Chromosome Numbers of *Rubus* Species at the National Clonal Germplasm Repository

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Abstract. The U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository (NCGR), Corvallis, Ore., maintains *Rubus* germplasm representing worldwide diversity of the genus. Chromosome numbers were counted for 201 plants representing 124 taxa (species and varieties). There are new reports for 42 taxa, confirmation for 72 previously reported, and 10 counts for plants unidentified to species. The basic chromosome number was seven, and ploidy levels ranged from 2x to 12x.

Rubus is a large genus with a worldwide distribution; species are found on all arable continents, from the lowland tropics to subarctic regions. The exact number of species is unknown because a worldwide taxonomic treatment of the genus has not been performed since that of Focke (1910, 1911, 1914). Since then, many new species have been described and several studies have been performed on local floras, clarifying species and synonyms (e.g., Davis et al., 1967, 1968a, 1968b, 1969a, 1969b, 1970; Edees and Newton, 1988; Grierson and Long, 1983; Kalkman, 1984, 1987; MacBride, 1938; Weber, 1972, 1981, 1986, 1988; Yü, 1985; Zandee and Kalkman, 1981). Estimates of the number of species range from 600 to 800. Disagreements by taxonomists about species, particularly in the subgenus *Rubus* in Europe and eastern North America, are common because of the prevalence of interspecific hybridizations, polyploidy, and various forms of apomixis, all of which blur species boundaries. Arriving at an exact number likely never will be possible; obviously, there is an enormous amount of genetic diversity throughout the genus.

Many species provide an important source of food from commercial production of raspberries and blackberries as well as from the abundant fruit picked from wild plants. Among the several hundred *Rubus* species, only a small fraction have been exploited in breeding programs.

The U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository (NCGR), Corvallis, Ore., has been assembling a collection of *Rubus* species, cultivars, and selections that greatly

expands the genetic diversity available for plant breeders and other scientists. As far as possible, seeds, propagules, or both are obtained directly from wild populations to ensure a more accurate species identity. However, some species have been obtained from botanical gardens, nurseries, and breeder collections. Plants from these secondary sources are more likely to be incorrectly identified. The current collection at the NCGR consists of only a fraction of the world's diversity.

There is an exceptionally wide range in chromosome numbers (2x to 14x) reported for *Rubus* species (Jennings, 1988; Nybom, 1980). Chromosome numbers are one aspect of germplasm characterization and as such can be helpful in verifying the plant identity. The numbers for cultivars and selections at the NCGR are reported separately (Thompson, 1995). My objective was to determine the chromosome number of one or more representatives of each species or variety growing at the NCGR.

Materials and Methods

Meristematic tissues used to obtain chromosome counts included shoot tips, root tips, and pollen mother cells (PMCs). Shoot tips on vigorous canes proved to be the most satisfactory. These rapidly growing meristems provided abundant mitotic metaphase figures throughout the growing season. In contrast, even when shoots were growing rapidly, root tips from pot-bound plants showed few cell divisions. PMCs provide reliable counts if the appropriate meiotic stages of late diakinesis, metaphase I, or metaphase II can be found. However, due to the varying flower bud sizes in the diverse germplasm, it is difficult to determine the correct stage of meiosis based on bud size. Furthermore, flower buds are available much less frequently than shoot tips. Samples were collected primarily from plants growing in screenhouses and less frequently from plants in a greenhouse or the field.

Detached shoot tips and root tips were placed immediately in cold water (2 to 4°C) and held overnight. To increase the frequency of

meristematic cells in the squash, meristems with only a few leaf primordia were dissected. Then, these were placed in Carnoy's solution (three parts 95% ethanol : one part glacial acetic acid) for 4 to 24 h. Finally, the killing-fixing solution was replaced with two changes of 70% ethanol before staining or storing tissues in a refrigerator. Flower buds were broken open to facilitate penetration of fluids, placed directly in the killing-fixing solution, and left for 20 to 24 h. This solution was replaced with two or three changes of 70% ethanol, and buds were stored in the refrigerator. All tissues were stained in alcoholic hydrochloric acid–carmin (Snow, 1963) at room temperature for 3 to 7 days and then rinsed in two or three changes of 70% ethanol. After the excess stain was rinsed out, tissues were squashed or stored again in 70% ethanol.

Before squashing, the shoot or root tips were hydrolyzed in 45% acetic acid at 60°C for 15 to 30 min to improve cell separation. Then, tissues were pulverized with a scalpel in a drop of acetic acid on a slide, and the coverslip was mounted with a small drop of Hoyer's medium (Anderson, 1954). Thumb pressure was applied on the coverslip to further separate cells, to flatten the metaphase plates, and to spread chromosomes. In some species with very high chromosome numbers, additional pressure applied directly above metaphase plates spread the chromosomes so that as many as 84 chromosomes could be counted accurately. For each accession, at least four counts of unambiguous chromosome configurations were made.

