A SYNOPSIS OF THE GENUS *PLANTAGO* L. IN TASMANIA

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(with one table)

An account of the genus *Plantago* in Tasmania is presented. The taxonomic, biogeographic and cytological relationships of the genus are reviewed. Current knowledge on ecological and cytological data for the Tasmanian taxa is included and a key to the Tasmanian species is presented.

Key Words: *Plantago*, cytology, breeding systems, taxonomy, Tasmania.

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INTRODUCTION

The family Plantaginaceae is composed of rosulate annual or perennial herbs and contains three genera: *Bougueria*, *Littorella* and *Plantago*. The flowers are usually in heads or spikes, bracteate, hermaphrodite, regular and predominantly anemophilous. The floral structure is described in detail in Curtis (1967), Willis (1973) and Briggs *et al.* (1977), and is characterised by: sepals four, (±) free, imbricate, diagonal, equal or unequal, persisting in the fruiting stage; a gamopetalous corolla with 3 or 4 imbricate and membranous lobes. The ovary is superior, 2-capellary (sometimes 1-capellary), (1)2-locular, sometimes up to 4-locular by the development of false septa. The fruit is a membranous capsule with circumscissile dehiscence (*Plantago*) or an indehiscent, one-seeded nut (*Littorella*, *Bougueria*).

The family occurs throughout the temperate and cold temperate regions of the world, including mountains of the tropics. The genus *Littorella* has one species in each of North America, South America and Europe. *Bougueria* is a monotypic genus restricted to the Andes. The genus *Plantago* contains about 260 species, of which 200 can be considered as local or regional endemics (i.e. occupying a limited range), and only 29 have a wide or discontinuous range (Good 1965). The genus therefore exhibits a fairly high degree of speciation apparently arising from geographical isolation.

CLASSIFICATION OF THE PLANTAGINACEAE

The affinities of the Plantaginaceae are not clear and, on the basis of the morphological characters, the family has been placed variously in the Scrophulariales near the Scrophulariaceae (Lawrence 1951, De Wit 1965, Takhtajan 1969, Willis 1973, Dahlgren 1975), in the Primulales (Bessey 1897) and in the Bignoniales (Thorne 1968). On the other hand, a number of authors consider that it belongs in the separate order Plantaginales (Bentham & Hooker 1862–83, Engler 1954 [quoted in Willis 1973], Benson 1957, Hutchinson 1959, 1969, Cronquist 1968).

The first systematic classification of the family was published by Barneoud (1845), who recognised three genera and subdivided the genus *Plantago* into six sections. Decaisne (1852) subsequently divided this genus into 17 sections. Engler & Prantl (1897) recognised 12 sections within *Plantago*; these were divided among two subgenera, one of which contained a single section. Pilger's (1937) classification recognised two subgenera within *Plantago*: *Euplantago*, with 247 species divided among 18 sections, and *Psyllium*, containing 13 species in a single section.

In Australia, only two of Pilger's sections (*Oliganthos*, *Mesembrynia*) are represented by native species. Briggs *et al.* (1973, 1977) reviewed the taxonomy of some of these species using cytological and morphological criteria. They stated that considerable revision of Pilger's classification is necessary and, in particular, they queried the division of the Australian species into two sections. Examples of species which combine "diagnostic" characteristics of both sections are not infrequent, and they cite as typical *P. cladarophylla*, a species which exhibits considerable similarity to some members of section *Oliganthos* whilst having fruit characters typical of *Mesembrynia*.

Species of the section *Oliganthos* are characterised by a bilocular ovary which has four to many ovules per loculus. Members of section *Mesembrynia* have a trilocular ovary which is formed by the development of a false septum. Some discrepancies from this classification have been found in the Tasmanian species, both by Curtis (1967) and during the present study. For example, *P. debilis*, *P. varia*, *P. bellidioides* and *P. antarctica* are assigned to section *Mesembrynia* by Pilger, but Curtis (1967) stated that *P. debilis* has a bilocular ovary, and that the presence of a trilocular ovary is not constant in the other three species. These observations have been confirmed in the present study but, for convenience, the classification of Pilger has been retained for the present.

