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CHROMOSOME NUMBERS OF HAWAIIAN FLOWERING PLANTS AND THE SIGNIFICANCE OF CYTOLOGY IN SELECTED TAXA¹

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ABSTRACT

Chromosome numbers are reported for 128 species of flowering plants indigenous or endemic to Hawaii, including first reports for 13 genera and 82 species. The special significance of reports for *Ilex*, *Tribulus*, *Keysseria*, *Pisonia*, *Boerhavia*, *Jacquemontia*, *Claoxylon*, *Lipochaeta*, *Railliardia*, and *Dubautia* are discussed. The cytological and morphological variation in *Railliardia* and *Dubautia* is considered and their treatment as congeners is advocated. The cytogeographic pattern in *Dubautia* and *Railliardia* and other factors suggest that the ancestral chromosome number of the Hawaiian tarweeds is $n = 14$. Their derivation from a western North American progenitor similar to *Adenothamnus* is considered plausible if not indeed likely.

CHROMOSOME NUMBERS have been reported for about 165 (11.4%) of Hawaii's 1,442 species of native flowering plants as enumerated by St. John (1973). The only extensive, general cytological survey of Hawaiian plants is that of Skottsberg (1955). Additional chromosome reports of Hawaiian taxa have resulted from concerted efforts in the genera *Bidens* (Gillett and Lim, 1970), *Pipterus* (Nicharat and Gillett, 1970), and *Wikstroemia* (Gupta and Gillett, 1969). Supplementary stray reports have been made mostly by mainland botanists interested in the Hawaiian representatives of their chosen taxonomic specialties. The most significant recent contribution is Gardner's study of *Lipochaeta* (1977).

The purpose of this paper is to present new data thus far accumulated in an ongoing cytological survey of the flowering plants of Hawaii. Intentional emphasis has been given to the Hawaiian tarweed genera *Dubautia* and *Railliardia*. The possible significance of chromosome numbers in these and certain other taxa is discussed below.

Chromosome numbers of 160 collections representing 128 species, 80 genera, and 50 families are presented herein. These include first reports for 82 species and 13 genera. This brings the total number of Hawaiian species cytologically determined to about 247 (17.1%).

All chromosome numbers reported here are gametic numbers determined by observation of meiotic configurations of microsporocytes.

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Floral buds for study were preserved and stored in modified Carnoy's fixative (6 chloroform:3 absolute ethanol:1 glacial acetic acid; v:v). Anthers were squashed in acetocarmine and slides were made permanent by addition of Hoyer's solution (cf. Beeks, 1955). Voucher specimens of taxa reported on here are deposited at HAW.

DISCUSSION—The counts of some of the species reported here (Table 1) are unique or otherwise distinctive enough to warrant their discussion in relation to other reports for the same or related taxa. For example, the counts for *Ilex anomala* ($n = 40$), *Tribulus cistoides* ($n = 18$), and *Keysseria maviensis* ($n = 27$) represent the highest polyploid levels known in these species. Likewise, the first count for *Pisonia* ($n = 68$, possibly an octoploid on base 17) reported here is the highest number recorded in the Nyctaginaceae. The second highest number in this family, $2n = 116$ (Thombre, 1959), reported for *Boerhavia diffusa* probably represents a nonaploid since $2n = 26$ has also been recorded for the species (Srivistava & Misra, 1966). The Hawaiian representatives of *Ilex* and *Boerhavia diffusa* ($n = 26$) are the only tetraploids known in these taxa. Likewise, Hawaiian material of *Tribulus cistoides* represents the only hexaploids known in that species. The only previous number recorded for *T. cistoides* is $n = 6$ (diploid) based on material from Mexico, Colombia and Jamaica (Porter, 1964, 1967). The only previous report for the genus *Keysseria* is based on *K. radicans* ($n = 18$) from New Guinea (Borgmann, 1964). The related genus *Lagenophora* has been reported to have $n = 9$ (Arano, 1965). Thus, it appears that *Keysseria maviensis* is a hexaploid and in this regard it is interesting to note that the Hawaiian material