All plants at the NCGR are identified by a *Rubus* accession number for each plant for which counts were made and are presented Table 1.

Results and Discussion

Chromosome numbers are reported for 201 plants representing 114 *Rubus* taxa (species and varieties) and 10 unidentified accessions (Table 1). Of the identified taxa, 42 are new counts while the other 72 are confirmations of previous reports. In Table 1 and the subsequent discussion, species are presented according to their respective subgenera. The geographic origin, where known, is given for plants that were obtained from wild-growing populations of either natural or introduced species. Accessions from secondary sources were obtained from botanical gardens, arboreta, breeding programs, or nurseries, where plants were cultivated before being sent to the NCGR. For these plants, the geographic origin is often uncertain and errors in identity have been discovered. Labeling errors become increasingly probable as plants are successively propagated. Even when seeds are collected from a correctly labeled plant in a collection, they may actually have arisen from interspecific hybridization due to cross-pollination from nearby plants of other species. In the reference column of Table 1, only the first chromosome number report for a species is cited.

The following subgenera, with the number

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¹Collaborator.

Table 1. Chromosome numbers of *Rubus* species at the U.S. Dept. of Agriculture, Agricultural Research Service, National Clonal Germplasm Repository, Corvallis, Ore.

Species	NCGR inventory no.	Chromosome no.	Geographic origin	Secondary source ^z	References
<i>European and southwestern Asian blackberries</i>					
Subgenus <i>Rubus</i>					
<i>armeniacus</i> Focke	45.001	28	Caucasus, Russia	1	Gustafsson, 1943
<i>axillaris</i> Lej.	1195.001	28	Sweden	2	Gustafsson, 1939
<i>caesius</i> L.	28.001	28	Stavropol, Russia		Longley, 1924
	757.001	28	Uzbekistan		Longley, 1924
	757.002	28	Uzbekistan		Longley, 1924
	1776.001	28	Unknown		Longley, 1924
<i>canescens</i> DC.	36.001	14	Former Yugoslavia	1	Gustafsson, 1933
<i>caucasicus</i> Focke	54.001	28 ^y	Afghanistan	1	
	822.001	28 ^y	Unknown	3	
<i>cissburiensis</i> Barton & Riddelsd. hybrid	753.001	28 ^y	New Zealand (introd.) ^w		
<i>conothrysoides</i> H.E. Weber	1159.001	28 ^y	Germany		
<i>cyri</i> Juz.	823.001	28 ^y	Unknown	3	
<i>drejeri</i> G. Jensen ex Lange	55.001	28	Unknown	1	Gustafsson, 1939
<i>erythrops</i> Edees & A. Newton	756.001	28 ^y	New Zealand (introd.) ^w	4	
<i>georgicus</i> Focke	824.001	28 ^y	Unknown	3	
<i>glandulosus</i> Bellardi	1186.001	28	Sweden	2	Heslop-Harrison, 1953
<i>grabowski</i> Weihe ex Gunther et al.	33.001	28 ^y	Former Yugoslavia	1	
	48.001	28 ^y	Former Yugoslavia	1	
