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egory J. Kenicer

University of Edinburgh, 2007

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Systematics and biogeography of *Lathyrus* L. (Leguminosae, Papilionoideae)

Gregory J. Kenicer

Doctor of Philosophy

The University of Edinburgh

2007

This thesis is dedicated to the late Dr Philip Smith

'like the Nepenthe of the Greeks, [Lathyrus linifolius] *exhilarates the mind'*

Thomas Pennant
A Tour in Scotland (1774)

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Declaration

I composed this thesis; the work is my own and has not been submitted for any other degree or professional qualification except as specified.

[redacted]

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Abstract

Lathyrus (Leguminosae, Papilionoideae) is the largest genus in tribe Fabeae and exhibits an intriguing extratropical distribution. This thesis presents a series of studies on the systematics and biogeography of *Lathyrus* and allied taxa at three taxonomic levels: (1) in tribe Fabeae, (2) in the genus *Lathyrus*, and (3) in section Notolathyrus.

The phylogenetic position of *Lathyrus* relative to the rest of tribe Fabeae (*Pisum* L., *Vicia* L., *Lens* Mill. and *Vavilovia* Al. Fed.) was estimated based on Bayesian and maximum parsimony analysis of DNA sequence data from the chloroplast *mat*K region. This study included 24 species of *Lathyrus* (including 19 newly sequenced) and is the first molecular phylogenetic investigation to include the monotypic genus *Vavilovia*. A clade containing *Lathyrus*, *Pisum* and *Vavilovia* is strongly supported as monophyletic. The results support the existing morphologically based hypothesis that *Pisum* and *Vavilovia* are sister genera. However, they are nested within *Lathyrus*, which may force a reappraisal of generic delimitations among this group and, significantly, synonymisation of *Pisum* into *Lathyrus*. *Lathyrus clymenum* (section Clymenum) is resolved as the sister group to the entire *Pisum–Lathyrus–Vavilovia* clade.

To study relationships within *Lathyrus*, accessions representing 53 of its species were sequenced for the internal transcribed spacers and 5.8S-coding region of nuclear ribosomal DNA, and the chloroplast *trn*L–F and *trn*S–G regions. These regions were also sequenced for *Pisum sativum* and three *Vicia* species. The position of *Pisum* is equivocal, nested inside *Lathyrus* in the Bayesian analysis and as sister to it in the maximum parsimony analysis. Most *Lathyrus* sections are centred on the Mediterranean region, which is indicated by the phylogeny to be the area of origin for the genus. Sections Orobus, Aphaca and Pratensis form a northern Eurasian–New World clade. Within this clade, the North American and eastern Eurasian species, including both Holarctic species (*L. palustris* and *L. japonicus*), form a transberingian clade of relatively recent origin and diversification.

In each phylogenetic analysis, the predominantly South American Notolathyrus group is resolved as monophyletic and unrelated to the transberingian clade. This provides support for long-standing morphologically based hypotheses that section Notolathyrus is a natural grouping and refutes the traditional view that the South American species of *Lathyrus* are derived from the extant North American–East Asian lineage. The South American lineage may be derived from long-distance dispersals from Eurasia. A synoptic revision provides the first taxonomic treatment to cover all members of section Notolathyrus. The treatment recognises 26 species endemic to South America, plus a subspecies of *L. pusillus* extending to the south-eastern USA. One species (*L. woodii* Kenicer) is described as new. Key morphological characters in species delimitation include presence or absence of dense pubescence on the ovary, structure of styles (bifid versus simple), stipule shape, and the colour of dry fruits and vegetative organs in herbarium specimens.

