

Systematics of *Libertia* (Iridaceae)

Spencer McIntyre, 16301056

Prof. John Parnell: MSc. Biodiversity and Conservation

BD7053: Desk Studies

31st Jan. 2017

6560 Words, excluding abstract, table of contents, acknowledgements, and literature cited

Signature: _____

Date: _____

I have read and I understand the plagiarism provisions in the General Regulations of the University Calendar for the current year, found at <http://www.tcd.ie/calendar>.

I have also completed the Online Tutorial on avoiding plagiarism 'Ready Steady Write', located at <http://tcd-ie.libguides.com/plagiarism/ready-steady-write>.

Abstract

Keywords: Iridaceae, *Libertia*, systematics, polyploidy, biogeography, bicentric distribution

Libertia Spreng. is a genus of monocotyledonous perennial herbs of bicentric distribution, from Australasia and South America. It contains sixteen species, with seven found in South America, seven endemic to New Zealand, one endemic to Australia, and one found in New Zealand, Tasmania, Australia, and New Guinea. Two species, *L. flaccidifolia* Blanchon and Weaver and *L. cranwelliae* Blanchon, Murray, and Braggins, are listed as Nationally Critical in New Zealand and *L. peregrinans* Cockayne and Allan is listed as Nationally Vulnerable. No South American species has been assessed for conservation status. The genus is best defined by its uniform $n=19$ chromosome count cytologically and 6 paired tepals morphologically.

Polyploidy and hybridization have played a critical role in the development of *Libertia* as a genus. Polyploidy is extremely common in perennial herbs, particularly the tribe Sisyrinchiae. In *Libertia*, only two of the eleven studied species are diploid, the remaining nine ranging from tetraploid to dodecaploid. The higher levels of polyploidy are particularly common in New Zealand, with all seven endemics being either hexaploid or dodecaploid. These levels of polyploidy are suggestive of a historic retreat into mountains during New Zealand's glacial periods, as polyploids are more productive and reproductively successful than diploids in high altitudes.

The bicentric distribution of *Libertia* and genera of similar distributions has been explained through three hypotheses, that of an Antarctic expansion, a Gondwanan distribution, or long range, random dispersal. In the case of *Libertia*, the Antarctic expansion is considered the most likely hypothesis. Evidence of a united flora between South America, Australasia, and Antarctica suggests these three regions were in contact more recently than the breakup of Gondwanaland, further reinforced by the evidence of Antarctic expansion and glaciation in New Zealand. The Gondwanan distribution is not a possibility in *Libertia* due to its phylogenetic age as a genus, as it would require a recombination event after the split of Gondwanaland, combined with extinction in Africa. Long range dispersal cannot be ruled out as a possibility, but due to the relatively large numbers and non-random distribution of bicentric genera, is unlikely.

Further study should include a phylogenetic study of *Libertia*, necessary to establish clades and relations intragenerically. Future research in *Libertia* should put a focus on South American studies, in particular the identification of clades within *L. chilensis* (Molina) Gunckel and the confirmation of chromosome count within the Juan Fernandez Islands group of *L. chilensis*. Establishment of a united and publicly available species description for the South American species is necessary as well.

Table of Contents

I. Background	4
II. Key and Characters	4
III. Taxonomy and Characters	7
a. Family Iridaceae	7
b. Subfamily Iridoideae	8
c. Tribe Sisyrinchieae	8
d. Genus <i>Libertia</i>	8
e. Species	9
IV. Polyploidy	15
a. Within Tribe Sisyrinchieae	15
b. Within Genus <i>Libertia</i>	16
c. Hybridization	18
V. Biogeography	18
a. Antarctic Expansion Hypothesis	19
b. Alternative Hypotheses	20
VI. Further Study	20
Literature Cited	22

Table of Figures

Fig 1. Phylogeny of Iridoideae, including tribes	8
Fig 2. Immature/mature seed capsules of <i>L. flaccidifolia</i> and <i>L. ixioides</i>	11
Fig 3. Seed of <i>L. ixioides</i>	13
Fig 4. Chromosomes of <i>L. ixioides</i> in Prometaphase I	16
Table 1. Cytology of genera from tribe Sisyrinchieae	16
Table 2. Cytology of species from genus <i>Libertia</i>	18

I. Background

Libertia Spreng. (Iridaceae) is a genus of perennial monocots, first named in 1824 by K.P.J. Sprengel, with the type species *L. ixioides* Spreng. It is a member of the tribe Sisyrinchieae under subfamily Iridoideae. *Libertia* has a bicentric distribution across Australasia, New Zealand, and southern South America. While no species within the genus are internationally regarded as threatened (IUCN, 2016), New Zealand listed *L. flaccidifolia* Blanchon and Weaver as Nationally Critical upon naming in 2009, due to its restricted range, furthered by herbivory of wild goats (NZPCN, 2017). *L. peregrinans* Cockayne and Allan was listed as Nationally Vulnerable in 2009 due to a decline in population and range, first documented in 2004. This has been attributed to urban development and the encroaching herbivory of farm animals. *L. cranwelliae* Blanchon, Murray, and Braggins was rediscovered in the wild in 2006, having been previously believed to be extinct in the wild and was listed in 2009 as Nationally Critical. South American species have not been studied to as large an extent as New Zealand species, though if studied, *L. falcata* Ravenna and *L. tricocca* Phil. would likely be listed as threatened due to limited ranges (Gardner *et al.*, 2006; Shaw, 2015).

II. Key and Characters

Key assembled using characters as described by Bentham, 1873; Cockayne and Allan, 1927; Hair *et al.*, 1967; Moore, 1967; Moore and Edgar, 1970; Smith, 1975; Rudall, 1984; Innes, 1985; Goldblatt *et al.*, 1989; Goldblatt, 1990; Harden, 1990; Curtis and Morris, 1984; Goldblatt and Takei, 1997; Huxley and Griffiths, 1999; Blanchon *et al.*, 2000; Bernadello *et al.*, 2001; Reeves *et al.*, 2001; Blanchon *et al.*, 2002; Tillich, 2003; Goldblatt and Celis, 2005; Gardner *et al.*, 2006; Goldblatt *et al.*, 2008; Blanchon and Weaver, 2009; Butler, 2016. Herbarium specimens from TCD Herbarium and online images from the Kew Royal Botanic Gardens, Auckland Museum, Harvard University, and Smithsonian Institute herbaria. Living specimens from the collection of the Dublin Zoo. Due to insufficient descriptions within the genus, *L. falcata* and *L. insignis* are excluded from the key.

a. Characters and States

Fans describe the tendency of leaves to form groups in some species of *Libertia*, described as being closely bunched, far spreading, or emerging from rhizomes or stolons. Closely bunched fans resemble a rose petal, fitting together with overlaps in a circular shape, where far spreading resemble a palm. This is a poor character as it is not definitive and has tremendous variation within a species

Leaves are described in terms of size, color, margins, veins, coating, rigidity, and shape. Size is related in terms of length and width from an objective value, as well as the presence of reduced leaves at the stem or attached to the scape. Colors center around green, with variation towards yellow or blue and expresses the tendency of some species to change to a copper or bright yellow color in sunlight. Margins are defined in terms of their difference

from the center of the leaf, being thick or thin, scabrid, or a difference in color. Veins are described as being few, crowded, or thick. Coating describes the thin layer on one or both sides of a leaf, present in some species, usually pale and cloudy. Rigidity is described as rigid, erect, half-erect, or flaccid, with rigid being difficult to bend and flaccid, as in the case of *L. flaccidifolia*, fully drooping to the ground. Shape is described as falcate, linear, or ensiform. These characters are good for field examination, but due to the large amounts of overlap and individual variation, can only be a contributing factor. Coatings and extremes of rigidity can be used as defining characters.

The *scape* is defined in terms of both objective and subjective size. The objective size refers to generally the length of the scape, as well as the diameter. Subjective size refers to the comparison between leaf length and scape length, usually in terms of $>$, $=$, $<$. This is a strong character in eliminating possible species, but is not defining.

Peduncles are described in terms of objective length, length relative to the total of the inflorescence, and whether they carry flowers directly. This is a very poor character due to tremendous intraspecific variation.