<i>hartmanii</i> Gand.	1187.001	28	Sweden	2	Gustafsson, 1943
<i>hirtus</i> Walldt. & Kit.	51.001	28	Former Yugoslavia	1	Gustafsson, 1933
	56.001	28	Former Yugoslavia	1	Gustafsson, 1933
<i>insularis</i> F. Aresch.	1188.001	28	Sweden	2	Gustafsson, 1933
<i>laciniatus</i> Willd.	1596.001	28	Australia (introd.) ^w		Crane and Darlington, 1927
<i>laciniatus</i> Willd. variant	413.001	28	Oregon (introd.) ^w		Crane and Darlington, 1927
<i>miszczenkoi</i> Juz.	825.001	28 ^y	Unknown	3	
<i>plicatus</i> Weihe & Nees	44.001	28	Unknown	1	Gustafsson, 1933
<i>pyramidalis</i> Kalt. hybrid	1193.001	28 ^y	Sweden	2	
<i>sanctus</i> Schreb.	482.001	14 ^y	Syria		
	483.001	14 ^y	Syria		
	484.001	14 ^y	Syria		
	813.001	14 ^y	Turkey	1	
	1053.001	14 ^y	Northern Pakistan		
	1054.001	14 ^y	Northern Pakistan		
<i>slesvicensis</i> Lange	1088.001	42 ^y	Unknown	1	
	1095.001	42 ^y	Unknown	1	
<i>ulmifolius</i> Schott	34.001	14	Former Yugoslavia	1	Crane and Darlington, 1927
	334.001	14	Ireland		Crane and Darlington, 1927
<i>ulmifolius</i> Schott inermis (Willd.) Focke	818.001	14	Oregon (introd.) ^w		
<i>wahlbergii</i> Arrh.	42.001	35	Unknown	1	Gustafsson, 1939
<i>North American blackberries</i>					
<i>canadensis</i> L.	785.001	14	North Carolina		Longley, 1924
	817.001	14	Georgia		Longley, 1924
	196.001	21	Unknown	1	Longley, 1924
<i>hispidus</i> L.	794.001	14	North Carolina		Aalders and Hall, 1966
<i>trivialis</i> Michx.	260.001	14	Georgia		Yarnell, 1936
	418.001	14	Texas		Yarnell, 1936
	419.001	14	Texas		Yarnell, 1936
	421.001	14	Texas		Yarnell, 1936
	434.001	14	Texas		Yarnell, 1936
	635.001	14	Louisiana		Yarnell, 1936
	832.001	14	Texas		Yarnell, 1936
<i>ursinus</i> Cham. & Schldtl.	30.001	84	Unknown	1	Darrow and Longley, 1933
	197.001	84	Oregon		Darrow and Longley, 1933
	611.001	84	Idaho		Darrow and Longley, 1933
	615.001	84	Washington		Darrow and Longley, 1933
	804.001	84	Northern California		Darrow and Longley, 1933
<i>South and Central American blackberries</i>					
<i>adenotrichos</i> Schldtl.	1250.001	14 ^y	Ecuador		
<i>robustus</i> C. Presl	1264.001	14 ^y	Ecuador		
	1273.001	14 ^y	Ecuador		
<i>urticifolius</i> Poir.	1288.001	14 ^y	Ecuador		
Subgenus <i>Idaeobatus</i> (Focke) Focke					
<i>cockburnianus</i> Hemsl.	1724.001	14	Unknown	5	Vaarama, 1954
<i>columellaris</i> Tutcher	1622.001	14	Guizhou, China		Thompson and Zhao, 1993
<i>corchorifolius</i> L. f.	1625.001	14	Guizhou, China		Iwatsubo and Naruhashi, 1993
	1628.001	14	Guizhou, China		Iwatsubo and Naruhashi, 1993
<i>coreanus</i> Miq.	1438.001	14	China	6	Longley and Darrow, 1924
<i>crataegifolius</i> Bunge	268.001	14	Unknown	7	Vaarama, 1954
<i>ellipticus</i> Sm.	1052.001	14	Northern Pakistan		Malik, 1965
<i>eustephanos</i> Focke ex Diels	1637.001	14 ^y	Guizhou, China		
	1637.002	14 ^y	Guizhou, China		
<i>flosculosus</i> Focke	424.001	14	China	8	Vaarama, 1954

