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THE CHROMOSOMES OF THE SPURIA IRISES AND THE EVOLUTION OF THE GARDEN FORMS[1]

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INTRODUCTION

The spuria[2] irises constitute a distinctive group of species and hybrids which have found considerable favor with horticulturists and are commonly found in gardens today. They may be characterized as: plants rhizotomous, sepals more or less panduriform and beardless, stigmas 2-toothed, capsules with double ribs at the three angles, and seeds with loose or somewhat loose parchment-like testa which may be smooth or wrinkled. The lateral branches of the inflorescence, when present, are held erect and held close to the main stem by subtending bracts, producing the effect of the flowers being borne one above the other on a single terminal spike. A feature not generally recorded since it is observable only in fresh material is the production of copious amounts of nectar which accumulates as droplets on the outside of the upper portion of the perianth tube, but well below the fusion of the segments. The spurias share this characteristic with two bulbous irises, *I. xiphium* L. and *I. tingitana* Boiss. et Reuter which have flowers superficially similar to those of the spurias. In the forms of *I. spuria*[3] which have been grown at the Botanic Garden the plants have produced quantities of nectar on the spathe valves as well as on the perianth tube. This has not been observed in any other iris.

No overall taxonomic evaluation of the spurias has been attempted since the publication of Dykes' *Handbook of Garden Irises* (1924). Since this is not a taxonomic treatment of the group the binomials used by us are not to be construed as necessarily recognition on our part of the specific distinctness of the taxa involved. A careful study will undoubtedly show that certain re-alignments are necessary, especially in the 22-chromosome *I. halophila* Pallas complex which may well include a number of specifically distinct entities. Present evidence indicates that among the 20-chromosome forms there may be at least one undescribed species.

MATERIALS AND METHODS

The plants used in this study were obtained from many sources as rhizomes or seeds. In the case of the species a special effort was made to obtain material collected in the field from naturally occurring populations rather than plants or seeds from gardens, the original sources of which are often unknown. When authentic wild-collected material was not available the plants were carefully checked to determine whether they agreed with the original description of the species. Horticultural forms were also obtained from many sources. Every attempt was

[1]This investigation was supported in part by grants from the National Science Foundation (NSF G-9322) and the American Iris Society.

[2]In this paper the word spuria is used in two ways, in the vernacular sense to include all the species and hybrids which are properly placed in the series *Spuriae* (Diels) Lawr., and as a specific epithet. In the latter case it will be indicated as *Iris spuria* L.

[3]The name *I. spuria* is here used in the strict sense and includes only the central and northern European forms with $n=11$ chromosomes. In this interpretation of the species we are following Bernatsky and Janchen (1910) and Westergaard (1938).

made to secure plants which were true to name. With recently introduced cultivars exact determinations could usually be made. In the case of the older varieties, some of which have been in the trade for as long as 80 years, it was impossible, due to lack of illustrations or exact descriptions, to be certain that they were divisions of the original plant bearing that name.

Chromosome determinations were made from root tip divisions obtained from plants grown in the greenhouse or from embryo-cultured seedlings. Pretreatment of the root tips consisted of chilling in ice water at 0° C for from 24 to 72 hours or treatment with a 0.2% aqueous solution of colchicine at 0° C for one-half to 3 hours. Fixation was in 3 : 1 absolute ethanol-glacial acetic acid. If storage was necessary the root tips were kept in the fixative rather than in 70% alcohol which tended to harden the tissues. Root tip squashes were made in 1% acetic-orcein after first hydrolyzing in a 1 : 1 mixture of the stain and 1 N HCl with slight heating. The edges of the coverslips were sealed with beeswax for temporary storage. All drawings were made with a camera lucida at bench level. Voucher specimens have been deposited in the Rancho Santa Ana Botanic Graden herbarium.

THE CHROMOSOMES OF THE SPECIES

Chromosome numbers of members of the spuria alliance have been reported by various investigators since the pioneer work of Simonet (1928) but in most instances the counts have been only incidental to a general survey of the genus. The first study specifically devoted to the group was that of Westergaard (1938) who made a karyotype analysis of the rare endemic found at Saltholm, a small island lying between Copenhagen, Denmark, and Malmo, Sweden, and compared it with the spurias found near Vienna, Austria. He concluded that while the karyotypes were somewhat different, the two groups might be considered as belonging to the central European stock. All chromosome counts of spuria species now known are shown in Table 1. Unless otherwise indicated the determinations are those of the authors.

The approximate geographical distribution of the different chromosome number groups is shown in figures 1–3. It will be noted that those of the low number series, i.e., n=8 (16), 9, 10 are found in southern Italy, the Balkans and the Near East. Plants with n=11 are found farther to the north and west with a discontinuous distribution in central Europe and with a few isolated localities in northern Europe. Before we can be certain of the total extent of distribution of the 11-chromosome forms additional counts should be made of plants from France as well as those reported growing along the fen ditches in Lincolnshire, England, where it is reported that they may be native (Clapham, Tutin & Warburg, 1962). Of the species with higher numbers, *Iris graminea* (n=17) is perhaps the most widely distributed, extending from Spain eastward through southern Europe to near the Black Sea. The related *I. humilis* (n=36) is more restricted being found in the area east and north of the Caspian Sea. From information presently available it would appear that the 19-chromosome forms are all native to the area around the western end of the Mediterranean. Plants from Algeria were not available for study and their chromosome determination must await the availability of seeds or plants. It is reasonable to assume however that they will be found to have the same number as those from Spain and southern France. The 20-chromosome taxa appear to have two areas of distribution, one in the Near East but extending into the Middle East, and a second in Kashmir. The taxonomically poorly understood 22-chromosome group is widely distributed from Afghanistan and the USSR eastward into China. This group has not been adequately sampled and further work is required before it can be stated with certainty that other chromosome numbers are not also present in the Far Eastern forms. There are other spuria species, some of which have never been in cultivation, and chromosome determinations of these plants must await the availability of suitable material.

Karyotype analyses (Fig. 4) have been made of the basic low number series (i.e. n=8, 9, 10, 11). In common with many species of *Iris*, each possesses one pair of long metacentric or submetacentric chromosomes. Although each species has a distinct and characteristic karyotype there are a number of features which they share in common; one is the absence of telocentric chromosomes (the location of the centromere in chromosome 10 of *I. brandzae* was not determined due to lack of adequate material). *Iris kerneriana* appears to have the greatest number of metacentric or submetacentric chromosomes. It also has two pairs of long chromosomes which are nearly equal in length. *Iris urumovii* is characterized by having a pair of very short metacentrics. The number of satellites varies from one pair in *I. kerneriana* to three pairs in *I. urumovii*. In *Iris brandzae* satellites are present on one pair of the longest, or next to longest, chromosomes. In all the others they are generally on the shortest, or one of the shortest pairs, and if a second pair is present they are often on one or more of the medium length chromosomes. With the exception of *I. urumovii* all species have satellites of about the same size. With more adequate sampling, karyotype differences within these taxa may well be detected as has been the case in some of the bearded irises (Randolph and Mitra, 1959).