Panicles are described in terms of branching, shape, and color. The branching patterns are laxly, sparsely, or closely branched. Shapes are described as narrow, broad, or lanceolate. Colors are a range of variation on green, including orange-green. This is a very poor character due to the large amount of overlap in states between species.

Pedicels are described in terms of length, shape, rigidity, and the presence of rhipidium. Shapes include stout, slender, and conical. Rigidity refers to pedicels being either erect or flaccid, with flaccid having a visible bend under its own weight. This is a good character and can be used as a defining character in its extremes, but has a fair amount of state overlap between many species.

The *bud* is described in terms of color, diameter, and shape. Colors are generally a variant of white to off-white, including pale yellow and tinges of green, yellow, or brown. The unique blue bud of *L. sessiliflora* is a defining character. Shapes include patent and cupiform. This is an excellent character in the singular case of *L. sessiliflora* and has little use for other species, due to the similarity of states.

Sepals and *petals* are described by shape, position, texture, color, and size. Shapes include obovate, oblong, elliptical, narrow, broad, orbicular, ovate, and lanceolate. Positioning refers to the overlapping or absence of overlapping of sepals and tepals. Structure is described as being thin, thick, semi-rigid, many veined, and sparsely veined. Colors center around white, with variants including tinges of red, green, brown, pink, and yellow. Size is both objective and subjective in comparison with between the sepals and petals. This subjective size is a useful character, but the remaining features do not vary interspecifically to a useful extent.

Anthers are described in terms of color and length. Colors center around yellow, but have a useful range of variation, while in living specimens, ranging from pale yellow to dark orange. Lengths tend to have little intraspecific variation and while interspecifically the states are similar, the spectrum of anther lengths allows for use of this character.

Ovaries are described in terms of color and shape. Colors have little variation and center around green, with variation to yellow-green or dark green. Shapes are more varied and each fairly unique to the species, including cupiform, globose, smooth (weakly furrowed), trigonous, flat, obovoid, and tapered making up the states. The shapes of ovaries form an excellent contributing character, but are not truly defining.

Style branches are described in terms of length, wings, and positioning. Wings can be present or absent and positioning can be described as either upwards or outwards. This character is capable of separating two species, but due to the broad similarities of states between many species, is not a useful or defining character in most cases.

Capsules are described by diameter, shape, color, dehiscence, valves, and seed count. Shapes include barrel, globose, teardrop, pyriform, oblong, trigonous, and elliptical. Colors vary widely, including brown, black, yellow, green, red, and orange with mixes in between. Capsules in some species also will change colors to black as they mature. Dehiscence describes the opening of capsules by loculicidal clefts or remaining closed until opened by an outside force. Valve shapes are described as recurved, keeled, or not patent. This forms an excellent character, as each capsule is unique and easily differentiated interspecifically in terms of shape and color. Seed counts are also unique to the species, but due to the variation within a species and often within the same individual, must be paired with the outside states of the capsule.

Seeds are described in terms of color, shape, texture, and diameter. Colors vary widely, including yellow, brown, orange, and red, with mixes in between. Shapes include globose, subglobose, and angular. Textures include smooth, reticulate, and foveolate. While this is a strong contributing character with good interspecific variation, it is difficult to observe in situ and thus is limited in use.

b. Dichotomous Key

1. Roots suckering and plant expands horizontally_____ *L. umbellata*
 Roots non-suckering and plant does not expand horizontally_____ 2
2. Flowers distinctly blue, tightly bunched, pedicels <3mm_____ *L. sessiliflora*
 Flowers distinctly not blue, white or close to white, pedicels >3mm_____ 3
3. Leaves with cloudy, white coating on upper surface, anthers white_____ *L. tricocca*
 Leaves lacking cloudy, white coating on upper surface, anthers not white_____ 4
4. Leaves highly flaccid, often touching ground_____ *L. flaccidifolia*
 Leaves half-erect or erect, rarely touching ground_____ 5
5. Fans half-erect, emerging from little-branched rhizomes_____ *L. pulchella*
 Fans erect, emerging from erect or branched rhizomes or horizontal stolons_____ 6
6. Fans emerging from horizontal stolons_____ 7
 Fans emerging from erect or branched rhizomes_____ 8
7. Leaves narrow, <5 mm wide, capsule dehiscing by loculicidal clefts_____ *L. edgariae*
 Leaves broad, >6 mm wide, capsule indehiscent_____ *L. cranwelliae*
8. Rhizomes horizontal and far-spreading, >12 cm long_____ *L. peregrinans*
 Rhizomes short, <10 cm long_____ 9
9. Style branches winged_____ 10
 Style branches not winged_____ 11
10. Style branch wings pointing upwards, scape \approx length of leaves_____ *L. grandiflora*
 Style branch wings pointing outwards, scape <1/2 length of leaves_____ *L. ixioides*
11. Leaves narrower, <4 mm wide_____ *L. mooreae*
 Leaves wider, >5mm wide_____ 12
12. Sepals oblong and hooded_____ *L. colombiana*
 Sepals obovate and unhooded_____ 13
13. Petals obovate, 6-10 mm long_____ *L. paniculata*
 Petals oblong, \geq 10 mm long_____ *L. chilensis*

III. Taxonomy and Characters**a. Family Iridaceae**

Iridaceae Juss., Gen. Pl. 57 (1789)

Perennial herb, cosmopolitan distribution, rooting with bulbs, corms, or rhizome. *Flowers* bisexual, actino- to completely zygomorphic. *Tepals* 6, connate basally into tube, subequal or 3 outer differ from inner. *Stamens* 3, opposite outer tepals, filaments free or partly connate. *Anther* 2-locular, opening extrorsely or laterally by longitudinal slits. *Ovary* inferior with axile placentae. *Style* 3-lobed in upper part, branches deeply lobed, usually winged, petaloid. *Styloid crystals* usually present. *Capsule* usually loculicidally dehiscent. *Seed* with cop. Endosperm. *Leaves* usually crowded at base of stem, mostly narrow-linear, isobilateral.

Iridaceae is made up of roughly 70 genera consisting of 2030 species (Goldblatt *et al.*, 2008). *Libertia* is the only genus of Iridaceae found in New Zealand (Blanchon *et al.*, 2000).

b. Subfamily Iridoideae

Iridoideae Eaton, Bot. Dict. 4: 28 (1836)

Perianth fugacious. *Septal nectaries* usually absent. *Tepals* clawed. *Style branches* thickened and hollow, associated with the stamens. *Terminal appendages* usually present. *Roots* with simple perforations, endothecium thickenings spiral.

Iridoideae's lineage separated 62 mya (Goldblatt *et al.*, 2008). It is a primarily New World subfamily, with only 9 of its 30 genera found outside of the Americas. Included in this are 4 genera of bicentric distribution of Australasian origin, including *Libertia*.

c. Tribe Sisyrinchieae

Sisyrinchieae Benth. And J.D.Hook., Gen. Pl. 3: 683 (1883)

Stamens 3. *Filaments* united in lower half or free, threadlike, loose adhesion to style branches. *Septal nectaries* absent.

Sisyrinchieae's lineage separated 51 mya (Goldblatt *et al.*, 2008). While phylogenetic analysis does not support the tribe as a monophyletic group, rejecting *Bobartia* and *Diplarrhena*, *Libertia* is a member of the best supported clade (Mildenhall, 1980; Reeves *et al.*, 2001). *Orthrosanthus* and *Libertia* split from the remainder of the tribe 27 mya and each other 5 million years later.