1

Thesis overview

Tribe Fabeae is based on Reichenbach's (1832), genus *Faba* (now treated under *Vicia*) which is the type genus of the Fabaceae (Leguminosae). The tribe is defined by its adaxially pubescent styles, leaves with terminal tendrils, unusual stem vasculature supplying the stipules, and several floral characters (Kupicha, 1974, 1977, 1981; Lavin & Delgado, 1990; Lock & Maxted, 2005). It is a well-established member of the 'temperate herbaceous' papilionoid legume clade (Gunn 1969, Polhill 1981, Lewis et al. 2005) and is distributed throughout the temperate northern hemisphere and temperate South America, but with most generic and species-level diversity in the Mediterranean. Its position as a recently evolved (Miocene), monophyletic group occupying a highly derived position in the legumes is generally accepted (Wojciechowski et. al., 2000; Steele &Wojciechowski, 2003; Lock & Maxted, 2005; Lavin et al., 2005). As well as a monotypic genus *Vavilovia*, Fabeae contains the peas (*Pisum* – 3 spp.), lentils (*Lens* – 5-6 spp.), true vetches (*Vicia* c.150 spp.) and the sweet peas and chickling vetches (*Lathyrus* c.160 spp.), and is a group of major economic importance. A thorough understanding of relationships among the taxa in tribe Fabeae is a critical starting point for any further research into the members of the tribe, whether for agronomic development, investigations of the origins of the Mediterranean and other temperate biomes, or studies of developmental genetics.

Elements of tribe Fabeae have been treated by many authors. These treatments have almost always considered only limited taxonomic groups, such as sections of

Lathyrus (e.g. Bässler, 1966, 1973, 1981), although Kupicha (1974, 1977; Clarke & Kupicha 1976) investigated the delimitations of the tribe, its genera (Kupicha 1974, 1981) and the sections of its two largest genera - *Vicia* (Kupicha, 1976) and *Lathyrus* (Kupicha, 1983). These studies were predominantly based on morphology. Since then, some molecular studies using amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP) and DNA sequencing techniques have examined relationships among members of the tribe or within *Lathyrus*. These molecular studies have had a limited taxonomic or geographical scope – predominantly focussing on *Lathyrus* sect. *Lathyrus* and its allies (Croft et al., 1999; Chtourou-Ghorbel et al., 2001; Badr et al., 2002; and Ben Brahim et al., 2002). The exceptions are Steele & Wojciechowski's (2003) work on tribes Fabeae and Trifoleae, and the study of Asmussen & Liston (1998) on the whole of *Lathyrus*. Steele & Wojciechowski (2003) demonstrated the monophyly of the tribe, and although their analysis included representatives of four of the five genera in Fabeae, only ten of the 220 or so species in the tribe were represented. Asmussen & Liston's (1998) work included around one third of the species of *Lathyrus*, and provided support for many of Kupicha's (1983) sections.

This thesis tests the morphology based classifications of Kupicha (1974, 1976, 1981, 1983) and expands the existing molecular systematic research at the tribal level in Fabeae and within *Lathyrus*. *Lathyrus*, the largest genus in the tribe, is the main focus for study of phylogenetic, biogeographical and systematic patterns. As an introduction to the genus, chapter two discusses the origin of its name and the significance of *Lathyrus* in human history. The distribution, ecological and morphological diversity of the genus are outlined, with a focus on the most important morphological characters for sectional classification in the genus. This is followed by a brief introduction to each of the currently accepted sections in the genus (Kupicha 1983, Asmussen & Liston 1998).

Chapter three places *Lathyrus* in the context of the other genera in tribe Fabeae. In order to assess the generic delimitations of Kupicha (1976, 1981, 1983) I expanded Steele & Wojciechowski's (2003) phylogenetic investigations using sequences of the *matK* gene in tribe Fabeae, including all five of its constituent genera.

Chapter four presents the results of a phylogenetic investigation using DNA sequence data from nuclear and chloroplast genomes to estimate phylogeny in *Lathyrus*. This research provides a comparison with Kupicha's (1983) morphological, and Asmussen & Liston's (1998) chloroplast RFLP-based studies. Questions addressed focus primarily on the existing sectional classifications of the group, which reflect morphological and geographical groupings. The biogeographic history of the genus is also assessed with particular attention to explaining its disjunct, antitropical distribution in temperate regions of the northern and southern hemisphere.