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Table 1. Continued.

Species	NCGR inventory no.	Chromosome no.	Geographic origin	Secondary source ^z	References
<i>hawaiiensis</i> A. Gray	399.001	14	Hawaii		Keep, 1958
<i>hirsutus</i> Thunb.	8.001	14	Japan	1	Jinno, 1951a
	266.004	14	Unknown	7	Jinno, 1951a
<i>hoffmeisterianus</i> Kunth & Bouche	1061.001	14 ^y	Northern Pakistan		
<i>ideaus</i> L.	1235.001	14	Southern Kazakhstan		Longley and Darrow, 1924
<i>ikenoensis</i> Lev. & Vaniot	1421.001	14	Japan		Iwatsubo and Naruhashi, 1992
<i>illecebrosus</i> Focke	838.001	14	Unknown	8	Longley, 1924
<i>innominatus</i> S. Moore	1039.001	14	Jiangxi, China		Longley and Darrow, 1924
	1039.002	14	Jiangxi, China		Longley and Darrow, 1924
	1039.003	14	Jiangxi, China		Longley and Darrow, 1924
	1039.004	14	Jiangxi, China		Longley and Darrow, 1924
<i>lasiosstylus</i> Focke	425.001	14	China	8	Longley and Darrow, 1924
<i>lasiosstylus</i> Focke var. <i>hubeiensis</i> T.T.Yu et al.	426.001	14 ^y	Hubei, China	8	
<i>leucodermis</i> Douglas ex Torrey & A. Gray	14.001	14	Unknown	1	Darrow and Longley, 1933
	414.001	14	Oregon		Darrow and Longley, 1933
<i>mcvaughianus</i> Rzed. & Calderon	1490.001	14 ^y	Mexico	10	
<i>microphyllus</i> L.f. var. <i>subcrataegifolius</i> Lev. & Vaniot	158.001	14 ^y	Japan		
	1608.001	14 ^y	Unknown	11	
<i>minusculus</i> Lev. & Vaniot	161.001	14	Japan		Iwatsubo and Naruhashi, 1993
	161.003	14	Japan		Iwatsubo and Naruhashi, 1993
<i>muelleri</i> F.M. Bailey	762.001	28 ^y	Australia	9	
	763.001	28 ^y	Australia	9	
	763.002	28 ^y	Australia	9	
<i>niveus</i> Thunb.	269.001	14	India	12	Thomas, 1940
	1295.001	14	Ecuador (introd.) ^w		Thomas, 1940
	1599.001	14	New Guinea	8	Thomas, 1940
<i>occidentalis</i> L.	541.001	14	Arkansas		Longley, 1924
	641.001	14	Illinois		Longley, 1924
<i>palmatus</i> Thunb. ex Murray	2.001	14	Japan		Jinno, 1951b
<i>palmatus</i> Thunb. ex Murray var. <i>coptophyllus</i> (A. Gray) Kuntze	1610.001	14 ^y	Unknown	11	
<i>parvifolius</i> L.	5.001	14	Japan	1	Jinno, 1951a
	180.001	14	Taiwan		Jinno, 1951a
	1615.001	14	Unknown	11	Jinno, 1951a
<i>parvifolius</i> L. (4x clone)	53.001	28	Unknown	1	
<i>phoenicolasius</i> Maxim.	163.001	14	Japan		Longley and Darrow, 1924
	1612.001	14	Unknown	11	Longley and Darrow, 1924
<i>pinfaensis</i> Lev. & Vaniot	1665.001	14 ^y	Guizhou, China		
	1665.002	14 ^y	Guizhou, China		
<i>pungens</i> Cambess.	46.002	14	Unknown	1	Iwatsubo and Naruhashi, 1992
<i>rosifolius</i> Sm.	188.001	14	Java, Indonesia		Thompson and Zhao, 1993
<i>rosifolius</i> Sm. var. <i>coronarius</i> (Sims.) Focke	1604.001	14 ^y	Unknown	11	
<i>sachalinensis</i> Lev.	167.001	28	Honshu Island, Japan		Rozanova, 1939
	626.001	28	Jilin, China		Rozanova, 1939
<i>simplex</i> Focke	428.001	14	China	8	Vaarama, 1954
<i>spectabilis</i> Pursh	4.001	14	California	1	Darrow and Longley, 1933
<i>strigosus</i> Michx.	17.001	14	Unknown	1	Longley and Darrow, 1924
	18.001	14	Unknown	1	Longley and Darrow, 1924
	20.001	14	Unknown	1	Longley and Darrow, 1924
	157.001	14	Wyoming		Longley and Darrow, 1924
	182.001	14	Alaska		Longley and Darrow, 1924
	183.001	14	Alaska		Longley and Darrow, 1924
	211.001	14	Idaho		Longley and Darrow, 1924
	212.001	14	Idaho		Longley and Darrow, 1924
	214.001	14	Oregon		Longley and Darrow, 1924
	257.001	14	Idaho		Longley and Darrow, 1924
	591.001	14	Unknown	13	Longley and Darrow, 1924
	592.001	14	Unknown	13	Longley and Darrow, 1924
	607.001	14	Idaho		Longley and Darrow, 1924
	610.001	14	Idaho		Longley and Darrow, 1924
	613.001	14	Alberta, Canada		Longley and Darrow, 1924
	1103.001	14	Alaska		Longley and Darrow, 1924
	1137.001	14	Wyoming		Longley and Darrow, 1924
<i>sumatramus</i> Miq.	7.001	14	Japan	1	Iwatsubo and Naruhashi, 1992
<i>thibetanus</i> Franch. hybrid	264.001	14 ^y	Unknown	7	
<i>trianthus</i> Focke	1044.001	14	Jiangxi, China		Thompson and Zhao, 1993
<i>trifidus</i> Thunb. ex Murray	3.001	14	Japan	1	Jinno, 1951b
	1429.001	14	Japan		Jinno, 1951b
Subgenus <i>Anaplobatus</i> (Focke) Focke					
<i>deliciosus</i> Torr.	1021.001	14 ^y	Oklahoma		
<i>neomexicanus</i> A. Gray	58.001	14 ^y	Unknown	1	
	436.001	14 ^y	Arizona	14	
<i>odoratus</i> L.	11.001	14	Unknown	1	Longley, 1924
<i>parviflorus</i> Nutt.	13.001	14	Unknown	1	Darrow and Longley, 1933

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Table 1. Continued.

