

## Chromosome Counts from the Flora of the Juan Fernández Islands, Chile. III.<sup>1</sup>

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**ABSTRACT:** Thirty-four chromosome counts are reported from populations in 20 species from Masafuera in the Juan Fernández Islands, Chile. New species counts are in *Abrotanella crassipes* ( $2n = 18$ ), *Carpobrotus aequilaterus* ( $n = 9$ ), *Coprosma pyrifolia* ( $n = 22$ ), *Drimys confertifolia* ( $n = \text{ca. } 43$ ), *Euphrasia formosissima* ( $n = 44$ ), *Parietaria debilis* ( $n = 8$ ), and *Urtica fernandeziana* ( $n = \text{ca. } 11$ ). A new chromosomal level for *Hypochoeris glabra* ( $n = 12$ ) also is provided. The taxonomic implications of certain of these counts are discussed. These data help extend chromosomal information for endemic taxa of the archipelago as part of broad evolutionary studies on the origin of the vascular plants. This study again emphasizes the absence of aneuploid or euploid chromosomal alterations during speciation within the archipelago.

ONE OF THE MOST FASCINATING oceanic archipelagoes of the Pacific is the Juan Fernández Islands. These small islands lie 600 km west of continental Chile at 33° S latitude. Having never been connected to the mainland, the Juan Fernández archipelago has been the site of evolutionary diversification of a unique flora. Sixty-nine percent of the species and 18 percent of the genera of flowering plants are endemic (Skottsberg 1956), and there also exists one endemic family (Lactoridaceae).

To understand patterns and processes of evolution in the endemic flora of the Juan Fernández Islands, collaborative studies have been carried out in the botanical laboratories of Ohio State University and the University of Concepcion, Chile. One of the emphases of these studies has been the investigation of chromosome numbers to reveal the importance of chromosomal change (i.e., aneuploidy and euploidy) in the evolution of the endemic flora. Two surveys have already been published from material collected on expeditions in 1980 (Sanders et al. 1983) and in 1984

(Spooner et al. 1987). The present paper adds new data regarding the flora of the archipelago from material collected from the younger island, Masafuera, on our expedition in 1986.

### MATERIALS AND METHODS

Flower buds were collected in the field, preserved in modified Carnoy's fixative (4 chloroform: 3 absolute ethanol: 1 glacial acetic acid), transferred to 70% ethanol back in the laboratory, and stored under refrigeration. Slide preparations were made by squashing young florets and examining developing anthers for meiotic divisions in the pollen mother cells. Acetocarmine stain was used and preparations were made semipermanent with Hoyer's medium. One count (for *Abrotanella crassipes*) was obtained by a squash of cells undergoing mitotic divisions in the developing embryo after fertilization.

### RESULTS

Thirty-four new chromosome counts for taxa growing on Masafuera are listed in Table 1. First counts are reported for seven species: *Abrotanella crassipes* (Asteraceae), *Carpobrotus aequilaterus* (Aizoaceae), *Coprosma pyri-*

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TABLE 1  
CHROMOSOME NUMBERS OF TAXA FROM MASAFUERA, JUAN FERNÁNDEZ ISLANDS, CHILE

