Chromosome Counts from the Flora of the Juan Fernández Islands, Chile. III.¹

BYUNG YUN SUN,² TOD F. STUESSY,³ and DANIEL J. CRAWFORD³

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 = ca. 43), *Euphrasia formosissima* (n = 44), *Parietaria debilis* (n = 8), and *Urtica fernandeziana* (n = 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-
<table>
<thead>
<tr>
<th>TAXON</th>
<th>MEIOTIC CHROMOSOME NUMBER&lt;sup&gt;a&lt;/sup&gt;</th>
<th>VOUCHER&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aizoaceae</td>
<td></td>
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</tr>
<tr>
<td><em>Carpobrotus aequilaterus</em> (Haw.) N.E. Br.</td>
<td>9</td>
<td>Quebrada Mono, SL 8329</td>
</tr>
<tr>
<td><em>Abrotanella crassipes</em> Skottsb.</td>
<td>2n = 18&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Los Inocentes, A 9350</td>
</tr>
<tr>
<td>Erigeron rupicola Phil.</td>
<td>27</td>
<td>Tierras Blancas, SR 8450</td>
</tr>
<tr>
<td><strong>Hypochoeris glabra</strong> L.</td>
<td>12</td>
<td>Cordon Atravesado, SV 9097</td>
</tr>
<tr>
<td><em>H. radicata</em> L.</td>
<td>4</td>
<td>Quebrada Pasto, SL 8391; Quebrada Ovalo, SG 9002; Cordon Atravesado, SV 9098</td>
</tr>
<tr>
<td>Lagenophora hariotii Franch.</td>
<td>7II + 4I</td>
<td>Cordon Inocentes, SP 9553</td>
</tr>
<tr>
<td>Brassicaceae</td>
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<td></td>
</tr>
<tr>
<td>Nasturtium officinale R. Br.</td>
<td>16</td>
<td>Quebrada Varadero, RA 8280</td>
</tr>
<tr>
<td>Campanulaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wahlenbergia masafuerae (Phil.) Skottsb.</td>
<td>11</td>
<td>Quebrada Casas, RL 8006; Quebrada Vacas, RL 8045; Quebrada Sandalo, V 8145; Quebrada Pasto, SL 8403; between Quebradas Vacas and Guaton, SRL 9317; Quebrada Mono, G. Lopez s.n.</td>
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<tr>
<td>Caryophyllaceae</td>
<td></td>
<td></td>
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<tr>
<td>Spergularia confertiflora Steud.</td>
<td>36</td>
<td>Chorro de Florida, V 8127; Quebrada Casas, SL 8317; Quebrada Tongo, SR 8465</td>
</tr>
<tr>
<td>Ericaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pernettya rigida (Bert.) DC.</td>
<td>33</td>
<td>Quebrada Pasto, AR 9201</td>
</tr>
<tr>
<td>Myrtaceae</td>
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<td></td>
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<tr>
<td>Myrceugenia schultzei Johow</td>
<td>11</td>
<td>Plano de Sanchez, RAV 8281</td>
</tr>
<tr>
<td>Myrteola nummularia (Poit.) Berg</td>
<td>22</td>
<td>Cordon Inocentes, SP 9550</td>
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<tr>
<td>Piiperaceae</td>
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<td></td>
</tr>
<tr>
<td>Peperomia berteroana Miq.</td>
<td>22II + 21</td>
<td>Quebrada Casas, RL 8004</td>
</tr>
<tr>
<td>Rubiaceae</td>
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<td></td>
</tr>
<tr>
<td><em>Coprosma pyrifolia</em> (Hook. et Arn.) Skottsb.</td>
<td>22</td>
<td>Quebrada Pasto, A 9387</td>
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<td>Nertera granadensis (L. f.) Druce.</td>
<td>22</td>
<td>Cordon Inocentes, SGP 9529</td>
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<td>Scrophulariaceae</td>
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<td></td>
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<tr>
<td><em>Euphrasia formosissima</em> Skottsb.</td>
<td>44</td>
<td>Quebrada Guaton, AG 9105; between Quebradas Vacas and Guaton, SRL 9318; Cordon Inocentes, AR 9591</td>
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<td>Urticaceae</td>
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<tr>
<td><em>Parietaria debilis</em> Forst.</td>
<td>8</td>
<td>Quebrada Sanchez, SL 8380; Quebrada Casas, SVAG 9063</td>
</tr>
<tr>
<td><em>Urtica fernandeziana</em> (Rich.) Ross.</td>
<td>ca. 11</td>
<td>Cordon Atravesado, SV 9090</td>
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<td>Verbenaceae</td>
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<td>Rhaphithamnus venustus (Phil.) Robins.</td>
<td>18</td>
<td>Quebrada Larga, RAV 8290</td>
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<tr>
<td>Winteraceae</td>
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<td></td>
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<tr>
<td><em>Drimys confertifolia</em> Phil.</td>
<td>ca. 43</td>
<td>Quebrada Ovalo, SVAG 9070; Quebrada Pasto, SL 9260; Cordon Inocentes, SP 9551</td>
</tr>
</tbody>
</table>

<sup>a</sup> First report for the taxon.

<sup>b</sup> New chromosome level for the taxon.

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

<sup>d</sup> From cells of the young embryo.
folia (Rubiaceae), Drimys confertifolia (Winteraceae), Euphrasia formossissima (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**


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° to 40° 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) referred *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 Ataviesado 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 masafuerana_ has been counted previously as _n_ = ca. 11 (Snooper 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. masafuerana_ 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.) Skottsb. 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. _Paradoxa_, 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. _Paradoxa_ 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. *Anagospermae* 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. *Anagospermae*, might also occur at this level.

**URTIACEAE:** *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 = 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:** *Rhaphithamus venustus* has been counted previously as n = 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 = 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 *Rhaphithamus*, 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 = 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 alloplloid 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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