A CYTOLOGICAL STUDY OF THE GENUS VIBURNUM[1]

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THE GENUS VIBURNUM includes some 250 species from diverse habitats in Asia, Europe, North America, and South America. Though viburnums are varied in form, the ideal ornamental that combines fragrance, colored flowers, small stature, evergreen or brilliantly colored foliage, and luxuriant fruit does not exist. The present cytological study was initiated to establish a basis for genetical research that might yield interspecific hybrids combining in one plant the ornamental characteristics of several species. Such a study of chromosomes is obligatory for the plant breeder to initiate and pursue intelligently an interspecific hybridization program. Many *Viburnum* species and varieties involve complexes that have not been adequately covered by any comprehensive taxonomic treatment. The data obtained from such related disciplines as cytology and genetics when combined with taxonomy may help to resolve the species complexes and clarify the classification of the genus.

To the extent that this publication is a portion of more extensive cytogenetical and cytotaxonomical studies in progress, only that portion of the research concerned with cytology is reported. Although the literature has been frequently consulted to verify the identification and relationships of the taxa studied, this paper is not intended as a taxonomic study. The author has followed the taxonomic nomenclature of Rehder's *Manual of Cultivated Trees and Shrubs* (30) and *Bibliography of Cultivated Trees and Shrubs* (31).

REVIEW OF LITERATURE

All the chromosome counts reported by various authors are incorporated under the respective species in TABLE I. The earliest cytological study of *Viburnum* was that of Sax and Kribs (32), who reported that eleven species had a gametic chromosome number of nine ($n = 9$). The Asiatic

[1] This study includes a portion of the research completed for the Ph.D. thesis in the Departments of Plant Breeding and Floriculture, Cornell University, Ithaca, N. Y., and later work in the United Kingdom and at the U. S. National Arboretum, Washington, D. C.

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and American species studied included six of the nine taxonomic sections of Rehder (30). Sax and Kribs stated that the chromosomes are large, have an affinity for chromosomal stains, and consequently provide favorable material for study. A second basic chromosome number of eight ($n = 8$) was reported for *V. fragrans* by Simonet and Miedzyrzecki (35), who also published counts for seven additional species as $n = 9$. The gametic and somatic number of *V. tinus* was determined by Feng (15) to be $n = 18$ and $2n = 36$. Sugiura (38) reported $2n = 20$ for *V. awabuki* (syn. *V. odoratissimum*). In 1946, Poucques (27) listed the gametic chromosome counts for five species, four of which were previously unpublished; in a later publication (28) he listed two additional species.

Janaki Ammal determined the chromosome number $2n = 16$ for *Viburnum fragrans* and *V. grandiflorum*, and for *V.* × *bodnantense*, a hybrid produced from a cross between these species. The chromosomes of the two species paired normally in the hybrid, and the pollen fertility was as high as one hundred per cent (36). The extensive cytological study of Janaki Ammal (18) included thirty-seven determinations, of which twenty-one were reported for the first time. Her survey reported somatic chromosome numbers for species in cultivation at the Royal Horticultural Society's Garden, Wisley, England; the Royal Botanic Gardens, Kew, England; and the Jardin des Plantes, Paris, France. Seventeen of these counts are at variance with the somatic chromosome numbers of the present study; while three are at variance with previous reports. These differences are considered in the discussion. She has interpreted the $2n = 18$ of the hybrid *V.* × *juddii* (*V. carlesii*, $2n = 20$, × *V. bitchiuense*, $2n = 16$) as a synthesis of a plant with $n = 9$, and in addition, proposed that *V. carlesii* ($2n = 20$) arose as a backcross between a chance triploid ($2n = 24$) and the normal diploid ($2n = 16$) of *V. bitchiuense*. This was considered to be an example of the possible manner of evolution of *Viburnum* species in nature, which finally resulted in a large number of species with the basic number $n = 9$. A chromosome count of *V. lobophyllum*, $2n = 20$, determined by Enoch for a plant grown at Exbury, Southampton, England, was included in the publication of Janaki Ammal (18).

The cytological study by Thomas (40) included twenty-nine of the plants cultivated in the Arnold Arboretum. A few of these counts were obtained from root tips, but most were made from pollen mother cells; however, only pártial designation is given as to which counts were gametic. Thomas concurs with the author that the origin of species with $n = 9$ as postulated by Janaki Ammal (18) is questionable. He states that it is more likely that species with basic chromosome numbers of eight and ten originated from species with a base number of nine by the loss or gain of a chromosome. His study indicates that translocations occur rather frequently, as evidenced by bridge formations observed in several of the species. He noted a relatively high percentage of aberrations in *Viburnum cassinoides*, *V. carlesii*, *V. dentatum*, *V. plicatum*, *V.* × *rhytidophylloides*, *V. sieboldii*, *V. trilobum* f. *compactum*, and *V. veitchii*.

MATERIALS AND METHODS

The seventy-seven species, sixty-one varieties and forms, thirteen hybrids, and two unidentified accessions of *Viburnum* investigated are presented with their sources, in TABLE I. Plant material was obtained as seed, cuttings, or plants from native habitats, botanic gardens, arboreta, and estate gardens throughout the world, exclusive of Central and South America. In all cases an effort was made to secure representatives of each taxon from three or more sources to provide a check on identification and chromosome counts of each taxon. Since commercial nurseries often propagate horticultural forms of *Viburnum* by grafting, all plant material for cytological study has been propagated from cuttings or from seed collected when possible in the native habitat of the species. Seed from native habitats have been used chiefly because seed from botanical collections may have been the result of cross pollinations with other species in the collection. The plants for cytological study were maintained during the summer months in frames or in a lath house. The remainder of the year the plants were grown under long-day conditions of twenty to twenty-two hours of light in a 70° F. greenhouse. Under these conditions it was possible to keep the plants actively vegetative and to avoid any dormant period.

In so far as feasible, plants propagated from seed and cuttings, and representatives of all sources, will be maintained at the Cornell Plantations and the U. S. National Arboretum for further study. Herbarium specimens, which are identified with the code accession numbers, were prepared for each collection that provided sufficient material. These are maintained as part of the permanent record and will be supplemented with flowering and fruiting material when the plants mature. Original descriptions and many of the type specimens have been studied to verify identifications. Photographs of type specimens and photostats of pertinent taxonomic literature were prepared to provide a basis for cytotaxonomic research. The identification of many of the plants previously studied (14) has been checked since they flowered and fruited. In those cases in which a positive determination was made, the alteration has been entered on TABLE I. However, the documentation numbers have not been altered and will be the same as in the previous list (14).

The root-tip smear technique was used exclusively in this study. Preliminary use of McClintock's permanent aceto-carmine (19) and La Cour's (20) acetic-orcein stain techniques revealed that the latter gave best results. In a portion of the early work the root tips were pretreated in aqueous paradichlorobenzene (22), fixed in Baldwin's modified Carnoy's (2), hydrolized in a solution of equal parts of 95% alcohol and concentrated hydrochloric acid, and smeared in acetic-orcein on the slide. After trial of numerous schedules and variations of these procedures a modification of La Cour's (20) technique was employed. Three- to five-millimeter-long root tips were pretreated in aqueous paradichlorobenzene for one to two hours. The root tips were placed in a watch glass contain-

ing one part 1.0 N. hydrochloric acid to nine parts 0.5% acetic-orcein stain. The watch glass with root tips was passed two or three times over the flame of an alcohol lamp to heat the mixture, but great care was taken to keep the solution under the boiling point. After the heated watch glass had cooled for several minutes, a root tip was placed in a drop of 0.5% acetic-orcein on a slide, smeared, and the cover slip applied.

The Feulgen technique (10) has been used in recent studies with excellent results. Root tips were collected and pretreated with 0.1% colchicine for two hours and fixed in La Cour's 2BD general fixative for twelve hours. The root tips were thoroughly washed with distilled water before immersion in a peroxide-oxalate bleach consisting of equal parts of ammonium oxalate in distilled water and hydrogen peroxide, and placed in direct sunlight or under a spot light for five minutes. After the root tips were washed again, they were hydrolized in 1.0 N. hydrochloric acid at 60° C. for twelve minutes, stained in leuco-basic fuchsin for 2 hours, and smeared. The edges of the cover slip were sealed with a mixture of gum mastic and paraffin in equal parts.

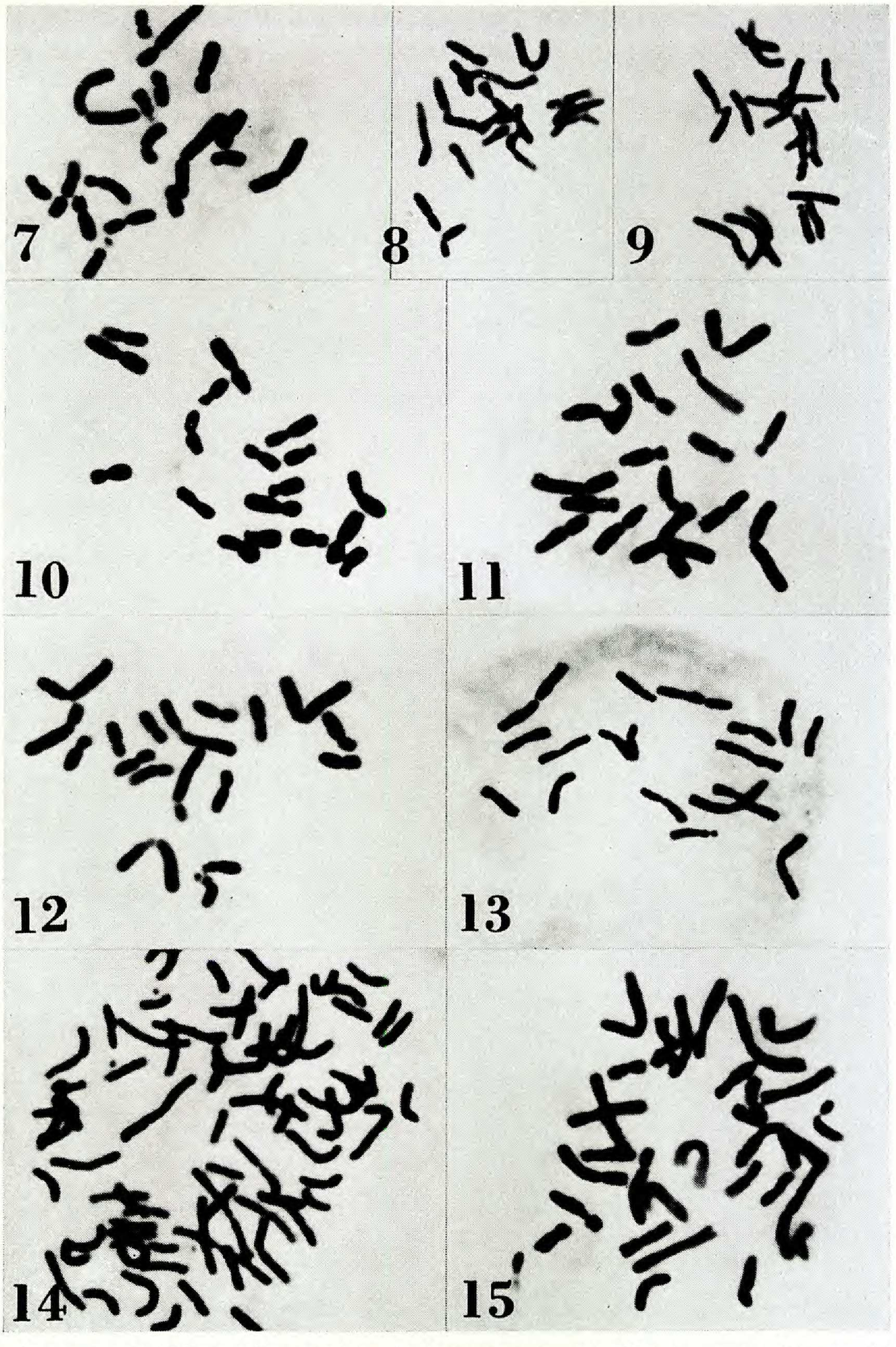
Slides were observed immediately or stored in a 40° F. refrigerator. After critical examination of the temporary smears was completed, camera lucida drawings made, and photomicrographs taken, selected slides were made permanent. The method of Conger and Fairchild (6) accomplishes the separation of the cover slip from the slide by freezing on dry ice. More recently, compressed carbon dioxide has been utilized for freezing slides to separate the cover slip from the slide. Immediately before thawing, the separated frozen slide and cover slip are placed in 95% alcohol which contains 5–10% acetic acid. After two or three minutes they are placed in absolute alcohol for another few minutes before mounting in diaphane. The permanent preparations made by this method are almost always equal in excellence and clarity to temporary slides and are superior for photomicrographs. Permanent slides of virtually all accessions here reported have been prepared.

Critical examination of the preparations was made with a binocular microscope equipped with 98 × fluorite objectives, N.A. 1.30, and 12.5 oculars. A minimum of ten countable cells was located before ascertaining the number of chromosomes in the somatic complement. Drawings were made with a camera lucida at table level, using 15 × oculars, giving the drawing a magnification of approximately 2400 ×. In addition to the drawings, photomicrographs were taken on 35 mm. microfilm at a magnification of approximately 1500 ×.