PLANTAGO IN TASMANIA

Eighteen species and a number of varieties and subspecies have been recorded for Tasmania at various times, but I have not been able to confirm the presence of *P. muelleri*. Four species are introduced: *P. lanceolata*, *P. major* and *P. coronopus* are of Eurasian origin whilst *P. australis* is from South America. Six of the native species are endemic to Tasmania (*P. glabrata*, *P. daltonii*, *P. paradoxa*, *P. bellidioides*, *P. gunnii* and *P. tasmanica*). Four of the species also occur on the Australian mainland (*P. varia*, *P. hisipida*, *P. debilis*, *P. antarctica*). *Plantago triantha* has a disjunct distribution, being found in Tasmania and on some of the offshore islands of New Zealand.

Some Tasmanian specimens of *P. glabrata* bear a strong superficial resemblance to the mainland species *P. alpestris* and *P. euryphylla*, but they differ in important respects. More detailed study is required to determine the status of these morphs.

The Tasmanian species fall fairly naturally into altitudinal groupings, and to some extent reflect differences in effective rainfall. Thus the coastal species *P. triantha* is restricted to the west and southeast coasts, and is replaced in similar habitats on the north and east coasts by *P. hispida*. With the possible exception of the introduced *P. major*, which preferentially grows in fertiliser-enriched pastures and lawns, and the cushion plant-epiphyte *P. gunnii*, the species do not appear to be specifically associated either with soil type or geological substrate. For example, *P. tasmanica* is restricted to the upland areas of Tasmania, and grows on sedimentary rocks of Permian age on Mt Maurice in northeastern Tasmania, on the Jurassic dolerite of the Central Plateau and southern mountains, and on Precambrian metaquartzites on Frenchmans Cap in the west.

The nomenclature used here for the Tasmanian species is essentially that of Curtis (1967). However, the review of New South Wales representatives by Briggs *et al.* (1973, 1977), and field and herbarium investigations during the present study have resulted in changes to the treatment by Curtis (see below).

A key to the genus in Tasmania is presented opposite.

SYNOPSIS OF SPECIES

The species are listed below according to Pilger's (1937) classification, with the exception of *P. australis* which has been placed in section *Virginica* by Rahn (1974).

Section Polyneuron

1. *Plantago major* L.

Description: Curtis (1967), Briggs et al. (1977).

Habitat: A widespread weed which is confined largely to fertiliser-enriched lawns and pastures in lowland areas.

Chromosome number: 2n = 12.

Distribution: Introduced, native in Europe and Asia.

Section Oliganthos

2. *Plantago tasmanica* Hook.f. ssp. *tasmanica* W.M. Curtis

Description: Curtis (1967), but see Brown (1981).

Habitat: Occurs in a wide range of habitats (*Astelia alpina* wet bogs, open shrublands, bare areas) in alpine Tasmania.

Chromosome number: 2n = 12.

Distribution: Tasmania (Victoria).

Comments: Although not listed as such by Curtis (1967), this species appears to be endemic to Tasmania. Reports of its occurrence in Victoria (e.g. Curtis 1967, Willis 1972) probably have resulted from confusion with *P. alpestris* (B. Briggs, pers. comm.). Its taxonomic status has been clarified by Brown (1981), using morphometric, seed germination and ecological characteristics. In that paper, the specific rank of *P. daltonii* was retained but varietal rank for *P. tasmanica* var. *tasmanica* and *P. tasmanica* var. *archeri* was recommended.

A KEY TO THE TASMANIAN SPECIES OF *PLANTAGO*

1\. Flowers cleistogamous (corolla lobes erect, appressed, persistent, anthers not exserted .... *P. australis*

1\. Flowers chasmogamous (corolla lobes spreading, anthers exserted) 2

2\. Scapes furrowed, anterior sepals fused for at least 1/2 their length .... *P. lanceolata*

2\. Scapes not furrowed, anterior sepals free ± to base 3

3\. Keels of posterior sepals winged 4

3\. Keels of posterior sepals not winged 5

4\. Scapes slender, 0.5–1.8 mm diam., mostly longer than leaves; bracts mostly longer than sepals; keel of anterior sepals ± equal to membranous margins .... *P. coronopus* ssp. *coronopus*

4\. Scapes stout, 1.3–2.3 mm diam., shorter than or equal to leaves; bracts mostly shorter than or equal to sepals; keel of anterior sepals much broader than membranous margins...... *P. coronopus* ssp. *commutata*

5\. Leaves broadly ovate, with 5–7 ± equal veins and narrowed abruptly to a long winged petiole; capsules with 8–16 seeds .... *P. major*