TAXON	MEIOTIC CHROMOSOME NUMBER <sup>a</sup>	VOUCHER <sup>b</sup>
Aizoaceae		
* <i>Carpobrotus aequilaterus</i> (Haw.) N.E. Br.	9	Quebrada Mono, <i>SL</i> 8329
Asteraceae		
* <i>Abrotanella crassipes</i> Skottsbo.	2n = 18 <sup>c</sup>	Los Inocentes, <i>A</i> 9350
<i>Erigeron rupicola</i> Phil.	27	Tierras Blancas, <i>SR</i> 8450
** <i>Hypochoeris glabra</i> L.	12	Cordon Atravesado, <i>SV</i> 9097
<i>H. radicata</i> L.	4	Quebrada Pasto, <i>SL</i> 8391; Quebrada Ovalo, <i>SG</i> 9002; Cordon Atravesado, <i>SV</i> 9098
<i>Lagenophora hariatii</i> Franch.	7II + 4I	Cordon Inocentes, <i>SP</i> 9553
Brassicaceae		
<i>Nasturtium officinale</i> R. Br.	16	Quebrada Varadero, <i>RA</i> 8280
Campanulaceae		
<i>Wahlenbergia masafuerae</i> (Phil.) Skottsbo.	11	Quebrada Casas, <i>RL</i> 8006; Quebrada Vacas, <i>RL</i> 8045; Quebrada Sandalo, <i>V</i> 8145; Quebrada Pasto, <i>SL</i> 8403; between Quebradas Vacas and Guaton, <i>SRL</i> 9317; Quebrada Mono, <i>G. Lopez s.n.</i>
Caryophyllaceae		
<i>Spergularia confertiflora</i> Steud.	36	Chorro de Florida, <i>V</i> 8127; Quebrada Casas, <i>SL</i> 8317; Quebrada Tongo, <i>SR</i> 8465
Ericaceae		
<i>Pernettya rigida</i> (Bert.) DC.	33	Quebrada Pasto, <i>AR</i> 9201
Myrtaceae		
<i>Myrceugenia schultzei</i> Johow	11	Plano de Sanchez, <i>RAV</i> 8281
<i>Myrteola nummularia</i> (Poit.) Berg	22	Cordon Inocentes, <i>SP</i> 9550
Piperaceae		
<i>Peperomia berteriana</i> Miq.	22II + 2I	Quebrada Casas, <i>RL</i> 8004
Rubiaceae		
* <i>Coprosma pyrifolia</i> (Hook. et Arn.) Skottsbo.	22	Quebrada Pasto, <i>A</i> 9387
<i>Nertera granadensis</i> (L. f.) Druce.	22	Cordon Inocentes, <i>SGP</i> 9529
Scrophulariaceae		
* <i>Euphrasia formosissima</i> Skottsbo.	44	Quebrada Guaton, <i>AG</i> 9105; between Quebradas Vacas and Guaton, <i>SRL</i> 9318; Cordon Inocentes, <i>AR</i> 9591
Urticaceae		
* <i>Parietaria debilis</i> Forst.	8	Quebrada Sanchez, <i>SL</i> 8380; Quebrada Casas, <i>SVAG</i> 9063
* <i>Urtica fernandeziana</i> (Rich.) Ross.	ca. 11	Cordon Atravesado, <i>SV</i> 9090
Verbenaceae		
<i>Rhaphithamnus venustus</i> (Phil.) Robins.	18	Quebrada Larga, <i>RAV</i> 8290
Winteraceae		
* <i>Drimys confertifolia</i> Phil.	ca. 43	Quebrada Ovalo, <i>SVAG</i> 9070; Quebrada Pasto, <i>SL</i> 9260; Cordon Inocentes, <i>SP</i> 9551

\* First report for the taxon.

\*\* New chromosome level for the taxon.

<sup>a</sup> Numbers represent bivalents except where noted otherwise.

<sup>b</sup> A = A. Landero, G = L. Gaete, L = T. Lammers, R = E. Ruiz, P = J. Sepulveda, S = T. Stuessy, and V = H. Valdebenito.

<sup>c</sup> From cells of the young embryo.

*folia* (Rubiaceae), *Drimys confertifolia* (Winteraceae), *Euphrasia formosissima* (Scrophulariaceae), *Parietaria debilis* (Urticaceae), and *Urtica fernandeziana* (Urticaceae). Twenty-two additional counts are for taxa reported previously, one of which is a new number.

#### DISCUSSION

Discussions are provided on some of the counts reported here, alphabetically by family, with focus on first reports for species. General statements on numbers of species counted within genera and their chromosomal data come from the standard chromosomal indices (Darlington and Wylie 1955, Cave 1958–1965, Ornduff 1967–1969, Fedorov 1969; Moore 1970–1977; Goldblatt 1981–1988).