RESULTS

The somatic chromosome counts of the 153 taxa of *Viburnum* included in this investigation are presented in TABLE I. The species are arranged alphabetically within the taxonomic sections, as designated by Rehder (31). Under each taxon the chromosome counts published by other authors precede those from this study. The general geographic distribution and

FIGS. 1–6. Photomicrographs of chromosomes of *Viburnum* to show variations in chromosome complements, approximately × 1100. 1, *Viburnum erubescens*, $2n = 32$; 2, *V. lobophyllum*, $2n = 18$; 3, *V. sieboldii*, $2n = 32$; 4, *V. carlesii*, $2n = 18$; 5, *V. bracteatum*, $2n = 72$; 6, *V. scabrellum*, $2n = 72$.



FIGS. 7–15. Photomicrographs of chromosomes of *Viburnum* to show variations in chromosome complements, approximately × 1100. 7, *V.* × *carlcephalum*, $2n = 18$; 8, *V. rigidum*, $2n = 18$; 9, *V.* × *rhytidocarpum*, $2n = 18$; 10, *V. cotinifolium*, $2n = 18$; 11, *V. schensianum*, $2n = 18$; 12, *V. macrocephalum* f. *sterile*, $2n = 18$; 13, *V. nudum*, $2n = 18$; 14, *V. dentatum* var. *pubescens*, $2n = 72$; 15, *V. odoratissimum*, $2n = 32$.

the source of material are given for each accession. A series of photomicrographs (FIGURES 1–15) illustrates variations in the chromosome complement.

In order to make the table more concise, the sources of material have been abbreviated as follows:

AA Arnold Arboretum, Jamaica Plain 30, Mass.
AB Arboretum des Barres, Loiret, France.
AN Arturo Ansaloni, Bologna, Italy.
AR Armstrong Nursery, Ontario, Calif.
B Botanisches Museum, Berlin-Dahlem, Germany.
BB Brooklyn Botanic Garden, Brooklyn 25, N. Y.
BC Birr Castle, Birr, County Kings, Ireland.
BE Collected near Bedford, Pa.
BG Bodnant Garden, Tal-y-Cafn, Denbighshire, N. Wales.
BH Borde Hill, Haywards Heath, Sussex, England.
BO U. S. Botanic Garden, Washington, D. C.
BR Collected near Brighton, Sussex, England.
BT Boyce Thompson Arboretum, Yonkers, N. Y.
C Botanic Garden of the University of Copenhagen, Copenhagen, Denmark.
CC Caerhays Castle, St. Austell, Cornwall, England.
CG Collected near Chattanooga, Tenn.
CH R. Chenault, Orleans, France.
CL W. B. Clarke & Co., San Jose 3, Calif.
CR Crathes Castle, Crathes, Kincardshire, Scotland.
CU Cornell Plantations, Ithaca, N. Y.
DA Dominion Arboretum, Ottawa, Ontario, Canada.
DO Collected near South Downs, England.
DS J. T. Dawson, Nantucket, Mass.
DU National Botanic Gardens, Glasnevin, Dublin, Ireland.
E Royal Botanic Garden, Edinburgh, Scotland.
EN Carl S. English, Seattle 7, Wash.
EX Exbury, Southampton, England.
FN Fruitland Nursery, Augusta, Ga.
G Conservatoire et Jardin Botaniques, Geneva, Switzerland.
GA Gardens of the Blue Ridge, Ashford, N. C.
GB Göteborgs Botaniska Trädgård, Göteborg, Sweden.
GP The Great Park, Windsor, Berkshire, England.
HA N. G. Hadden, West Porlock, Somerset, England.
HB Hattori Botanical Laboratory, Nichinan, Miyasaki, Japan.
HC Headford Court, Kells, County Meath, Ireland.
HF Henry Foundation for Botanical Research, Gladwyne, Pa.
HH Hermann A. Hesse, Weener, Germany.
HI Highdown, Worthing, Sussex, England.
HL Hillier and Sons Nursery, Winchester, Hampshire, England
HM Unknown Source, Hong Kong.
HN Hong Kong Dept. of Agriculture, Hong Kong.
HP Highland Park, Rochester, N. Y.
IC Collingwood Ingram, Cranbrook, Kent, England.
JG George Jackman & Son, Woking, Surrey, England.
JI John Innes Institute, Bayfordbury, Hertfordshire, England.
JP Jackson and Perkins Co., Newark, N. Y.
K Royal Botanic Gardens, Kew, Richmond, Surrey, England.
KB Botanic Gardens of Indonesia (Kebun Raya), Bogor, Indonesia.
KH Henry Kohankie and Son, Painesville, Ohio.
KN Kingsville Nurseries, Kingsville, Md.
KR Kornik Gardens, Kornik, Poland.
LA Collected east shore of Lake Cayuga, Ithaca, N. Y.
LE V. Lemoine & Fils, Nancy, France.
LI Linn County Nurseries, Center Point, Iowa.
LO Los Angeles State & County Arboretum, Arcadia, Calif.
LS Lu Shan Botanic Garden, Kiukiang, China.

MA C. J. Marchant, Wimborne, Dorset, England.
MC W. L. McAtee, Chapel Hill, N. C.
ML McLean Bog, McLean, N. Y.
MR Morris Arboretum, Philadelphia 18, Pa.
MT Morton Arboretum, Lisle, Ill.
MY Myddelton House, Enfield, Middlesex, England.
NB Nanking Botanic Garden, Nanking, Kiangsu, China.
NN R. C. Notcutt, Ltd., Woodbridge, Suffolk, England.
NS Nymans Gardens, Haywards Heath, Sussex, England.
NY New York Botanical Garden, New York 58, N. Y.
ON Onarga Nursery Co., Onarga, Ill.
P Muséum National d'Histoire Naturelle, Paris, France.
PE Pennsylvania State University, University Park, Pa.
PI U. S. Plant Introduction Garden, Glenn Dale, Md.
PN Princeton Nurseries, Princeton, N. J.
PO Unknown Source, Warsaw, Poland.
RE Regel & Kesselring, Rome, Italy.
RF Ringwood Forest, Ithaca, New York.
RH Royal Horticultural Society's Garden, Wisley, Surrey, England.
RU B. Ruys, Ltd., Dedemsvaart, Holland.
SN Siebenthaler Co., Dayton 5, Ohio.
SO Collected South Hill, Ithaca, N. Y.
SP L. Späth, Berlin, Germany.
ST Bergius Botanic Garden, Stockholm, Sweden.
SY Swyncombe House, Oxford, England.
TA Taiwan Forest Research Institute, Taipei, Taiwan, China.
TC Taiwan Pineapple Corp., Taipei, Taiwan, China.
TG Tokyo University Botanic Gardens, Tokyo, Japan.
UC Univ. of California Botanical Garden, Berkeley, Calif.
UW Univ. of Washington Arboretum, Seattle, Wash.
VN Vaughan Nursery, Chicago 6, Illinois.
VO Arnold Vogt, Erlenbach-Zurich, Switzerland.
WA Wakehurst Place, Ardingly, Sussex, England.
WG Wayside Gardens, Mentor, Ohio.
WL Wildlife Research Laboratory, Delmar, N. Y.
WM Isaac L. Williams, Exeter, N. H.
WW Willowwood Farm, Gladstone, N. J.
WY Wyman's Garden Centers, Inc., Framingham, Mass.
WZ Wyoming Nurseries, Cincinnati 15, Ohio.

TABLE I. Chromosome Numbers of Viburnum

SPECIES	2*n*	AUTHOR-ITY [a]	DOCUMEN-TATION [b]	SOURCE OF MATERIAL [c]	GENERAL DISTRIBU-TION
Sect. I. **Thyrsosma** (Raf.) Rehd.					
V. × *bodnantense* Aberc. (*V. fragrans* × *grandiflorum*)	16	9	76E	CL	cult.
"	16	9	874E	UW539–50(HL) [d]	"
"	16	9	902E	RH	"
"	16	9	1007E	K660–48(BG)	"
"	16	9	1102E	HL	"
'Dawn'	16	6*	—	—	cult.
"	16	9*	1357E	BG	"
'Deben'	16	9*	1937E	NN	cult.
V. erubescens Wall.	48	6	—	—	Himal.
"	32	9	972E	AA7602–A	"
"	32	9	1149E	K	"
"	32	9*	1170E	EX	"
var. *gracilipes* Rehd.	32	9	100E	HP2158	Himal.
"	32	9	502E	RU	"
"	32	9	1092E	HL	"
"	32	9*	1594E	DU183P	"
V. foetens Decne.	16	6	—	—	Himal.
"	16	9	441E	RH	"
"	16	9	1061E	K	"
"	16	9	1091E	HL	"
"	16	9*	1571E	HA	"
V. fragrans Bge.	16	2	—	—	n. China
"	16	6*	—	HI	"
"	16	9	25E	CU	"
"	16	9	27E	PI–82380	"
"	16	9	174E	AA11588(K)	"
"	16	9	597E	MT1007–39	"
"	16	9	1074E	RH	"
"	16	9*	1154E	HA	"
var. *album* Krüss.	32	6	—	—	n. China
(as var. *candidissimum*)	16	8	AA55–50–B	AA55–50–B	n. China
"	16	9	250E	MT35–38	"
"	16	9	598E	MT235–38(VN)	"
"	16	9	896E	RH	"
"	16	9*	1419E	MY	"

[a] 1, Sax and Kribs (1930); 2, Simonet and Miedzyrzecki (1932); 3, Feng (1934); 4, Sugiura (1936); 5, Poucques (1946); 5*, *ibid.* (1949); 6, Janaki Ammal (1953); 6*, *ibid.* (1950); 7, Enoch (1953); 8, Thomas (1961); 9, Egolf (1956); 9*, *ibid.*, reported here for the first time.

[b] The numbers listed in this column are the accession numbers and voucher herbarium specimen numbers for the plants studied. Specimens of others are given as "AA" (Arnold Arboretum) and "K" (Kew).

[c] The number or designation after the code letters identifies specific plants. The abbreviation "sd." signifies that the accession was obtained as seed.

[d] Source of material reference in parentheses refers to the original source from which the seed or plants were procured.

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
var. *nanum* Boom	16	9	431E	UW198–41	cult.
"	16	9	504E	RU	"
"	16	9	600E	MT685–50(CL)	"
'Roseum'	16	9	438E	RH	cult.
"	16	9*	1422E	JG	"
V. grandiflorum Wall.	16	6*	—	—	Himal.
"	16	9	1022E	K	"
"	16	9	1082E	RH	"
"	16	9	1093E	HL	"
"	16	9*	1426E	GP	"
"	16	9*	1427E	BG	"
"	16	9*	1428E	E3025 (Cooper)	"
"	16	9*	1576E	NN	"
V. henryi Hemsl.	48	6	—	—	c. China
"	32	9	984E	C	"
"	32	9	1039E	K	"
"	32	9	1069E	DU	"
"	32	9	1097E	HL	"
"	32	9*	1168E	EX	"
"	32	9*	1175E	HI	"
"	32	9*	1435E	BH1398	"
"	32	9*	1441E	DU10–39 (Henry)	"
V. × *hillieri* Stern (*V. henryi* × *erubescens*) 'Winton'	32	9*	1442E	HL	cult.
V. odoratissimum Ker-Gawl. (as *V. awabuki*)	40	4	—	—	Malaysia
"	40	6	—	—	"
"	32	9	68E	CU (Wash.)	"
"	32	9	119E	FN	"
"	40	9	293E	UW	"
"	32	9	371E	LO	"
"	40	9	392E	NY(BO)	"
"	32	9	427E	LO	"
"	32	9	919E	HL	"
"	32	9	983E	C	"
"	32	9	1011E	K	"
V. photinioides Fashiro	32	9	691E	KB	Malaysia
V. sieboldii Miq.	16	6	2454K	RH	Japan
"	32	8	AA616–6–B	AA616–6–B	"
"	32	9	62E	CU	"
"	32	9	105E	HP2161	"
"	16	9	270E	SN	"
"	32	9	656E	MT159–38(KH)	"
"	32	9	718E	MR2143	"
"	32	9	839E	AA616–6–B	"
"	32	9	903E	RH	"
"	32	9	1120E	P	"
f. *reticulatum* Rehd.	32	9	657E	MT281–51(AB)	Japan
"	32	9	878E	VO	"
"	32	9*	1056E	K986–36(LE)	"

TABLE I (*Continued*)

SPECIES	2n	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
V. suspensum Lindl. (as *V. sandankwa*)	18	5	—	—	Malaysia
"	16	6	—	—	"
"	16	9	289E	UC	"
"	16	9	389E	NY	"
"	16	9	692	KB	"
Sect. II. **Lantana** Spach.					
V. bitchiuense Makino	16	6	—	—	w. Japan
"	18	9	4E	PI–82381	"
"	18	9	70E	sd. PI–82381	"
"	18	9	307E	KR, sd.	"
"	18	9	522E	WZ, sd.	"
"	18	9	788E	AA (Wilson)	"
"	18	9	980E	MR3	"
"	18	9	998E	K	"
"	18	9	1078E	RH	"
"	18	9	1143E	CU	"
"	18	9*	1354E	K	"
"	18	9*	1355E	E430–29	"
V. buddleifolium Wright	18	2	—	—	c. China
"	20	6	—	—	"
"	18	9	7E	PI–111380	"
"	18	9	8E	CU	"
"	18	9	422E	BB	"
"	18	9	423E	KN	"
"	18	9	710E	MR	"
"	18	9	808E	AA7533 (Veitch)	"
"	18	9	1049E	K	"
"	18	9*	1328E	JI	"
"	18	9*	1360E	EX	"
V. burejaeticum Rgl. & Herd.	18	9	278E	GB, sd.	n. China
"	18	9	428E	LO	"
"	18	9	434E	UW160–46	"
"	18	9	585E	MT546–32(AA, sd)	"
"	18	9	586E	MT475–40(ST, sd.)	"
"	18	9	628E	MT1144–40	"
"	18	9	675E	KH	"
"	18	9	772E	AA4942(RE)	"
V. × *burkwoodii* Burk. & Skip. (*V. carlesii* × *utile*)	18	8	AA815–41–B	AA815–41–B	cult.
"	18	9	11E	CU	"
"	18	9	518E	WZ, sd.	"
"	18	9	587E	MT295–36(SN)	"
"	18	9	1006E	K1923HK	"
"	18	9*	1363E	SY	"
'Park Farm Hybrid'	18	9	923E	HL	cult.
V. × *carlcephalum* Burk. ex. Pike (*V. carlesii* × *macrocephalum*)	18	8	AA618–53–A	AA–618–53–A	cult.