TABLE 1. *Chromosome Numbers of Spuria Species*

SPECIES	CHROMOSOME NUMBER		AUTHOR	SOURCE[4]
	n	*2n*		
1. *Iris sintenisii* Janka		16, 32	Simonet, 1934	
2. *Iris sintenisii* Janka		16		1
3. *Iris kerneriana* Aschers & Sint.		18	LaCour, unpub.[5]	
4. *Iris kerneriana* Aschers & Sint.		18		6
5. *Iris kerneriana* Aschers & Sint.		18		4
6. *Iris brandzae* Prodan		20	Tarnavschi, 1938[5]	
7. *Iris brandzae* Prodan		20		3
8. *Iris brandzae* Prodan (as *I. sintenisii* Janka ssp. *brandzae* Prodan)		20		8
9. *Iris urumovii* Vel.		20	Simonet, 1934	
10. *Iris urumovii* Vel.		20		2
11. *Iris urumovii* Vel.		20		3
12. *Iris urumovii* Vel. (as *I. sintenisii* Janka ssp. *urumovii* Vel.)		20		8
13. *Iris urumovii* Vel. (as *I. ruthenica* Ker.-Gaw.)		20		3
14. *Iris spuria L. (sensu stricto)*		22	Westergaard, 1938	
15. *Iris spuria* L.		22		3
16. *Iris spuria* L.		22		9
17. *Iris spuria* L.		22		10
18. *Iris spuria* L. (as *I. spuria* L. var. *danica* Dykes)		22	Westergaard, 1938	
19. *Iris graminea* L.	17	34	Simonet, 1932	
20. *Iris graminea* L.		34		5

[4]Key to sources: 1–Ben Hager, Modesto, California; 2–Marion R. Walker, Ventura, California; 3–Rudolf Hanselmayer, Graz, Austria; 4–Leonard W. Brummitt, Banbury, Oxon, England; 5–Paul Cook, Bluffton, Indiana; 6–Edith Cleaves, Los Gatos, California; 7–United States Department of Agriculture, Washington, D. C.; 8–Botanical Garden, Cluj, Rumania; 9–Max Steiger, Lauf/Pegnitz, Germany; 10–F. Ehrendorfer, Vienna, Austria; 11–Museum of Natural History, Paris, France; 12–Botanical Garden, Leningrad, USSR; 13–Botanical Garden, Munich, Germany; 14–Botanical Garden, Palermo, Sicily; 15–Homer Metcalf, Bozeman, Montana; 16–Botanical Garden, Barcelona, Spain; 17–Roy Davidson, Seattle, Washington; 18–Haydar Bagda, Ankara, Turkey.

[5]*In* Darlington, C. D., & A. P. Wylie, 1955, *The Chromosome Atlas of Flowering Plants*. London, 519 p.

TABLE 1. *Chromosome Numbers of Spuria Species (continued)*

SPECIES	CHROMOSOME NUMBER		AUTHOR	SOURCE[4]
	n	*2n*		
21. *Iris graminea* L. (as *I. colchica* Kem.-Nat.)		34		12
22. *Iris graminea* L. (as *I. pseudocyperus* Schur.)		34		8
23. *Iris maritima* Lam. (as *I. spuria* L. var. *maritima* Dykes)	19	38	Simonet, 1932	
24. *Iris maritima* Lam.		38		11
25. *Iris maritima* (as *I. spuria* L.)		38		16
26. *Iris crocea* Jacq. ex Baker		40		3
27. *Iris crocea* Jacq. ex Baker (as *I. aurea* Lindl.)	20	40	Simonet, 1932	
28. *Iris ochroleuca* L.	20	39–40	Simonet, 1932	
29. *Iris ochroleuca* L.		40		?
30. *Iris ochroleuca* L.		40		2
31. *Iris ochroleuca* L.		40		7
32. *Iris ochroleuca* L. (as *I. ochroleuca* L. var. *sulphurea* hort.) clone 1		40		2
33. *Iris ochroleuca* L. (as *I. ochroleuca* L. var. *sulphurea* hort.) clone 2		40		2
34. *Iris monnieri* DC		40		2
35. *Iris monnieri* DC		40		1
36. *Iris* sp. (Turkey Yellow)		40		18
37. *Iris carthaliniae* Fom.		44	Simonet, 1932	
38. *Iris carthaliniae* Fom.		44		15
39. *Iris carthaliniae* Fom. (as *I. violacea* Sweet)		44		14
40. *Iris halophila* Pal. *(sensu lato)*		44	Simonet, 1934	
41. *Iris halophila* Pal. (as *I. lilacina* Borb.)		44	LaCour, unpub.[5]	
42. *Iris halophila* Pal. (as *I. musulmanica* Fom.)	22	44	Simonet, 1928	
43. *Iris halophila* Pal. (as *I. musulmanica* Fom.)		44		12
44. *Iris halophila* Pal. (as *I. spuria* L.)		44		3
45. *Iris halophila* Pal. (as *I. spuria* L. var. *alba* hort.)	22	44	Simonet, 1928	
46. *Iris halophila* Pal. (as *I. spuria* L. var. *alba* hort.)		44		13
47. *Iris halophila* Pal. (as *I. spuria* L. var. *kashmiriana* hort.)	22	44	Simonet, 1932	
48. *Iris halophila* Pal. (as *I. spuria L.* var. *lilacina* Borb.)		44		18
49. *Iris halophila* Pal. (as *I. spuria* L. var. *notha* M.B.)		44		13
50. *Iris halophila* Pal. (as *I. spuria* L.)		66		?
51. *Iris halophila* Pal. (as *I. sp.*)		44		7
52. *Iris klattii* Kem. Nat.		44		12
53. *Iris humilis* M.B.		72	Simonet, 1934	

Westergaard (1938) found it difficult, due to unsatisfactory fixation to set up complete idiograms for the two forms of *I. spuria* which he studied. He did, however, report two pairs of satellites in each. One pair was found on one of the shortest chromosome pairs and the