The final chapter provides a taxonomic revision of section Notolathyrus which is almost exclusively endemic to South America. Section Notolathyrus shows nearly as much morphological variation as the entire remainder of the genus and it is widespread throughout the temperate part of the continent. The group has not been the subject of a large-scale revision for more than 60 years and this taxonomic treatment is the first to address the section in its entirety.

In summary, the principal aims of this study were to:

1. Provide improved estimates of phylogenetic relationships of genera in Fabeae and species in *Lathyrus* both by using DNA sequence data from more loci, and by sampling more taxa than in previous studies.
2. Investigate the phylogenetic positions of *Pisum* and *Vavilovia* within Fabeae.
3. Evaluate the monophyly of *Lathyrus.*
4. Estimate the sister group to *Lathyrus.*
5. Evaluate the potential of several traditionally important morphological characters to diagnose monophyletic groups in Fabeae and *Lathyrus*:
    - Adaxial stylar pubescence
    - Reflexed stylar margins
    - Leaflet vernation patterns (conduplicate vs. supervolute)
6. Answer biogeographical questions:
    - Is the Mediterranean region the centre of origin for *Lathyrus*?
    - From where are the N. American species of *Lathyrus* derived?
    - What is the origin of the S. American species of *Lathyrus*?

2

Lathyrus L. (Leguminosae)

2.1 Introduction

This chapter introduces the genus *Lathyrus*, providing an overview of its taxonomic history and diversity. The origin of the generic name and the use of the plants by humans are briefly discussed, and an outline of its distribution and biogeography is given.

Throughout, I have adopted Kupicha's 1983 sectional classification of the genus. This is the most comprehensive classification and the one most widely accepted in recent literature. Recent modifications based on molecular phylogenetic analyses are discussed where relevant, particularly those based on Asmussen & Liston's (1998) chloroplast RFLP-based phylogenetic analysis. Furthermore, Kupicha's classification is generally well supported by the findings presented in chapter 4 of this thesis. The introduction to chapter 4 contains a discussion of the history of infrageneric classification in *Lathyrus*. Please see appendix 1 for a glossary of general morphological terms for tribe Fabeae.

2.2 Origins of the name

Lathyrus is a Linnaean genus (Linnaeus, 1753). The name is almost certainly derived from λα–τουρισ (la-thyris) of Dioscorides and Theophrastus. The 'thyris' element of the name is usually interpreted as 'powerful' or 'vigorous'. The 'la' prefix indicates a diminutive form. It is unclear from the classical descriptions whether this name relates to the vigorous growth habit of a small plant, or some medicinal action, although the latter is more probable. In either case, it is fairly clear that the classical descriptions relate to a different plant from the ones we know as *Lathyrus* today. By far the most likely candidate from the descriptions is *Euphorbia lathyris* L., a powerful purgative.

It is unclear how the name made the transition from a *Euphorbia* to a legume. Throughout the literature there is considerable interchange of names. Dioscorides describes the fruit of lathyris (i.e. the *Euphorbia*) as 'about the size of an ervum seed'. Although 'ervum' was later applied to some members of *Vicia* L., it appears, from Dioscorides' descriptions to have been *Lathyrus sativus* L. in classical times. Dioscorides records ervum as being used to make ervina, or farina ervi, a medicinal flour used as a purgative. Not only were the medicinal actions of ervum and lathyris plants comparable, but Pliny (XXVI: 60, 63) records ervina being mixed with the juice of tithymallus, a coastal spurge to make a substitute for Scamonium, another purgative (Jones, 1992). Thus we have a connection between the appearance of the fruit in *Euphorbia lathyris* and the seed of *Lathyrus sativus*, as well as their medicinal actions.