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	77E	CL	"
"	18	9	433E	UW	"
"	18	9	689E	WG	"
"	18	9	1023E	K	"
V. carlesii Hemsl.	18	2, 5*	—	—	Korea
"	20	6	—	—	"
"	18	8	AA17981–A	AA17981–A	"
"	18	9	112E	HP2193	"
"	18	9	421E	BB	"
"	18	9	521E	WZ, sd.	"
"	18	9	536E	JP, sd.	"
"	18	9	676E	KH	"
"	18	9	785E	AA17981(Gibbs)	"
"	18	9	1009E	K972–34(Trickett)	"
"	18	9	1144E	CU	"
"	20, 22	9	1145E	HN, sd.(Korea)	"
"	20, 22	9	1146E	TA, sd.	"
"	20, 22	9	1147E	HM, sd. (s. China)	"
"	18	9*	1369E	DU	"
"	18	9*	1596E	E529–38	"
V. × *carlotta* Hort. (*V.* × *burkwoodii* × *carlesii*)	18	9	78E	CL	cult.
V. × *chenaultii* Chenault	18	9	406E	RU	cult.
"	18	9	469E	MT741–50	"
"	18	9	519E	WZ, sd.	"
"	18	9	592E	MT218–51(SN)	"
"	18	9	1057E	K227–48(AB)	"
V. cotinifolium D. Don	18	5	—	—	Himal.
"	18	9	819E	AA1236–52(K)	"
"	18	9	871E	UW17493 L&S (Bhutan, sd.)	"
"	18	9	1037E	K56–81	Himal.
"	18	9	1040E	K1067–83	"
"	18	9	1067E	DU	"
"	18	9	1086E	HL	"
V. glomeratum Maxim.	18	9	817E	AA, W180–5(K, sd.)	China
"	18	9	992E	MT406–44	"
"	18	9	1052E	K	"
V. × *juddii* Rehd. (*V. carlesii* × *bitchiuense*)	18	6	—	—	cult.
"	18	9	81E	CL	"
"	18	9*	97E	MR	"
"	18	9	606E	MT451–48(AA)	"
"	18	9	756E	AA1107–27(Gibbs)	"
"	18	9*	823E	AA813–49	"
"	18	9*	824E	AA284–44	"
"	18	9	973E	HP	"
"	18	9*	1312E	RH	"
V. lantana L.	18	1	—	AA	Eur., w.As.

TABLE I (*Continued*)

SPECIES	*2n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
"	18	5*, 6	—	—	"
"	18	9	31E	CU	"
"	18	9	239E	MT1010–39	"
"	18	9	301E	KR, sd.	"
"	18	9	385E	NY	"
"	18	9	607E	MT437–37 (PI–107644)	"
"	18	9	608E	MT640–34	"
"	18	9	722E	BT78–38	"
"	18	9	996E	K40–33	"
"	18	9	1041E	K	"
"	18	9	1142E	P	"
"	18	9*	1325E	DO	"
"	18	9*	1456E	BR	"
"	18	9*	1467E	E(B193–36)	"
'Aurea Marginata'	18	9	609E	MT838–37(B)	cult.
'Floribundum'	18	9	1138E	P	cult.
'Lanceolatum'	18	9	612E	MT616–39	cult.
"	18	9	940E	P	"
'Lees'	18	9	825E	AA(K)	cult.
'Macrophyllum'	18	9	472E	MT	cult.
var. *rugosum* Lange	18	8	AA907–27–A	AA907–27–A	cult.
"	18	9	99E	HP2167	"
"	18	9	456E	MT352–46	"
"	18	9	615E	MT213–41(KH)	"
"	27	9	679E	KH	"
"	18	9*	775E	AA907–27(DA, sd.)	"
f. *variegatum* (West.) Rehd.	18	9	618E	MT1053–41	cult.
"	18	9*	1470E	E	"
V. macrocephalum Fort. f. *sterile* Dipp.	18	9	82E	CL	cult.
"	18	9	424E	KN	"
"	18	9	713E	MR47–121	"
"	18	9	975E	HP	"
"	18	9	1015E	K	"
"	18	9*	1597E	E	"
V. microphyllum (Oerst.) Hemsl.	18	9	624E	MT642–36	Mexico
V. mongolicum (Pall.) Rehd.	16	6	—	—	e. As.
"	18	9	277E	GB, sd.	"
"	18	9	673E	MT501–53	"
V. × *rhytidocarpum* Lemn. (*V. buddleifolium* × *rhytidophyllum*)	18	9	418E	RU	cult.
"	18	9	643E	MT503–53	"
"	18	9	806E	AA412–36(LE)	"
V. rhytidophylloides Suring. (*V. rhytidophyllum* × *lantana*)	18	8	AA711–36–A	AA711–36–A	cult.
"	18	9	102E	HP	"
"	18	9	426E	KN(WW)	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	449E	NY	"
"	18	9	671E	MT265–37	"
"	18	9	754E	AA711–36(LE)	"
"	18	9	826E	AA1481–52(WW)	"
"	18	9	1038E	K387–29	"
V. rhytidophyllum Hemsl.	18	2	—	—	c. & w. China
"	18	6	2451K	RH	"
"	18	9	51E	CU	"
"	18	9	52E	PI–58813	"
"	18	9	91E	MR	"
"	18	9	304E	KR, sd.	"
"	18	9	1048E	K201–07(Veitch)	"
"	18	9*	1203E	E401–37	"
"	18	9*	1205E	E493–36	"
"	18	9*	1259E	RH	"
"	18	9*	1278E	HI(Wilson)	"
"	18	9*	1505E	E493–36(CR)	"
f. *roseum* (Gard. Chron.) Rehd.	18	9	295E	UW(CL)	cult.
"	18	9	800E	AA510–41(HL)	"
f. *aureovariegatum* Boom	18	9	822E	AA266–54	cult.
V. schensianum Maxim.	18	9	128E	AA15570	nw. China
"	18	9	397E	NY(HP)	"
"	18	9	465E	MT1051–401	"
"	18	9	652E	MT795–35(AA)	"
"	18	9	726E	NY	"
"	18	9	1014E	K(AA562–30)	"
"	18	9	1090E	HL	"
V. stellulatum Hemsl.	18	9	506E	DU	Himal.
"	18	9	1017E	K131–38(DU)	"
V. utile Hemsl.	18	6	—	—	c. China
"	18	9	214E	DA, sd.	"
"	18	9	425E	KN	"
"	18	9	507E	DU	"
"	18	9	694E	PI–111380	"
"	18	9	1008E	K	"
"	18	9*	1528E	BH	"
"	18	9*	1529E	WA	"
"	18	9*	1530E	E	"
V. veitchii Wright	18	8	AA7198	AA7198	c. China
"	18	9	113E	HP2177d	"
"	18	9	261E	MT1101–36	"
"	18	9	685E	KH	"
"	18	9	727E	NY67480	"
"	18	9	753E	AA7198(Veitch)	"
"	18	9	1005E	K101–13(Veitch)	"
"	18	9*	1560E	DU1288W	"

TABLE I (*Continued*)

SPECIES	2n	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
		Sect. III. **Pseudotinus** Clarke			
V. furcatum Bl. ex Maxim.	18	6	—	—	Japan
"	18	9	740E	AA17988(Wilson)	"
"	18	9	1099E	HL	"
V. lantanoides Michx. (as *V. alnifolium*)	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	497E	RF	"
"	18	9*	1876E	GA	"
V. sympodiale Graebn.	18	9	451E	NY(LS)	China
V. urceolatum S. & Z.	18	8	AA876–51	AA876–51	Japan
"	18	9*	1645E	PI–227284	"
		Sect. IV. **Pseudopulus** (Dipp.) Rehd.			
V. plicatum Thunb.	16	8	AA18016–1	AA18016–1	e. As.
"	18	9	92E	MR681	"
"	18	9	103E	HP2165	"
"	18	9	157E	AA18016–1	"
"	16	9	577E	PN	"
"	16	9	578E	PN	"
"	16	9	779E	AA933–4	"
"	16	9	1002E	K629(HH)	"
f. *glabrum* (Nakai) Rehd.	16	9	532E	TI, sd.(Ozegahara)	Japan
'Lanarth'	16	9	436E	RH	cult.
"	16	9	843E	AA134–53	"
f. *lanceolatum* Rehd.	16	8	AA6122–1	AA6122–1	cult.
"	16	9	658E	MT1204–41	"
"	16	9	763E	AA6122–1(Sargent)	"
f. *mariesii* (Veitch) Rehd. (as *V. tomentosum* var. *mariesii*)	18	6	2456K	RH	cult.
"	18	8	AA870–51–A	AA870–51–A	"
"	16	9	500E	RU	"
"	16	9	762E	AA19355(K)	"
"	16	9	1010E	K	"
"	16	9	1079E	RH	"
'Roseum'	16	9	580E	PN	cult.
f. *roseum* (Doney) Rehd.	16	8	AA856–34	AA856–34	cult.
"	16	9	737E	BB	"
"	16	9	742E	AA856–34(BB)	"
'Rowallane'	16	9	437E	RH	cult.
'St. Keverne'	16	9	505E	RU	cult.
f. *tomentosum* (Thunb.) Rehd. (as *V. tomentosum*)	18	1	—	AA	e. As.
"	18	6	2452K	RH	"
"	18	9	43E	CU	"
"	16	9	95E	MR1218	"
"	16	9	110E	HP2195	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	484E	MT176–37, 1204–41	"
"	16	9	688E	KH	"
"	16	9	846E	CU	"
"	16	9	1001E	K257–33(NN)	"
"	18	9	1084E	RH	"
Sect. V. **Lentago** DC.					
V. cassinoides L.	18	8	AA17997	AA17997	e. N. Am.
"	18	9	12E	CU	"
"	18	9	106E	HP2790	"
"	18	9	575E	ML, sd.	"
"	18	9	590E	MT, 570–43	"
"	18	9	677E	KH	"
"	18	9	1000E	K	"
var. *nanum* Krüss.	18	9	1088E	HL	cult.
V. × *jackii* Rehd. (*V. lentago* × *prunifolium*)	18	9	257E	MT1037–40(AA)	cult.
"	18	9	965E	AA17992–1–B	"
V. lentago L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	166E	AA18021–A	"
"	18	9	535E	CU	"
"	18	9	574E	SO	"
f. *sphaerocarpum* (Fern.) Rehd.	18	9	619E	MT892–35	e. N. Am.
"	18	9	968E	AA11316	"
V. nudum L.	18	6	—	—	e. N. Am.
"	18	9	570E	MC	"
"	18	9	681E	KH	"
"	18	9	988E	MT	"
"	18	9	1059E	K961–31(Gibbs)	"
"	18	9	1151E	CG	"
V. obovatum Walt.	18	9*	982E	C	se. U.S.
"	18	9*	1802E	HF(Fla.)	"
V. prunifolium L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	46E	CU	"
"	18	9	47E	BE	"
"	18	9	156E	AA1805–2	"
"	18	9	223E	DA, sd.	"
"	18	9	960E	CU	"
"	18	9	1020E	K	"
V. rufidulum Raf.	18	9	517E	WZ	se. U.S.
"	18	9	569E	MC	"
"	18	9	645E	MT1012–39	"
"	18	9	1150E	PE	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
		Sect. VI. **Tinus** Maxim.			
V. atrocyaneum Clarke	18	9	918E	HL	Himal.
"	18	9	1043E	K566–48(HL)	"
"	18	9*	1173E	HI	"
"	18	9*	1267E	DU9198K.W.	"
V. calvum Rehd.	18	9	922E	HL	w. China
"	18	9	1054E	K(E23–48)	"
"	18	9*	1285E	E16–52(HL)	"
V. cinnamomifolium Rehd.	18	6	—	—	w. China
"	18	9	85E	CL	"
"	18	9	884E	UW163–41(AR)	"
"	18	9	895E	RH	"
"	18	9*	1270E	DU963W	"
"	18	9*	1276E	HC	"
"	18	9*	1372E	BH	"
"	18	9*	1374E	WA	"
V. davidii Franch.	18	6	—	—	w. China
"	18	9	86E	CL	"
"	18	9	181E	E2485, sd.	"
"	18	9	415E	RU	"
"	18	9	877E	VO	"
"	18	9	885E	UW	"
"	18	9	900E	RH	"
"	18	9	1029E	K	"
"	18	9*	1390E	E963W	"
"	18	9*	1391E	WA	"
'Femina'	18	9	503E	RU	cult.
"	18	9*	1315E	DU(MA)	"
V. harryanum Rehd.	18	5	—	—	w. China
"	18	9	917E	HL	"
"	18	9*	1165E	EX	"
"	18	9*	1194E	E56–42	"
"	18	9*	1275E	BC	"
"	18	9*	1314E	DU	"
V. propinquum Hemsl.	18	5	—	—	w. China
"	18	9	559E	K	"
"	18	9	875E	VO	"
"	18	9	886E	UW79–50	"
'Lanceolatum'	18	9	924E	HL	cult.
V. rigidum Vent.	18	9	556E	K	Canary Is.
"	18	9	858E	C	"
"	18	9*	1174E	HI	"
V. tinus L.	36	2, 3, 5, 6	—	—	Eur.
"	36	9	118E	FN	"
"	36	9	267E	AN, sd.	"
"	36	9	291E	UW	"
"	36	9	314E	C	"
"	36	9	1035E	K	"