Species	NCGR inventory no.	Chromosome no.	Geographic origin	Secondary source ^z	References
Subgenus <i>Malachobatus</i> (Focke) Focke					
<i>assamensis</i> Focke	1701.002	28	Guizhou, China		Thompson and Zhao, 1993
<i>bambusarum</i> Focke	1602.001	28	Unknown	11	Keep, 1958
<i>buergeri</i> Miq.	1603.001	56	Unknown	11	Jinno, 1951a
<i>formosensis</i> Kuntze	174.001	28	Taiwan		Thompson and Zhao, 1993
<i>hayata-koidzumii</i> Naruh.	178.001	28	Taiwan		Thompson and Zhao, 1993
<i>henryi</i> Hemsl. & Kuntze	152.001	28	China		Keep, 1958
<i>hillii</i> F. Muell.	1199.001	42 ^y	Australia		
	1199.002	42 ^y	Australia		
	1199.012	42 ^y	Australia		
<i>hunanensis</i> Hand.-Mazz.	1715.001	28 ^y	Guizhou, China		
	1715.002	28 ^y	Guizhou, China		
<i>ichangensis</i> Hemsl. & Kuntze	1606.001	28	Unknown	11	Iwatsubo and Naruhashi, 1992
<i>irenaeus</i> Focke	1607.001	42	Unknown	11	Thompson and Zhao, 1993
	1697.001	42	Guizhou, China		Thompson and Zhao, 1993
	1697.002	42	Guizhou, China		Thompson and Zhao, 1993
<i>lambertianus</i> Ser.	181.001	28	Japan		Iwatsubo and Naruhashi, 1992
	1210.001	28	Japan	15	Iwatsubo and Naruhashi, 1992
<i>lambertianus</i> Ser. var. <i>glaber</i> Hemsl.	429.001	28 ^y	Hubei, China		
<i>multibracteatus</i> Lev. & Vaniot	1642.001	28	Guizhou, China		Thompson and Zhao, 1993
	1645.001	28	Guizhou, China		Thompson and Zhao, 1993
<i>setchuenensis</i> Bureau & Franch.	1613.001	28	Unknown	11	Thompson and Zhao, 1993
<i>setchuenensis</i> Bureau & Franch.	1695.001	28	Guizhou, China		Thompson and Zhao, 1993
<i>swinhoei</i> Hance	1671.001	28 ^y	Guizhou, China		
	1671.002	28 ^y	Guizhou, China		
<i>tephrodes</i> Hance	1041.001	28	Anhui, China		Vaarama, 1954
	1713.002	28	Guizhou, China		Vaarama, 1954
<i>tephrodes</i> Hance var. <i>ampliflorus</i> (Lev. & Vaniot) Hand.-Mazz.	1043.001	28 ^y	Jiangxi, China		
Subgenus <i>Cylactis</i> (Raf.) Focke					
<i>arcticus</i> L.	710.001	14	Finland		Vaarama, 1939
<i>arcticus</i> L. subsp. <i>x stellarcticus</i> G. Larsson	32.001	14 ^y	Sweden	1	
<i>lasiococcus</i> A. Gray	261.001	14 ^y	Oregon		
	1619.001	14 ^y	Oregon		
<i>nepalensis</i> (Hook. f.) Kuntze	1609.001	28 ^y	Uncertain	11	
<i>pedatus</i> Sm.	191.001	14	Washington		Taylor and Mulligan, 1968
<i>pubescens</i> Raf.	1094.001	14	Oregon	1	Vaarama, 1954
Subgenus <i>Dalibardastrum</i> (Focke) Yü & Lu					
<i>amphidasys</i> Focke ex Diels	1693.001	42	Guizhou, China		Thompson and Zhao, 1993
<i>tricolor</i> Focke	1614.001	28	Unknown	11	Keep, 1954
<i>tsangorum</i> Hand.-Mazz.	1674.001	28 ^y	Fujian/Hunan, China	6	
Subgenus <i>Orobatus</i> Focke					
<i>glabratus</i> Kunth	1251.001	42 ^y	Ecuador		
<i>nubigenus</i> Kunth	1257.001	42 ^y	Ecuador		
	1257.002	42 ^y	Ecuador		
<i>roseus</i> Poir.	1266.002	42 ^y	Ecuador		
Subgenus <i>Chamaebatus</i> (Focke) Focke					
<i>nivalis</i> Douglas ex Hook.	1374.001	14 ^y	Oregon		
<i>pectinellus</i> Maxim.	179.001	42	Taiwan		Jinno, 1951a
	1426.001	42	Honshu Island, Japan		Jinno, 1951a
Subgenus <i>Micranthobatus</i> (Fritsch.) Kalkman					
<i>cissoides</i> A. Cunn.	722.001	28 ^y	New Zealand		
<i>schmidelioides</i> A. Cunn.	741.001	28 ^y	New Zealand		
<i>squarrosus</i> Fritsch	739.001	28 ^y	New Zealand		
Natural inter-subgeneric hybrid					
<i>glaucus</i> Benth.	759.001	28	Ecuador	4	Williams et al., 1949
Undetermined species					
sp.	219.001	28	Scotland		
	248.001	28	England		
	328.001	28	Ireland		
	542.002	14	Missouri		
	580.001	28	Missouri		
	582.001	28	Missouri		
	1150.001	14	Pennsylvania		
	1151.001	35	Pennsylvania		
	1152.001	35	Pennsylvania		
	1675.001	14	Guizhou, China		