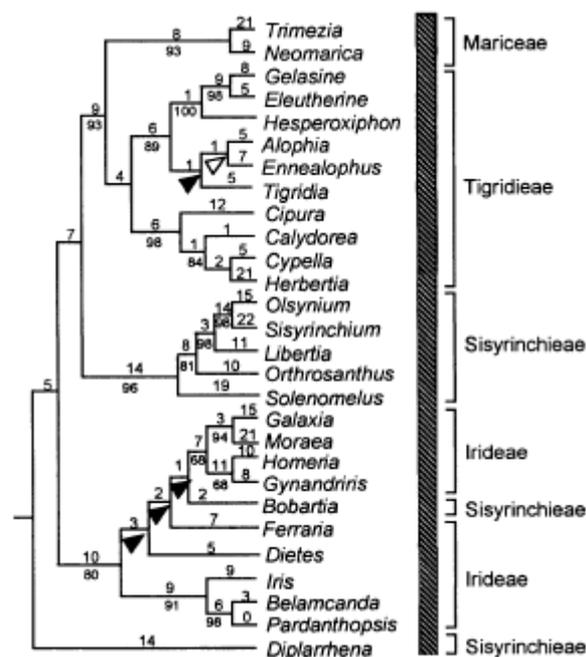


Fig 1. Phylogeny of Iridoideae, including tribes (Reeves *et al.*, 2001)

d. Genus *Libertia*

Libertia Spreng., Syst. Veg. 1: 127 (1824)

Synonyms: *Tekel* Adans., Fam. Pl. 2:497 (1763); *Tekelia* Scop., Introd. 88 (1777); *Renealmia* R.Br. Prodr. Add. [591] (1810); *Nematostigma* A.Dietr. Sp. Pl. 2:509 (1833);

Orthrosanthus Sweet, Fl. Australas. (1827); *Choeradodia* Herb., Amar. 87 (1837); *Ezeria* Raf., Fl. Tellur. 4:51 (1838)

Nom. illeg.: *L. azurea* Baker, Handb. Irid. 118 (1892) (*O. multiflorus* Sweet, Fl. Austral. (1827)); *L. graminea* Endl., Pl. Preiss. 2(1): 32 (1846) (*O. laxus* var. *gramineus* (Endl.) Geerinck, Bull. Jard. Bot. Natl. Belg. 44(1-2): 38 (1974)); *L. laxa* Endl., Pl. Preiss. 2(1) (1848) (*O. laxus* (Endl.) Benth., Fl. Austral. 6:411 (1873)); *L. stricta* Endl., Pl. Preiss. 2(1) (1848) (*O. multiflorus* Sweet)

Tufted, short rhizomatous or stoloniferous herb. Where rhizomes are present, usually short and many-branched, completely or almost completely glabrous. *Roots* contractile. *Flowers* usually white, actinomorphic, pedicillate, bracts membraneous, peripherally spreading. *Tepals* free, usually 3 sepals < 3 petals. *Staminal filaments* free or connate at base, flattened. *Panicles* laxly branched or with dense clusters of flowers. *Style branches* not winged. *Styloid crystals* usually present. *Sterile spathes* foliaceous. *Inflorescences* terminal and branched. *Anthers* versatile, usually linear-sagittate. *Ovary* 3-locular, inferior. *Capsule* subglobose to oblong or pyriform, 3-valved. *Seeds* rounded to angular, foveolate, lacking umbilicus. *Leaves* in flattened fans. *Peripheral vascular tissue* as a poorly defined plexus. Distribution bicentric Australasian-South American. n=19.

A point of contention in the genus description (Moore, 1967) includes the characterization by Sprengel, 1824 of the sepals < tepals. In *L. paniculata*, *L. chilensis* var. *formosa*, and *L. pulchella* this is not always the case (Moore, 1967; Moore and Edgar, 1970). As such, *Libertia* should be described as ‘Usually 3 sepals < 3 tepals.’

e. Species

Species descriptions of *L. falcata*, *L. insignis*, and *L. umbellata*, are limited due to a restricted publication of their respective naming articles. The naming author, Ravenna, self-published the series ‘Onira Botanical Leaflets’ to name species without peer review and has a history of superfluous and erratic naming (Gibbs and Semir, 2003). As such, no copies of the naming articles are available worldwide and the copies are found only in several major botanical institutions, including the Royal Botanic Gardens, Kew and Missouri Botanical Garden.

L. chilensis (Molina) Gunckel, Rev. Chil. Hist. Nat. 31:87 (1927)

Synonyms: *Strumaria chilensis* Molina, Sag. Stor. Nat. Chili 2(130): 284 (1810); *L. crassa* Graham, Edinb. N. Phil. Journ. 15:383 (1833); *L. formosa* Graham, Edinb. N. Phil. Journ. 15:383 (1833); *L. elegans* Poepp., Fragm. Syn. Pl. 1 (1833); *Choeradodia chilensis* (Molina) Herb., Amar. 87 (1837); *Sisyrrinchium fernandezianum* Steud, Nomencl. Bot. 2(2):595 (1841); *L. ixioides* Gay, Fl. Chil. 6:31 (1854); *L. grandiflora* Phil., Bot. Zeit. 14:648 (1856); *Sisyrrinchium formosum* (Graham) F.Muell Fragm. 7(54): 91 (1870); *L. formosa* var. *crassa*

(Graham) Baker, J. Linn. Soc. Bot. 16:153 (1877); *O. chilensis* Klotzsch ex Baker, J. Linn. Soc. Bot. 16:121 (1877); *Tekel formosa* (Graham) Kuntze, Revis. Gen. Pl. 2:702 (1891); *L. formosa* var. *grandiflora* Johow, Estud. H. Juan Fern. 150 (1896)

Fans closely bunched on stout, erect rhizomes. *Leaves* 12-95 x 0.6-1.5 cm, linear and erect, dark blue-green. *Scape* > leaves, 60-135 cm long. *Pedicels* 6-12 mm long. *Bud* white-pale yellow, cupiform. *Sepals* obovate, thin-textured, white-green. *Petals* oblong, green-brown, 1-1.5 cm long. *Style* branches not winged. Native to Chile, Argentina, and Juan Fernandez Islands. Flowers Apr. to early June. Known to hybridize x *L. ixioides* in culture in varied forms, including *L. x Butleri* and the commercial *Libertia* 'Amazing Grace.'

L. chilensis has 3 variants. *L. chilensis* var. *elegans* Poepp. is the smallest form of *L. chilensis*, with the inflorescences open and umbellate. Seeds are yellow-brown with an average of 10 seeds per capsule. *L. chilensis* var. *formosa* Graham is the most varied and common form of *L. chilensis* and does not always have sepals smaller than petals. Seeds are yellow-brown with 25-30 seeds per capsule. *L. chilensis* var. *procera* is a commercial name for the largest form (Butler, 2016), usually scape > leaves > 1m and has dramatically larger, cupiform flowers, with 4 per inflorescence. Seeds are pale brown with 50-60 seeds per capsule.

L. colombiana R.C.Foster, Contr. Gray Herb. 127:44 (1939)

Synonym: *L. boliviana* R.C.Foster, Contr. Gray Herb. 161:4 (1946)

Fans emerging from creeping rhizome 5-18 cm long, elongated internodes. *Leaves* 3-10 mm wide, linear and erect. *Bud* white-green. *Sepals* oblong, average 3 x 1.25 mm. *Petals* ovate-obovate, average 4.5 x 3 mm. *Style branches* not winged, pointing outwards. Native to Colombia, Ecuador, Peru, and Bolivia. Flowers Nov.

L. cranwelliae Blanchon, Murray, and Braggins, New Zeal. J. Bot. 40(3): 441 (2002)

Fans crowded from horizontal stolons. *Leaves* 15-90 x 0.6-1.1 cm, rigid, surfaces similar, turn yellow exposed to full sunlight, median nerves thick and crowded, margins not scabrid. *Scape* 2/3 length of leaves, to 40 x 0.4 cm. *Peduncles* 2/3 length of total inflorescence. *Panicle* narrow, sparsely branched, lanceolate, orange-green. *Pedicels* 5-16 mm long, stout. *Bud* white-yellow, 2-3.5 cm diam. *Sepals* elliptical, narrow, 1/2 length of petals. *Petals* ovate-elliptical, shortly unguiculate, not overlapping sepals. *Anthers* 3 mm long, yellow. *Ovary* yellow-green, cupiform. *Style branches* not winged, pointing outwards. *Capsule* 20 mm diam., barrel-shaped, yellow-orange, matures to black, indehiscent, to 70 seeds each. *Seeds* 1.5 mm diam., globose, reticulate-foveolate texture, orange-brown. Formerly endemic to Awatere and Kopuaponunamu Valleys, New Zealand. Flowers Sept. to Nov. Nationally critical.