TABLE I (*Continued*)

SPECIES	*2n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	36	9	1064E	K	"
"	36	9*	1180E	E	"
"	36	9*	1260E	RH	"
'French White'	36	9	915E	HL	cult.
var. *hirtulum* Ait.	36	9	1028E	K22–11–47	Eur.
"	36	9	1100E	HL	"
var. *lucidum* Ait.	72	9	288E	UC	Eur.
"	72	9	292E	UW	"
"	72	9	343E	DU, sd.	"
"	72	9	997E	K	"
"	72	9*	1198E	E	"
'Variegatum'	72	9	999E	K	cult.
'Purpureum'	36	9	1046E	K1936	cult.
var. *variegatum*	36	9	1096E	HL	cult.
"	36	9	1181E	E	"
Sect. VII. Megalotinus Maxim.					
V. coriaceum Bl.	18	9	879E	VO	e. As.
"	18	9	1026E	K90–51(E)	"
"	18	9	1101E	HL	"
"	18	9*	1167E	EX	"
"	18	9*	1274E	BC	"
V. sempervirens Koch.	18	9	276E	HN, sd.	Malaysia
Sect. VIII. Odontotinus Rehd.					
V. *acerifolium* L.	18	1	—	AA	e. N. Am.
"	18	6	—	—	"
"	18	9	1E	CU	"
"	18	9	2E	SO	"
"	18	9	357E	DU	"
"	18	9	581E	MT202–38(WM)	"
"	18	9	799E	AA19181	"
"	18	9	1066E	K258–53(HP)	"
"	18	9	1144E	LA	"
V. betulifolium Batal.	18	6	—	—	c. & w. China
"	18	9	297E	UW(CL)	"
"	18	9	447E	NY	"
"	18	9	674E	KH	"
"	18	9	757E	AA550–26 (Rock 13476)	"
"	18	9	1003E	K61–08	"
"	18	9*	1187E	E346F	"
"	18	9*	1247E	RH	"
"	18	9*	1338E	NS	"
"	18	9*	1340E	WA	"
"	18	9*	1342E	HL	"
"	18	9*	1347E	DU238A–W	"
'Aurantiacum'	18	9*	283E	C	cult.

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
V. bracteatum Rehd.	72	9	455E	MT960–37	se. U.S.
"	72	9	552E	K	"
V. dasyanthum Rehd.	18	9	294E	UW	c. China
"	18	9	736E	BB	"
"	18	9	1055E	K910–39(LE)	"
"	18	9	1386E	E910–39(LE)	"
V. dentatum L.	54	6	—	—	e. N. Am.
"	36	8	AA17985	AA17985	"
"	36	9	16E	CU	"
"	36	9	107E	HP2212	"
"	36	9	142E	AA17985–B	"
"	36	9	391E	NY(HP)	"
"	36	9	572E	SO	"
"	36	9	593E	MT639–34(ON)	"
"	36	9	890E	RH	"
"	36	9	1036E	K(JG)	"
"	36	9	1148E	BE	"
var. *deamii* (Rehd.) Fern.	72	9	144E	AA100–38–A	c. U.S.
"	72	9	636E	MT1006–39 (Deam)	"
var. *pubescens Ait.*	36	8	AA18008	AA18008	e. N. Am.
"	36	8	AA18009	AA18009	"
"	72	9	49E	CU	"
"	36	9	179E	AA18009	"
"	36	9	639E	MT355–46 (AA2106–4A)	"
"	36	9	743E	AA18008(DS)	"
"	72	9	777E	AA5070–1	"
"	72	9	974E	HP	"
"	72	9	1019E	K1938HK	"
V. dilatatum Thunb.	18	8	AA229–46–B	AA229–46–B	e. As.
"	18	9	19E	CU	"
"	18	9	23E	PI–76383	"
"	18	9	30	PI–C3R29	"
"	18	9	93E	MR4	"
"	18	9	525E	TG, sd. (Japan)	"
"	18	9	526E	TG, sd. (Japan)	"
"	18	9	564E	HB, sd. (Japan)	"
"	18	9	784E	AA7665–D(CH)	"
"	18	9	832E	AA137–52 (Japan, sd.)	"
"	18	9	835E	AA138–52	"
"	18	9	888E	UW248–49(E, sd.)	"
"	18	9	1021E	K	"
f. *hispidum* Nakai	18	8	AA17486–1–A	AA17486–1–A	e. Asia
"	18	9	146E	AA17986–1–A	"
"	18	9	386E	NY(TG)	"
"	18	9	731E	NY2311–36(TG, sd.)	"
"	18	9	818E	AA647–53 (Japan, sd.)	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	828E	AA567–53 (Japan, sd.)	"
"	18	9	831E	AA569–53 (Japan, sd.)	"
"	18	9	833E	AA139–52 (Japan, sd.)	"
"	18	9	870E	UW91–46(NY, sd.)	"
f. *pilosum* (Thunb.) Nakai	18	9	446E	NY(TG)	e. As.
"	18	9*	534E	TG, sd.(Japan)	"
"	18	9*	562E	HB, sd.(Japan)	"
"	18	9	563E	"	"
f. *xanthocarpum* Rehd.	18	8	AA10140	AA10140	cult.
"	18	9	149E	AA10140	"
"	18	9	373E	NY	"
"	18	9	594E	MT457–45(KH)	"
"	18	9*	1397E	E(IC)	"
V. ellipticum Hook.	18	9	430E	LO	w. U.S.
"	18	9	1060E	K316–32(EN)	"
V. erosum Thunb.	18	9	24E	PI–4276P	e. As.
"	18	9	89E	MR2015	"
"	18	9	515E	HB, sd.(Japan)	"
"	18	9	595E	MT499–53(AA11596)	"
"	18	9	734E	NY179752	"
"	18	9	810E	AA11596 (Wilson)	"
"	18	9	881E	UW168–50(NY, sd.)	"
"	18	9	1081E	RH	"
"	18	9*	1398E	E15163 Yii	"
var. *punctatum* Franch.	18	9	511E	TC(Japan, sd.)	e. As.
"	18	9	512E	"	"
"	18	9	527E	TG, sd.(Mt. Tawa)	"
var. *taquetii* Rehd.	18	9*	1401E	E	Korea
V. flavescens W. W. Sm.	18	9*	202E	E2486, sd.	China
"	18	9*	882E	UW274–49(E, sd.)	"
"	18	9*	1407E	E	"
V. foetidum Wall.	16	6	—	—	Himal.
"	18	9	440E	RH	"
"	18	9	1087E	HL	"
var. *rectangulatum* (Graebn.) Rehd.	16	6	—	—	w. China
"	18	9*	1158E	HA	"
"	18	9*	1163E	EX	"
V. hanceanum Maxim.	72	9	477E	MT564–39	China
"	72	9	821E	AA1507–51(HL)	"
"	72	9	1033E	K124–26(AA)	"
"	72	9	1132E	P	"
V. hirtulum Rehd.	18	9	883E	UW264–49(LS, sd.)	China
"	18	9*	1784E	WY	"
V. hupehense Rehd.	18	1	—	AA	c. China
"	18	2	—	—	"
(as *V. hirtulum*)	18	8	AA708–37–B	AA708–37–B	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
"	18	9	302E	KR, sd.	"
"	18	9	355E	DU, sd.	"
"	18	9	463E	MT, 390–39	"
"	18	9	678E	KH	"
"	18	9	711E	MR601A (Wilson)	"
"	18	9	738E	BB	"
"	18	9	765E	AA18020 (Wilson 601)	"
"	18	9	769E	AA708–37–B (LS, sd.)	"
"	18	9	978E	MR601A–5	"
"	18	9	995E	K650–10 (Wilson 601)	"
"	18	9	1080E	RH	"
V. ichangense (Hemsl.) Rehd.	18	9	80E	CL	c. & w. China
"	18	9	695E	PI–114819	"
"	18	9	838E	AA(KN)	"
"	18	9	1072E	RH	"
"	18	9	1085E	HL	"
"	18	9*	1162E	EX	"
"	18	9*	1319E	BC	"
V. japonicum (Thunb.) Spreng.	18	9	560E	K	Japan
"	18	9	566E	HB, sd. (Japan)	"
"	18	9	876E	VO	"
"	18	9	887E	UW631–50(HL)	"
"	18	9	1047E	K167–37(DA)	"
"	18	9*	1159E	CC	"
V. lobophyllum Graebn.	18	1	—	AA	c. & w. China
"	20	6	—	—	"
"	22	7	—	EX	"
"	18	9	108E	HP2152	"
"	18	9	131E	AA19494–C	"
"	18	9	351E	Du, sd.	"
"	27	9	620E	MT1303–35 (NB, sd.)	"
"	18	9	730E	NY67491(LS)	"
"	18	9	967E	AA19498–A	"
"	18	9*	1004E	K88–08(AA238w)	"
"	18	9	1128E	P	"
"	18	9*	1472E	HL	"
V. molle Michx.	36	9	391E	NY(HP)	c. U.S.
"	36	9	625E	MT1044–40	"
"	36	9	803E	AA18294–A (Palmer)	"
"	36	9	1016E	K104–35(DU)	"
f. *leiophyllum* Rehd.	18	8	AA4643–1–A	AA4643–1–A	c. U.S.
"	36	9	804E	AA4643(Bush)	"
"	36	9	985E	MT1097–36	"
V. ovatifolium Rehd.	18	1	—	AA	w. China
"	18	8	AA20078A	AA20078A	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	290E	UW(MT, sd.)	"
"	18	9	764E	AA20078 (Wilson 590)	"
"	18	9	1025E	K1008–34(NN)	"
"	18	9	1076E	RH	"
V. parvifolium Hayata	18	9	889E	RH	Formosa
V. phlebotrichum S. & Z.	36	9	531E	TG, sd. (Japan)	Japan
"	36	9	723E	BT37–39	"
"	36	9	869E	UW38–49(HL)	"
"	36	9	1095E	HL	"
V. rafinesquianum Roem & Schult.	36	9	365E	K	e. N. Am.
"	36	9	573E	SO	"
"	36	9	576E	LA	"
var. *affine* (Schneid.) House	20	8	AA4622–2–B	AA4622–2–B	e. N. Am.
"	36	9	571E	MC	"
"	36	9	768E	AA17972(Bush)	"
"	36	9	1051E	K378–36	"
V. *recognitum* Fern.	36	9	707E	MR54–94	e. N. Am.
V. *scabrellum* Chapm.	72	9	96E	MR	se. U.S.
"	72	9	396E	NY(BT)	"
"	72	9	567E	MC	"
"	72	9	579E	PN(Va.)	"
"	72	9	714E	MR2200	"
"	72	9	745E	AA11549–B (Harbison)	"
V. setigerum Hance (as *V. theiferum* Rehd.)	18	2	—	—	c. & w. China
"	36	8	AA20189	AA20189	"
"	36	9	55E	CU	"
"	18, 36	9	57E	PI–104128	"
"	36	9	88E	MR11(Wilson)	"
"	36	9	654E	MT807–40(MR)	"
"	36	9	655E	MT522–50	"
"	36	9	709E	MR218A(Wilson)	"
"	36	9	744E	AA20189 (Wilson 236)	"
f. *aurantiacum* Rehd.	36	8	AA812–32	AA812–32	c. & w. China
"	36	9	59E	PI–023027	"
"	36	9	60E	PI–TN–R8	"
"	36	9	94E	MR12(Wilson 236)	"
"	36	9	815E	AA19085–2(Wilson 236)	"
V. wilsonii Rhed.	18	9	1053E	K262–23(HL)	w. China
"	18	9	1068E	DU	"
"	18	9*	1562E	E262–33(HL)	"
V. wrightii Miq.	16	6	2450K	RH	Japan
"	18	9	84E	CL	"
"	18	9	116E	HP2202	"
"	18	9	286E	C	"