TABLE 1. *Chromosome numbers of Hawaiian flowering plants*

Taxon	Gametic no.	Coll. no. ^a	Island:Locality
GRAMINEAE			
** <i>Dissochondrus biflorus</i> (Hbd.) Ktze. ex Hack.	18	C986	O:Waianae Kai
* <i>Eragrostis variabilis</i> (Gaud.) Hbd.	20	C852	O:Diamond Head
	20	C869	O:Waianae Mts., Makaleha
* <i>Panicum torridum</i> Gaud.	9	C875	O:Kaena Point
LILIACEAE			
<i>Dianella sandwicensis</i> H. & A.	Ca. 16	C11 Oct 75	O:Mt. Kaala, summit
MORACEAE			
<i>Streblus sandwicensis</i> (Deg.) St. John	14	S1141	O:Waianae Mts., Pahole
URTICACEAE			
<i>Boehmeria grandis</i> (H. & A.) Heller	14	S1166	O:Mt. Kaala, summit
<i>Urera kaalae</i> Wawra	13	S1188A	O:Waianae Mts., Pahole
SANTALACEAE			
** <i>Exocarpus gaudichaudii</i> A. DC.	10	C840	O:Waianae Mts., Pahole
* <i>Santalum ellipticum</i> Gaud.	20	S1185	O:Waianae Mts., rd. to Mauna Kapu
* <i>S. freycinetianum</i> Gaud.	20	C979	O:Waianae Mts., above Manini
* <i>S. paniculatum</i> H. & A.	20	S798	H:Pohakuloa
CHENOPODIACEAE			
* <i>Chenopodium oahuense</i> (Meyen) Aellen	18	C900	O:Bluffs above Kaena Point
NYCTAGINACEAE			
<i>Boerhavia diffusa</i> L.	26	C877	O:Kaena Point
** <i>Pisonia brunoniana</i> Endl.	68	C981	O:Waianae Kai
AIZOACEAE			
<i>Sesuvium portulacastrum</i> (L.) L.	Ca. 24	C902	H:Beach near Punaluu
CARYOPHYLLACEAE			
* <i>Silene hawaiiensis</i> Sherff	12	C920	H:HVNP, Kau Desert
MENISPERMACEAE			
* <i>Cocculus ferrandianus</i> Gaud.	39	C829	O:Waianae Mts., Mauna Kapu
LAURACEAE			
** <i>Cassytha filiformis</i> L.	24	R144	K:Polihale Beach
CAPPARACEAE			
* <i>Capparis sandwichiana</i> DC. var. <i>zoharyi</i> Deg. & Deg.	20	C933	O:Barbers Point
CRUCIFERAE			
* <i>Lepidium serra</i> Mann	16	R131	K:Nualolo Gulch
SAXIFRAGACEAE			
** <i>Broussaisia arguta</i> Gaud.	16	S1184	O:Waianae Mts., near Palikea
PITTOSPORACEAE			
* <i>Pittosporum glabrum</i> H. & A.	12	C858	O:Waianae Mts., Pahole
ROSACEAE			
* <i>Osteomeles anthyllidifolia</i> Lindl.	17	O1	O:Koolau Mts., Lanipo Trail
LEGUMINOSAE			
<i>Acacia koa</i> Gray	26	C939	K:Kokee St. Park
* <i>Cassia gaudichaudii</i> H. & A.	14	C984	O:Waianae Kai
<i>Erythrina sandwicensis</i> Deg.	21	S1162	O:Waianae Mts., Mt. Kaala Rd.
* <i>Mezoneuron kawaiense</i> (Mann) Hbd.	11	H5251	O:Waianae Mts., Makaleha
* <i>Sesbania tomentosa</i> H. & A.	12	C881	O:Kaena Point
<i>S. tomentosa</i> H. & A.	12	C	H:(Waimea Arboretum 745920)
<i>S. tomentosa</i> f. <i>arborea</i> Rock	12	Ch56	Mo:Kamiloloa Ridge
GERANIACEAE			
* <i>Geranium arboreum</i> Gray	Ca. 25	C906	M:Puu Nianiau
ZYGOPHYLLACEAE			
<i>Tribulus cistoides</i> L.	18	C885	O:Kaena Point
<i>T. cistoides</i> L.	18	C935	K:0.6 mi SE of Kekaha on Hwy 50