L. edgariae Blanchon, Murray, and Braggins, New Zeal. J. Bot. 40(3): 442 (2002)

Fans crowded from horizontal stolons. *Leaves* 12-62 x 0.1-0.5 cm, green to pale yellow, surfaces similar, median nerves crowded, margins scabrid towards tip. *Scape* = length of leaves. *Peduncles* 1/2 length of inflorescence. *Panicle* broad, laxly branched. *Pedicels* 10-35 mm long, slender. *Bud* white, 1-2 cm diam. *Sepals* elliptical, narrow, 1/2 length of petals. *Petals* orbicular, unguiculate, overlapping sepals. *Anthers* 2-3 mm long, bright yellow. *Style branches* not winged, pointing upwards. *Capsule* 5-9 x 3-6 mm, barrel-shaped, green, matures to black, dehiscing by loculicidal clefts, long valves recurved. *Seeds* 1.5 x 1 mm, globose, reticulate-foveolate texture, bright orange. Native to New Zealand, along coastlines and marine terraces, in low scrub cover. Flowers Sept. to Nov.

L. falcata Ravenna, Onira 10:2. (2005)

Leaves 4-20 cm long, <3 mm wide. *Scape* > 2x leaves, to 45cm. *Capsule* globose, indehiscent, 2.5-4 mm diam. Endemic to el Parque Nacional Nahuelbuta, Chile. A poorly defined species due to limited publication.

L. flaccidifolia Blanchon and Weaver, New Zeal. J. Bot. 47(3): 319 (2009)

Fans closely bunched on short, branched rhizomes. *Leaves* 70-96 x 0.7-1.4 cm, highly flaccid, falcate, green to yellow-green, median nerves crowded, margins coarsely scabrid. *Peduncles* 1/5-2/5 length of inflorescence. *Panicle* broad, laxly branched. *Pedicels* 10-20 mm long, slender. *Sepals* narrow, elliptical, red-brown, < 1/2 length of petals. *Petals* orbicular, unguiculate, overlapping sepals. *Anthers* 1-2 mm long, yellow. *Ovary* dark green, 1/2 length of perianth bud. *Style branches* not winged, pointing upwards. *Capsule* 6-18 x 4-9 mm, teardrop-shaped, green-yellow, matures to black, dehiscing by loculicidal clefts. *Seeds* 1-1.5 mm diam., globose, yellow-orange. Endemic to the south face of Mt. Tamahunga between 200-400m, New Zealand. Flowers Sept. to Nov. Nationally critical.



Fig 2. Immature/mature seed capsules of *L. flaccidifolia* (left) and *L. ixiooides* (right) (Blanchon and Weaver, 2009). Key features to compare include the body shapes and loculicidal clefts.

L. grandiflora (R.Br.) Sweet, Hort. Brit. 2:498 (1830)

Synonyms: *R. grandiflora* R.Br., Prodr. Fl. Nov. Holland. 592 (1810); *L. orbicularis* Colenso, Trans. And Proc. New Zeal. Inst. Xv. 329 (1883); *Tekel grandiflora* (R.Br.) Kuntze Revis. Gen. Pl. 2:702 (1891)

Fans closely bunched on short, erect rhizomes. *Leaves* average 50 x 0.3-1.5 cm, surfaces similar, median nerves thick and crowded, margins finely scabrid. *Scape* ≈ length of leaves. *Peduncles* long, usually carry flowers above leaves. *Panicle* broad, usually laxly branched, upper bracts narrow and pale. *Pedicels* to 25 mm long, slender, erect. *Bud* white, ≥ ovary, 1.5-3 cm diam. *Sepals* narrow, 1/2 length of petals. *Petals* orbicular to broad-oblong, shortly unguiculate, overlapping sepals. *Anthers* 3 mm long, bright yellow. *Ovary* dark, smooth, globose. *Style branches* winged, pointing upwards. *Capsule* 15 x 10 mm, globose to long-pyriform, green-red, matures to black, dehiscing by loculicidal clefts, long valves recurved. *Seeds* 1.5-2 x 1.5 mm, globose to angular, reticulate texture, brown-red to bright red. Found in dwarf and rhizomatous forms. Native to New Zealand, along streamsides and on forest floors, often above 1000m altitude. Flowers Oct. to Nov. Known to hybridize x *L. ixioides* in nature.

L. insignis Ravenna, Onira 10:3. (2005)

Native to Chile. A poorly defined species due to limited publication.

L. ixioides (G.Forst.) Spreng, Syst. Veg. 16(1): 168 (1824)

Synonyms: *Sisyrinchium ixioides* G.Forst., Fl. Ins. Austr. 61 (1786); *Moraea ixioides* (G.Forst.) Thunb. (1787); *Ferraria ixioides* (G.Forst.) Willd. (1800); *R. ixioides* (G.Forst.) Ker Gawl. (1827); *Nematostigma ixioides* (G.Forst.) A.Dietr. (1833); *L. macrocarpa* Klatt (1862); *L. restioides* Klatt (1862); *L. tricolor* Lem. (1863); *Tekel ixioides* (G.Forst.) Kuntze (1891)

Fans closely bunched on short, erect rhizomes, growing into circular fan pattern. *Leaves* average 50 x 0.3-1.5 cm, surfaces similar, green, darker towards edge, turn yellow exposed to full sunlight, median nerves thick and crowded, margins finely scabrid. *Scape* < leaves. *Peduncles* 1/2 length of total inflorescence, not carrying flowers. *Panicle* narrow, closely branched, upper bracts pale. *Pedicels* to 20 mm long, stout. *Bud* white-yellow, 1-2 cm diam. *Petals* orbicular to broad-oblong, shortly unguiculate, overlapping sepals. *Anthers* 2 mm long, pale yellow. *Ovary* pale, trigonous, flat-sided. *Style branches* winged, pointing outwards. *Capsule* 10-15 mm diam. globose to oblong, yellow, dehiscing by short loculicidal clefts, older valves pale and not widely patent, 70 seeds per capsule. *Seeds* 2 x 1.5 mm, angular-globose, reticulate texture, orange-yellow. Native to New Zealand, along streamsides and in bogs. Flowers Oct. to Dec. Known to hybridize x *L. peregrinans* and possibly x *L. chilensis* in nature and x *L. grandiflora* in situ.

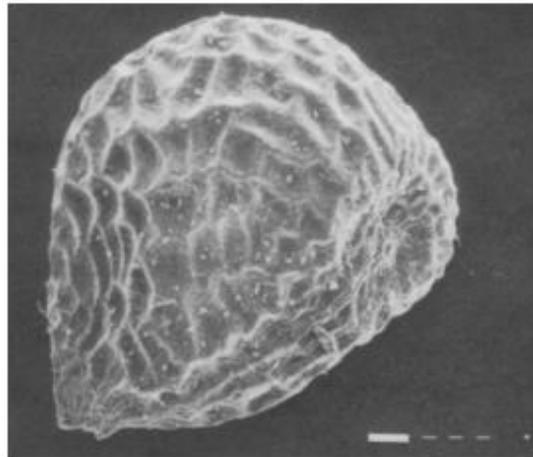


Fig 3. Seed of *L. ixiooides* (Goldblatt, 1989). Key features to note include the angular point and globose body of the seed, and reticulate texture.

L. mooreae Blanchon, Murray, and Braggins, New Zeal. J. Bot. 40(3): 444 (2002)

Fans closely bunched on short, branched rhizomes. *Leaves* 10-40 x 0.1-0.4 cm, slightly falcate, green, surfaces similar. *Peduncles* 2/3 length of inflorescence, carrying flowers above leaves. *Panicle* broad, laxly branched. *Pedicels* 10-35 mm long, slender. *Bud* white, 1-2 cm diam. *Sepals* narrow, elliptical, beige-pink, 1/2 length of petals. *Petals* orbicular, overlapping sepals. *Anthers* 2-3 mm long, yellow. *Ovary* dark green. *Style branches* not winged, pointing upwards. *Capsule* 5-8 x 3-5 mm, barrel-shaped, green-brown, matures to black, fully dehiscent by short loculicidal clefts. *Seeds* 1-1.5 mm diam., globose, reticulate-foveolate texture, yellow to yellow-orange. Native to New Zealand, along rocky ridges, cliffs, and river banks. Flowers Aug. to Nov.