TABLE I (*Continued*)

SPECIES	2*n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
"	18	9	516E	HB, sd.(Japan)	"
"	18	9	667E	MT165–37	"
"	18	9	686E	KH	"
"	18	9	781E	AA18015(Sargent)	"
"	18	9	912E	RH	"
var. *eglandulosum* (Miq.) Nakai	18	9	565E	HB, sd.(Japan)	Japan
var. *hessei* (Koehne) Rehd.	18	9	402E	NY	Japan
"	18	9	1031E	K	"
Sect. IX. **Opulus** DC.					
V. edule (Michx.) Raf.	18	9	873E	UW1053–50 (White R.)	n. N. Am.
"	18	9*	1098E	HL	"
V. kansuensis Batal.	18	9	1083E	RH	w. China
"	18	9	1094E	HL	"
"	18	9*	1453E	GP13248 L&S	"
V. opulus L.	18	1	—	AA	Eur., n. Afr.
"	18	6	—	—	"
(as *V. sargentii*)	20	6	2459K	RH	"
"	18	9	39E	CU	"
"	18	9	191E	K2491, sd.	"
"	18	9	324E	PO	"
"	18	9	344E	DU	"
"	18	9	375E	NY	"
"	18	9	400E	NY(Austria)	"
"	18	9	459E	MT1189–35	"
"	18	9	545E	K	"
"	18	9	672E	MT49–52(AA)	"
"	18	9	687E	KH	"
"	18	9	741E	AA	"
"	18	9	786E	AA20736(E, sd.)	"
"	18	9	1013E	AA562–30	"
"	18	9	1030E	K53–46(RH)	"
"	18	9	1032E	K94–29(G)	"
"	18	9	1063E	K106–63	"
'Aureum'	18	9	629E	MT1046–40(SP)	cult.
"	18	9	842E	AA997–52	"
"	18	9	892E	RH	"
"	18	9	1012E	K	"
'Compactum'	18	9	417E	RU	cult.
"	18	9*	1485E	JG	"
var. *nanum* (David) Zabel.	18	9	524E	CU	cult.
"	18	9	630E	MT118–53(HL)	"
"	18	9	981E	C	"
'Notcutt'	18	9	670E	MT211–51	cult.
"	18	9	747E	AA814–38(NN)	"

TABLE I (*Continued*)

SPECIES	*2n*	AUTHORITY	DOCUMENTATION	SOURCE OF MATERIAL	GENERAL DISTRIBUTION
f. *roseum* (L.) Heg. (as *V. tomentosum* var. *sterile*)	18	6	2463K	RH	cult.
"	18	9	41E	CU	"
"	18	9	246E	MT156–38	"
"	18	9	632E	MT1098–36(AA)	"
"	18	9	790E	AA26–47–A	"
"	18	9	1107E	P	"
"	18	9	1118E	P	"
f. *variegatum* (West) Zabel	18	9	316E	DA	cult.
"	18	9	633E	MT528–51(DA)	"
f. *xanthocarpum* (Endl.) Rehd.	18	8	AA1298–28–A	AA1298–28–A	cult.
"	18	9	104E	HP2157	"
"	18	9	403E	RU	"
"	18	9	634E	MT1099–36(HP)	"
"	18	9	791E	AA1298–28–A	"
V. orientale Pall.	18	9	175E	AA677–33	w. As.
"	18	9	296E	UW(MT, sd.)	"
"	18	9	837E	AA934–52	"
V. sargentii Koehne	18	1	—	AA	ne. As.
"	18	9	74E	PI–81798	"
"	18	9	300E	KR	"
"	18	9	337E	PO	"
"	18	9	404E	RU	"
"	18	9	794E	AA18012–B(Korea)	"
"	18	9	827E	AA571–53(Japan, sd.)	"
"	18	9	829E	AA572–53(Japan, sd.)	"
"	18	9	830E	AA570–53(Japan, sd.)	"
"	18	9	834E	AA646–53(Japan, sd.)	"
"	18	9	901E	RH	"
f. *calvescens* (Rehd.) Rehd.	18	8	AA467–26	AA467–26	ne. As.
"	18	9*	494E	AA467–26	"
"	18	9	797E	AA2144(Hers, sd.)	"
"	18	9	798E	AA467–26(Rock 13485)	"
"	18	9	1042E	K234–38 Marsh	"
f. *flavum* Rehd.	18	9	117E	HP2159	cult.
"	18	9*	130E	AA21419	"
"	18	9	647E	MT2195–22(HP)	"
"	18	9	795E	AA11037(HP)	"
'Puberulum'	18	9	649E	MT975–38(GB)	cult.
V. trilobum Marsh.	18	1	—	AA	n. N. Am.
"	18	6	—	—	"
"	18	9	327E	PO	"
"	18	9	659E	MT1228–38	"
"	18	9	816E	AA15673	"
"	18	9	1058E	K205–48(KR)	"

TABLE I (*Continued*)

SPECIES	*2n*	AUTHOR-ITY	DOCUMEN-TATION	SOURCE OF MATERIAL	GENERAL DISTRIBU-TION
'Andrews'	18	9	248E	MT1055–40	cult.
"	18	9	793E	AA292–42(LI)	"
"	18	9*	1663E	WLA66–104	"
'Compactum'	18	8	AA871–51	AA871–51	cult.
"	18	9	664E	MT216–53(KH)	"
"	18	9	684E	KH	"
'Hans'	18	9	661E	MT801–40	cult.
"	18	9	789E	AA293–42(LI)	"
'Wentworth'	18	9	663E	MT1057–40	cult.
"	18	9	783E	AA294–42(LI)	"
Unidentified species	18	9	693E	PI–22978	
"	18	9	700E	PI–111382	

CONTROVERSIAL CHROMOSOME COUNTS

Poucques (27, 28) reported $2n = 18$ in *Viburnum sandankwa*, a synonym of *V. suspensum*, while a somatic chromosome number of 16 is reported here. However, since several different evergreen forms have been referred to *V. sandankwa*, it is possible that Poucques' plant was not the same as *V. suspensum*. Simonet and Miedzyrzecki (35) reported a chromosome number $2n = 18$ for *V. setigerum* (*V. theiferum*). In the present study a single plant of this species was found with a chromosome number $2n = 18$; whereas other determinations, including that of Thomas (40), revealed a chromosome number of $2n = 36$.

The somatic chromosome counts reported in this study for thirteen species and four varieties differ from those reported by Janaki Ammal (18). In order to check Janaki Ammal's counts, and, if possible, to resolve the differences between our studies, an attempt was made to secure all the species grown at the Royal Horticultural Society's Garden, Wisley; at the Royal Botanic Gardens, Kew; and in the Jardin des Plantes, Paris. It is assumed that plants from these sources are similar to the material studied by her, but there is no assurance that the same plants were sampled. Since she published no record of the particular plants involved, it is uncertain whether she studied the same species in all three gardens or in only one. In any case, it seems logical to assume that some of the plants included in this study were the same as some of those she studied.

As with most cytological investigations, many of the studies must be made with cultivated plants that may be variants of the native species. The plant material used or the technique used could result in differences of chromosome counts. In a personal letter from Janaki Ammal it was stated that she had used the lacmoid leaf-bud technique (10), whereas

in the present study root-tip smears were used. A critical comparison of her cytological study with the present one is impossible, for no slides, drawings, or photomicrographs and only a limited number of herbarium specimens were available. For clarity of discussion the differences between her and my counts are grouped into two classes: 1) species differing by a few chromosomes per complement and, 2) those differing in the number of sets of chromosomes in each complement.

In the first category, *Viburnum bitchiuense*, *V. foetidum* var. *foetidum*, *V. foetidum* var. *rectangulatum*, *V. mongolicum*, and *V. wrightii* were determined to have $2n = 18$ chromosomes, two more than reported by Janaki Ammal (18). Among the plants studied were *V. bitchiuense*, from Kew, and *V. bitchiuense*, *V. foetidum* vars. *foetidum* and *rectangulatum*, and *V. wrightii* from the R.H.S. Garden, Wisley. In the collection at Wisley is a plant identified as *V. foetidum* var. *rectangulatum* which is probably the plant studied by Janaki Ammal. Plant 1084E of this study, which was received from the R.H.S. Garden as *V. foetidum* var. *rectangulatum* and which has horizontally spreading branches, oblong-ovate leaves, and an inflorescence with fertile flowers surrounded by sterile marginal flowers, is correctly identified as *V. plicatum* f. *tomentosum*. Upon visiting the R.H.S. Garden the author further verified the identification of this individual plant.

The present study has revealed that *Viburnum carlesii* is composed of a complex $2n = 18$, 20, and 22 chromosome forms. All the plants studied that were obtained from cultivation, including a plant from Kew, had $2n = 18$ chromosomes, which agrees with the reports by Poucques (28) and by Simonet and Miedzyrzecki (35). Janaki Ammal (18) reported this species have $2n = 20$ chromosomes.

The present study agrees with the previously reported counts of $2n = 18$ in *Viburnum buddleifolium* (35) and in *V. lobophyllum* (32), but Janaki Ammal (18) reported $2n = 20$ and 22 (the count of Enoch) for *V. lobophyllum*. Included in my study was a plant of *V. lobophyllum* from Kew.

In this study both *Viburnum plicatum* f. *plicatum* and f. *tomentosum* were determined to have forms with $2n = 16$ and $2n = 18$. Janaki Ammal (18) reported both these and f. *mariesii* to have $2n = 18$. The plants of f. *mariesii* and f. *tomentosum* from Kew and of f. *mariesii* from the R.H.S. Garden used in this study have chromosome complements of $2n = 16$. The herbarium specimens deposited at Kew by Janaki Ammal clarify the discrepancies, and this documentation has been added to TABLE I. Specimen *2456K* of *V. plicatum* f. *mariesii* (*V. tomentosum mariesii*) has an annotation note "$2n = 16$?" which definitely indicates that her published count was questionable. The specimen of *V. plicatum* (*V. tomentosum sterile*), *2463K*, collected at the R.H.S. Garden, is identified by me as *V. opulus* f. *roseum*. Likewise, specimen *2459K* of *V. sargentii*, collected at the R.H.S. Garden, is *V. opulus*. The plants of *V. odoratissimum* from Kew were found to be of the $2n = 32$ variation. Janaki Ammal reports $2n = 40$ for this species. This last number, however, was found elsewhere

in the *V. odoratissimum* complex in this study and has likewise been reported by Sugiura (38).

The number of genomes reported by Janaki Ammal (18) in the complements of four species and one variety differ from those found in this study. *Viburnum erubescens*, *V. henryi*, and *V. dentatum*, including in the present study specimens of all three from Kew and of *V. dentatum* from R.H.S., were found to be tetraploid, whereas Janaki Ammal reported them all to be hexaploid. Janaki Ammal's theory that the species evolved after spontaneous doubling of an unstable triploid obviously is not supported by this new evidence. *Viburnum sieboldii*, reported by Janaki Ammal (18) to be a diploid, was determined in this study to have both diploid and tetraploid forms, the tetraploid occurring much more frequently. The plant from the R.H.S. Garden studied was the tetraploid form. Janaki Ammal (18) reported *V. fragrans* 'Album' to be a tetraploid, but plants of this variety from R.H.S. Garden, and from other sources utilized in this study, were determined to be diploids. Thomas (40) also reports this variety to be diploid.

Among the 536 counts listed by the author (14) were a number of plants procured from the Arnold Arboretum. Thirteen of the plants studied by Thomas (40) are identical with those from which the author acquired material, while another six plants have the same Arnold Arboretum accession number but are not necessarily the same individual plant. The author lists the counts of an additional sixty-six plants from the Arnold Arboretum. Two of Thomas' counts, those for *Viburneum rafinesquianum* var. *affine* ($2n = 20$) and *V. molle* f. *leiophyllum* ($2n = 18$), differ significantly from the present work. *Viburnum rafinesquianum* var. *affine* was determined to be $2n = 36$ for all plants studied. A plant of *V. molle* f. *leiophyllum* bearing the Arnold Arboretum accession number 4643 was determined to be $2n = 36$, while Thomas reports $2n = 20$ for plant 4643–1–A, the latter having been propagated vegetatively from one of the original lot. Quite possibly, either a mixed lot or a mistake in labeling may be involved.

VARIATION IN CHROMOSOME NUMBERS WITHIN SPECIES AND VARIETIES

Differences in chromosome number were found within six species and five varieties. These differences can be placed in two classes for discussion: 1) those species that differ by a few chromosomes and, 2) those species that differ by a number of genomes.

The first category includes *Viburnum plicatum* and *V. carlesii*. Morphologically indistinguishable plants of *V. plicatum*, with $2n = 16$ and $2n = 18$, have been found. Comparison of the chromosome complements of these two forms reveals that the form with $2n = 18$ has an extra pair of metacentric chromosomes. This species will be discussed later in more detail. All plants of *V. carlesii* from cultivation have $2n$ chromosome complements of 18. However, among plants produced from seeds col-

lected in Korea, the native habitat of the species, chromosome complements of $2n = 18$, 20, and 22 have been found.