5\. Leaves either not 5–7 nerved, *or* having capsules with 2–5 seeds 6

6\. Rootstocks short and lateral roots spreading......... 7

6\. Taproots long (sometimes branched) 13

7\. Plants with thick leaves which are densely tomentose, shortly petiolate; spikes cylindrical; seeds pigmented a deep, matte, purple-brown 8

7\. Plants with leaves glabrous or sparingly hispid, *or* if tomentose, then spikes capitate and seeds pale brown, glistening.........9

8\. Fruiting scapes approximately twice leaf length ....*P. tasmanica* var. *tasmanica*

8\. Fruiting scapes scarcely as long as the leaves ....*P. tasmanica* var. *archeri*

9\. Leaves spathulate with an indumentum of long pilose hairs spread evenly over the upper surface. Small plants growing in alpine cushion plants.........*P. gunnii*

9\. Leaves ± glabrous, or with hairs confined to bands on the upper surface 10

10\. Scapes (sub-)sessile at anthesis......... 11

10\. Scapes elongate at anthesis......... 12

11\. Plants with an axillary tuft of golden brown hairs; leaves glabrous; seeds (1–)4 ....*P. muelleri*

11\. Plants with an axillary tuft of silvery-white hairs (if present); leaves with bands of hairs ± across the blade; seeds (4–)8 .... *P. paradoxa*

12\. Flowers crowded in a cylindrical (but sometimes reduced) spike; petioles about as long as the blade; axillary hairs silvery-white and with a tuft of hairs in the axil of the bract......... *P. daltonii*

12\. Flowers (1–)2–3(–5) on a capitate spike; petioles shorter than the blade; axillary hairs golden brown; tuft of hairs absent from the axil of the bract.........*P. glacialis*

13\. Leaves ± glabrous, fleshy, 3–5 cuspid, bracts and sepals glabrous; plants of coastal rocks......*P. triantha*

13\. Leaves, bracts and/or sepals pilose 14

14 Keels of the bracts and sepals pilose......... 15

14\. Keels of sepals ± glabrous; bracts glabrous or with fimbriate-iliate margins 18

15\. Bracts minute, or if long, then less than half the calyx length; hairs in leaf axils short, whitish or pale yellow-brown .... *P. hispida*

15\. Bracts greater than half sepal length; hairs in leaf axils long, tufted, deep golden brown 16

16\. Leaves broadly obovate, anterior sepals, 1.8–2 mm long, narrowly elliptic; bracts ± 2/3 sepals .... *P. bellidioides*

16\. Leaves linear to lanceolate; anterior sepals 2.8–3.5 mm long, broadly elliptic-obovate; bracts ± equal sepals 17

17\. Leaves narrow-elliptic to lanceolate, pilose, length 5–10 times the breadth ....*P. varia*

17\. Leaves linear to narrow elliptic ± glabrous, length more than 15 times than breadth ....*P. gaudichaudii*

18\. Bracts fimbriate-ciliate, as long or longer than the calyces .... *P. glabrata*

18\. Bracts entire, shorter than the calyx.........19

19\. Scapes slender bearing interrupted spikes of small, distant flowers ....*P. debilis*

19\. Spikes dense; flowers closely imbricate .... *P. antarctica*

3. *Plantago tasmanica* Hook.f. ssp. *archeri* (Hook.f.) W.M. Curtis

Description: Curtis (1967) but see Brown (1981).

Habitat: Occurrence as *P. tasmanica* var. *tasmanica.*

Chromosome number: 2n = ?

Distribution: Endemic.

4. *Plantago daltonii* Decne

Description: Curtis (1967), but see Brown (1981).

Habitat: Edges of streams, lakes and sites of frequent flooding in sub-alpine and alpine Tasmania. Also on river banks to sea level on the west coast.

Chromosome number: 2n = 12.

Distribution: Endemic.

5. *Plantago paradoxa* Hook.f.

Description: Curtis (1967), but see Brown (1983).

Habitat: Grasslands, herbfields in depressions and margins of lakes and streams of sub-alpine and alpine areas, river banks to sea level on the west coast. Also found in bolster moor communities.

Chromosome number: 2n = 48.

Distribution: Endemic.

6. *Plantago gunnii* Hook.f.

Description: Curtis (1967).

Habitat: Found only in bolster moor communities on the dolerite mountains of Tasmania.

Chromosome number: 2n = 36.

Distribution: Endemic.

7. *Plantago triantha* Sprengel

Description: Curtis (1967).