Many of the accounts following Dioscorides are somewhat vague as to the identity of Lathyris / Lathyrus, perhaps because it was such a commonplace drug. Pliny the Elder's description is appropriately hazy, but sounds rather more like a *Euphorbia* than a modern *Lathyrus* (XXVII: 95; Johnson, 1975):

> *Lathyris folia habet multa lactucae similia, tenuoira, germina multa in quibus semen tuniculis continentur ut capparisque quae cum inaruere eximuntur grana piperis magntiudine, candida, dulcia, facilia purgatu. . .*

> *. . .qui vehementius purgari volunt cum folliculus ipsis summunt ea. . .*
> ‘Lathyris has leaves somewhat like lettuce, although more slender, it has many buds, in which the seeds are covered by tunicae, like a caper. When dry, the seeds are easily removed and are similar in size to a pepper grain, white, sweet and facilitate purging. . .
> . . .those who wish a stronger purge, eat also the follicles [i.e. tunicae]’

Fuchs’s beautifully illustrated herbal (1543) follows the classical authors closely – he applied the name Lathyris solely to the *Euphorbia*, using the name ervum for the modern *Lathyrus sativus*. Turner’s 1551 herbal gives the first indication of some confusion between the two names. He stated that the plant known as fichlynge [i.e. vetchling] or cicercula in English (Chapman & Tweddle, 1995):

> *is called in Greke lathyros*

Johnson, in his 1663 edition (Johnson, 1975) of John Gerard’s herbal appeared to be aware of the confusion, explaining that the plant is:

> *called* Lathyrus*, to make a difference betweene it and* Lathyris*, or Spurge*

In spite of Johnson’s attempt to straighten this problem out, the name *Lathyrus* sensu Turner had stuck and was being used by pre-Linnaean botanists for the tendrilous, bijugate plants now recognised as members of *Lathyrus* sect. Lathyrus. The species initially included by Linnaeus in his genus also correspond largely with the members of the modern sect. Lathyrus.

2.3 Modern distribution of *Lathyrus*

Lathyrus is an almost exclusively temperate genus. Its members are distributed throughout the northern hemisphere, with a disjunction in South America. A few species reach tropical East Africa and of these *Lathyrus hygrophilus* Taubert is the only certain native (ILDIS, 2002) The subtropical and tropical species are typically found in temperate (often montane) habitats. An assemblage of crop, fodder and ornamental species including *L. cicera* L., *L. sativus*, *L. tuberosus* L., *L. latifolius* L. and *L. odoratus* L. are fairly ubiquitous escapes from cultivation worldwide. These examples are all members of sect. *Lathyrus* and the first four have been in cultivation since pre-Classical times. *Lathyrus aphaca* L., *L. hirsutus* L., *L. pratensis* L. and *L. clymenum* L. do very well as weedy aliens and can also be found almost anywhere.

The stronghold of the genus is Western Eurasia, particularly around the Eastern Mediterranean with over a third of the species native to Turkey (Davis, 1970; Fig. 2.1). Secondary centres of diversity are found in East Asia and North and South America. Central Asia has a relative paucity of *Lathyrus* species, with perhaps only five truly native to the Himalaya (Hara & Williams, 1979; Tsui, 1998) and even less on the Indian subcontinent east of Pakistan. Further north, in Siberia, in spite of the low diversity, there are a number of endemic species with cryptic affinities such as *L. pisiformis* L. and *L. humilis* Fischer ex Seringe as well as some with stronger affinities to species in western Eurasia (e.g. *L. mulkalk* Lipsky)