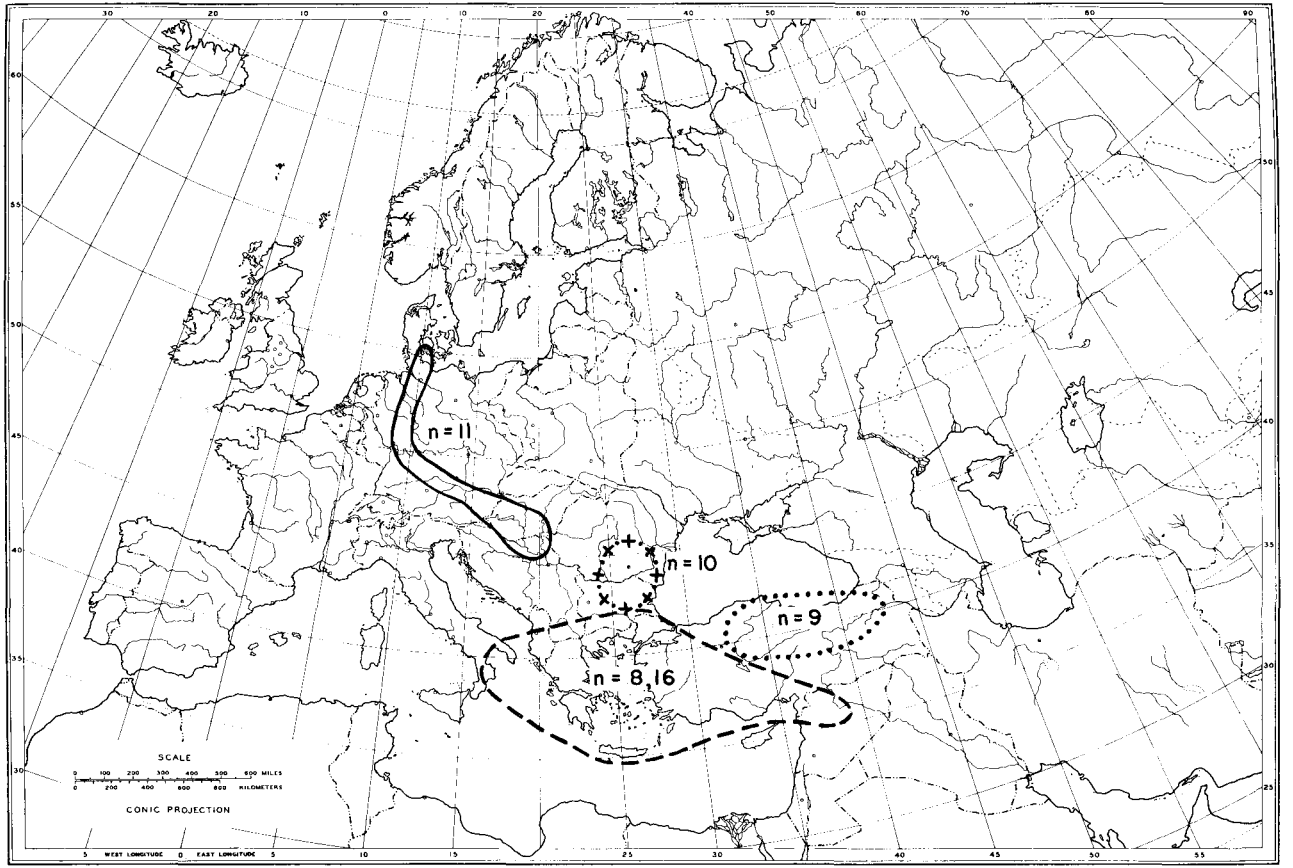

Fig. 1. Approximate geographical distribution of different chromosome number groups in the series *Spuriae* (Diels) Lawr. as determined from standard floras. See Table 1 for the species included within each group. The map used is one of the Goode Base Map Series, published and copyrighted by the University of Chicago Press and used with their permission.

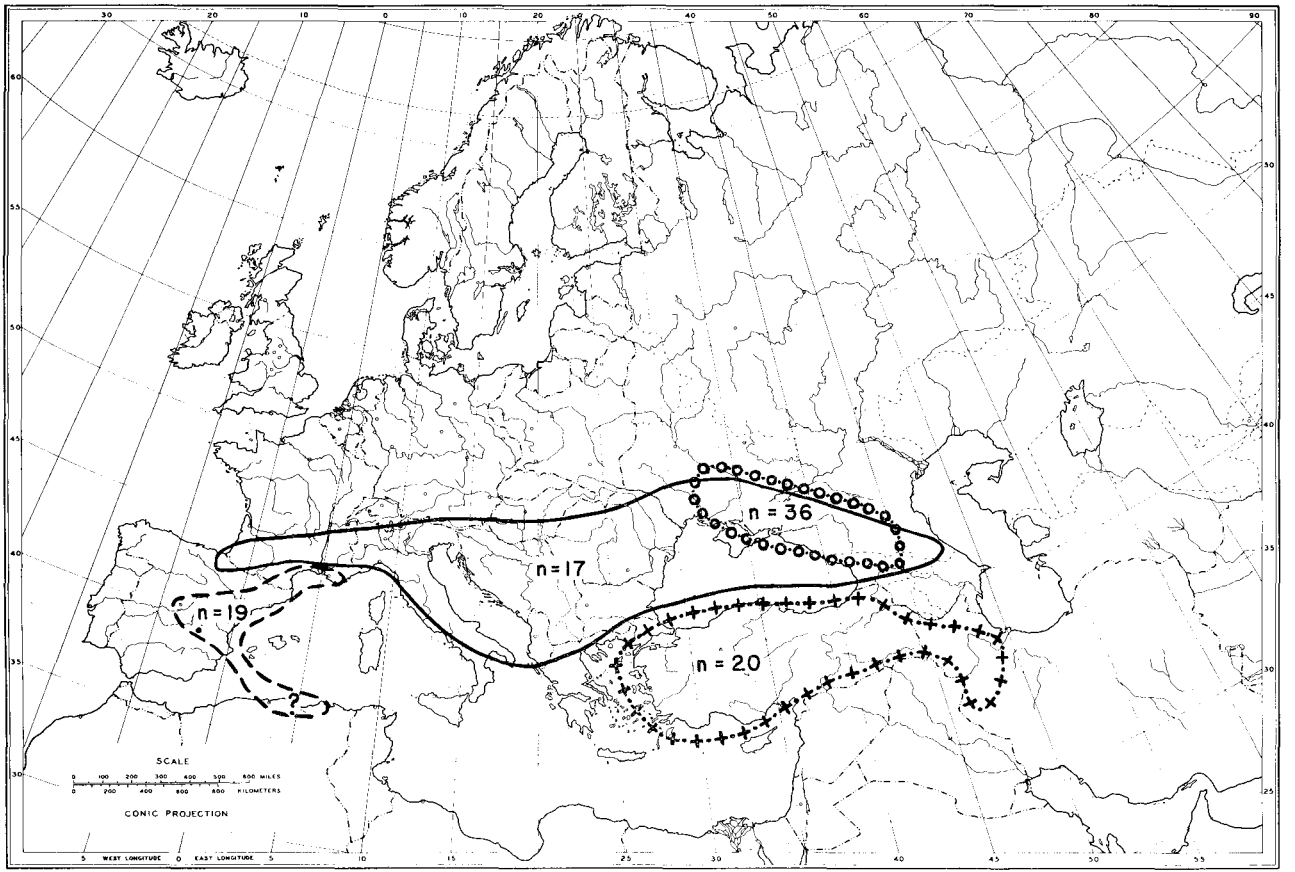

Fig. 2. Approximate geographical distribution of different chromosome number groups in the series *Spuriae* (Diels) Lawr. as determined from standard floras. See Table 1 for the species included within each group. The map used is one of the Goode Base Map Series, published and copyrighted by the University of Chicago Press and used with their permission.