L. paniculata (R.Br.) Spreng., Syst. Veg. 1:168 (1824)

Synonyms: *R. paniculata* R.Br., Prodr. Add. [592] (1810); *Sisyrrinchium paniculatum* R.Br., Prod. Fl. Nov. Holl. (1810); *Nematostigma paniculatum* (R.Br.) A.Dietr., Sp. Pl. 2:510 (1833); *Sisyrrinchium paniculatum* (R.Br.) ex F.Muell., Fragm. 7:91 (1870); *Tekel paniculata* (R.Br.) Kuntze, Rev. Gen. Pl. 2 (1891)

Leaves 20-60 x 0.4-1.2 cm, linear, half-erect, not arranged as fans. *Scape* < leaves, 1-3 mm diam., 0/1 reduced leaf present. *Pedicels* average 10 mm, carry 3-6 flowers as rhipidium. *Spathes* lanceolate, 10-40 mm long. *Bud* white, 2-3 cm diam. *Sepals* obovate, 8-13 mm long. *Petals* ovate, 6-10 mm long. *Anthers* 2 mm long. *Ovary* obovoid. *Style branches* not winged. Lacks styloid crystals. *Capsule* 5-8 mm diam., globose-trigonous, black. *Seeds* average 1 mm diam., angular, dark brown. Native to eastern Australia, in warm temperate rainforests and moist gullies in wet sclerophyll forest. Flowers Nov. to Jan.

L. peregrinans Cockayne and Allan, Trans. and Proc. N. Z. Inst. Ivii. 56 (1927)

Fans crowded or emerging from far spreading (12-15 cm long) horizontal rhizomes. *Leaves* 15-70 x 0.5-1.5 cm, surfaces similar, turn copper exposed to full sunlight, median nerves thick and crowded, margins finely scabrid and brightly colored. *Scape* < leaves, to 30 x 0.2 cm. *Peduncles* 1/2 length of inflorescence, not carrying flowers. *Panicle* narrow, closely branched, upper bracts brown. *Pedicels* 15-30 mm long, slender. *Bud* white-brown, averages 2 cm diam. *Sepals* narrow, 1/2 length of petals, pale yellow-white. *Petals* to 15 x 10 mm, orbicular, shortly unguiculate, not overlapping sepals. *Anthers* 3-3.5 mm long, dark orange to brown. *Ovary* green, smooth, tapered to pedicel. *Style branches* with narrow wings. *Capsule* <1 cm diam., pyriform, brown to yellow, matures to black, indehiscent, containing to 30 seeds each. *Seeds* average 1.2 mm diam., subglobose, reticulate texture, light brown. Does not flower annually and produces sparse inflorescences. Native to New Zealand, in sandy, peaty, and pumice soils at altitude <1000m. Known to hybridize x *L. ixioides* in culture. Nationally threatened.

L. pulchella (R.Br.) Spreng, Syst. Veg. 1 (1824)

Synonyms: *R. pulchella* R.Br., Prodr. Add. [592] (1810); *Nematostigma pulchellum* (R.Br.) A.Dietr., Sp. Pl. 2:510 (1833); *L. micrantha* A.Cunn, Comp. Bot. Mag. 2:375 (1837); *L. laurencei* Hook.F., Fl. Tasman. 2:34 (1858); *Sisyrinchium pulchellum* (R.Br.) R.Br. ex F.Muell., Fragm. 7:92 (1870); *Tekel pulchella* (R.Br.) Kuntze, Revis. Gen. Pl. 2 (1891); *Tekel micrantha* (A.Cunn.) Kuntze, Revis. Gen. Pl. 2:702 (1891); *L. pulchella* var. *laurencei* (Hook.F.) Domin., Biblioth. Bot. 85:536 (1915); *L. pulchella* Spreng. var. *pygmaea* D.I.Morris, Stud. Fl. Tasman. 4B:425 (1994)

Fans emerging from little branched rhizomes 5-8 cm long, wiry roots. *Leaves* 3-18 x 0.2-0.7 cm, linear to falcate, half erect, downward surface dull, few nerves. *Scape* > leaves, 1-2 mm diam., 0/1/2 reduced leaves present. *Panicle* simple, narrow-lanceolate, green. *Pedicels* 10-40 mm long, carry 2-6 flowers as rhipidium. *Bud* white, 1-1.5 cm diam. *Sepals* narrow, ovate, sparse veins, average 5 mm long. *Petals* wide, ovate, many veins, average 10 mm long. *Anthers* 2 mm long. *Ovary* globose. *Capsule* 3-5 mm diam., globose-trigonous, brown, valves keeled and recurved. *Seeds* 1-1.5 mm diam., globose, smooth texture, pale yellow, long funicle persistent. Native to New Zealand, Tasmania, eastern Australia, and New Guinea, in high altitudes on damp, mossy forest floor. Flowers in Nov.

L. pulchella var. *pygmaea* endemic to Tasmania. *Leaves* 3-5 cm x 0.1-0.6 cm. *Scape* roughly = leaves, to 5 cm long. *Anther* to 1 mm long. *Capsule* 2-3 mm diam.

L. sessiliflora (Poepp.) Skottsbo., Nat. Hist. Juan. Fern. Bot. 2(6): 778 (1953)

Synonyms: *Sisyrinchium sessiliflorum* Poepp., Notiz. Gebiet Natur-u. Heilk. 1(23): 277 (1829); *Sisyrinchium sessiliflorum* Hook. And Arn., Bot. Beechey Voy. 47 (1830); *L. caerulescens* Kunth and Bouche, Index Sem. 9 (1845); *Sisyrinchium huismo* Dombey ex Baker, J. Linn. Soc. Bot. 16:120 (1877); *Bermudiana sessiliflora* (Poepp.) Kuntze, Revis. Gen. Pl. 2:700 (1891); *Tekel sessiliflora* (Poepp.) Kuntze, Revis. Gen. Pl. 2:703 (1891)

Fans emerging from little-branched rhizomes. *Leaves* usually 30-45 x 1-1.2 cm, up to 85 cm long, erect, green. *Scape* > leaves. *Pedicels* <3 mm long, conical, bunching flowers tightly. *Bud* sky blue. *Sepals* 4-5 x 2-3 mm, ovate to lanceolate, semi-rigid. *Petals* 7-8 x 5-6 mm, ovate, thin-textured. *Anther* orange-yellow. *Ovary* avg. 4 mm diam. *Capsules* elliptical, 7-10 x 5-6 mm, containing 3-4 seeds. Native to upland Chile. Flowers Jan. to Mar. A large commercial cultivar referred to as *L. sessiliflora* 'Ballyrogan Blue' with leaves to 85 cm, scape to 100 cm, and paler, closely bunched inflorescences.

L. tricocca Phil., Linn. 29:63 (1858)

Synonyms: *Sisyrinchium tricoccum* (Phil.) F.Muell., 7(54):92 (1870); *Tekel tricocca* (Phil.) Kuntze, Revis. Gen. Pl. 2:703 (1891)

Rhizomes to 2 cm long. *Leaves* to 30 x 0.1-0.3 cm long, not arranged as fans, erect, thick margins, ensiform, upper surface with cloudy, white coating. *Pedicels* long. *Bud* white. *Petals* < sepals. *Tepals* avg. 4.5 mm long. *Style branches* 2-3 mm long. *Anthers* 1-1.3 mm, white. *Capsules* 3 x 2 mm. Endemic to el Parque Nacional Nahuelbuta, Chile. Flowers Jan. to Mar.

