parts are of extreme value as both authors have carried out very important investigations on this topic. Several new results are published here for the first time, often with original drawings and photographs.

The physiology of the lichens is treated in a concise chapter. Lichen chemistry is dealt with by a specialist, Dr JOHAN SANTESSON, Uppsala. This subject, introduced more than a hundred years ago for diagnostic purposes, has developed immensely during the last few decades and has become an important source of information for the understanding of the metabolism of lichens. Symbiosis, parasitism and related problems are briefly discussed, as well as synthesis in vitro between mycobionts and phycobionts. There are also short accounts of growth, diaspores, ecology (including sociology and the effects of air pollution), distribution and economic importance.

Nomenclature and classification are treated in some detail. A new lichen system is presented, differing essentially from ZAHLBRUCKNER's classical arrangement and also from the system proposed by J. POELT (cf. review above). HENSSEN and JAHNS have founded their taxonomy on modern views on the ontogeny of the fruitbodies of the non-lichenized ascomycetes. Much attention has been paid to ascolocular or ascohymenial development, bitunicate or unitunicate asci, etc. As experts in this field it is not unreasonable that the authors have laid stress upon taxonomic characters derived from ontogeny. Though the place of some families is described as tentative so far, the reviewer believes that the main features of the future lichen system will much resemble the taxonomy outlined by HENSSEN and JAHNS.

An extensive list of references to literature and another of lichenological terms conclude this well-organized volume. No effort will be made here to compare it with the major work reviewed above, "The Lichens", but it seems highly probable that a translation of "Lichenes" into English would be appreciated in many parts of the world.

OVE ALMBORN

TRALAU, H. (ed.) 1974. Index Holmensis, IV. A World Index of Plant Distribution Maps. Dicotyledoneae A—B. — Scientific Publishers Ltd., Zürich.

Three volumes of Index Holmensis have been published previously, viz. Vol. I: Vascular cryptogams and gymnosperms; Vol. II: Monocotyledoneae A—I; and Vol. III: Monocotyledoneae J—Z. The last two were reviewed in Bot. Notiser 125 p. 199. The fourth volume, Dicotyledoneae A—B, which has now appeared is especially welcome as it promises a full continuation of the Index for the rest of the higher plants.

An innovation for Vol. IV is that in addition distributions of plant species incorporated in vegetation maps have been included in the Index (but only where Latin names of the species concerned are given). This extends the coverage of the Index considerably and adds much useful information.

The present volume, like the previous one, contains a tremendous amount of information. *Astragalus,* a genus of c. 1,600 species, contributes references of maps extending over approx. 65 columns. Important tree genera such as *Betula, Alnus,* and *Acacia* are also included, with numerous columns of reference each, which should be of immeasurable importance to forest ecologists all over the world.

It is hardly necessary to repeat that I consider Index Holmensis to be of great importance. It should be found in any biological institute or library with effective research and service respectively. The Index provides information that is of primary importance to ecologists in the fields of botany as well as zoology, and to systematists, horticulturalists and plant geographers. It can also be used to trace literature supplying information on other aspects of the species concerned.

As the number of maps being published is rapidly increasing Dr TRALAU appeals for assistance in collecting information on new maps published, and in getting reprints of publications with distribution maps (see Bot. Notiser 128 p. 201 and Taxon 24 p. 142). This is a matter of utmost urgency. There are numerous maps printed in publications that are difficult to obtain and that in addition may have mixed contents.

Index Holmensis is an undertaking that is deserving of all support. It is without doubt an investment that is a means of saving time and money for the research worker.

ROLF DAHLGREN

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