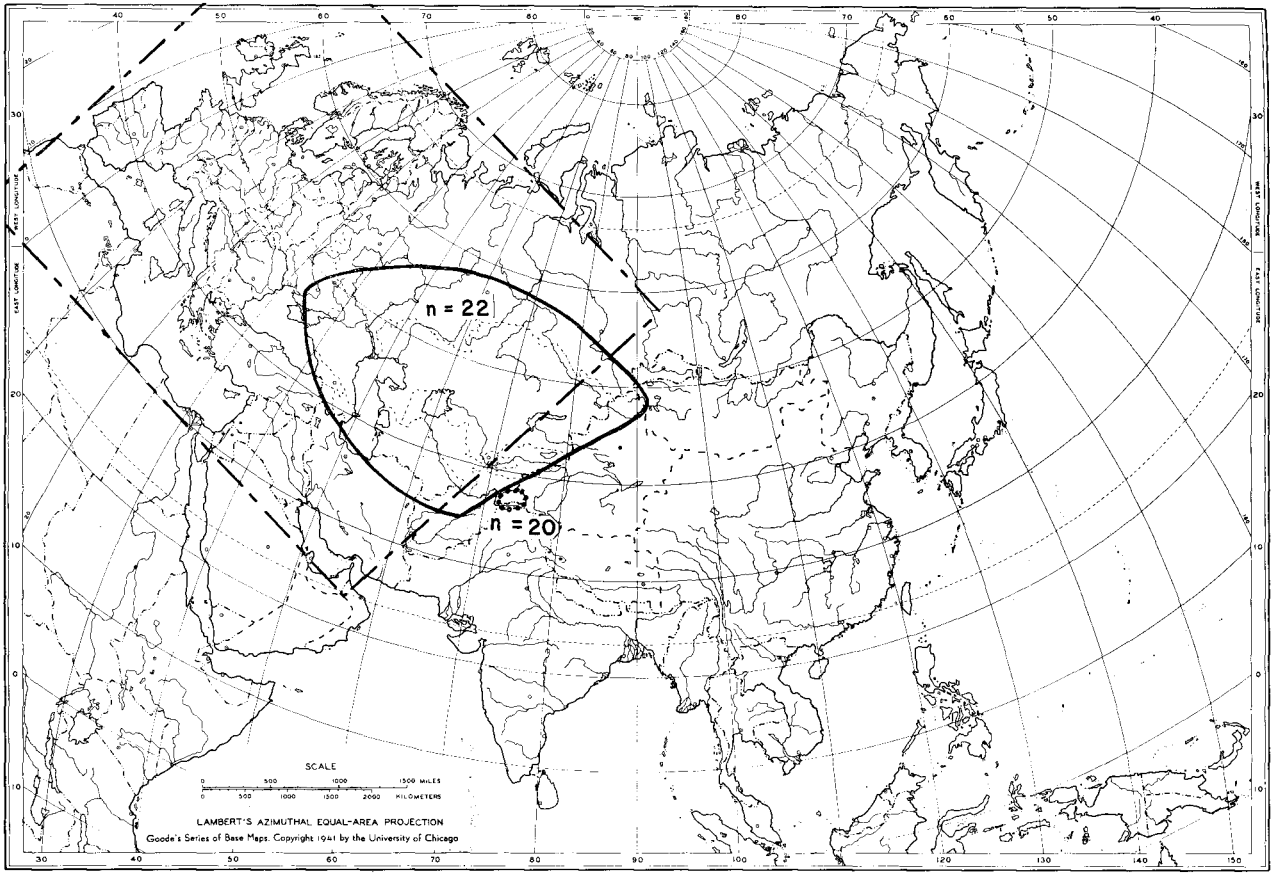

Fig. 3. Approximate geographical distribution of different chromoscme number groups in the series *Spuriae* (Diels) Lawr. as determined from standard floras. See Table 1 for the species included within each group. The map used is one of the Goode Base Map Series, published and copyrighted by the University of Chicago Press and used with their permission.

other appeared to be on one of the longest. In the material from Austria he found the satellites to be about the diameter of the rest of the chromosome, whereas in the Danish form one pair was very small and easily overlooked. Considering the differences in source of material and techniques, our collection from Germany appears to correspond very closely with Westergaard's Austrian form.

CHROMOSOMES OF THE HORTICULTURAL FORMS

The garden spurias, mostly of hybrid origin, are plants with flower stalks from about three to as much as six feet tall ('Shelford Giant') and flowers ranging in color from white and pale blue or lavender to deep blue-purple, and from cream color to deep golden-yellow. There are also forms with brown or bronze-colored flowers and some of the more recent introductions combine two colors in a single flower. Many of the flowers are heavily veined on the sepals.

The only cytological study of the garden varieties is that of Hadley (1958) who reported a uniform $2n=40$ for 18 clones. Difficulty in determining the exact number of chromosomes in root tip divisions, as well as the desire to observe meiotic chromosome behavior, led Hadley to confine his investigations to microsporocytes. He reported the presence of univalents and multivalents but found that anaphase I was apparently normal in all varieties with the possible exception of 'Russet Flame' in which he detected a cell with an anaphase bridge. He also found laggards in some divisions. Hadley concluded that on the basis of their meiotic behavior the forms which he had examined appeared to be cytologically highly stable. In the present investigation we did not find the strict uniformity of numbers reported by Hadley but this is due perhaps only to our broader sampling of the horticultural clones. Table 2 shows the chromosome numbers of all garden forms so far determined. Of the 64 cultivars, 84% have $2n=40$ and 16% have numbers ranging from 41–44, with one exception, a hybrid with $2n=28$. The significance of these variant numbers in the evolution of the garden spurias will be discussed in a later section.