L. umbellata Ravenna. Onira 10:1. (2005)

Synonyms *L. formosa* Graham, Edinb. N. Phil. Journ. 15:383 (1833); *L. ixioides* Klatt, Fl. Bras. Mart. 3(1): 530 (1871); *L. chilensis* (Molina) Gunckel, Rev. Chil. Hist. Nat. 31:87 (1927)

Rhizomes suckering, horizontally expanding. *Leaves* to 60 x 1 cm, pale green with a cloudy, white coating, turn bright yellow to orange exposed to full sunlight, not arranged as fans, falcate, flaccid. *Scape* > leaves, to 80 x 0.4 cm. *Sepals* > petals, 5 x 1 mm. *Petals* 9 x 6 mm, broad oblong. *Anther* yellow. *Seeds* 5-8 per capsule, yellow-brown. Native to Chile.

IV. Polyploidy

a. Within Tribe Sisyrinchieae

Libertia has a high rate of polyploidy, with nine species confirmed as polyploid and only two confirmed as diploid (five have not been assessed) (Blanchon *et al.*, 2000). However, the ploidy levels of *Libertia* are not unprecedented within the family or tribe, with varied base numbers and rampant polyploidy a common feature of Iridaceae and Sisyrinchieae (Golblatt

and Takei, 1997). A defining feature of *Libertia* is the distinct $x=19$, as well as the uniform base number intragenerically, found only in half of Sisyrinchieae genera (Hair *et al.*, 1967; Goldblatt and Takei, 1997; Blanchon *et al.*, 2000). Other members of the tribe Sisyrinchieae have varied base numbers, with as many as four in *Olsynium*, ranging between 8 and 11 (Goldblatt and Takei, 1997). The ploidy levels of 2x, 4x, 6x, and 12x for *Libertia* are present elsewhere in the tribe as well (Goldblatt, 1982; Goldblatt and Takei, 1997). While polyploidy is present across the distribution, the species in *Libertia* with the highest rates of polyploidy are all endemic to New Zealand, with three dodecaploids and four hexaploids making up the seven endemic species (Hair *et al.*, 1967; Moore 1967; Blanchon *et al.*, 2000, 2002; Blanchon and Weaver, 2009). This is consistent as well with the high ploidy found amongst many species of plants in New Zealand (Rendle, and Murray, 1989; Murray *et al.*, 1992).

Genus	Base Number	Ploidy Levels	Chromosome Count
<i>Libertia</i>	19	2x, 4x, 6x, 12x	38, 76, 114, 228
<i>Diplarrhena</i>	16	2x	32
<i>Olsynium</i>	8, 9, 10, 11	2x, 4x, 6x, 12x	18, 20, 22, 40, 60, 96
<i>Orthrosanthus</i>	9, 10, 12	4x, 5x, 6x, 7x	40, 50, 54, 84
<i>Sisyrinchium</i>	8, 9, 17	2x, 4x, 6x, 8x, 12x	16, 18, 32, 36, 48, 64, 72, 96
<i>Solenomelus</i>	8	6x	48

Table 1. Cytology of genera from tribe Sisyrinchieae (Goldblatt, 1982; Goldblatt and Takei, 1997)

b. Within Genus *Libertia*

The cytology of *Libertia* has several points of contention, usually revolving around the difficulty of counting chromosomes due to large satellites and small chromosome size (Kenton and Heywood, 1984; Blanchon *et al.*, 2000). The proper identification of species has proved to be a significant hurdle to the cytological study of the genus as well. As such, studies with such questionable results should be re-examined where appropriate, to establish confirmation of questionable results (Blanchon and Weaver, 2009).

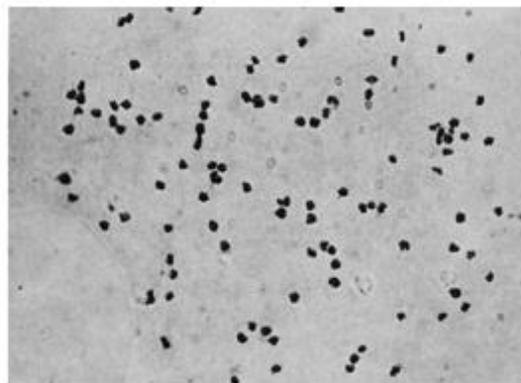


Fig 4. Chromosomes of *L. ixiooides* in Prometaphase I (Hair *et al.*, 1967). Key features to note include the obstructive satellite at the bottom left and clumping of small chromosomes.

The difficulties of counting chromosomes were prevalent in the 2000 study by Blanchon *et al.* In this study, *L. ixioides* was described as having 228 chromosomes (12x), though the authors described the counts as ranging between 220 and 230 at times. Sanders *et al.* in 1983 counted 114 chromosomes in *L. chilensis* from the Juan Fernandez Islands. Upon further examination in 2000, Blanchon *et al.* found 76 chromosomes in *L. chilensis*, in samples from mainland Chile. If a new study of *L. chilensis* from the Juan Fernandez Islands found identical results to Sanders *et al.*, it could be argued for the establishment of a new name for this group.

Larger issues arose during Kenton and Heywood's 1984 cytological study. Their findings were complicated by a likely misidentification of a sample, stating *L. ixioides* had a chromosomal count of 72. This is unlikely on several counts, as the sample was from Chile and *L. ixioides* is a New Zealand endemic (Moore and Edgar, 1970), 72 is an improbable value for a uniformly 19-base number genus such as *Libertia* (Hair, 1967), and other literature ascribing 228 as the count for *L. ixioides* (Hair *et al.*, 1967; Blanchon *et al.*, 2000, 2002). This sample was more likely a misidentified *L. chilensis*, known to be found in Chile and to have a tetraploid chromosomal count, coupled with a miscounting of the chromosomes. As such, with these confounding factors, this finding should be disregarded entirely.

The study further stated the chromosomal count of *L. grandiflora* to be $12x = 230$ in the rhizomatous form. While the chromosomal count not being equal to a base count of 19 can be attributed to a miscounting (Blanchon *et al.*, 2000), the sample being dodecaploid, rather than the confirmed hexaploid of *L. grandiflora* (Hair *et al.*, 1967; Moore, 1967; Blanchon *et al.*, 2000), is a possible case of misidentification. This count, as with Moore in 1967, may likely have been a misidentified *L. flaccidifolia* sample, before the 2009 naming of the species by Blanchon and Weaver. In 1967, Moore found a single rhizomatous sample of *L. grandiflora* to be dodecaploid. This sample may have been an early specimen of *L. flaccidifolia*, however, as brief examination of the photo sample provided suggests it presents several characters of the latter named species, coupled with its collection from the only known location of *L. flaccidifolia*, on Mt. Tamahunga. In this way, the samples and subsequent cytological examinations should be considered synonymous to *L. flaccidifolia* (Blanchon and Weaver, 2009).

Species	Ploidy Level	Chromosomal Count
<i>L. chilensis</i>	4x (6x)	76 (72, 114)
<i>L. colombiana</i>	No data available.	No data available.
<i>L. cranwelliae</i>	12x	228
<i>L. edgariae</i>	6x	114
<i>L. falcata</i>	No data available.	No data available.
<i>L. flaccidifolia</i>	12x	228
<i>L. grandiflora</i>	6x	114 (228, 230)
<i>L. insignis</i>	No data available.	No data available.
<i>L. ixioides</i>	12x	228 (220-230, 230)
<i>L. mooreae</i>	6x	114
<i>L. paniculata</i>	4x	76
<i>L. peregrinans</i>	6x	114
<i>L. pulchella</i>	2x	38
<i>L. sessiliflora</i>	2x	38
<i>L. tricocca</i>	No data available.	No data available.
<i>L. umbellata</i>	No data available.	No data available.