Six species that differed in number of genomes were studied. One plant of *Viburnum lobophyllum* ($2n = 27$) was determined to be a triploid, with three cytologically identical genomes. All other specimens of this species studied were diploid, with $2n = 18$. Since the triploid plant appears identical with the diploid, it does not seem likely that this is a hybrid between the diploid *V. lobophyllum* and one of the tetraploid species. It is possible that this triploid could have resulted from the fertilization of an unreduced functional gamete by a normal gamete. Likewise, it could have originated as a cross between diploid and tetraploid plants of *V. lobophyllum*, although this does not seem probable since no tetraploid *V. lobophyllum* is known.

One species, *Viburnum odoratissimum*, is represented by tetraploid and pentaploid forms. These two forms, which have distinct vegetative differences, comprise a taxonomic complex that is given further consideration later. The pentaploid form, with $2n = 40$, has five similar genomes, each of which is morphologically identical with the genomes of the tetraploid. It is unknown whether the four pentaploids and seven tetraploids are representative of the variation that occurs in native populations.

Individual diploid plants of *Viburnum sieboldii* and *V. setigerum* were discovered in species that otherwise are tetraploid. The diploid plant of *V. setigerum* was isolated from a group of plants grown from seed obtained from the U. S. Plant Introduction Garden, Glenn Dale, Maryland. This plant probably resulted from parthenogenesis wherein an unreduced gamete developed without syngamy. The diploid plant of *V. sieboldii* was secured from a commercial nursery and it is not known whether the plant was propagated asexually or from seed. The diploid plants of these species are still immature, making it impossible to compare them critically with tetraploid plants. Although at this time they do not appear morphologically distinct from the tetraploid, they are obviously somewhat weaker, and growth has been slower. This may be partially or entirely due to environmental conditions, however.

Only six of the sixty-one varieties observed in this study had chromosome complements with numbers different from the species (i.e., the typical varieties). *Viburnum tinus* var. *luciàum*, *V. dentatum* var. *deamii*, and *V. dentatum* var. *pubescens*, all $2n = 72$, had double the number of genomes of the typical variety of the species. One of the five collections of *V. lantana* var. *rugosum* was found to be a triploid, $2n = 27$. Though there are three cytologically identical genomes in this particular plant, it does not appear to be morphologically distinct from the other collections. It is conceivable that this plant developed from a chance unreduced gamete that was fertilized by a normal gamete.

In *Viburnum plicatum* f. *tomentosum* and *V. plicatum* f. *mariesii*, as well as in *V. plicatum* f. *plicatum*, occur both $2n = 16$ and 18 chromosome forms which cannot be distinguished by vegetative characteristics. All other taxa of this species which have been examined (*V. plicatum* f.

glabrum, *V. plicatum* 'Lanarth,' *V. plicatum* f. *lanceolatum*, *V. plicatum* f. *mariesii*, *V. plicatum* 'Roseum,' *V. plicatum* 'Rowallane,' and *V. plicatum* 'St. Keverne') have chromosome complements of $2n = 16$. The forms with $2n = 18$ differ from those with $2n = 16$ by an additional pair of metacentric chromosomes. Since the $2n = 16$ plants produced the most abundant fruit, it is to be expected that these forms should have a higher rate of survival. The evidence indicates that most of the minor variations in *Viburnum* that have been given varietal rank are the result of genic or intrachromosomal changes, rather than the result of changes in chromosome numbers.

CYTOTAXONOMIC COMPLEXES

Differences in the chromosome numbers of different collections of *Viburnum odoratissimum*, *V. carlesii*, and *V. dentatum* suggest that each of these is a species complex.

VIBURNUM ODORATISSIMUM. Two distinct forms are evident in *V. odoratissimum*, the plants of which were secured from nine different sources. The one has smooth-barked branches; thin, coriaceous, elliptic-ovate leaves; and indistinct axillary buds. The other has stout, lenticular branches; thick, coriaceous, elliptic-obovate leaves; and prominent axillary buds. The illustrations of *V. odoratissimum* by Dippel (13) and of *V. awabuki* by Nakai (23) portray two types which are respectively similar to the two forms observed in the present study. Nakai (23) recognized *V. odoratissimum*, *V. liukiuense*, *V. awabuki*, and *V. awabuki* var. *serratum* in this complex, but other taxonomists generally have accepted only one species, *V. odoratissimum*. Because all the plants used in this study have not yet produced flowers, it is impossible to make a positive identification of these variants. Chromosome counts of $2n = 32$ (tetraploid) and $2n = 40$ (pentaploid) have been observed among both morphological forms of this species complex. Two of the three plants with $2n = 40$ are from the same original source and are of the variant with coriaceous leaves and stout, lenticular branches. Sugiura's (38) report of $2n = 40$ in *V. awabuki* also indicates that his *V. awabuki* may be different from *V. odoratissimum*. Do these represent species or are they variants of one species? Although the cultivated material studied probably does not differ from representatives of the native populations of this species complex, additional material from known populations and further study will be necessary to determine the relationships within the species.

VIBURNUM CARLESII. In this study all plants of *V. carlesii* received from cultivation have chromosome counts of $2n = 18$. However, seeds supposedly collected from native populations in China and Korea produced an array of plants with $2n = 18$, 20, or 22 chromosomes. It is difficult, if not impossible, to explain this variation if this is a true species. Of course, there is no assurance that this seed was from isolated plants and not from

plants growing near other species with which there could be cross-pollination.

As previously noted, Janaki Ammal (18) proposed that *Viburnum carlesii* arose as a backcross between a chance triploid ($2n = 24$) and the normal diploid ($2n = 16$) of *V. bitchiuense*. In view of the present study, her explanation appears inadequate, for *V. bitchiuense* has $2n = 18$ chromosomes, rather than the 16 chromosomes required by her proposal. If triploid plants exist in nature, this variation in the chromosome complement of seedlings might be the result of self-pollination or cross-pollination between the triploid and diploid forms, which would produce progeny with additional chromosomes. It is doubtful, even if the triploid does exist, that fruit would normally result from self-pollination.

Most taxonomists consider *Viburnum bitchiuense* and *V. carlesii* to be closely related. However, few have gone to the extreme of Nakai (24), who not only reduced *V. bitchiuense* to a variety of *V. carlesii*, but also put both of these in a new genus *Solenolantana*. It is doubtful if this complex requires the latter action. Pollinations by the author of *V. bitchiuense* ($2n = 18$) $\times$ *V. carlesii* ($2n = 18$) produced no seed, while the reciprocal cross between these species produced, from ninety-nine flowers pollinated, forty-three seed which have yielded forty-one plants. A meiotic chromosome study of these plants should indicate more clearly the natural relationships of these species. Until a sporocyte study is made of authentic materials collected from native populations, this remains an unsolved cytotaxonomic complex.

VIBURNUM DENTATUM. *Viburnum dentatum* var. *dentatum* and *V. dentatum* var. *pubescens*, represented by $2n = 36$ and $2n = 72$, form the third cytotaxonomic complex. According to Rehder (31), *V. pubescens* is a synonym of *V. dentatum* var. *pubescens*. In the *V. dentatum–pubescens* complex specific delimitation has been based almost entirely on the presence and distribution of pubescence on petioles, leaf surfaces, and inflorescence branches or combinations of these. Blake (4), who examined Solander's manuscript of *Hortus Kewensis*, an early treatment of this complex, and who also studied native material, recognized *V. pubescens*, *V. pubescens* var. *canbyi*, and *V. pubescens* var. *longifolium*. Rehder (29) described two new varieties from Indiana, *V. pubescens* var. *deamii* and *V. pubescens* var. *indianense*, which have only minor differences from each other.

Svenson (39) commented on the variations of this group, which he separated on the basis of leaf shape and pubescence into *Viburnum dentatum*, *V. dentatum* var. *lucidum*, *V. dentatum* var. *pubescens* and *V. pubescens* var. *semitomentosum*. He also concluded that *V. pubescens* var. *deamii* probably is a separable variation.

Fernald (16) was in disagreement with Svenson's reduction of the glabrous-twigged form of *Viburnum dentatum* to varietal rank as *V. dentatum* var. *lucidum*, and elevated this glabrous variation to the rank of species with the specific name *V. recognitum*. *Viburnum recognitum* is dis-

tinguished from *V. dentatum* by its glabrous branchlets and cyme, glabrous or glabrate foliage, and flowers produced ten days to three weeks earlier. Fernald further stated that *V. dentatum* and its variations and *V. recognitum* "are both hopelessly variable in leaf outline and toothing of leaves, each of them with blades varying from lance-ovate to ovate-oblong to orbicular, with veins prominent beneath or obscure, with length from 2.5 to 10 cm. and breadth from 2 to 8 cm." *Viburnum recognitum*, *V. recognitum* var. *alabamense*, *V. crenatum*, *V. dentatum*, *V. carolinianum*, *V. carolinianum* var. *deamii*, and *V. pubescens* are entities recognized by McAtee (21) in this species complex.

The present study follows Rehder's treatment which reduces this complex to *Viburnum dentatum*, *V. dentatum* var. *pubescens*, and *V. dentatum* var. *deamii*. The material studied here was received under practically every one of the different names applied by past authors to these variations. Many of these collections were from cultivated plants, since materials from native populations were not available for all species or varieties. Therefore, it must be realized that the material studied is not necessarily an adequate sampling of variability of the native population, but it does give indications which may establish a basis for further research. The plants are being maintained for further study and identification.

Two chromosomal forms, $2n = 36$ and $2n = 72$, were located among plants of *Viburnum dentatum* var. *pubescens*. All plants of *V. dentatum* var. *deamii* had $2n = 72$. Are these plants of another variety or polyploid forms of the same species? Are these variations within a species the result of natural hybridization that has been followed by segregation and selection? The variations between *V. dentatum* var. *dentatum*, var. *pubescens*, and var. *deamii* have been described taxonomically but are only of minor magnitude. Likewise, *V. recognitum* is only slightly different from *V. dentatum*, though it has been elevated to specific rank. Are these cases in which speciation is resulting from natural hybridization but in which divergence of types is not yet great enough for complete delimitation? Is the glabrous-branched *V. recognitum* a plant of a segregating hybrid population or does it represent another species?

It has been suggested that *Viburnum dentatum* may have crossed with *V. rafinesquianum*, another related species, to produce by introgressive hybridization a different ecological population. Normally, however, these species are isolated by season of bloom, *V. dentatum* flowering approximately ten days later than *V. rafinesquianum*, and by habitat, *V. dentatum* being located on moist soil and *V. rafinesquianum* on dry upland. It is possible that a few late flowers of *V. rafinesquianum* may be shedding viable pollen when the first *V. dentatum* flowers open, and the distance between plants would not prevent cross-pollination. The offspring produced by such crosses could, over a period of time, produce a population of a type differing from the original species of the locale. In the particular area of South Hill, near Ithaca, N.Y., where plants were used for controlled pollinations in this study, there is no evidence of natural hybridization, but in similar situations elsewhere the densely pubescent *V. rafinesquianum* may

have crossed with the nearly glabrous *V. dentatum* to produce a population with additional variations.

A further complication arises from the report by Janaki Ammal (18) that *Viburnum dentatum* has a chromosome number of $2n = 54$. In the present study, $2n = 36$ has been counted in all cases. It is logical to think that her plant was a hybrid, unless the count was incorrectly determined, since all of her work was done on cultivated plants growing in close proximity and hence subject to crossing. Since it is the custom of many botanic gardens to raise plants from seed, not realizing the seed may be from cross-pollination and not true for the species type, it is possible that the plants studied by her may have originated in this way.

One approach to the problem is experimental; that is, to reproduce a similar plant by controlled hybridization. All the possible pollination combinations between *Viburnum dentatum* var. *dentatum*, *V. dentatum* var. *pubescens*, and *V. rafinesquianum* were made in the present study. From 386 flowers of *V. dentatum* pollinated by *V. rafinesquianum* were produced 190 seeds from which 123 plants have been grown. From 130 flowers pollinated in the cross *V. dentatum* var. *dentatum* × var. *pubescens*, 49 seed and 15 plants were obtained. The only other combination to yield seed was *V. dentatum* var. *pubescens* × *V. rafinesquianum* which, from 329 pollinations, produced five seed that yielded two plants. The other combinations failed to produce seed, but this cannot be attributed necessarily to sterility or incompatibility, for climatic conditions and technique may have been variable factors. That seeds and plants were procured from crosses between these species and varieties indicates a relationship within the complex. As these plants attain flowering size, a study of the meiotic chromosome configurations of the sporocytes should reveal the interrelationships more definitely. It will be desirable to repeat those crosses that produced no seed and to attempt additional crosses with other related species from section Odontotinus.

Because polyploids are found in this complex, a study of the native populations will be required to resolve the problem. Such experimental studies should not be concentrated within a few isolated populations but should cover the distribution range of this species complex so that differences and relationships between populations, as well as within populations, can be determined. With the union of the evidence from cytology, genetics, and taxonomy the intricate relationships of this complex should eventually be clarified further.