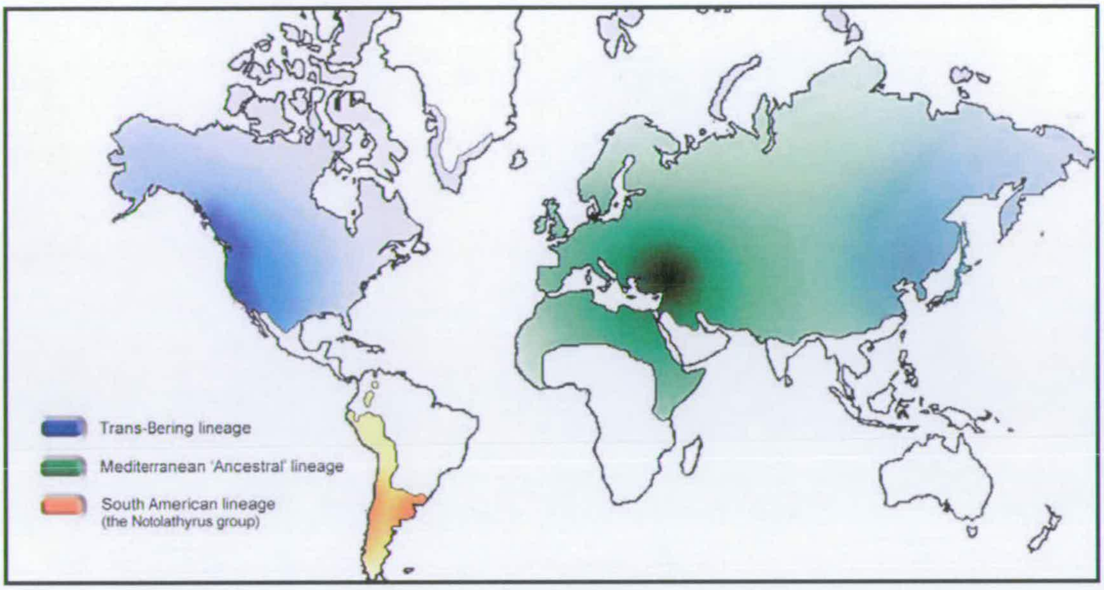


Figure 2.1 Worldwide distribution of *Lathyrus*.
Colour density on this map indicates diversity of species in each area. Colours reflect biogeographic groups recognised in this study (chapter 4).

Both Bässler (1973) and Kupicha (1983) classified all of the East Asian species in the species-rich and morphologically variable sect. Orobus (p.40). The only exceptions are introduced crops, ornamentals and weeds, and the possible native *L. pratensis* (sect. Pratensis p.34). Endemic species in East Asia are found in Siberia and Primorsky as far as Kamchatka; Mongolia and much of China (excluding the subtropical south), and in Japan from Hokkaido to Kyushu. Although they are treated as members of the same section, this East Asian group is comprised of morphologically disparate species (Bässler, 1973; Kupicha, 1983).

Only two species, *L. palustris* L. and the sea dispersed *L. japonicus* Willdenow, are native to both the Old and New Worlds, being distributed across the whole of the temperate Northern hemisphere. The former of these is morphologically similar to a number of the East Asian and North American species, so it may represent one member of a wider group linking the two continents. In North America, the greatest diversity is found in the West, particularly on the shoulders of the Rocky Mountains and in coastal Oregon and California. *Lathyrus pusillus* Elliot is a predominantly South American species that has a disjunction in the Southeastern states of the USA. It is interpreted (Kupicha, 1983) as being distinct from the other North American species and is a part of the South American 'Notolathyrus' group (a section of Kupicha's later included in sect. Orobus by Asmussen and Liston 1998). Section Notolathyrus sensu Kupicha contains 23 species and is represented by five species in the tropical Andes (over 2500m – see p.40, under sect. Orobus). The section is more diverse in the subtropical and temperate lowlands of S. America, where they spread to coastal regions. A total of 24 species is known from subtropical and temperate areas of S. America. Burkart (1937) listed 20 species he believed to be indigenous to Argentina, concentrated mainly in the Paraná river delta, Mediterranean climatic zone (pampa) and on the slopes of the central Andes.