**AIZOACEAE:** *Carpobrotus* N.E. Br., once included in *Mesembryanthemum* s.l., which is now divided into a hundred or more genera or sometimes even treated as a separate family, Mesembryanthemaceae (Herre 1971), is a genus with 24 species mainly distributed in South Africa, Australia, New Zealand, and Pacific regions (Shaw 1973). Only four species are known chromosomally and all are  $2n = 18$  (Vos 1947, Snoad 1951). Our new count of  $n = 9$  for *C. aequilaterus*, native to coastal sands of Chile from  $30^\circ$  to  $40^\circ$  S (Blake 1969) and apparently introduced to the islands, is consistent with other counts within the genus.

**ASTERACEAE:** *Abrotanella* Cass. is a genus of 14 species distributed in Australia, Tasmania, New Guinea, New Zealand, and the Falkland Islands. *Abrotanella crassipes* is endemic to the Juan Fernández Islands and is confined to the highest ridge (Los Inocentes) of the younger island, Masafuera. The relationships of the genus are still problematical. It has usually been placed in the Anthemideae (Heywood and Humphries 1977), but Robinson and Brettell (1973) suggested that it belongs in the Senecioneae based on microfeatures of the anthers and corollas. They favor a position with *Ischnea* (also placed by most workers in the Anthemideae) in the Senecioneae near *Crocidium*. Based upon pollen ultrastructural features, Skvarla and Turner (1966) re-

ferred *Crocidium* to the Senecioneae. Nordenstam (1977), however, believed that these genera are out of place geographically and morphologically in the Senecioneae. The basic chromosome number of the Anthemideae is  $x = 9$  with many numbers  $n = 9$  and  $n = 18$  (Heywood and Humphries 1977). Known chromosome numbers in *Ischnea* are  $2n = 18$  (Borgmann 1964), and  $n = 9$  in *Crocidium* (Ornduff et al. 1963, Spellenberg 1964, Schaack et al. 1974). Our first count of  $2n = 18$  for *Abrotanella crassipes* and the previous report of  $2n = 18$  for *A. emarginata* Cass., endemic to the Falkland Islands (Moore 1967), coincides with counts for related taxa whether one emphasizes placement in the Anthemideae or Senecioneae. *Abrotanella crassipes* is apparently related most closely to *A. mosleyi* Skotts. (Skottsberg 1922), but the latter species from Patagonia is still unknown chromosomally.

*Hypochoeris* L., with about 70–100 species mainly distributed in South America and Europe, is divided into two subgenera based on characteristics of the pappus (Burkart 1974, Gustav 1987). Subgenus *Hypochoeris* comprises only two species (*H. glabra* and *H. radicata*), which are native to Europe and have been introduced to South America, including the Juan Fernández Islands (Skottsberg 1922, Burkart 1974, Gustav 1987). Chromosomally, *H. glabra* has been consistently counted from 13 populations as  $n = 5$  except for three reports documenting two other levels ( $n = 4$ , Turner 1970;  $n = 6$ , Negodi 1935, Heiser and Whitaker 1948). The island populations of *H. glabra* (e.g., Solbrig 3693, SV 9097, AR 9256, A 9380) look very different from typical *H. glabra* in overall habit. They are much shorter (4–7 cm) than typical representatives (30–40 cm) and have fewer flowers per head. We have seen one specimen similar to the island form collected from the Province of Pichincha, Ecuador at 3600 m (Little & Paredes 6945, US). We regard these variations as ecological races of *H. glabra* rather than distinct species. However, our count of  $n = 12$  from a population located in Cordon Atravesado at 1200 m on Masafuera (SV 9097) is very unusual compared with previous reports, which have not yet revealed polyploidy. Parker (1975) reported frequent natural and artifi-

cial hybridizations between *H. glabra* and *H. radicata* and suggested possible gene flow between them. The voucher specimen of our count is clearly *H. glabra* and shows no tendency toward *H. radicata*. The meiotic chromosomes show clear bivalents, which also help exclude the possibility of hybrid origin for our material.