TABLE 2. *Chromosome Numbers of Garden Spurias*

NAME OF CULTIVAR	REGISTRAR	2n	DATE OF REGISTRATION	AUTHOR	SOURCE[6]
1. 'A. J. Balfour'	Barr	40	1889		1
2. 'Alice Eastwood'	Brannin	40	1929		2
		40		Hadley, 1958	
3. 'Alice White's Sdlg.'	—	28			1
4. 'Autumn Glow'	Nies-Walker	40	1959		2
5. 'Azure Dawn'	Nies	40	1942	Hadley, 1958	
6. 'Bathsheba'	Washington	40	1936		1
7. 'Ben Lomond'	Washington	42	1935		2
8. 'Big Cloud'	Craig	40	1950		1
9. 'Black Point'	Nies-Walker	40	1955		1
10. 'Blue Display'	Nies	40	1947		2
11. 'Blue Nightshade'	Nies-Walker	40	1956		1
12. 'Blue Pinafore'	Craig	40	1950		1
13. 'Blue Zephyr'	Washington	44?	1943		1
14. 'Bronze Butterfly'	Brennan	40	1950		2
15. 'Bronzspur'	Nies	40	1940	Hadley, 1958	

[6]See footnote 4, p. 259.

TABLE 2. *Chromosome Numbers of Garden Spurias (continued)*

NAME OF CULTIVAR	REGISTRAR	2n	DATE OF REGISTRATION	AUTHOR	SOURCE
16. 'Cambridge Blue'	Barr	42	1924		2
17. 'Canary Island'	Walker	40	1948		2
18. 'Cherokee Chief'	Nies	40	1949	Hadley, 1958	
19. 'Driftwood'	Nies-Walker	40	1956		2
20. 'Dresden Blue'	Nesmith	41	1954		1
21. 'Dutch Defiance'	Nies	40	1943	Hadley, 1958	
22. 'El Camino'	Walker	40	1958		2
23. 'Fairy Lantern'	Nies-Walker	40	1955		2
24. 'Fairy Light'	Thorup	40	1948		2
25. 'Fifth Symphony'	Nies	40	1942		1
26. 'Gay Lark'	Walker	40	1958		2
27. 'Golden Agate'	Nies	40	1944		1
28. 'Golden Lady'	Combs	40	1957		1
29. 'Golden Sceptre'	Washington	40	1948		2
30. 'Good Nature'	Ferguson	40	1958		1
31. 'Grace Perry Nies'	Nies-Walker	40	1955		2
32. 'Katrina Nies'	Nies-Walker	40	1949		2
33. 'Lark Song'	Nies	40	1942	Hadley, 1958	
34. 'Lord Wolsely'	Barr	40	1899		2
		40			1
35. 'Lumiere'	Washington	42	1935		1
		41			2
36. 'Michigan State'	Nies	40	1942	Hadley, 1958	
37. 'Monaurea'	Bonnewitz	41	1920		1
38 'Monspur' clone 1	Foster	40	1890		2
clone 2		40			2
39. 'Morningtide'	Walker	40	1955		2
40. 'Mrs. Tait'	Farr	42	1912		1
(as 'A. W. Tait')		42			2
41. 'Mt. Wilson'	Milliken	40	?	Hadley, 1958	
42. 'Orange Delight'	Nies-Walker	40	1956		2
43. 'Pastoral'	Nies	40	1942	Hadley, 1958	
44. 'Peaches and Cream'	Taylor	40	1947		1
45. 'Perky Maid'	Nies	40	1949		1
46. 'Premier'	Barr	42	1899		1
		42			2
47. 'Royal Toga'	Nesmith	43–44	1954		2
48. 'Ruffled Gold'	Taylor	40	1947		1
49. 'Russet Flame'	Nies	40	1944	Hadley, 1958	
50. 'Ruth Nies Cabeen'	Nies-Walker	40	1949		2
51. 'Saugatuck'	Nies	40	1941		1
52. 'Shelford Giant'	Foster	40	1913		2
		40			1
53. 'Skyline'	Washington	44	1936		1
54. 'Sun and Shadow'	Craig	40	1950	Hadley, 1958	
55. 'Sunlit Sea'	Nies-Walker	40	1956		2
56. 'Sunny Day'	Sass	40	1931		1
57. 'Sweet Butter'	Craig	40	1950		2
58. 'Two Opals'	Nies	40	1944		1
59. 'Violet Veil'	Walker	40	1956		2
60. 'Wadi Zem Zem'	Milliken	40	1943		2
61. 'Wakerobin'	Ferguson	40	1958		1
62. 'White Crane'	Milliken	40	?	Hadley, 1958	
63. 'White Heron'	Milliken	40	1948	Hadley, 1958	
64. 'Yellow Swallowtail'	Nies	40	1948		1

EVOLUTION OF THE GARDEN FORMS

Any attempt to trace the history and evolutionary development of a group of plants long in cultivation is beset with obstacles and often there is little factual material on which to build an hypothesis. Cytological information has contributed substantially to a better understanding of the development of a number of garden plants, among them the hyacinths (Darlington, *et al,* 1951), the daffodils (Wylie, 1952), the garden mock orange (Janaki Ammal, 1951) and the cultivated nerines (Janaki Ammal, 1951). Stearn's (1946) paper on the evolution and history of the tall bearded irises was made possible only through earlier cytological investigations of Longley (1928), Simonet (1934) and Randolph (1944). Although it would be desirable to have additional counts of the spurias it is felt that the ones already obtained indicate lines along which the garden forms may have evolved.

Counts of more than 60 registered clones (Table 2) show 84% with $2n$=40 and 16% with $2n$=41–44 (with the exception of the previously mentioned $2n$=28 hybrid). According to Hadley (1958) the 40-chromosome garden forms are probably polyploids but he did not elaborate. Somatic counts of 40 might well indicate a polyploid condition, either ancient or recent, and in the tall bearded irises with $2n$=48(49) it has been clearly demonstrated that they do represent a group of tetraploids produced in recent times through hybridization between diploid ($2n$=24) and tetraploid ($2n$=48) species.

An examination of Table 1 shows that there is a group of species with $2n$=40 chromosomes, the number found in the majority of the garden forms. These are *I. ochroleuca, I. crocea* and *I. monnieri.* It is generally agreed among horticulturists that many of the garden varieties are similar to, if not identical with, some of the forms of *I. ochroleuca* (e.g., 'Shelford Giant') and there can be little doubt but that *I. ochroleuca* has played a major role in the evolution of the garden plants. This species, native to the Near East but extending perhaps into the Middle East, was introduced into cultivation at an early date and was illustrated in the *Botanical Magazine* (t. 61) in 1788 where it was reported that "it appears perfectly naturalized in this country [i.e., England], growing luxuriantly in a moist rich soil and increasing . . . very fast by its roots." It thrives in many parts of the world and due to its ease of cultivation and the beauty of the flowers it has been a garden favorite for many years. So far as is known, *I. ochroleuca* is always white-flowered with a yellow spot, or signal patch, on each of the sepals. The extent of the yellow varies but no form is known in which it completely absent.