The section Odontotinus of Rehder's classification includes other species that occur in the same geographical areas as members of the *Viburnum dentatum–pubescens* complex. Other taxa related to this complex and warranting study include *V. molle*, *V. scabrellum*, *V. bracteatum*, and *V. rafinesquianum*. The Chinese *V. hanceanum* appears to be allied closely to this complex. When the plants studied have produced fruit and the identification has been checked, a more valid interpretation of *V. hanceanum* may result.

This cytotaxonomic complex in eastern North America and the two com-

plexes in Asia may be representative of those that exist in other species groups of this genus. The author is inclined to believe that a similar complex may exist with *V. cassinoides*, *V. nudum*, and *V. lentago* of eastern North America.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships within a genus can be accurately formulated only when the number, morphology, and behavior of chromosomes are correlated with anatomy, morphology, and taxonomy of the species. A tentative scheme for the species of *Viburnum* has been constructed utilizing all the available data (FIG. 16).

The genus *Viburnum* includes polyploid series with the basic numbers of eight and nine. Polyploidy can take place effectively only in one direction; the diploid must nearly always be the parent of the polyploid (11, 33). Stebbins (37) emphasizes the point that diploid members must be older than the polyploids, although they are not necessarily more primitive in the sense that they are less specialized in structure. Since higher polyploids (tetraploids, hexaploids, etc.) usually cannot revert to the diploid without abnormalities in the reproductive cycle, it is likely that one of the lower gametic numbers, i.e., 8 or 9, is primitive.

Wilkinson (44) presented additional evidence of the natural relationships of selected species in the genus. She reported on fourteen species, representing all but two of the sections of the genus, which were placed in five groups on the basis of their internal morphology and the vascular anatomy of their flowers. *Viburnum sieboldii* ($n = 8$) is the most primitive of those studied, with only two characteristics that might be considered advanced: reduction of peripheral bundles to five and the reduction of the sepal supply to a single unbranched trace. In no other species included in her study were so many primitive characteristics present. A group of relatively primitive species includes *V. carlesii*, *V. lantana*, and *V. dentatum*, all $n = 9$. Another group of less primitive species would include *V. lantanoides* ($n = 9$), *V. plicatum* f. *tomentosum* ($n = 9$), and *V. lentago* ($n = 9$). The group of more advanced nine-chromosome species includes *V. rhytidophyllum*, *V. nudum*, *V. cassinoides*, *V. dilatatum*, and *V. trilobum*. *Viburnum opulus* ($n = 9$) is considered the most advanced. Her work supports the theory that the species with the basic number of eight are primitive, while those with a basic number of nine are more advanced.

From a study of the stem anatomy, De Vos (12) concurred that *V. opulus*, *V. lentago*, and *V. cassinoides* are the most advanced and that *V. plicatum* f. *tomentosum*, *V. lantanoides*, and *V. sieboldii* are the most primitive.

To date, this is the extent of comparative morphological and anatomical studies of *Viburnum* species. *Viburnum sieboldii* ($n = 8$) is on these grounds considered to be the most primitive species of the genus. All other species with a basic number of eight have many characteristics in common with *V. sieboldii*, so that it can be assumed that this group is more primitive

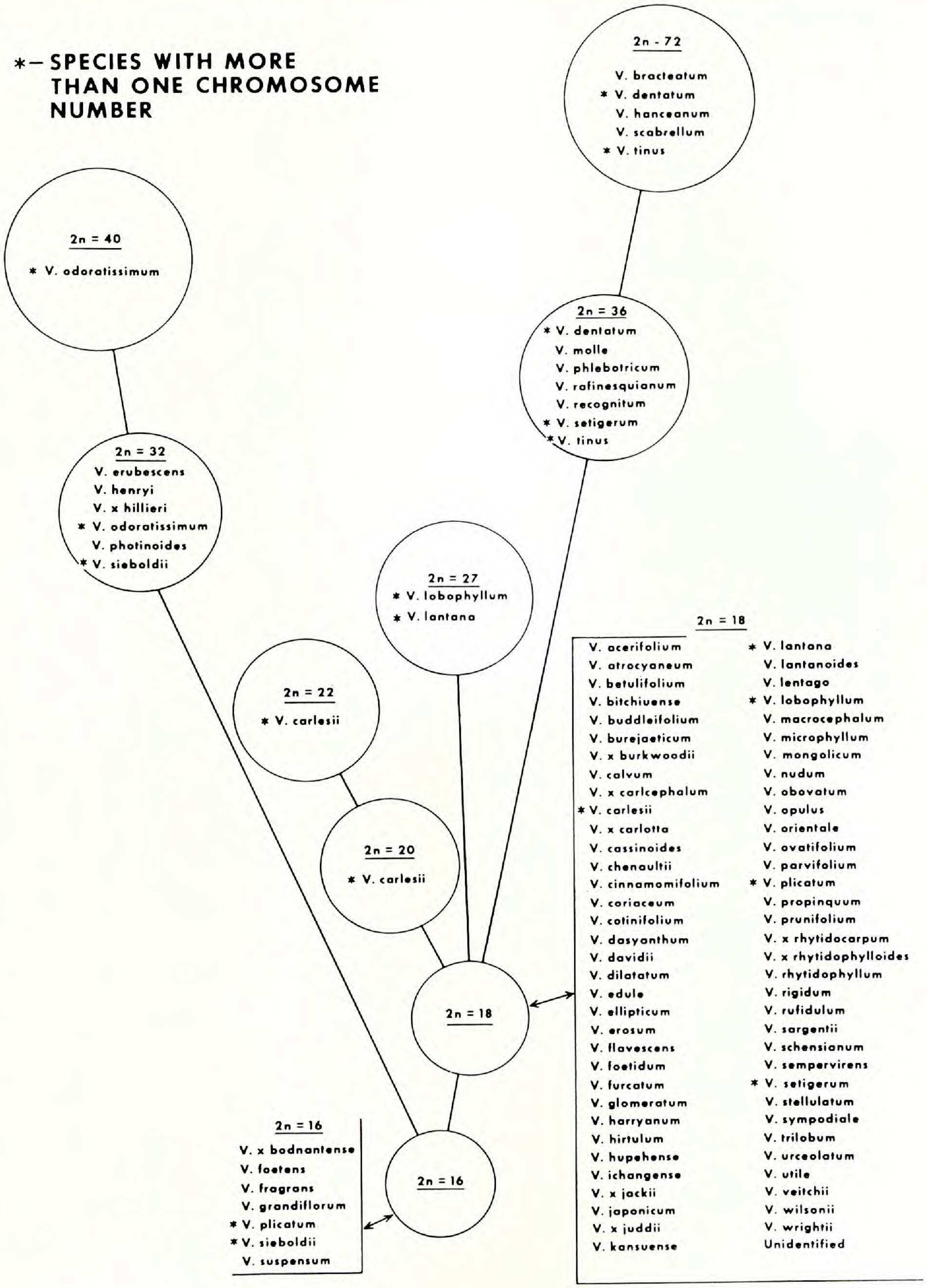


FIG. 16. Diagram based on chromosome complements to show interrelationships of species of *Viburnum*.

than those species with a basic number of nine. But the possibility remains that another species within the $n = 8$ group may be more primitive than *V. sieboldii*, and likewise that *V. opulus* need not necessarily be the most advanced species of the genus. Only a small sample of species and of the variation that exists in this widely distributed genus has been evaluated critically. Opinion concerning the relative position of species in regard to primitiveness may shift when additional evidence is available, but the basic cytological relationships of the various chromosome groups appear to be well established.

On the basis of floral anatomy Wilkinson (43, 45) postulates that there are in the Caprifoliaceae two lines of development. Through a form resembling the prototype postulated for *Viburnum* one line leads to *Viburnum* and *Sambucus*; the other stems through *Leycesteria* and branches separately to the Loniceraeae and Linnaeeae. The evidence at hand is inadequate to hazard an interpretation or conclusion as to what was the prototype for the family and from whence *Viburnum* arose, but the present evidence favors the $n = 8$ forms as the more primitive.

ALTERATION OF BASIC CHROMOSOME NUMBER

Evolutionary changes within a genus may be due to polyploidy, to the addition or subtraction of one or a few chromosomes of a complement, to gross structural rearrangements of the chromosomes, to submicroscopic changes, probably involving the chemistry of the chromosomal material, or to any combination of these. It can be assumed that all these changes have probably functioned in speciation in *Viburnum*. However, the genus has not been studied sufficiently to ascertain the evolutionary significance of each. For this reason, this discussion of phylogenetic relationships will be centered primarily around the evolutionary significance of the basic chromosome numbers of the genus.

Navashin (25) realized that changes in the basic number must involve loss or gain of the existing kinetochore, since kinetochores or kinetochore modifications cannot arise *de novo*. In this light, the increase or decrease in chromosome number attributed to "fragmentation" and "fusion" (7) could occur only when it involved a gain or loss of the kinetochore.

Darlington (8) presented a procedure favoring the loss or gain of a chromosome by means of an equal translocation between two different nonhomologous chromosomes with subterminal kinetochores. An interchange involving the long arm of one and the short arm of the other would produce one long metacentric chromosome and one very short chromosome or fragment. It has been pointed out that the consequences of unequal translocation depend on whether the regions about the kinetochore are genetically active or inert. An inert centric fragment may be eliminated, with a consequent reduction in chromosome number. If the fragment chromosome is genetically active it may persist as a univalent and be passed at meiotic metaphase to the same pole as the other interchange chromosome. This will yield, in addition to normal gametes, gametes

with both or none of the interchange chromosomes. The union of gametes with additional chromosomes may yield trisomic or eventually tetrasomic plants which evolve into species with permanently increased basic numbers. Morphological differences may arise by virtue of either dosage effect or by divergent gene mutation in the duplicated chromosomes. Further cytological divergence may arise from reciprocal translocation between one of the new extra chromosomes and another chromosome of the complement (5, 37, 1).

Tobgy (41) confirmed Darlington's postulate with the demonstration that a reciprocal translocation between two chromosomes of *Crepis neglecta* ($n = 4$) gave rise to one chromosome of *Crepis fuliginosa*. Of the two chromosomes resulting from this translocation, the one with a genetically inactive region adjacent to the kinetochore was lost. Likewise, Sherman (34) obtained evidence that the origin of the *Crepis kotschyana* ($n = 4$) complement involved reciprocal translocation in the reduction from five to four pairs of chromosomes.

Chromosome number can also be increased or decreased by aberrations such as the translocations observed by Thomas (40) in the meiotic cycle. Asynapsis, desynapsis, nondisjunction, and chromosome lagging may be responsible for the production either of gametes with a single extra chromosome, several extra chromosomes, or with the entire unreduced complement, or of other gametes with chromosomal deficiencies. The union of such gametes may result in individuals deficient in or with additional chromosomes.

Chromosome numbers may be increased by supernumeraries or by misdivision of the kinetochore. White (42) considers the formation of supernumeraries, fragments produced by deletion or translocation, and fragmentation of the kinetochore to be probably the chief method whereby chromosome numbers have become increased in the course of evolution in animals. The fragment lacking the kinetochore region is lost in subsequent divisions unless it is translocated to another chromosome. Thus, fragmentation, in association with translocation, provides a mechanism for chromosome number increase. According to Darlington and Mather (11), misdivision of the kinetochore is the only single change that can affect both the number and structure of the chromosomes in a single stroke. The kinetochore, rather than dividing lengthwise, divides crosswise, resulting in two telocentric chromosomes which at a later division may produce two pairs of unlike isochromosomes (9). Races of *Campanula persicifolia* (11) have been found in which two telocentric chromosomes occur instead of a single chromosome and thus add an additional chromosome to the haploid number.

The backcrossing of a triploid, produced by a cross between a tetraploid and diploid plant, to a diploid has experimentally produced a great variety of segregant types, from among which have been recovered a small proportion of fertile types. Examples of such results have been reported in *Triticum* by O'Mara (26) and in *Gossypium* by Beasley and Brown (3) and have been summarized for *Nicotiana* by Goodspeed (17). This

system of hybridization has artificially changed the basic chromosome number but has not been established as occurring in the natural evolution of species.

These examples individually, or in combination, illustrate numerous means whereby the basic chromosome number could increase or decrease as the taxonomic group evolved. Likewise, the progressive increase or decrease in basic number could be followed or accompanied by amphidiploidy to produce a complicated aneuploid series such as occurs in *Carex*, *Iris*, *Sedum*, *Viola*, and other genera. Stebbins' (37) summary of the types of aneuploid series in higher plants shows that the number of descending basic series is far greater than either the ascending basic or interchange amphidiploid series.

It is possible that in *Viburnum* the change in the basic chromosome number from eight to nine was adequate to keep the two types isolated and to allow each to evolve independently. As the types were exposed to new and changing environments the selection pressure further subdivided the major groups into minor groups with differential adaptability. It is conceivable that under certain circumstances the polyploid was favored over the diploid, or in others vice versa, thus increasing the variability. During this interval adaptive mutations could arise in certain subgroups. As the minor groups became further subdivided and isolated for survival in specific environmental niches, the variability within the genus expanded until today many *Viburnum* species have great morphological divergence. Although the phylogenetic relationships suggested by the chromosome numbers of *Viburnum* species provide a basic framework from which the specific differences evolved, the pathway remains obscure.