CAMPANULACEAE: *Wahlenbergia masafueriae* has been counted previously as  $n = ca. 11$  (Spooner et al. 1987). Our exact counts here from six populations all with  $n = 11$  confirm the previous report. The previous count came from a population located in Quebrada Casas (Pacheco & Ruiz 6408), and we have counted other individuals from this same locality (RL 8006). We have also now sampled three populations toward the northern part of the island (SL 8403, V 8145, and G. Lopez s.n.), as well as from the highest ridge (1050 m, S et al. 9317). This latter material is small in habit, and the vegetative parts are more hispid than other known collections. An even more striking morphological variant is confined to the dry coastal cliffs between Quebrada Casas and Quebrada Vacas at 3 m elevation. Here the plants have shorter internodes (2–3 mm), resulting in a more compact habit, and they are only weakly hispid. All of the sampled populations are now known as  $n = 11$ , which suggests that *W. masafueriae* contains considerable morphological variation and/or plasticity that is unrelated to change in chromosome number.

*Spergularia confertiflora* has been counted previously as  $n = 36$  from two populations on Masatierra (Sanders et al. 1983). Our three new counts also of  $n = 36$  are the first from populations on Masafuera and are consistent with previous reports for this species. The relationships of the species of the Juan Fernández Islands to those of mainland Chile are not yet clear. *Spergularia confertiflora* may be related to *S. remotiflora* Steud. (Skottsberg 1922), and *S. masafuerana* may be related to the cosmopolitan species *S. media* (L.) Presl. (Skottsberg 1953). Cytological study of *S. masafuerana* and mainland species would be helpful in this regard.

Two species of *Coprosma*, the only ones

known from the eastern side of the Pacific (Fosberg 1968), have been described as endemic to the Juan Fernández Islands (Skottsberg 1922): *C. pyrifolia* (H. & A.) Skottsberg and *C. oliveri* Fosberg [the earlier name of the latter, *C. hookeri* (G. Don) Oliver, was determined to be a later homonym of *C. hookeri* Stapf of Borneo by Fosberg (1968), who renamed it *C. oliveri*]. Our first chromosome count of  $n = 22$  for *C. pyrifolia* is consistent with most of the previous counts of this genus (36 of the 56 species have been counted as  $n = 22$ ). This probably represents the tetraploid level on an ancestral base of  $x = 11$  (Sanders et al. 1983). Skottsberg (1922) remarked that *C. pyrifolia* is most closely related to *C. laevigata* of Rarotonga, New Zealand, and *C. oliveri* (= *C. hookeri*) is closest to *C. foliosa* of Hawaii, and that the affinity between the two Juan Fernández island species is remote. Fosberg (1986), however, suggested that the two island species are not only the closest to each other, but also close to Polynesian species such as *C. cookei* Fosberg. Among the above-mentioned species, only *C. laevigata* is known chromosomally, and it is  $n = 22$  (Beuzenberg 1983). Considering the uniformity of chromosome numbers throughout the genus, it would not be surprising if all these close relatives were also  $n = 22$ .

SCROPHULARIACEAE: Of the 19 South American species of *Euphrasia* (Barker 1982), only one has been counted chromosomally, as  $n = 44$  from a population from the Falkland Islands (*E. antarctica* Benth.: Moore 1967). Our first count for *E. formosissima* of  $n = 44$  from three populations places this species also at the octoploid level within the genus, which appears to be based on  $x = 11$  (Barker et al. 1988). The relationship of *E. formosissima*, the only species of sect. *Paradoxae*, to the other groups is inconclusive. Although there has been some agreement of a remote tie to the South American species of sect. *Trifidae*, *E. formosissima* also has been suggested to be related to taxa of New Zealand (Du Rietz 1932, 1948) or even the northern hemisphere (Skottsberg 1922). In the most recent monograph, Barker (1982) speculated that sect. *Paradoxae* of the Juan Fernández Islands is

closely related to sect. *Novaezeelandiae*, a group of four small New Zealand annuals with unique acropetal patterns of branch development and pubescence of the anther slits. Among taxa of the southern Pacific region, Barker (1982) recognized four sections that appear to be very closely related: sect. *Paradoxae* of Juan Fernández, sect. *Trifidae* of South America, sect. *Novaezeelandiae* of New Zealand, and sect. *Anagosperrae* also of New Zealand. Among these, the two sections for which chromosomal information is now available, sect. *Trifidae* (*E. antarctica*,  $n = 44$ ) and sect. *Paradoxae* (*E. formosissima*,  $n = 44$ ), are both at the octoploid level. All other counts known in the genus are  $n = 11$  or  $n = 22$ , except for a recent report of seven Australian species showing hexa, deca, and dodecaploidy (Barker et al. 1988). The octoploid level, therefore, stands out as a distinctive chromosomal line within the genus. In this context, it is possible that the other Pacific sections, sect. *Novaezeelandiae* and sect. *Anagosperrae*, might also occur at this level.