^zPlant material received from an intermediary source where plants were grown, rather than directly from the original geographic region where collected. 1 = Western Washington Research and Extension Center, Puyallup, Wash.; 2 = Fredrikssdal Botanical Gardens, Helsingborg, Sweden; 3 = Vavilov Institute, St. Petersburg, Russia; 4 = Riwaka Research Station, Crop Research Division, Motueka, New Zealand; 5 = Arnold Arboretum, Jamaica Plains, Mass.; 6 = Nanjing Botanical Garden, Nanjing, China; 7 = East Malling Research Station, Maidstone, Kent, England; 8 = Dept. of Botany and Plant Pathology, Oregon State Univ., Corvallis; 9 = Australian National Botanical Gardens, Sydney; 10 = Agriculture Canada Research Station, Vancouver, B.C.; 11 = Heronswood Nursery, Kingston, Wash.; 12 = U.S. Dept. of Agriculture Plant Introduction Station, Miami; 13 = Washington State Univ., Pullman, Wash.; 14 = Washington Park Arboretum, Seattle; and 15 = Toyama Univ., Toyama, Japan.

^yNew chromosome number report.

^wIntroduced to that country; originated elsewhere.

of species or varieties of each, were available for study: *Rubus* (34), *Idaeobatus* (41), *Anaplobatus* (4), *Malachobatus* (17), *Cylactis* (6), *Dalibardastrum* (3), *Orobatus* (3), *Chamaebatus* (2), and *Micranthobatus* (3). Plants were not available yet from the subgenera *Chamaemorus*, *Lampobatus*, and *Comaropsis*, each of which consists of very few species. Counts are given for 10 taxa as yet unidentified.

Subgenus *Rubus* (blackberries). In this study, the subgenus *Rubus* is discussed according to the geographic origin of the species. In the European–West Asian group, chromosomes were counted for 40 accessions representing 27 taxa. Chromosome numbers for species in the section *Rubus* include the previously reported diploids *R. canescens* and *R. ulmifolius*. The new report of $2x$ for *R. sanctus* might be expected because of its close relationship to *R. ulmifolius*. The other 19 species in the section *Rubus* are tetraploid. Species for which $4x$ is reported for the first time include *R. caucasicus*, *R. cissburiensis* hybrid, *R. conothrysoides*, *R. cyri*, *R. erythrops*, *R. georgicus*, *R. grabowski*, and *R. miszczekoi*. The count of $4x$ for *R. grabowski* is inconsistent with the $3x$ counts that have been reported for its proposed synonyms *R. thrysanthus* Focke and *R. thrysoideus* Wimm. Either *R. grabowski* is not synonymous with these species or the NCGR has a misidentified accession. Only two species were available in the section *Corylifolii*: *R. slesvicensis* ($6x$) is a new report, and *R. wahlbergii* ($5x$) was confirmed. The only species in the section *Caesii*, *R. caesius*, ($4x$) was confirmed.

The chromosome numbers that I report for the limited sampling of the abundant European species are consistent with Gustafsson's (1943) conclusion regarding the ploidy levels in the major *Rubus* sections. That is, the section *Rubus* (*Moriferi veri*) has predominantly tetraploids, with only two basic diploid species and a few triploids that are mainly associated with two form complexes, *R. nitidus* Weihe & Nees and *R. thyrsoideus* Wimm. (now collectively called *R. grabowski* Weihe ex Gunther et al.). Section *Corylifolii* consists of tetraploids but also a few pentaploid and hexaploid species.