Table 2. Cytology of species from genus *Libertia* (Hair *et al.*, 1967; Moore, 1967; Sanders *et al.*, 1983; Kenton and Heywood, 1984; Blanchon *et al.*, 2000; Blanchon *et al.*, 2002; Blanchon and Weaver, 2009)

c. Hybridization

Hybridization is a common occurrence in *Libertia*, in both cultivation and the wild (unpublished, Blanchon, 1999; Blanchon *et al.*, 2000; Butler, 2016, 2017), and this capability is further suggested by the high level of polyploidy (Stebbins, 1971). *L. ixioides* is capable of hybridizing with *L. peregrinans* (unpublished, Blanchon, 1999), *L. grandiflora* (Blanchon *et al.*, 2000), and possibly *L. chilensis* (Butler, 2016). *L. ixioides* x *peregrinans* and *L. grandiflora* x *ixioides* both have $2n = 9x = 171$, as expected from such crosses (Blanchon *et al.*, 2000), and *L. ixioides* x *chilensis* has not been examined cytologically. Due to the well-established cytology of New Zealand species of *Libertia*, these hybrids are easily confirmed, allowing for confirmation of the origins of questionable samples. The artificial cross by Blanchon *et al.* in 2000 further provided evidence toward the practical application of crossings between *Libertia* to establish parentage through cytology, as the *L. ixioides* x *grandiflora* produced the expected chromosomal count of 171, between the parents with counts 228 and 114 respectively. As such, the final unanalyzed hybrid, *L. x Butleri* (Butler, 2016), could be studied to establish proper identification.

V. Biogeography

The bicentric distribution of *Libertia* has raised a number of questions as to how a genus could be spread across a seemingly Gondwanan distribution, while not being present in any

form in Africa, and having diverged more recently than New Zealand's detachment from Gondwanaland 80 mya (McQueen, 1992; Goldblatt *et al.*, 2008). This is one of the rarest disjunct distributions, with only five other genera having such a distribution of bicentric endemism between South America and Australasia, each with similar patterns of distribution and lineage divergence (Blanchon *et al.*, 2002). Furthermore 48 genera across seven families are present in both South America and Australasia, though not in as restricted a range as the *Libertia*-type distribution (Thorne, 1972). As such, a discussion regarding these distributions must acknowledge that random dispersion in common patterns, while difficult to truly falsify (Morrone and Crisci, 1995), is unlikely to occur in such a consistent manner, with such a large number of cases (Sanmartin and Ronquist, 2004).

a. Antarctic Expansion Hypothesis

The foremost hypothesis explaining these distributions centers around a "Greater New Zealand" directly connected to South America through an expanded Antarctic ice shelf and repeated glaciation (Skottsberg, 1915; Campbell, 1923; McQueen, 1992; Blanchon *et al.*, 2002). New Zealand has shallow seas surrounding it that were exposed by lowered global sea levels during glacial periods, expanding the coastlines greatly and allowing its biodiversity to reach further from the current center of distribution in modern New Zealand (Campbell, 1923; McQueen, 1992). This expanded range was then met more closely by ice caps of a glacial period Antarctica (Campbell, 1923), allowing for an interchange of biodiversity between all landmasses connected to this Antarctic expansion, including New Zealand, South America, and many Subantarctic islands (Skottsberg, 1915; Blanchon *et al.*, 2002). Through these connections, species and genera previously thought endemic to New Zealand have appeared in Southern Ocean islands, such as Seymour Island (Skottsberg, 1915) and the submerged Kerguelen plateau (Carpenter *et al.*, 2010). As such, there is distinct evidence that the Southern Hemisphere, including Australasia, South America, Africa, Antarctica, and the islands of Oceania were joined through a common flora.

Upon the separation of these landmasses as ice caps retreated, Blanchon *et al.* in 2002 argued that the New Zealand lineage of *Libertia* developed separately from the South American and Australian lineages. This is evidenced by the distinct characters of the group and hybrid success within New Zealand species but not without (Blanchon, 1999; Blanchon *et al.*, 2000), suggesting New Zealand species are much more closely related to each other, than other *Libertia*. With the possible hybrid of *L. x Butleri* (Butler, 2016), this support may prove to be more circumstantial than evidential, as *L. ixioides* and *L. chilensis* hybridizing successfully would contradict this point of argument. This lineage hypothesis is further supported by the cytology of New Zealand endemics in comparison to other lineages with the high levels of ploidy found not just in *Libertia*, but many genera within the New Zealand flora (Rendle and Murray, 1989; Murray *et al.*, 1992). The unique levels of polyploidy in comparison with outside

New Zealand suggests a unique lineage, but also provides support of the use of glacial refugia by *Libertia*. At higher altitudes, higher polyploids are found and polyploids are more successful within their ecosystems (Kenton *et al.*, 1986), as well as being capable of outcompeting their diploid relatives in direct competition (Stebbins, 1971). McQueen in 1992 argues that the high polyploidy within the New Zealand flora thus is a relic of periods of repeated retreats into the high mountains of the islands during glacial periods, followed by rapid recolonization of its lowlands during interglacials. During these refugia periods, high polyploidy develops and remains in the lineages of New Zealand endemics (McQueen, 1992; Blanchon *et al.*, 2002).

b. Alternative Hypotheses

The first alternate hypothesis explaining bicentric distribution argues that *Libertia* had a fully Gondwanan distribution, but the lineage died out in Africa, leaving only descendants in South America and New Zealand. This is easily discredited through molecular phylogeny with the establishment of divergence periods within Iridaceae (Goldblatt *et al.*, 2008). As New Zealand split from Gondwanaland 80 mya (McQueen, 1992), the ancestral lineage of *Libertia* must have been present across the distribution during this time period. As the genus *Libertia* was formed 22 mya (Goldblatt *et al.*, 2008), this is not a viable explanation of the historical spread of *Libertia* across its distribution.

An alternative explanation of this distribution rests in random long-range dispersal. As *Libertia* generally is wind or insect pollinated (Bernadello *et al.*, 2001; Thorsen *et al.*, 2009), a migration of significant size or indeed a single plant is tremendously unlikely (Skottsberg, 1960). While there have been cases of animal-based dispersal through birds and sea animals, the low possibility of animal-based dispersal is further reduced by the observation in zoo collections that few animals will eat *Libertia* (Butler, 2017), reducing the likelihood of seed dispersion. It cannot be factually ruled out as a possibility (Morrone and Crisci, 1995), though the evidence of an Antarctic expansion during the dispersal period combined with the low chance of a random tide-based migration marks this as an insignificant hypothesis (Skottsberg, 1915; Skottsberg, 1960; Blanchon *et al.*, 2002).

VI. Further Study

Libertia has many potential routes of further examination, primarily revolving around the study of its South American species. Due to the greater access to resources, the New Zealand flora has such been better accounted for. The most obvious gap in knowledge of these South American species is the lack of uniform description and identification keys for the region (Sanders *et al.*, 1983; Kenton and Heywood, 1984). Without proper species descriptions and tools to identify them, future South American studies run the risks of repeating the same mistakes as the past in misattributing data. Furthermore, a reexamination of *L. chilensis* is necessary to establish recognized names for its variants and straighten out the misnaming that has become overly common in commercial botany (Butler, 2016).

Due to the cytological confusion throughout the genus, a comprehensive analysis of questioned and unstudied species should be undertaken. Five *Libertia* spp., *L. colombiana*, *L. falcata*, *L. insignis*, *L. tricocca*, and *L. umbellata*, have no cytological data on record, three have had questionable results in past studies as discussed above, and the 1983 study by Sanders *et al.* sets a precedent for further examination of a potential cryptic species from the Juan Fernandez Islands. Known and suspected hybrids, such as *L. x Butleri*, should be analyzed as well, to assist in the confirmation of parent species (Blanchon *et al.*, 2000; Butler, 2016).

Another critical point of future study is that of the phylogeny within the genus. As the molecular phylogeny of *Libertia* has not been assembled, it is more difficult to conclusively state the point of origin of the genus and its dispersal routes (Sanmartin and Ronquist, 2004). With the phylogeny assembled, a more complete view of its species and their relations in terms of clades can be ascertained as well.

Acknowledgements

This paper was written under guidance of Prof. John Parnell of Trinity College Dublin. My thanks to Trinity College at the University of Dublin, Trinity College Herbarium, the Hamilton Library, and the Dublin Zoo for their resources, Prof. John Parnell for his guidance and laying the foundations of this paper, and Stephen Butler for his aid and expertise in *Libertia*.