URTICACEAE: *Parietaria*, with about 30 species mainly distributed in temperate regions (Skottsberg 1956) contains diverse chromosome numbers of  $n = 7, 8, 10$ , and 13. Our first count of  $n = 8$  for *P. debilis* is consistent with the above reports. Larsen (1963) speculated the base numbers of the genus to be  $x = 7$  and 13 (perhaps also  $x = 10$  for *P. arborea*). However, it is more likely that the base number is  $x = 7$  or 8, with  $n = 13$  already at the tetraploid level.

Our first count of  $n = \text{ca. } 11$  for *Urtica fernandeziana*, endemic to Masafuera, is consistent with previous reports of  $x = 11, 12$ , or 13 for the genus. Skottsberg (1956) stressed that this species is very distinctive morphologically and regarded it as an ancient type. This seems improbable because of the young geological age of Masafuera (1–2 m.y.).

VERBENACEAE: *Rhaphithamnus venustus* has been counted previously as  $n = \text{ca. } 18$  from a population on Masatierra (Sanders et al. 1983). Our first count from a population on Masafuera as  $n = 18$  confirms the previous report. The only other species in the genus, *R. spinosus* (Juss.) Moldenke from continental

Chile, is also known as  $n = \text{ca. } 18$  (Spooner et al. 1987). Sanders et al. (1983) suggested the basic number of the genus to be  $x = 19$ , based on  $n = 38$  from the closest genus, *Citharexylum* (*C. spinosum* L., Mehra 1976), but it seems more likely now that the base is  $x = 18$ . Sanders et al. (1983) suggested that the ancestral base for this entire group was probably  $x = 9$ , and our exact count of  $n = 18$  for *R. venustus* helps support this contention. The two species of *Rhaphithamnus*, therefore, would be at the tetraploid level. More chromosome counts of *Citharexylum* in mainland Chile would be helpful.

WINTERACEAE: *Drimys* has four species confined to Central and South America (Smith 1943). Two of them are already known chromosomally, as  $n = 43$  for *D. winteri* J. R. & Forst. (Raven and Kyhos 1965) and  $n = 43$  for *D. granadensis* var. *mexicana* (DC.) Sm. (Ehrendorfer et al. 1968). Our first count of  $n = \text{ca. } 43$  for *D. confertifolia* from three populations on Masafuera is consistent with previous reports for this genus. It also suggests that there has been no change in chromosome number during speciation of *D. confertifolia* from its closest relative on the continent, *D. winteri*. Raven and Kyhos (1965) speculated that the ancestral base of *Drimys* might be  $x = 7$ , and therefore *D. confertifolia* would be a dodecaploid. Raven and Kyhos (1965) suggested the base number of Winteraceae to be  $x = 43$ , but with the related genus *Tasmannia* R. Br. as  $x = 13$ , it would seem that *Drimys* is probably an aneuploid at least at the hexaploid level.

Once again the chromosomal data suggest that few aneuploid or euploid changes have occurred during speciation in the vascular plants of the Juan Fernández Islands. Examination of 35% of the endemic species shows no aneuploid nor allopolyploid evolutionary relationships. This situation appears similar to the results from Hawaii obtained by Carr (1978, 1985) and for the Bonin Islands by Ono (in press). The reason for this tendency toward chromosomal conservatism in oceanic settings may be related to the disruptive nature of such chromosomal alterations in upsetting adaptive character complexes that

are essential for survival in the microhabitats in the islands. For adaptive radiation to proceed along lines of strong directional selection, such drastic alterations may lead to ill-adapted progeny.

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