Yellow-flowered, 40-chromosome spurias are found as naturally occurring taxa and as garden plants. *Iris crocea* (*I. aurea* of gardens) has been in cultivation well over a century and was illustrated in the *Botanical Register* (t. 59) in 1847 where it was recorded as having been grown by Messrs. Whittley and Osborne of Fulham, England, from seed sent by Dr. Royle from India. At that time it was pointed out that it differed from *I. ochroleuca* in that the sepals and petals were lanceolate and wavy on the edges and the flowers a bright golden-yellow color. It also blooms much later than *I. ochroleuca.* The natural distribution of the species is not accurately known. According to Dykes (1913) it is Kashmir. Hooker (1894) records it as "Western Himalaya; Kashmir." Blatter (1928) in *Beautiful Wild Flowers of Kashmir* reports it as Kashmir but also makes the interesting comment, "not known to me." We have had no seed or plants of this species from its native habitat. Nevertheless there are in cultivation plants which approximate very closely the original description of the species as well as the published illustrations. However, many of the forms presently grown as *I. crocea* are obvious hybrids, many of them probably with *I. ochroleuca* with which it is highly fertile.

Another interesting but poorly understood yellow-flowered, 40-chromosome taxon is *I. monnieri* described by De Candolle in 1808. The original plant was discovered growing in the garden of M. Lemonnier at Versailles where it was called 'Iris de Rhodes', the name

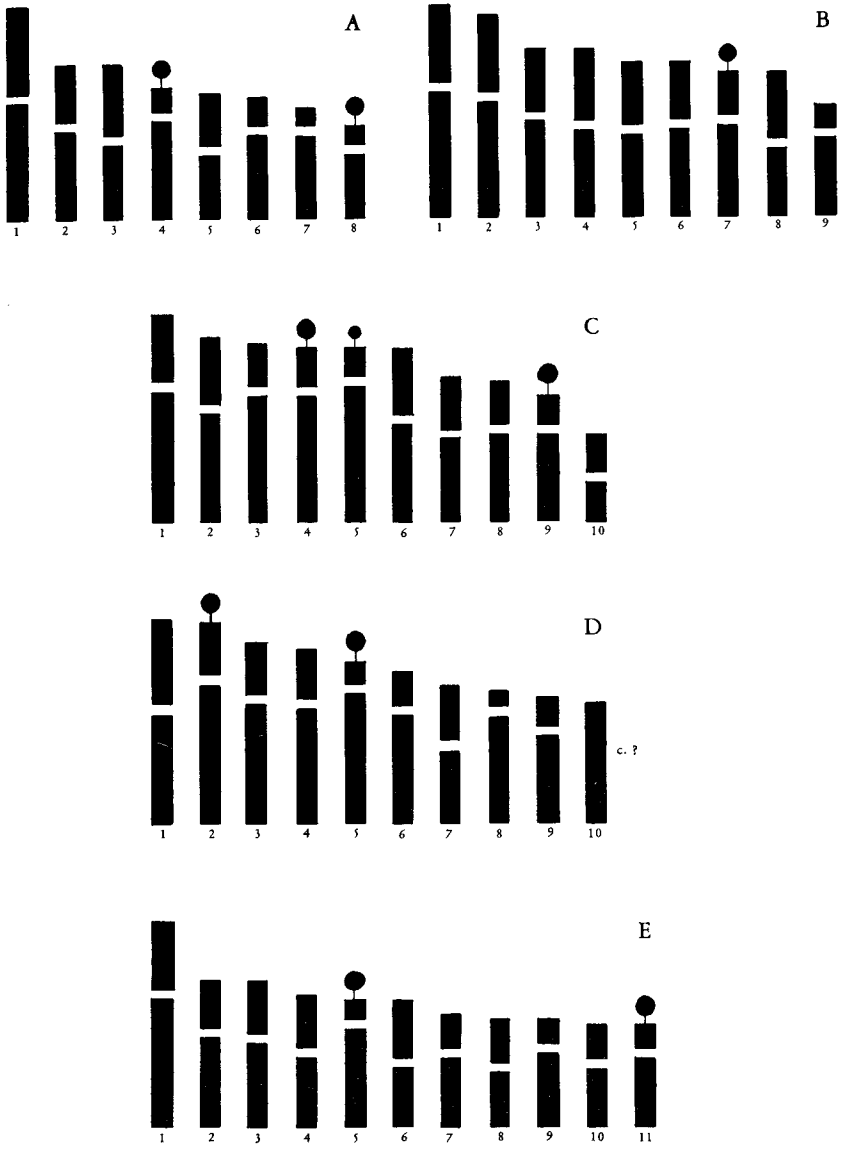

Fig. 4. Ideograms of metaphase chromosomes in root tips of (A) *Iris sintenisii,* (B) *I. kerneriana,* (C) *I. urumovii,* (D) *I. brandzae,* (E) *I. spuria.*

referring presumably to its place of origin. Dykes was of the opinion that it was probably not a good species as evidenced by the fact that the majority of the seedlings raised from self-fertilized flowers approached *I. ochroleuca.* According to him *I. monnieri* is dis-

tinguished from both *I. ochroleuca* and *I. crocea* by color differences and in the case of *I. crocea* also by the shape of the sepals which are orbicular in *I. monnieri* and lanceolate with crimped edges in *I. crocea.* First generation hybrids between *I. ochroleuca* and *I. crocea* have falls somewhat tapered like those of *I. crocea* and quite unlike those of *I. monnieri* as shown in Redouté's painting which accompanied the original description. Perhaps the most significant floral feature of the three is the shape and size of the style crests which are triangular and over half an inch long in *I. ochroleuca,* and are small and deltoid in *I. monnieri* (Dykes, 1913). For *I. crocea* Dykes merely says that they are deltoid. The original illustration of *I. monnieri* shows the crests to be short and very recurved, quite distinct from those observed by us in *I. crocea* or any form of *I. ochroleuca* which we have grown.

In 1885 Sir Michael Foster received from Amasia (i.e., north-central Turkey) a plant with golden-yellow flowers, the edges on the segments of which were crimped. In 1948 we received seed collected in the vicinity of Ankara, Turkey, by Haydar Bagda. Plants grown from this seed (our Turkey Yellow) produce deep golden-yellow flowers with sepals varying in shape from lanceolate to rounded. The most striking feature of the flowers is the very short, strongly recurved style crests which are distinct from *I. ochroleuca* or *I. crocea* but similar to, though more extreme than those shown in the illustration of *I. monnieri.*

Recently Peter Davis collected an iris in Anatolia which, according to the herbarium label has "the color of *aurea* and shape of variety *monnieri.*" There are, therefore, in Asia Minor deep golden-yellow-flowered spurias which in the single collection grown by us, show very short and strongly recurved style crests unlike those of the more common *I. ochroleuca.* A plausible explanation for the origin of *I. monnieri* would be that it is a hybrid, possibly a natural hybrid, between the white-flowered *I. ochroleuca* and one of the deep yellow-flowered irises found in Turkey. Such an explanation would fit all the facts now known about *I. monnieri.* On morphological grounds (as well as on a geographical basis) it would seem doubtful whether *I. crocea,* as now understood, could have been involved. *Iris monnieri* has been used many times in breeding programs and if the proposed hybrid origin for it is true, it would mean that it could contribute to the production of both white and yellow-flowered hybrids.