TABLE 1. *Continued*

Taxon	Gametic no.	Coll. no. ^a	Island:Locality
RUTACEAE			
** <i>Pelea elliptica</i> (Gray) Hbd.	18	S1145	O:Waianae Mts., Pahole
** <i>Platydesma cornuta</i> Hbd.	18	C859	O:Waianae Mts., Pahole
EUPHORBIACEAE			
* <i>Claoxylon sandwicense</i> Muell.-Arg.	22	S1189	O:Waianae Mts., Pahole
AQUIFOLIACEAE			
* <i>Ilex anomala</i> H. & A.	40	C873	H:2 mi SW of HVNP on Hwy 11
SAPINDACEAE			
* <i>Dodonaea eriocarpa</i> Sm.	14	C823	O:Waianae Mts., Mauna Kapu
RHAMNACEAE			
** <i>Gouania gagnei</i> St. John	23	C983	O:Waianae Mts., Kamaileunu
MALVACEAE			
<i>Abutilon incanum</i> (Link) Sweet	7	C	Mo:(Waimea Arboretum 75P250)
* <i>Gossypium sandwicense</i> Parl.	26	C884	O:Kaena Point
* <i>Hibiscadelphus distans</i> Bishop & Herbst	20	C	K:(Waimea Arboretum 74P245)
<i>H. hualalaiensis</i> Rock	20	C13 Mar 76	H:(cultivated plant, HVNP)
* <i>H. giffardianus</i> Rock	20	C13 Mar 76	H:(cultivated plant, HVNP)
<i>Sida</i> sp.	14	C	Mo:(Waimea Arboretum 75P249)
* <i>S. fallax</i> Walp.	14	C998	O:Kaena Point
* <i>S. meyeniana</i> Walp.	14	C	K:(Waimea Arboretum 75S655)
VIOLACEAE			
* <i>Viola trachelifolia</i> Gingins	40	C891	O:Waianae Mts., near Palikea
FLACOURTIACEAE			
* <i>Xylosma hawaiiense</i> Seem.	10	S1118	P:Waianae Mts., Pahole
THYMELAEACEAE			
<i>Wikstroemia recurva</i> (Hbd.) Skottsbo.	9	C839	O:Waianae Mts., Pahole
MYRTACEAE			
* <i>Eugenia sandwicensis</i> Gray	11	S1138	O:Waianae Mts., Pahole
<i>Metrosideros collina</i> (J. R. & G. Forst.) Gray ssp. <i>polymorpha</i> (Gaud.) Rock var. <i>fauriei</i> (Levl.) Rock	11	S2020	Mo:Kapuiki, Wailau
<i>Metrosideros collina</i> (J. R. & G. Forst.) Gray ssp. <i>polymorpha</i> (Gaud.) Rock var. <i>glaberrima</i> (Levl.) Rock	11	C867	O:Waianae Mts., Makaleha
	11	C874	H:2 mi SW HVNP on Hwy 11
* <i>M. tremuloides</i> (Heller) Knuth	11	G76	O:Koolau Mts., Manoa Cliffs
ARALIACEAE			
** <i>Munroidendron racemosum</i> (Forbes) Sherff	24	S19 Sep 76	K:Nonou Mts. (cultivated)
** <i>Tetraplasandra</i> cf. <i>meiandra</i> (Hbd.) Harms	24	S1203	O:Koolau Mts., Summit Trail
ERICACEAE			
<i>Vaccinium reticulatum</i> Sm.	12	S1157	H:Saddle Rd.
EPACRIDACEAE			
* <i>Styphelia tameiameia</i> (Cham.) F.Muell.	10	C872	H:Mauna Loa Strip Rd.
	10	S1156	H:Kilauea, Crater Rim Rd.
	10	Y11 Dec 76	O:Kahuku Military Reservation
PRIMULACEAE			
<i>Lysimachia hillebrandi</i> Hook f. ex Gray	36	R122	Mo:Makapupai Ridge
* <i>L. kalalauensis</i> Skottsbo.	36	C940	K:Kokee, near Kalalau Lookout
<i>L. mauritiana</i> Lam.	10	C6 Nov 76	M:6 mi E of Paia (cultivated)
PLUMBAGINACEAE			
<i>Plumbago zeylanica</i> L.	14	C899	O:Kaena Point, bluffs
LOGANIACEAE			
** <i>Labordia fagroidea</i> Gaud.	Ca. 40	C932	O:Mt. Kaala, summit
** <i>L. hirtella</i> Mann	Ca. 40	C808	M:Upper Waikamoi Stream