Literature Cited

- Bentham, G., 1873. *Flora Australiensis: A description of the plants of the Australian territory*. London, L. Reeve and Co.
- Bernadello, G., Anderson, G.J., Stuessy, T.F., and D.J. Crawford, 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Botanical Review* 67(3), pp. 255-308.
- Blanchon, D.J., 1999. The genus *Libertia* Sprengel: systematics, hybridization and evolution. Unpublished PhD thesis, The University of Auckland, Auckland, New Zealand.
- Blanchon, D.J., 2000. Chromosome numbers in the genus *Libertia*. *New Zealand Journal of Botany* 38(2), pp. 245-250.
- Blanchon, D.J., Murray, B.G., and J.E. Braggins, 2002. A taxonomic revision of *Libertia* (Iridaceae) in New Zealand. *New Zealand Journal of Botany* 40, pp. 437-456.
- Blanchon, D.J. and J.S. Weaver, 2009. *Libertia flaccidifolia* (Iridaceae), a new species from Mt. Tamahunga, Northland, New Zealand. *New Zealand Journal of Botany* 47, pp. 317-324.
- Butler, S., 2016. Naming those *Libertias*. *The Irish Garden Plant Society Blog*, [online] 20 May. Available at: <<https://igpsblogs.wordpress.com/tag/stephen-butler/>> [Accessed 5 January 2017]
- Butler, S., 2017. *Libertia in the Dublin Zoo. Interview with Spencer McIntyre on 23rd Jan*. Dublin.
- Campbell, D.H., 1923. Australasian Botanical Notes. III. New Zealand. *American Journal of Botany* 10(10), pp. 515-536.
- Carpenter, R.J., Truswell, E.M., and W.K. Harris, 2010. Lauraceae fossils from a volcanic Palaeocene oceanic island, Ninetyeast Ridge, Indian Ocean: ancient long-distance dispersal? *Journal of Biogeography* 37(7), pp. 1202-1213.

- Cockayne, L. and H.H. Allan, 1927. The bearing of ecological studies in New Zealand on botanical taxonomic conceptions and procedure. *Journal of Ecology* 15(2), pp. 234-277.
- Curtis, W.M. and D. I. Morris, 1994. *The Student's Flora of Tasmania*. Hobart, Tasmania, St. David's Park Publishing.
- Gardner, M.F. *et al.*, 2006. *Threatened plants of central and south Chile*. Edinburgh, Royal Botanic Gardens Edinburgh Publications Department.
- George, A.S., 1986. *Flora of Australia vol. 46: Iridaceae to Dioscoreaceae*. Netley, Australia, Griffin Press Ltd.
- Gibbs, P. and J. Semir, 2003. A taxonomic revision of the genus *Ceiba* Mill. (Bombacaceae). *Anales Jardin Botanico de Madrid* 60(2), pp. 259-300.
- Goldblatt, P., 1982. Chromosome cytology in relation to suprageneric systematics of neotropical Iridaceae. *Systematic Botany* 7(2), pp. 186-198.
- Goldblatt, P., 1990. Phylogeny and classification of Iridaceae. *Annals of the Missouri Botanical Garden* 77(4), pp. 607-627.
- Goldblatt, P. and M. Celis, 2005. Notes on *Libertia* (Iridaceae: Sisyrinchieae) in South America. *SIDA, Contributions to Botany* 21(4), pp. 2105-2112.
- Goldblatt, P., Henrich, J.E., and R.C. Keating, 1989. Seed morphology of *Sisyrinchium* (Iridaceae-Sisyrinchieae) and its allies. *Annals of the Missouri Botanical Garden* 76(4), pp. 1109-1117.
- Goldblatt, P. and M. Takei, 1997. Chromosome cytology of Iridaceae-patterns of variation, determination of ancestral base numbers, and modes of karyotype change. *Annals of the Missouri Botanical Garden* 85(2), pp. 285-304.
- Goldblatt, P. *et al.*, 2008. Iridaceae 'out of Australasia'? Phylogeny, biogeography, and divergence time based on plastid DNA sequences. *Systematic Botany* 33(3), pp. 495-508.
- Hair, J.B., Beuzenberg, E.J., and B. Pearson, 1967. Contributions to a chromosome atlas of the New Zealand flora – 9. Miscellaneous families. *New Zealand Journal of Botany* 5, pp. 185-196.
- Harden, G.J., 1990. *Flora of New South Wales vol 4*. Sydney, UNSW Press.

- Huxley, A. and M. Griffiths, 1999. *The New Royal Horticultural Society Dictionary of Gardening*. London, MacMillan.
- Innes, C., 1985. *The World of Iridaceae*. London, Holly Gate International.
- IUCN, 2016. *The IUCN Red List of Threatened Species. Version 2016-3*, [online]. Available at <<http://www.iucnredlist.org>> [Accessed 13 January 2017].
- Kenton, A. and C.A. Heywood, 1984. Cytological studies in South American Iridaceae. *Plant Systematics and Evolution* 146, pp. 87-104.
- McQueen, D.R., 1992. Disjunction of tree species in mountain forests, southern North Island, New Zealand: a review of paleobotanical evidence. *Pacific Science* 46(2), pp. 269-275.
- Mildenhall, D.C., 1980. New Zealand late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 81, pp. 197-235.
- Moore, L.B., 1967. The New Zealand species of *Libertia* (Iridaceae). *New Zealand Journal of Botany* 5(2), pp. 255-275.
- Moore, L.B. and E. Edgar, 1970. *Flora of New Zealand vol II*. Wellington, Government Printer.
- Morrone, J.J. and J.V. Crisci, 1995. Historical biogeography: introduction to methods. *Annual Review of Ecological Systems* 26, pp. 373-401.
- Murray, B.G., Cameron, E.K., and L.S. Standring, 1992. Chromosome numbers, karyotypes, and nuclear DNA variation in *Pratia* Gaudin (Lobeliaceae). *New Zealand Journal of Botany* 30, pp. 181-187.
- New Zealand Plant Conservation Network (NZPCN), 2017. *New Zealand's Flora*, [online]. Available at <<http://www.nzpcn.org.nz/page.aspx?flora>> [Accessed 13 January 2017].
- Reeves, G. *et al.*, 2001. Molecular systematics of Iridaceae: evidence from four plastid DNA regions. *American Journal of Botany* 88(11), pp. 2074-2087.
- Rendle, H. and B.G. Murray, 1989. Chromosome relationships and breeding barriers in New Zealand species of *Ranunculus*. *New Zealand Journal of Botany* 27, pp. 437-444.
- Rudall, P., 1984. Taxonomic and evolutionary implications of rhizome structure and secondary thickening in Iridaceae. *Botanical Gazette* 145(4), pp. 524-534.
- Sanders, R.W., Stuessy, T.F., and R. Rodriguez, 1983. Chromosome numbers from the flora of the Juan Fernandez Islands. *American Journal of Botany* 70, pp. 799-810.

- Sanmartin, I. and P. Ronquist, 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. *Systematic Biology* 53(2), pp. 216-243.
- Shaw, J., 2015. An overview of *Libertia*. *Plantsman: New Series* 14(2), pp. 104.
- Skottsberg, C., 1915. Notes on the relations between the floras of Subantarctic America and New Zealand. *The Plant World* 18(5), pp. 129-142.
- Smith, J.M.B., 1975. Notes on the distributions of herbaceous angiosperm species in the mountains of New Guinea. *Journal of Biogeography* 2(2), pp. 87-101.
- Sprenkel, C., 1824. *Linnaeus Systema Vegetabilium ed. 16 vol. 1*.
- Stebbins, G. L., 1971. *Chromosomal evolution in higher plants*. London, Edward Arnold Publishers Ltd.
- Tillich, H., 2003. Seedling morphology in Iridaceae: indications for relationships within the family and to related families. *Flora* 198, pp. 220-242.
- Thorne, R.F., 1972. Major disjunctions in the geographic ranges of seed plants. *The Quarterly Review of Biology* 47(4), pp. 365-411.
- Thorsen, M.J., Dickinson, K.J.M., and P.J. Seddon, 2009. Seed dispersal systems in the New Zealand flora. *Perspectives in Plant Ecology, Evolution and Systematics* 11, pp. 285-309.