At the NCGR collection, North American blackberries are represented by plants of only four species. The three species from eastern North America, *R. trivialis*, *R. hispidus*, and *R. canadensis*, have previously been reported to be diploids, counts which I confirmed. However, in *R. canadensis*, $3x$ forms also are found commonly, one of which is among the NCGR accessions. Aalders and Hall (1966) found *R. hispidus* to be $2x$, as reported in my study, whereas Longley (1924) reported $5x$ for this species; he may have had a misidentified plant, perhaps an interspecific hybrid.

The one species native to the Pacific states, *R. ursinus*, consists of a polyploid complex with $2n$ numbers of 42, 56, 63, 70, 77, and 84 (Brown, 1943). This species' range is throughout the western regions of California, Oregon, Washington, and Idaho, and British Columbia, Canada. In most of California, the pre-

dominant $2n$ number is 56, whereas 84 predominates from northern California through Oregon, Washington, and Idaho. The other chromosome numbers occur less frequently and mostly in the central California coastal region or in northern California, where 56- and 84-chromosome forms overlap. The NCGR accessions, all of which are $12x$, were collected from regions where this high number is expected: in northern California and Oregon, Idaho, and Washington.

South and Central American blackberry species are poorly represented at the NCGR, with only three species, all from Ecuador. To my knowledge, this paper is the first to report the chromosome numbers for *R. adenotrichos* ($2x$), *R. robustus* ($2x$), and *R. urticifolius* ($2x$). These counts are consistent with that of *R. bogotensis* ($2x$), the only other South American blackberry species that has a reported chromosome number (Dale and Ingram, 1981; Gustafsson, 1939). These four species are all included in Focke's (1910, 1911, 1914) section *Floribundi*. More plant collections are needed from South and Central America so that the extent of the primary diploid basic number in *Rubus* from this region can be determined.

Subgenus *Idaeobatus* (raspberries). Of the 41 accessions in this subgenus whose chromosomes were counted, all but three were diploids. New counts are reported for 10 taxa: *R. eustephanos* ($2x$), *R. hoffmeisterianus* ($2x$), *R. lasiostylus* var. *hubeiensis* ($2x$), *R. mcvaughianus* ($2x$), *R. microphyllus* var. *subcrataegifolius* ($2x$), *R. muelleri* ($4x$), *R. palmatus* var. *coptophyllus* ($2x$), *R. pinfaensis* ($2x$), *R. rosifolius* var. *coronarius* ($2x$), and a presumed hybrid of *R. thibetanus* ($2x$).

Polyploidy is not common in this subgenus. Of the 40 species counted, only two are tetraploid. Stanley and Ross (1983) reported that *R. muelleri* ($4x$) from Australia is a synonym of *R. fraxinifolius* Poir. However, A.R. Bean (personal communication) considers *R. muelleri* to be a separate species. The other $4x$ species, *R. sachalinensis*, which is widespread in Northeast Asia, was reported to have arisen through autotetraploidy from the wild *R. idaeus* (Rozanova, 1939). Two accessions of *R. sachalinensis* from East Asia (one from northern Japan and one from China) confirm the $4x$ count. The $2x$ count for the wild raspberry accession collected near Almaty, Kazakhstan, indicates that this plant is *R. idaeus*. Unless the two species overlap, *R. sachalinensis* may not extend to this region. Based on morphological traits, Rozanova (1939) reported that *R. strigosus* in western North America was more similar to *R. sachalinensis* in northeastern Asia than it was to *R. strigosus* in eastern North America. Hitchcock et al. (1961) perpetuated the concept that *sachalinensis* (albeit as a subspecies of *R. idaeus*) is one of the wild raspberry forms in northwestern North America. To help clarify this taxonomy, the chromosome number for 17 accessions of wild raspberry from the northwestern states, including Alaska, was determined; in all cases, these accessions were diploid. Therefore, based on cytological criteria only, all North Ameri-

can raspberries are designated *R. strigosus*, rather than the northwestern populations being included in *R. sachalinensis*. The third $4x$ *Idaeobatus* accession was an induced tetraploid *R. parvifolius* clone whose ploidy level was confirmed.

Subgenus *Anaplobatus*. This subgenus is represented by four species, all of which are diploid. To my knowledge, I am the first to report that *R. neomexicanus* is $2x$; I also confirm *R. odoratus* ($2x$) and *R. parviflorus* ($2x$). I found *R. deliciosus* to be $2x$, whereas Longley (1924) reported it as $3x$. Counts of more individuals in this species are necessary to determine if, indeed, $2x$ and $3x$ forms exist in wild populations. I suspect, however, that Longley (1924) may have had an aberrant individual $3x$ plant arising from an unreduced gamete or from interspecific hybridization.