TABLE 1. *Continued*

Taxon	Gametic no.	Coll. no.*	Island:Locality
GENTIANACEAE			
* <i>Centaurium sebaeoides</i> (Griseb.) Druce	Ca. 22	S25 Apr 76	O:Kaena Point, bluffs
APOCYNACEAE			
* <i>Rauvolfia mauiensis</i> Sherff	22	S1228	M:4.5 mi E of Ulupalakua
CONVOLVULACEAE			
* <i>Bonomia menziesii</i> Gray	15	C866	O:Waianae Mts., Makaleha
* <i>Jacquemontia sandwicensis</i> Gray	10	C883	O:Kaena Point
* <i>J. sandwicensis</i> Gray	10	C907	K:Beach near Hanapepe
HYDROPHYLLACEAE			
<i>Nama sandwicensis</i> Gray	7	L6 May 76	M:Waiehu, sand dune
	7	S838	Mo:Moomomi sand dunes
BORAGINACEAE			
* <i>Heliotropium anomalum</i> H. & A. var. <i>argenteum</i> Gray	14	C879	O:Kaena Point
VERBENACEAE			
* <i>Vitex ovata</i> Thunb.	17	C876	O:Kaena Point
LABIATAE			
* <i>Phyllostegia</i> n. sp.	Ca. 33	S1130	H:Kilauea Forest Reserve
* <i>P. glabra</i> (Gaud.) Benth.	33	C861	O:Waianae Mts., Pahole
* <i>P. grandiflora</i> (Gaud.) Benth.	32	C836	O:Mt. Kaala, summit
* <i>Stenogyne</i> n. sp.	32	S1131	H:Kilauea Forest Reserve
* <i>S. crenata</i> Gray	32	S905	M:Haleakala 8,500 ft elev.
* <i>S. kaalae</i> Wawra	32	W559	O:Waianae Mts., rim above Makua
SOLANACEAE			
* <i>Lycium sandwicense</i> Gray	12	C896	O:Kaena Point
SCROPHULARIACEAE			
<i>Bacopa monniera</i> (L.) Wettst.	34	C904	H:beach near Punaluu
GESNERIACEAE			
* <i>Cyrtandra stapantha</i> St. John & Storey	17	Ga29 Nov 75	O:Koolau Mts., near Hauula
RUBIACEAE			
<i>Coprosma montana</i> Hbd.	22	C871	H:Mauna Loa Strip Rd.
CUCURBITACEAE			
* <i>Sicyos</i> n. sp.	12	C898	O:bluff above Kaena Point
* <i>S. microcarpus</i> Mann	12	C918	O:Waianae Mts., Makua Valley
LOBELIACEAE			
* <i>Clermontia kakeana</i> Walp.	14	S826	Mo:Kaluaaha
<i>C. oblongifolia</i> Gaud.	14	C888	O:Waianae Mts., Palikea
<i>Cyanea angustifolia</i> (Cham.) Hbd.	14	W13 Nov 76	O:Koolau Mts. Vic. Kawaiiki Str.
<i>Lobelia grayana</i> E. Wimm.	14	C806	M:Haleakala, Upper Waikamoi Str.
* <i>L. yuccoides</i> Hbd.	14	C889	O:Waianae Mts., near Palikea
** <i>Rollandia calycina</i> (Cham.) D. Don var. <i>kaalae</i> (Wawra) E. Wimm.	14	W1126	O:Waianae Mts., Puu Hapapa
** <i>Trematolobelia</i> n. sp.	14	Ob29 Aug 76	O:Koolau Mts., Waialae Nui
** <i>T. macrostachys</i> (H. & A.) Zahlbr.	14	C847	O:Koolau Mts., Poamoho Summit
GOODENIACEAE			
<i>Scaevola chamissoniana</i> Gaud. var. <i>bracteosa</i> Hbd.	8	S1100	M:Haleakala, Kaupo Gap
* <i>S. coriacea</i> Nutt.	8	C919	M:Waihee Point
* <i>S. gaudichaudi</i> H. & A.	8	C978	O:Waianae Mts., above Manini
<i>S. gaudichaudiana</i> Cham.	8	C814	O:Waianae Mts., near Palikea
* <i>S. glabra</i> H. & A.	16	Ob29 Aug 76	O:Koolau Mts., Waialae Nui
<i>S. procera</i> Hbd.	8	C911	K:Kokee, Awaawapuhi Trail
<i>S. taccada</i> (Gaertn.) Roxb. var. <i>sericea</i> (Vahl) St. John	8	C892	O:Kaena Point