Habitat: A halophyte which colonises salt-spray zones of coastal rocks in northwest, west and southeast Tasmania.

Chromosome number: 2n = 12.

Distribution: Tasmania, New Zealand.

8. *Plantago muelleri* Pilger

Description: Briggs *et al.* (1977).

Habitat: See remarks below.

Chromosome number: 2n = ? Briggs (1973) reports 2n = 36 for NSW plants. W.D. Jackson (pers. comm.) found 2n = 12 in plants from the ACT, but his voucher specimens are *P. glacialis.*

Distribution: NSW, not confirmed for Tasmania.

Comments: I have not seen any of Curtis' material, but her description of *P. muelleri* (Curtis 1967) differs from typical *P. muelleri* in having scapes which are elongated at anthesis. It appears to be nearer to *P. glacialis*, a species formerly included in *P. muelleri.* However, both *P. muelleri* and *P. glacialis* have a tuft of golden-brown hairs in the leaf axils, a character not mentioned by Curtis. *P. muelleri sensu* Curtis (1967) has bracts "about as long as the calyces, elliptical, mucronulate" whereas *P. glacialis* has bracts "triangular acute 1.5–3mm long" and sepals "2–2.2mm long" (Briggs *et al.* 1977).

The description given by Curtis is most similar to depauperate specimens of *P. daltonii.* In the field, such plants are characterised by short scapes with flowers frequently reduced to 1(–4) to a head, but on transplantation they assume the typical *P. daltonii* form. These plants occur in alpine areas, frequently forming mats in habitats similar to those described by Curtis for *P. muelleri.* The situation is further confused by the occurrence of forms of *P. paradoxa* which accord closely with the vegetative descriptions of *P. muelleri sensu* Curtis, but which, in respect of floral characters and on transplantation, are "good" *P. paradoxa.* Clearly the status of *P. muelleri sensu* Curtis requires clarification. For clarity, *P. muelleri sensu* Briggs *et al.* (1977) has been included, but its presence in Tasmania remains unconfirmed.

9. *Plantago glacialis* Briggs, Carolin et Pulley

Description: Briggs *et al.* (1977)

Habitat: Forms mats in apine areas, found at Mt Rufus and Mt Geryon in Tasmania.

Chromosome number: 2n = ? Briggs (1973) and Jackson (see 8. above) report 2n = 12 for mainland material.

Distribution: Tasmania, NSW, Victoria.

Comments: The Tasmanian specimens bear strong resemblance to some forms of *P. paradoxa*, which exhibits considerable phenotypic plasticity (Brown 1983). The status of the Tasmanian populations could be clarified by chromosome counts since *P. paradoxa* has 2n = 48 and *P. glacialis* has 2n = 12.

Section Coronopus

10. *Plantago coronopus* L. ssp. *coronopus*

Description: Curtis (1967), Briggs *et al.* (1977), Briggs B. G. (ined).

Habitat: A widespread weed, naturalised in dunes, swales and saltmarshes.

Chromosome number: 2n = 10.

Distribution: Introduced, native in Europe and Asia.

11. *Plantago coronopus* L. ssp. *comutata* (Guss.) Pilger

Description: B. G. Briggs (pers. comm.), Pilger (1937).

Habitat: Recorded from the Jordan River and the South Esk River at Perth.

Chromosome number: 2n = ?

Distribution: Introduced, native of southern and eastern Mediterranean region.

Section Virginica

12. *Plantago australis* Lam.

Description: Rahn (1974).

Habitat: Naturalised in pastures, dune swales and ruderal areas of lowland western Tasmania.

Chromosome number: 2n = ? Rahn (1974) reported 2n = 24, 48 for South American plants.

Distribution: Introduced from South America.

Comments: This species contains a number of subspecies (Rahn 1974). A Tasmanian specimen at Kew has been identified by Rahn as *P. australis* spp. *cumingiana* (B. G. Briggs, pers. comm.), but specimens at MELB (B. G. Briggs, pers. comm.) and those at HO key to *P. australis* spp. *sodiorana*.

Section Mesembrynia

13. *Plantago varia* R. Br.

Description: Briggs *et al.* (1977).

Habitat: Widespread on the dry plains and rocky slopes of the eastern half of the state in grassland, savanna woodland and dry sclerophyll communities.

Chromosome number: 2n = 24 (Brown and Jackson 1982). Curtis (1967) reported 2n = 12, 24. All of the Australian mainland plants studied by Briggs (1973) were 2n = 24.