In addition to white and yellow-flowered garden forms there are numerous blue, lavender, brown and bronze-colored varieties, many of them heavily veined. If the 64 cultivars shown in Table 2 are separated according to whether anthocyanin is present or absent (i.e., those with blue, lavender, brown and bronze flowers, assuming that brown and bronze colors are produced through the presence of both yellow and blue pigments) it will be seen that 59% of the clones are cyanic and 41% acyanic. At the present time no blue- or lavender-flowered, 40-chromosome spuria species is known. The source of genes for blue or lavender pigments must be sought among the non-40-chromosome species unless, of course, these colors have appeared spontaneously among the garden hybrids. There is no evidence that this has happened. Among the species having cyanic flowers are *I. brandzae* and *I. urumovii* both $2n=20$, *I. graminea,* $2n=34$, and *I. humilis,* $2n=72$. All are low-growing plants usually referred to as the dwarf spurias. The taller species include *I. spuria,* $2n=22$; *I. halophila (sensu lato),* $2n=44$; *I. carthalinae,* $2n=44$; and *I. klattii,* $2n=44$. Table 2 of chromosome numbers of the garden forms shows that 16% of the clones examined had somatic counts of $2n=41–44$. Of these 8 out of 10 had colored flowers. It might be postulated that the 41–44-chromosome cultivars are hybrids between 40- and 44-chromosome plants. There is some historical basis for such an assumption. One of the oldest garden hybrids is 'Monspur' produced by Sir Michael Foster in 1882. In *The Garden* for November 1890 (p. 463) Sir Michael wrote: "In 1882 I crossed *I. monnieri* with the pollen of a small, but dark-flowered *I. spuria* of unknown origin, and obtained some dozen or so seedlings of which

the one figured is perhaps the most handsome. The several seedlings differed in the size and depth of colour of the flower, all being different shades of purple, more or less conspicuously veined with darker lines . . . In fact, the offspring were what might have been expected from the two parents." Foster used the name *I. spuria* to include such plants as *I. notha* M.B., *I. guldenstaedtiana* Lep., *I. stenogyna* Delarbe, etc., all plants which are now generally included in the 44-chromosome *I. halophila* complex. If *I. monnieri* was the second parent, then Foster's 'Monspur' should be $2n=42$. The plant which we obtained as 'Monspur' was found to have 40 chromosomes rather than the expected 42. It is possible that in the 80 years since the hybrid was produced another plant has become associated with the name, or a seedling from 'Monspur' may also have been given the same name. It is also possible, though not probable for reasons given below, that Foster had a 40-chromosome blue-flowered *I. spuria*. *The American Iris Society Alphabetical Check List* (Peckham, ed., 1924) lists, in addition to 'Monspur', 'Monspur A. J. Balfour', 'Monspur Cambridge Blue', 'Monspur Dorothy Foster', 'Monspur Juno', and 'Monspur Premier', clones registered between 1910 and 1915 by Barr & Sons. In their catalogue for 1913 under beardless irises they describe Monspur as a group of "handsome new hybrids raised by the late Sir Michael Foster from *I. monnieri* × *I. spuria* . . ." They then describe each of the 5 clones listed above. In their catalogue for 1938 the wording has been changed and they write of Monspur as "the result of *crosses* [ital. ours] between *monnieri* and *spuria* . . ." and they then list 4 of the 5 originally listed in 1913. The variety named 'Cambridge Blue' is described in the 1913 catalogue as new for 1910 and it seems doubtful whether a plant originally produced in 1882 would first be listed as new 28 years later. It may be assumed then that the word Monspur has been used at times as a collective name for crosses between *I. monnieri* and *I. halophila* (*I. monnieri* × *I. spuria* sensu auth.). Foster on the other hand appears to have used the word Monspur as a cultivar name for a single seedling selected from his original cross. Today these clones are usually referred to merely as 'Cambridge Blue', 'Premier', etc. We have examined three of them and have found 'Premier', $2n=42$; 'Cambridge Blue', $2n=42$; and 'A. J. Balfour', $2n=40$. The latter was registered by Barr and Sons in 1889 but was not offered by them in their catalogue for 1913 or 1914. Cytological evidence from 'Cambridge Blue' and 'Premier' would lend support to the assumption that these plants were produced as hybrids of 40 and 44-chromosome plants. It has been our experience that at least some of the 42-chromosome hybrids are partially fertile and in advanced generations it would be possible to obtain plants with somatic numbers ranging from 40–44. A clone registered by Nesmith in 1954 as 'Royal Toga' appears to be similar, if not identical with 'Premier' but we have found that the chromosome numbers are different; 'Premier' has $2n=42$ and 'Royal Toga', $2n=43$–44. The parents of 'Royal Toga' were not available for study and no further information is available.

In addition to *I. halophila* there are other 44-chromosome spurias which could contribute color to the garden hybrids. *Iris carthaliniae* Fom. was described in 1909 from plants collected in the Caucausus Mts. near Tbilisi. It is an attractive species and from the horticultural standpoint may be more desirable than *I. halophila*. There is no evidence that it has been used in breeding programs in the past, but results from first generation hybrids indicate that it may be a valuable source of genes for color. *Iris klattii* Kem.-Nat., also a 44-chromosome species, is presently in cultivation but there is no evidence that it has contributed to the garden spurias.

If any species with colored flowers other than one of the 44-chromosome forms had been used, the resulting hybrids should show counts of less than $2n=40$ since the others have $2n=16$, 20, 34, 38. (The dwarf *Iris humilis* with $2n=72$ is an exception). Table 2 shows only a single clone with less than 40 chromosomes, a plant know only as 'Mrs. White's Hybrid'

with $2n$=28. The parentage of this hybrid is reported (pers. com.) to be *I. desertorum* Ker. (♀) × *I. graminea* L. (♂). The latter species is a distinctive and easily identified dwarf plant and the identification is probably correct. *Iris desertorum* is a synonym for *I. halophila.* According to Mrs. White the seed parent of her hybrid was smaller in every way than *I. halophila* and was probably not that species. If *I. graminea* was one parent it would have normally contributed 17 chromosomes to the hybrid and the second parent would have had to contribute 11. The only spuria with n=11 is *I. spuria,* a species that might be confused with some forms of *I. halophila.* On morphological grounds this hybrid could have arisen between *I. spuria* and *I. graminea.* Interspecific crosses made by us and to be reported on later prove that hybrids can be produced between members of the *Spuriae* having very different chromosome numbers.