TABLE 1. *Continued*

Taxon	Gametic no.	Coll. no. ^a	Island:Locality
COMPOSITAE			
* <i>Argyroxiphium kauense</i> (Rock & Neal) Deg. & Deg.	14	S1127	H:Kahuku Ranch
<i>A. sandwicense</i> DC.	14	C801	M:Haleakala Crater
* <i>Artemisa hillebrandii</i> Skottsb.	9	C897	O:Kaena Point
<i>A. mauiensis</i> (Gray) Skottsb.	9	Hi1202	M:Haleakala, Waipoi Gulch
* <i>Bidens cuneata</i> Sherff	36	C853	O:Diamond Head Summit
<i>Dubautia knudsenii</i> Hbd.	14	C946	K:Kokee, Awaawapuhi Trail
<i>D. laxa</i> H. & A.	14	C817	O:Waianae Mts., Palikea
	14	S1208	O:Koolau Mts., Summit Trail
	14	C845	O:Koolau Mts., Poamoho Trail
* <i>D. microcephala</i> Skottsb.	14	C915	K:Kokee, Kaluapuhi Trail
* <i>D. paleata</i> Gray	14	Ch76014	K:Alakai Swamp
* <i>D. plantaginea</i> Gaud.	14	C825	O:Waianae Mts., near Palikea
	14	S1171	O:Waianae Mts., Ekahanui Ridge
<i>Hesperomannia arbuscula</i> Hbd. ssp. <i>oahuensis</i> (Hbd.) Carlquist	10	C985	O:Waianae Kai
* <i>Keysseria maviensis</i> (Mann) Cabrera	27	Al2476	M:Puu Kukui
<i>Lipochaeta</i> cf. <i>acris</i> Sherff	26	R152	K:Kalalau Tr., Hanakapiai Beach
	26	R153	K:near Haena Dry Cave
<i>L. integrifolia</i> (Nutt.) Gray	15	C882	O:Kaena Point
	15	R107	Mo:Moomomi Beach
	15	R148	K:Haula Beach
	15	C964	M:Waihee Point
<i>L. lavarum</i> (Gaud.) DC.	15	H5784	L:Kaoha
	15	S1225	M:Haleakala, Lualailua Hills
<i>L. lobata</i> (Gaud.) DC. var. <i>albescens</i> Sherff	26	C851	O:Diamond Head
<i>L. lobata</i> (Gaud.) DC. var. <i>denticulata</i> (Wawra) Sherff	26	R114	O:Kaena Point
<i>L. lobata</i> (Gaud.) DC. var. <i>hastulatoides</i> Deg. & Sherff	26	C908	Mo:East Ohia Ridge
* <i>L. profusa</i> Sherff var. <i>robustior</i> Deg. & Sherff	26	C908	K:Kokee Rd.
<i>L. remyi</i> Gray	15	S863	O:Waianae Mts., Manini Gulch
<i>L. rockii</i> Sherff	26	C963	M:Haleakala, Lualailua Hills
	26	R118	Mo:Makakupaia Ridge
<i>L. succulenta</i> (H. & A.) DC.	26	R150,151	K:Kalalau Tr., Hanakapiai Beach
* <i>Raiiardia montana</i> Mann var. <i>longifolia</i> Sherff	13	Hi5020	M:Haleakala, Wai Anapanapa
* <i>R. arborea</i> Gray	13	C921	H:Manuna Kea, near Puu Laau
<i>R. ciliolata</i> DC.	13	C850	H:HVNP, Kilauea
	13	Hi27 Nov 75	H:Mauna Kea, E slope
* <i>R. latifolia</i> Gray	14	C941	K:Kokee, Mohihi Rd.
	14	C942	K:Kokee, Mohihi Rd.
	14	C943	K:Kokee, Mohihi Rd.
* <i>R. linearis</i>	13	C927	H:7 mi W of Pohakuloa Camp
<i>R. menziesii</i> Gray	13	C793	M:Haleakala Mt., summit
	13	C794	M:Haleakala, Puu Nianiau
	13	C967	M:Haleakala, Poli Poli St. Park
<i>R. molokaiensis</i> Hbd.	13	Ch24 Oct 76	Mo:near Waikolu Lookout
* <i>R. reticulata</i> Sherff	13	C795	M:Haleakala, Puu Nianiau
	13	C949	M:Haleakala, upper Waikamoi Str.
* <i>R. cf. rockii</i> Sherff	13	C969	M:Haleakala, Poli Poli St. Park
<i>R. scabra</i> DC.	14	C849	H:HVNP, Kilauea
	14	C905	H:5 mi W of Waiohinu
	14	J570	H:Puna District
	14	Hi1099	M:Haleakala, Paliku Gap
* <i>R. sherffiana</i> (Fosb.) Sherff	13	C837	O:Mt. Kaala Summit
	13	S1172	O:Waianae Mts., Ekahanui Ridge
	13	W561	O:Waianae Mts., rim above Makua
* <i>Tetramolopium filiforme</i> Sherff	9	H5333	O:Waianae Mts., Ohikilolo Ridge
<i>T. humile</i> (Gray) Hbd.	9	C800	M:Haleakala Crater
<i>Wilkesia gymnoxiphium</i> Gray	14	R157	K:Kokee, Awaawapuhi Trail