Distribution: Tasmania, temperate Australia.

14. *Plantago debilis* R. Br.

Description: Curtis (1967), Briggs *et al.* (1977).

Habitat: Localised in dry sclerophyll forests in northeastern Tasmania.

Chromosome number: 2n = 12.

Distribution: Tasmania, Victoria, NSW, Queensland, South Australia, and southern parts of the Northern Territory.

15. *Plantago bellidioides* Decne.

Description: Curtis (1967).

Habitat: Common in dune herbfields and grasslands of northeastern and northwestern or western Tasmania.

Chromosome number: 2n = 12.

Distribution: Endemic.

16. *Plantago hispida* R. Br.

Description: Briggs *et al.* (1977).

Habitat: Widespread in grasslands and *Allocasuarina stricta* low open forests along the coastal cliffs and rocky headlands of north, east and southeast Tasmania.

Chromosome number: 2n = 12.

Distribution: Tasmania, temperate Australia.

Comments: Since the work by Curtis (1967), this species has been returned to specific rank by Briggs *et al.* (1973). In Tasmania, the species is very much habitat limited, and shows consistent morphological variation from its nearest ally, *P. varia*. The differentiation is maintained when plants of the two species are grown in a common environment.

17. *Plantago antarctica* Decne.

Description: Curtis (1967), Briggs *et al.* (1977).

Habitat
Local in sub-alpine and alpine grasslands of the Central: Plateau and North-East.

Chromosome number: 2n = 12.

Distribution: Tasmania, Victoria, NSW.

Comments: See comments under *P. glabrata*.

18. *Plantago gaudichaudii* Decne.

Description: Briggs *et al.* (1977).

Habitat: Grassy dry sclerophyll.

Chromosome number: 2n = 24. Briggs (1973) reports 2n = 12, 24, 36 for mainland plants.

Distribution: Recorded from Rosny Esplanade (MJB) and by L. Rodway in 1928 from Blackmans Bay in Tasmania, temperate Australia.

Comments: This species is not included by Curtis (1967).

19. *Plantago glabrata* Hook.f.

Description: Curtis (1967).

Habitat: Sub-alpine grasslands and shrublands of the Central Plateau and Eastern Tiers.

Chromosome number: n = 12, 2n = 24; found in both the narrow- and broad-leaf variants of this species.

Distribution: Endemic.

Comments: This species typically shows the development of a trilocular ovary and should be referred to section *Mesembrynia* pending a review of Pilger's classification.

Some forms of *P. glabrata* may be mistaken for *P. antarctica* if the key characters given by Curtis (1967) are used to identify them, viz. "leaves with 3–7 almost equal parallel veins" (*P. antarctica*) or "leaves with midrib distinct but lateral veins not, or scarcely conspicuous" (*P. glabrata*). Consequently, some common variants of *P. glabrata* which have broad leaves would key to *P. antarctica* on the basis of the above characteristics. However, the two species have different chromosome numbers (*P. antarctica*, 2n = 12; *P. glabrata*, 2n = 24) and can be more satisfactorily distinguished as follows. *P. glabrata* has leaves with an elongate, narrow petiole and floral bracts which have fimbriate-ciliate margins and are as long or longer than the calyces. *P. antarctica* has leaves which narrow gradually to a short, broad petiole and floral bracts which have entire margins and are only $^1/_2$ to $^3/_4$ as long as the calyces. These characteristics can readily be used to distinguish plants in the field, because the bracts and sepals are persistent in both species and old scapes remain on the plants for most of the year.

P. glabrata exhibits both within population and clinal variation in leaf-form across the Central Plateau, the cline being correlated with precipitation rather than temperature (Brown 1979). The westernmost narrow and broad leaf-forms exhibit close morphological resemblances to the upland mainland Australian species *P. alpestris* and *P. euryphylla* respectively (Briggs *et al.* 1973, 1977, Costin *et al.* 1979.) However, these two species differ from *P. glabrata* in the following respects: both mainland species lack the development of the trilocular ovary typical of *P. glabrata*, neither species produces the long, persistent tap-root of *P. glabrata* and the diploid chromosome number of both species is 2n = 12, whereas *P. glabrata* has 2n = 24. Further study is required to determine whether the western morphs of *P. glabrata* warrant specific recognition.

Section Arnoglosum

20. ***Plantago lanceolata*** **L.**

Description: Curtis (1967), Briggs *et al.* (1977).