CHROMOSOMES AND THE TAXONOMIC SECTIONS

The nine taxonomic sections of the genus, based on morphological characters, as recognized by Rehder (30) may be correlated with the pattern of cytological relationships. Section THYRSOSMA, which includes *Viburnum sieboldii*, is composed entirely of species with a basic chromosome number of eight. This number occurs in only one other section, PSEUDOPULUS, in which, however, *V. plicatum* and *V. plicatum* f. *tomentosum* have forms with both $n = 8$ and $n = 9$. The question arises as to whether *V. plicatum* and *V. plicatum* f. *tomentosum*, both with cytological forms that are morphologically indistinguishable, represent the connecting link in the evolution of the genus between the basic numbers of eight and nine. Wilkinson (43) concluded from the study of floral anatomy and morphology that *V. plicatum* f. *tomentosum* was relatively primitive, but not as primitive as *V. carlesii*, $n = 9$, of sect. LANTANA, and *V. dentatum*, of sect. ODONTOTINUS. This does not support the proposition that *V. plicatum* forms an evolutionary bridge between the groups of species with $n = 8$ and $n = 9$. It is probable that $n = 9$ may have evolved more than once and in various places. However, with additional study this relationship may be clarified.

Only diploids are found in sects. PSEUDOPULUS, LENTAGO, MEGALOTINUS, OPULUS, and LANTANA, with the exception of *V. carlesii* ($2n = 18, 20, 22$) and *V. lantana* var. *rugosum* ($2n = 27$).

Tetraploids and higher polyploids are found in sects. THYRSOSMA, TINUS, and ODONTOTINUS. The scheme showing the relationship between chromosome complements is presented in FIG. 16, which shows the evolutionary trend to be from $2n = 16$ to $2n = 32$, and from 16 to 18 to 36 to 72. In the evolution of the genus the diploids probably have had the highest adaptive value and today are represented by the largest number of species. At the present time it appears impossible to separate the diploid species into taxonomic sections on the basis of chromosome morphology. The distinct gross morphological differences used by the taxonomist to divide the genus into sections appear to be the result of genic rather than structural chromosomal changes. When karyotype analysis has been completed for these species, differences of arm length, secondary constrictions, kinetochore position, satellites, and size of chromosomes may reveal natural relationships between species and sections.

A study of the chromosome complements of polyploid species reveals that the genome is duplicated. These species, preceded by an asterisk in FIG. 16, provide additional evolutionary information. For example, in sect. ODONTOTINUS the tetraploid *V. setigerum* has the same genomes duplicated that occur in the diploid. In the same section, *V. dentatum* var. *pubescens* and *V. dentatum* var. *deamii* are represented by octoploid forms with eight genomes duplicating the four genomes of the tetraploid. *Viburnum carlesii* (sect. LANTANA) and *V. plicatum*, *V. plicatum* f. *mariesii*, and *V. plicatum* f. *tomentosum* (sect. PSEUDOPULUS) are the only aneuploid species yet found in *Viburnum*. The forms with $2n = 20$ and $2n = 22$ can be considered to have developed from the $2n = 18$ form which is the most common. The plants with 20 and 22 chromosomes have, respectively, one and two pairs of chromosomes not found in the $2n = 18$ form, but at present the origin and relationship of these additional chromosomes to the usual 18 in *V. carlesii* is unknown.

The geographical distribution of polyploids is much more restricted than that of diploids. *Viburnum* species from all the major centers of distribution, except Central and South America, are well represented in this study. Since the origin of most of the varieties, whether natural or by man's selection, is uncertain, in many cases they cannot be assigned to a specific geographic area and are omitted in the following discussion. The greatest number of species studied is in the 18-chromosome group, and these are distributed over a wide geographic area. The diploid species include fifty from Asia, four from Europe, and twelve from North America, while the polyploids include eight species from Asia Minor, one from Europe, and six from North America.

From the foregoing it is obvious that the distribution of polyploids in *Viburnum* provides little evidence for one distinct center of origin of the genus. It is probable that polyploidy has evolved several to many times and in various places: eastern Asia, the Himalayan and Mediter-

ranean regions and eastern North America. In eastern Asia occur all the species with the basic number of eight, along with a large number of diploids and a few polyploid forms with the basic number of nine. The Mediterranean species are few in number and belong to the group with a basic number of nine. The eastern North American species include the greatest number of octoploids, possibly indicating that this geographical niche has been more favorable for their evolution and establishment.

Only for certain sections does a relationship exist between the geographical distribution and the taxonomic sections of the genus. Sections THYRSOSMA and MEGALOTINUS are entirely of Asiatic distribution. *Viburnum plicatum* and its varieties, composing sect. PSEUDOPULUS, are native only to China and Japan. All species of sect. LENTAGO are limited to eastern North America. Representative species of sects. TINUS and LANTANA are distributed both in Asia and in Europe. Sections ODONTOTINUS and PSEUDOTINUS are represented both by North American and Asiatic species. The species of the sect. OPULUS occur both in Europe and in North America.

At present, the cytological evidence suggests that Rehder's sectional classification of *Viburnum* corresponds favorably with the natural relationships. It is hoped that as this study is continued and expanded a more accurate evaluation of the classification can be achieved.

PROPOSED RESEARCH

Portions of the preceding discussion are based principally on inference which indicates where the problems lie and suggests methods of approach. Definite conclusions cannot be drawn until much additional research is completed. Therefore, the present study is basic both for plant breeding and for cytological studies to be continued in the genus *Viburnum*.

To the present, it has been impossible to secure the species native to Mexico and Central and South America, but by expedition or otherwise, it is hoped that these may become available for future study. Within these areas are many species of diverse form which, when secured from higher elevations, should prove hardy and noteworthy ornamentals in this and other latitudes. These species not only may provide additional genetical variability for interspecific hybridization, but also are representatives of one of the centers of diversity in the evolution of the genus.

Cytological studies, in addition to providing a basis for plant breeding, have provided a useful tool for taxonomists in classifying certain plant groups, and there is every indication that such information can likewise be useful in studies of *Viburnum*. It is anticipated that a sporocyte study and karyotype analysis, associated with genetical and taxonomic studies, will aid materially in revealing natural relationships which can be utilized in the classification of the genus *Viburnum*.

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BIBLIOGRAPHY

1. Babcock, E. B. Cytogenetics and speciation in *Crepis*. *In*: Advances in Genetics, pp. 161–206. Academic Press, Inc., New York, 1947.
2. Baldwin, J. T., Jr. *Kalanchoe*: the genus and its chromosomes. Am. Jour. Bot. **25**: 572–579. 1938.
3. Beasley, J. O., & M. S. Brown. The production of plants having an extra pair of chromosomes from species hybrids of cotton. Rec. Genet. Soc. Am. **12**: 43. 1943.
4. Blake, S. F. On the names of some species of *Viburnum*. Rhodora **20**: 11–15. 1918.
5. Clausen, Jens. Stages in the evolution of plant species. 206 pp. Cornell Univ. Press, Ithaca, N.Y., 1951.
6. Conger, A. D. & L. M. Fairchild. A quick freeze method for making smear slides permanent. Stain Tech. **28**: 281–283. 1953.
7. Darlington, D. C. Chromosomes and plant breeding. 112 pp. Macmillan and Co., London, 1932.
8. ———. Recent advances in cytology. Ed. 2. 671 pp. J. and A. Churchill, Ltd., London, 1937.
9. ———. Misdivision and the genetics of the centromere. Jour. Genet. **37**: 341–364. 1939.
10. ——— & L. F. La Cour. The handling of chromosomes. Ed. 2. 180 pp. George Allen and Unwin, Ltd., London, 1947.
11. ——— & K. Mather. The elements of genetics. 446 pp. Macmillan Co., New York, 1949.
12. De Vos, F. The stem anatomy of some species of the *Caprifoliaceae* with reference to phylogeny and identification of the species. 81 pp. Ph.D. thesis, Cornell University, 1951.
13. Dippel, L. Handbuch der Laubholzkunde Beschreibung der in Deutschland heimischen und im Freien kultivierten Baüme und Sträucher **1**: 172–200. 1889.
14. Egolf, D. R. Cytological and interspecific hybridization studies in the genus *Viburnum*. 131 pp. Ph.D. thesis, Cornell University, 1956.
15. Feng, Y. A. Observations sur la présence de centrosomes et d'asters présidant à la caryocinèse dans un genre de Caprifoliacées: *Lonicera*. Le Botaniste **26**: 3–20. 1934.
16. Fernald, M. L. Another century of additions to the flora of Virginia. Rhodora **43**: 635–657. 1941.
17. Goodspeed, T. H. The genus *Nicotiana*. 536 pp. Chronica Botanica Co., Waltham, Mass., 1954.
18. Janaki Ammal, E. K. Chromosomes and the species problem in the genus *Viburnum*. Curr. Sci. Bangalore **22**: 4–6. 1953.
19. Johansen, D. A. Plant microtechnique. 533 pp. McGraw-Hill Book Co., New York and London, 1940.
20. La Cour, L. Acetic-orcein a new stain fixative for chromosomes. Stain Tech. **16**: 169–174. 1941.
21. McAtee, W. L. A review of the nearctic *Viburnum*. 125 pp. Chapel Hill, North Carolina, 1956.
22. Meyer, J. R. Prefixing with paradichlorobenzene to facilitate chromosome study. Stain Tech. **20**: 121–125. 1945.
23. Nakai, T. Tentamen systematis *Caprifoliacearum* japonicarum (System-

atic treatment of *Caprifoliaceae* of Japan). Tokyo Imp. Univ. Jour. Coll. Sci. **42:** Art. 2, 139 pp. 1921.

24. ———. Classes, ordines, familiae, subfamiliae, tribus, genera nova quae attinent ad plantas Koreanas. Jour. Jap. Bot. **24:** 8–14. 1949.
25. NAVASHIN, M. The dislocation hypothesis of evolution of chromosomal numbers. Zeits. Ind. Abst. Ver. **63:** 224–231. 1932.
26. O'MARA, J. G. Cytogenetic studies on *Triticale*. I. A method for determining the effects of individual *Secale* chromosomes in *Triticum*. Genetics **25:** 401–408. 1940.
27. POUCQUES, M. L. DE. Etude caryologique de quelques *Viburnum*. Compt. Rend. Soc. Biol. Paris **141:** 183–185. 1946.
28. ———. Recherches caryologiques sur les Rubiales. Revue Gén. Bot. **56:** 5–27, 74–138, 172–188. 1949.
29. REHDER, A. New species, varieties and combinations from the herbarium and the collections of the Arnold Arboretum. Jour. Arnold Arb. **5:** 49–59. 1924.
30. ———. Manual of cultivated trees and shrubs. Ed. 2. 996 pp. Macmillan Co., New York, 1940.
31. ———. Bibliography of cultivated trees and shrubs. 825 pp. Arnold Arboretum, Harvard University, 1949.
32. SAX, K. & D. A. KRIBS. Chromosomes and phylogeny in Caprifoliaceae. Jour. Arnold Arb. **11:** 147–153. 1930.
33. SHARP, L. W. Introduction to cytology. Ed. 3. 567 pp. McGraw-Hill Book Co., New York and London, 1934.
34. SHERMAN, M. Karyotype evolution: a cytogenetic study of seven species and six interspecific hybrids of *Crepis*. Univ. of Calif. Publ. Bot. **18:** 369–408. 1946.
35. SIMONET, M., & C. MIEDZYRZECKI. Etude caryologique de quelques espèces arborescentes ou sarmenteuses d'ornement. Compt. Rend. Soc. Biol. Paris **111:** 969–973. 1932.
36. STEARN, W. T. × *Viburnum bodnantense*, Caprifoliaceae. Bot. Mag. **167:** *t. 113*. 1950.
37. STEBBINS, G. L., JR. Variation and evolution in plants. 643 pp. Columbia Univ. Press, New York, 1950.
38. SUGIURA, T. Studies on the chromosome numbers in higher plants with special reference to cytokinesis. I. Cytologia **7:** 544–595. 1936.
39. SVENSON, H. K. Plants of the southern United States. I. *Viburnum dentatum*. Rhodora **42:** 1–6. 1940.
40. THOMAS, J. L. The cytology of some cultivated species of *Viburnum*. Jour. Arnold Arb. **42:** 157–164. 1961.
41. TOBGY, H. A. A cytological study of *Crepis fuliginosa*, *Crepis neglecta* and their F_1 hybrid and its bearing on the mechanism of phylogenetic reduction in chromosome number. Jour. Genet. **45:** 67–111. 1943.
42. WHITE, M. J. D. Animal cytology and evolution. 454 pp. Cambridge Univ. Press, Cambridge, 1954.
43. WILKINSON, A. M. The floral anatomy and morphology of some species of *Cornus* and the Caprifoliaceae. 148 pp. Ph.D. thesis, Cornell University, 1945.
44. ———. Floral anatomy and morphology of some species of the genus *Viburnum* of the Caprifoliaceae. Am. Jour. Bot. **35:** 455–465. 1948.
45. ———. Floral anatomy and morphology of *Triosteum* and of the Caprifoliaceae in general. *Ibid.* **36:** 481–489. 1949.