Subgenus *Malachobatus*. Chromosome studies in the subgenus *Malachobatus* have been performed only recently (Naruhashi and Iwatsubo, 1993; Nybom, 1986; Thompson and Zhao, 1993), so that, currently, chromosome numbers are available for ≈ 37 species, all of which are polyploid ($4x$, $6x$, $8x$, and $14x$), with $4x$ being the predominant ploidy level. In my study, I report chromosome numbers of 17 taxa—only three of these are new counts: *R. humanensis* ($4x$), *R. swinhoei* ($4x$), and *R. hillii* ($6x$). Although Stanley and Ross (1983) consider *R. hillii* to be a synonym of *R. moluccanus* L., A.R. Bean (personal communication) and Kalkman (1984) prefer to keep *R. hillii* separate from the typical *R. moluccanus* var. *moluccanus*, which also is present in northern Australia. Nybom (1986) reported *R. moluccanus* from Indonesia, a close relative of *R. hillii*, to be $4x$. I made the counts of $6x$ for *R. hillii* on three plants grown from one seed lot received from northern Australia. These different counts for *R. hillii* and *R. moluccanus* support the concept of their being two separate species. *Rubus moluccanus* is an extremely variable species that may represent a species complex, including *R. hillii*, with varying chromosome numbers. I found two new counts for varieties of species whose numbers were previously reported [i.e., *R. lambertianus* var. *glaber* ($4x$) and *R. tephrodes* var. *ampliflorus* ($4x$)].

Subgenus *Cylactis*. Of the six taxa available in this subgenus, five are diploid and one (*R. nepalensis*) is tetraploid. I report new counts for *R. arcticus* subsp. *x stellarcticus* ($2x$), *R. lasiococcus* ($2x$), and *R. nepalensis* ($4x$) and confirm counts for previously established *R. arcticus* ($2x$), *R. pedatus* ($2x$), and *R. pubescens* ($2x$).

Subgenus *Dalibardastrum*. The three species for which counts were made are all polyploid. This paper is a new report for *R. tsangorum* ($4x$) and a confirmation of previous reports for *R. amphidasys* ($6x$) and *R. tricolor* ($4x$).

Subgenus *Orobatus*. All three species counted in this subgenus, *R. glabratus* ($6x$), *R. nubigenus* ($6x$), and *R. roseus* ($6x$), are hexaploid and represent new reports. This number is consistent with the only other published report for a species in this subgenus, *R.*

macrocarpus Benth. (6x) (Dale and Ingram, 1981).

Subgenus *Chamaebatus*. The two species available have different ploidy levels. To my knowledge, *R. nivalis* (2x) is newly reported in my study, whereas *R. pectinellus* (6x) was previously reported.

Subgenus *Micranthobatus*. This subgenus was originally published by Fritsch (1886) as a section that included a few *Rubus* species in New Zealand and Australia. Focke (1910, 1911, 1914) then placed these species in *Lampobatus*, a subgenus that included a small group of diverse, geographically scattered species. Kalkman (1987) considers that the New Zealand and Australian *Rubus* species, along with a few others, are distinct enough to warrant their separate subgenus (i.e., *Micranthobatus*). To my knowledge, this is the first report on the chromosome numbers of three species in this subgenus: *R. cissooides* (4x), *R. schmidelioides* (4x), and *R. squarrosus* (4x). The number is consistent with the only other report for this subgenus, *R. parvus* Buchanan (4x), by Beuzenberg and Hair (1983).

Natural intersubgeneric hybrid. The count presented here for *R. glaucus* (4x) confirms previous reports. Darrow (1952) first proposed that this species arose from an interspecific hybrid between the black raspberry and a diploid tropical blackberry, followed by chromosome doubling that created a fertile allopolyploid. Jennings (1978) provided further evidence for this hypothesis based on the nature of anthocyanin pigments in the fruit of *R. glaucus* and its putative parents. The relatively true breeding behavior when selfed further supports this concept (Darrow, 1952).

Undetermined species. Counts are given for 10 accessions that have not been identified to species yet. All but one were blackberries (subgenus *Rubus*) collected from wild populations in North America or in Great Britain. The other one, in the subgenus *Ideaobatus*, was collected in Guizhou Province, China. Chromosome numbers will assist in the eventual identification of these plants.

This list of chromosome numbers for 124 *Rubus* taxa represents only ~55% of the species currently held at the NCGR. Counts could not be made on the 97 other accessions that are stored as seeds only. Knowledge of the chromosome number is important for use of germplasm by breeders who want to make effective interspecific hybridizations and for taxonomic and evolutionary studies.

Plant materials are available to researchers on request, depending on the accession, either as seeds, cuttings, or in vitro cultures. An inventory list of available plants can be obtained from Kim Hummer, curator, National Clonal Germplasm Repository, 33447 Peoria Rd., Corvallis, OR 97333.

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