Habitat: Widespread in lawns, pastures, roadsides and rough grazing areas. In some areas, e.g. Mt Nelson, the species is invading woodlands occupied by *P. varia*.

Chromosome number: 2n = 12.

Distribution: Introduced, native in Europe and Asia.

DISCUSSION

Cytology

Cytological studies (e.g. McCullagh 1934) have been of little assistance in demonstrating affinities at the family level, although they have been valuable in suggesting probable lines of diversification within the genus *Plantago*.

There appear to be at least three series of multiple chromosome numbers in the genus. The probable primitive base number is x = 6, giving rise to the polyploid series 12, 24, 36, 48 and 72. The other two series appear to derive from aneuploids, with bases x = 5 (2n = 10, 20, 30) and x = 4 (2n = 8, 16) (McCullagh 1934, Maude 1939, Rahn 1957, Bassett 1967, Groves & Hair 1971, Briggs 1973, Brown & Jackson 1982).

Polyploid races are known to occur within some species of the genus, but the occurrence of polyploidy does not appear to be well correlated with morphological variation at either the intra or interspecific level. For example, Rahn (1974) found that polyploid races of *P. australis* (2n = 24, 48) did not exhibit obvious morphological differences, and a similar result was found by Briggs (1973) for *P. gaudichaudii* (2n = 12, 24, 36). Bassett & Crompton (1968) found no overall correlation between chromosome number and pollen size of North American taxa. Bocher *et al.* (1953, 1955), in an investigation of the cytogeographic variation of *P. coronopus*, found diploid and hexaploid races within the species, but found that the morphological differences between the ploidy levels were less than those observed among the races of the diploid type. McCullagh (1934) found some agreements between chromosome number and Decaisne's division of the genus (1852).

The consensus of these reports has been put succinctly by Briggs (1973):

> "Polyploidy is fairly common, but the primary diversification within the genus has apparently not been accompanied by change of either base number or level of ploidy."

The chromosome numbers of the Tasmanian representatives of the genus *Plantago* are given in table 1. Polyploids occur in both sections of the genus native to Tasmania. In section *Oliganthos*, reported chromosome numbers are 2n = 12 *(P. tasmanica, P. daltonii, P. triantha)*, 2n = 36 *(P. gunnii)* and 2n = 48 *(P. paradoxa)*. In section *Mesembrynia*, the species are either 2n = 12 *(P. debilis, P. bellidioides, P. hispida, P. antarctica)* or 2n = 24 *(P. varia, P. glabrata)*. Curtis (1967) reports diploid (2n = 12) and tetraploid (2n = 24) populations of *P. varia* in Tasmania, but Briggs (1973) found that all of the Australian mainland plants studied were tetraploid. Brown and Jackson (1982) found only 2n = 24 in *P. varia* from Tasmania.

Breeding Systems

The genus has hermaphrodite flowers which are protogynous, largely wind-pollinated and outbreeding, although exceptions do occur. Thus *P. media* produces flowers which are scented, have coloured stamens and are at least partly insect-pollinated. Members of the section *Novorbis* produce cleistogamous flowers and these species were held by Pilger (1937) to be apomictic, although no evidence for this was found by Rahn (1974). Pilger reported dioecy in *P. tubulosa* Decne. and *P. rigida* Kunth., and gynogioecy in *P. lanceolata*.

The occurrence of protogyny provides a measure of facultative outbreeding, at least in the early part of the season, but unless self-incompatability mechanisms are present, selfing can occur by fertilisation of younger inflorescences of the same plant. In a survey of the breeding systems of eleven species of *Plantago*, Ross (1970) found a diversity from facultative inbreeding to obligate outbreeding. Of particular interest was the occurrence of both self-incompatibility mechanisms and gynodioecy in populations of three species. Even more remarkably, it was found that, whilst both self-incompatibility and gynodioecy occurred in populations of *P. maritima* located in Europe, the American populations of the same species were self-compatible and not gynodioecious.

No detailed studies of the breeding systems of the native Tasmanian species have been reported in the literature, but my own field observations suggest that, with the possible exceptions of *P. paradoxa* and *P. gunnii*, all of the species are perennial, protogynous, outbreeding and wind-pollinated. *P. paradoxa* and *P. gunnii* are perennial and protogynous, but produce flowers on scapes which are (sub-)sessile at anthesis, so self-pollination may be more common in these species. However, both species probably are capable of outbreeding to some degree. *P. paradoxa* occupies wet sites where cross-pollination could occur via water-borne pollen. Plants of *P. gunnii* occur within "cushion plants", where they are elevated above the ground surface. Their stamens have versatile anthers on very long filaments so that some wind-pollination is likely.