^a Collectors of cytological and voucher material are abbreviated as follows: A = J. M. Arakawa, C = G. D. Carr, Ch = W. P. Char, G = G. C. Gerrish, Ga = R. J. Gaber, H = D. R. Herbst, Hi = P. K. Higashino, J = J. D. Jacobi, L = C. H. Lamoureux, O = K. A. O'Malley, Ob = J. K. Obata, R = E. Rabakonandrianina, S = R. L. Stemmermann, W = F. R. Warshauer, and Y = L. K. Yoshida. Likewise, islands are abbreviated: H = Hawaii, K = Kauai, L = Lanai, M = Maui, Mo = Molokai, and O = Oahu. Numbers printed in boldface type differ from those previously reported for the taxa concerned. Previously unreported species are preceded by an asterisk (*); genera, by a double asterisk (**).

has nine large pairs of chromosomes and 18 smaller pairs.

Robertson (1974) treated *Jacquemontia sandwicensis* as a subspecies of *J. ovalifolia* (Choisy) Hallier f. However, St. John (1976) reaffirmed the status of *J. sandwicensis* as a Hawaiian endemic species on morphological grounds. Since *J. sandwicensis* has $n = 10$ (Table 1) and *J. ovalifolia* ssp. *obcordata* (Millspaugh) Robertson is reported to have $n = 9$ (Jones, 1968; as *J. subsalina*), Robertson's treatment is not supported by cytological evidence.

The report here for *Claoxyylon sandwicense* ($n = 22$) sharply contrasts with the only other report for the genus ($n = 54$; Mehra and Hans, 1969). At the very least the cytological evidence suggests that the subtribe Claoxylynae of the Euphorbiaceae may be unnatural, particularly since the morphological characters are none too conclusive (G. L. Webster, pers. comm.).