Among the more recently registered clones with numbers ranging from $2n$=41–44 are 'Ben Lomond', $2n$=42; 'Blue Zephyr', $2n$=44?; 'Dresden Blue', $2n$=41; 'Lumiere', $2n$=41–42; and 'Royal Toga', $2n$=43–44. Except for 'Dresden Blue' and 'Royal Toga', the latter already referred to, these hybrids were produced by Thomas A. Washington of Nashville, Tenn. All but 'Lumiere' are blue-lavender-flowered. Washington kept no record of his crosses but it is known (Nesmith, 1958) that he had in his garden *I. halophila,* 'Mrs. Tait', *I. crocea, I. monnieri, I. ochroleuca* and either 'A. J. Balfour' or 'Cambridge Blue'. Available to him then were clones with $2n$=40, 42, 44, and it is not surprising that some of his hybrids would be plants with numbers similar to, or intermediate between, those growing in his garden.

Another early and successful spuria breeder was Eric Nies of Los Angeles, California. According to Walker (pers. comm.) Nies' original cross was between *I. ochroleuca* and 'Monspur'. Afterwards Nies followed a strict pattern of line breeding. It is possible that the 'Monspur' used by Nies is the same one we examined. If this is true, then the Nies strain of spurias were all produced from 40-chromosome plants. Of the hybrids registered by Nies, Nies-Walker, and later by Walker using the Nies strain, those that we have examined (27 clones) have all had 40 chromosomes.

From the evidence available it might be postulated that the modern garden spurias have arisen as hybrids between a series of white or yellow-flowered 40-chromosome species and members of the 44-chromosome blue-lavender-flowerd *I. halophila* complex. Due to the vigorous growth habits and larger and more attractive flowers of the 40-chromosome species the early 42-chromosome hybrids were probably more often backcrossed to the 40 rather than to the 44-chromosome species with the result that in advanced generations the number has been stabilized at 40 and fertility, lowered in the 41–43 chromosome hybrids, has again been increased in the modern cultivars. If this hypothesis is correct it could explain the presence of occasional meiotic irregularities found in the garden forms by Hadley (1958), i.e., laggards, occasional univalents, and multivalent associations.

Hadley reported pollen fertility in the 18 clones examined (as indicated by stainability) to be 81–100%. Pollen fertility as determined by us was generally lower even when identical clones were used. Such differences may be due in part to the personal factor rather than to actual differences in plant fertility. However, cultural and environmental factors may sometimes affect fertility. The material used by Hadley was grown at Houston, Texas, ours was grown in southern California. Because of the large number of intermediate type pollen grains scoring is difficult. In order to minimize the personal element all our determinations were made by one of us (AD). Results are shown in Table 3. From the results it will be seen that the average pollen fertility of the garden forms is considerably lower than that found in the species, and forms having anthocyanin, genes for which may have come from the 44-chromosome complex, have lower pollen fertilities than those with nonanthocyanin

flowers. This is true whether all chromosome groups are considered or whether only the 40-chromosome forms are included.

TABLE 3. *Pollen Stainability*

	NUMBER OF CLONES	PERCENTAGE OF STAINABLE POLLEN	
		RANGE	AVERAGE
Spuria species	10	71–99	89.1
Garden spurias (all)	30	18–87	57.8
(acyanic)	11	56–87	69.9
(cyanic)	19	18–68	45.7
Garden spurias (40-chromosome)			
(acyanic)	8	56–87	71.0
(cyanic)	13	18–68	51.0

SUMMARY

Chromosome determinations were made of 53 collections representing 15 species of *Iris* belonging to the series *Spuriae* (Diels) Lawr., section *Spathula* Tausch, em. Lawr. Root tip counts reveal a series of five species with numbers of $2n$=16, (32), 18, 20, 22 and a series of species with higher numbers of $2n$=34, 38, 40, 44, 72.

Karyotype analyses of the low number series showed that each of the five species possessed a characteristic karyotype, and different collections of the same species showed similar karyotypes. With more adequate sampling karyotype differences within the taxa may, however, be detected. Using standard floras the geographical distribution of the different chromosome number groups was plotted.

The chromosome numbers of 64 horticultural varieties are reported. Of these 84% were found to have 40 somatic chromosomes and 16% had numbers ranging from 41 to 44. One hybrid was found to be $2n$=28.

Using cytological data, as well as available information from the literature, an origin for the garden cultivars has been postulated.

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LITERATURE CITED

Ammal, E. K. Janaki. 1951. Chromosomes and the evolution of garden Philadelphus. J. Roy. Hort. Soc. 76: 268–275.

———. 1951. The chromosome history of the cultivated nerines, J. Roy. Hort. Soc. 76: 365–375.

Bernatsky, J., and E. Janchen. 1910. Über *Iris spuria* L., *I. spathulata* Lam. und *I. subbarbata* Joo. Osterreichische Botan. Zeitschr. 60: 335–343.

Candolle, A. P. de. 1808. *in* Redouté, P.P., Les Liliacées, t. 236.

Clapham, A. R., T. G. Tutin, and E. F. Warburg. 1962. Flora of the British Isles. 2nd ed. Cambridge. 1269 p.

Dykes, W. R. 1913. The Genus Iris. Cambridge. 245 p.

———. 1924. A Handbook of Garden Irises. London. 250 p.

Darlington, C. D., J. B. Hair, and R. Hurcombe. 1951. The history of the garden hyacinths. Heredity 5: 233–252.

Fomin, A. 1909. *In* Monit. Jard. Botan. Tiflis. No. 14, p. 44.

Hadley, H. H. 1958. Chromosome number and meiotic behavior in commercial varieties of spuria iris. Bull. Am. Iris Soc. No. 150: 108–115.

Longley, A. E. 1928. Chromosomes in Iris species. Bull. Am. Iris Soc. No. 29: 43–55.

Nesmith, E. N. 1958. The Washington spurias. Bull. Am. Iris Soc. No. 150: 82–83.

Peckham, W. H. (Mrs.). 1929. Alphabetical Iris Check List. Am. Iris Soc. Baltimore. 300 p.

Randolph, L. F. 1944. Chromosome numbers of tall bearded irises. Bull. Am. Iris. Soc. No. 95: 37–45.

———, and J. Mitra. 1959. Karyotypes of *Iris pumila* and related species Am. J. Botan. 46: 93–102.

Simonet, M. 1928. Le nombre des chromosomes dans le genre *Iris*. Comptes Rendus Societé Biologie 99: 1314–1316.

———. 1934. Nouvelles recherches cytologiques et génétiques chez les *Iris*. Ann. Sci. Nat., Botan., Sér. 10. 16: 229–378.

Stern, F. C. 1946. The evolution of the garden iris. J. Roy. Hort. Soc. 71: 286–290.

Westergaard, M. 1938. Karyotypes of the collective species *Iris spuria* L. Dansk Botan. Arkiv. No. 5: 1–11.

Wylie, A. P. 1952. The history of the garden narcissi. Heredity 6: 137–156.