All of the known native Tasmanian species have been grown in isolation at some stage and all appear to be fully self-compatible. No evidence for gynodioecy was found in any of the species. Populations of some members of section *Mesembrynia* (*P. glabrata*, *P. varia*, *P. hispida*, *P. debilis*, *P. bellidioides*) appear to show polymorphism in flowering time, but this does not occur in species from section *Oliganthos* (*P. paradoxa*, *P. triantha*, *P. daltonii*) or in the introduced species (*P. lanceolata*, *P. major* and *P. australis*) (Brown 1979).

In the field, flowers are produced during spring–summer (September–January) in all species, and seed-set occurs from late spring to the end of summer (November–February). It is probable that all species produce only one generation per year, although it may be possible for an early flowering phenotype to produce plants which set seed prior to the onset of winter. This aspect of the life cycle of the species requires further study.

Phenotypic Modification

Many of the species exhibit extensive phenotypic plasticity (Marsden-Jones & Turrill 1930–45, Salisbury 1952, Gregor & Watson 1961, Brown 1979, 1981, 1983) and some of the habitat-induced modifications have been shown to correspond closely to previously described infra-specific taxa. Thus Marsden-Jones & Turrill (1939–45) were able to demonstrate the correspondence between edaphically induced modifications of *P. major* and varieties described by Pilger (1937). Similarly, Salisbury (1952) showed that the form adopted by plants described as *P. coronopus* var. *pygmaea* was habitat-induced as, on transplanting, the plants assumed the "typical" form of *P. coronopus*. However, Bocher *et al.* (1955) also demonstrated that in some cases this dwarf form is genetically fixed. Brown (1979, 1983) demonstrated a similar propensity for phenotypic plasticity and stability in *P. paradoxa*.

Ecotypic and ecoclinal variation in a variety of characters has been demonstrated for a number of species. Much of this variation is genetically based. Gregor (1930) found quantitative differences in the spike:scape length ratio in *P. maritima* from different habitats were under genetic control. Groot & Boschhuizen (1970) have found heritable differences of leaf-form along populations of *P. major* and Bocher *et al.* (1955) found that geographically distinct races of *P. coronopus* are maintained genetically.

From the examples given here it can be seen that, within a single species of the genus, there are characters capable of exhibiting morphological differences which are habitat-correlated, and which may simultaneously be genetic in origin and yet exhibit plastic modification.

The studies by Brown (1979, 1981, 1983) demonstrated a widespread capacity for phenotypic and more directly genetically-based variability in the Tasmanian species of *Plantago*. For example, there is evidence of ecotypic variation in *P. tasmanica* and ecoclinal variation in *P. glabrata*, the variation being made manifest in a range of vegetative, floral and ecophysiological characteristics. Of particular significance is the ability exhibited by many species to produce canalised phenotypic responses, which frequently may mask underlying genetic variation. Such variability or apparent lack thereof makes the task of the field botanist and the taxonomist particularly difficult!

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TABLE 1
Chromosome Numbers of Tasmanian *Plantago* Species

Chromosome number		**Species**	**Authority***
n	2n		
–	10	*P. coronopus*	2, 4†
		P. major	2, 4†
		P. lanceolata	2, 4†
		P. tasmanica var. *tasmanica*	4†
		P. daltonii	4†
		P. triantha	4†
–	12	*P. glacialis*	2, 4
		P. debilis	2, 4†
		P. bellidioides	5†
		P. hispida	2, 4†
		P. antarctica	2, 4†
–	24	*P. varia*	2, 4†
		P. glabrata	4†
–	36	*P. gunnii*	4†
		P. muelleri	2
–	48	*P. paradoxa*	4†
–	12, 24	*P. varia*	1†
–	12, 24, 36	*P. gaudichaudii*	2
–	24, 48	*P. australis*	3
12	24	*P. glabrata* (narrow leaf form)	4†
12	24	*P. glabrata* (broad leaf form)	4†

* Authority: 1 – Curtis (1967); 2 – Briggs (1973); 3 – Rahn (1974); 4 – Brown & Jackson (1982).

† Determinations made on Tasmanian material.