The interesting cytological situation in *Lipochaeta* has been discussed in some detail by Gardner (1977), who suggests that species of *Lipochaeta* with $n = 26$ may have been derived from Hawaiian diploids ($n = 15$) through tetraploidy and subsequent aneuploidy. It seems just as likely that the two groups of *Lipochaeta* in Hawaii are the products of two independent introductions of a *Wedelia*-like ancestor, one with $n = 15$ and the other with $n = 26$. This interpretation is enhanced by the lack of intermediate aneuploid chromosome numbers in *Lipochaeta* and by the impressive cytological variation known in the very widespread and closely related genus *Wedelia* ($n = 11, 12, 14, 15, 22, 23, 25, 26, 28, 29, \text{ and } 33$; Federov, 1974; Moore 1973, 1974). Biosystematic investigations of *Lipochaeta* in progress may eventually clarify this situation.

St. John (1973) treats *Railliardia* and *Dubautia* as distinct genera, but as such they are poorly marked. *Railliardia* tends to be xerophytic with relatively thick leaves and small surface area, but certain species occur in what must be regarded comparatively wet sites. In general contrast *Dubautia* often occurs in very wet areas and typically has broad, thin leaves. The receptacular bracts are generally not coalescent in *Dubautia*, but those of *D. knudsenii*, *D. raillardiioides* Hbd., and *D. magnifolia* Sherff are coalescent as is typical for *Railliardia* (cf. Carlquist, 1959). Chromosome numbers of $n = 13$ and $n = 14$ occur in *Railliardia*, but most of its species have $n = 13$, while all of those of *Dubautia* have $n = 14$ (Table 1). Previous reports for certain taxa appear to be in error (see Table 1) or perhaps, in one instance, based on hybrid material. Considering the overall patterns of morphological and cytological variation and the recurrence of partially fertile hybrids between

TABLE 2. Distribution of known cytotypes of *Railliardia* and *Dubautia* in the Hawaiian Islands

G.N. ¹	Biogeographic unit							
	KAUAI		OAHU		MAUI-MOLOKAI		HAWAII	
	N.S. ²	%	N.S.	%	N.S.	%	N.S.	%
14	6	100	2	67	4	40	2	29
13	0	0	1	33	6	60	5	71

¹ Gametic number.

² Number of species.

these two taxa (Carr, unpubl.), it seems more appropriate to regard them as congeners (cf. Keck, 1936) than as separate genera.

If one considers the geographical distribution of the species of *Railliardia* and *Dubautia* whose chromosome numbers are known (Table 1), a rather striking trend is apparent (Table 2). Only species with $n = 14$ are known from the island of Kauai, the northwesternmost and geologically oldest major island of the windward group (see Macdonald and Abbott, 1970 for a discussion of Hawaiian geology). The progressively younger islands to the southeast have concomitantly higher frequencies of species with $n = 13$. Of the cytologically investigated species on Hawaii, the southeasternmost and geologically youngest island in the Hawaiian archipelago, 71% have $n = 13$ and only 29% have $n = 14$. Furthermore, based on morphological and ecological considerations it can be predicted with near certainty that all of the cytologically unknown species on Hawaii and Maui have $n = 13$. On the other hand the same criteria leave little doubt that all of the cytologically unknown species on Kauai have $n = 14$. Thus there is virtually no chance that further investigation will significantly alter the trend seen in Table 2 and in fact the percentage of species with $n = 13$ in the Hawaii and Maui-Molokai biogeographic units undoubtedly will increase as more species become cytologically known. Given the cytogeographic pattern discussed above, one may logically conclude that $n = 14$ is the ancestral chromosome number in the Hawaiian tarweeds and that species with $n = 13$ have evolved comparatively recently from the product of an aneuploid reduction event. The ecological amplitude and morphology of *Railliardia scabra* ($n = 14$) make it a good candidate as the nearest living relative of the 13-paired species.

The fact that the widest ranging and most highly differentiated species have $n = 14$ while species with $n = 13$ tend to be poorly differentiated and highly restricted in distribution supports the contention that $n = 14$ is the ancestral chromosome number in this group. This conclusion is also consistent with data from cytogenetic

analyses of hybrids that will be presented elsewhere. Finally, it is consistent with the view that the Pacific Coast tarweed *Adenothamnus validus* (Brand.) Keck ($n = 14$; Solbrig et al., 1972) is a reasonable ecological, morphological, and cytological prototype for a putative ancestor of the Hawaiian tarweeds (Carlquist, 1970; Kyhos, pers. comm.; Moran, 1972).

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