Lathyrus japonicus is the only Eurasian species that extends as far as South America, ranging from the East coast of North America, through Greenland, Iceland, Atlantic Europe and the Barents Sea to Kamchatka, Korea, northern China and Japan. It is common on the Aleutian chain and down as far as coastal Oregon with some populations on the great lakes. The plants of the isolated Chilean localities were believed by Burkart (1937) to be introduced. Although this opinion has gained general acceptance, there is no conclusive evidence and *L. japonicus* is certainly capable of long distance dispersal by sea. Indeed, the seeds are known to remain viable in seawater for up to five years (Nelson, 2000). This particularly widespread distribution has attracted recent attention for population genetic analysis (Conny Asmussen personal communication, Oliver 2005).

Species counts for unequivocal natives from some standard Floras are as follows:

- Flora Europaea (Ball, 1968): 54
- Flora of Turkey (Davis, 1970): 58
- Flora of the USSR (Fedchenko, 1948): 50
- Flora Iranica (Rechinger, 1979): 25
- Flora of China (Kenicer, this thesis, Appendix 2): 14
- North America (Broich, in press): 31
- South America (Kenicer, chapter 5, this thesis): 26

2.4 Cultivation and uses

Lathyrus includes species of prehistoric, historic and modern importance as food crops, fodder plants, ornamentals, medicines, environmental improvers and weeds. In addition, the genus includes some important taxa for agronomic, ecological and genetic research.

2.4.1 *Ornamentals*

Species and cultivars of *Lathyrus* are of major importance in commercial horticulture as ornamentals. More than 70 species of *Lathyrus* (c. 50% of the genus) are commercially available in the UK today and 'sweet pea' clubs are to be found in countries throughout the world.

The most important ornamental species are *L. odoratus* and *L. latifolius* (the garden 'sweet' and 'broadleaved everlasting' peas, respectively – Figures 2.2, 2.3), with well over 100 modern cultivars between them and many more historical cultivars. Both of these species are relatively large members of sect. Lathyrus (p. 38) – a group characterised by its climbing habit.

Ornamental *Lathyrus*

Figure 2.2 (top right) *L. latifolius* 'White Pearl' RBGE accession 19561017

Figure 2.3 (top) *L. odoratus* 'Beaujolais'

Figure 2.4 (right) *Lathyrus vernus*

Other commercially significant ornamentals from this section include *L .grandiflorus*, *L. rotundifolius*, and *L. undulatus*. *Lathyrus aureus* and *L. vernus* (sect. Orobus – Figure 2.4) are also popular (Brickell, 1999). Both of the latter species are clump-forming perennials without climbing tendrils. The wild species and cultivars of *L. vernus* are popular for foreground display in herbaceous borders and are particularly shade tolerant.

2.4.2 *Food and fodder*

Many of the larger species have been suggested as suitable fodder for livestock (Fedchenko, 1948) and several species, including *L. ochrus* DC, *L. tingitanus* L. and *L. sativus* are grown in large quantities for this purpose. The drought tolerance of these species makes them suitable for cultivation in arid areas. *Lathyrus sativus* in particular, is a significant crop in Ethiopia, Sudan and India, with 1.6 million hectares producing around 0.5 million tonnes of seed annually in India (van der Maesen & Somaatmadja, 1989; Mathur et al., 1999). The seeds form an important part of the human diet during times of famine. Unfortunately, the toxicity of the seeds above levels of 40% of total diet or when consumed over extended periods makes them suitable for use in only the direst situations. A vast body of work has been devoted to research on *L. sativus* and closely related species in efforts to breed less toxic cultivars and document genetic diversity (discussed in Mathur et al., 1999, and chapters therein). Although low toxicity strains have been produced in the past, uptake was relatively limited in the areas where the plant is traditionally cultivated as local growers tend to regard seeds with an unfamiliar look or taste with suspicion. Recently developed Syrian strains are said to be very close in taste and appearance to traditional cultivars (Raloff, 2000). However, these improved germlines will not breed true for low toxicity unless they are grown in isolation from high toxicity strains to reduce the risk of cross pollination.

Apparently, seeds of *Lathyrus japonicus* have also been eaten (without recorded toxic effects), in Suffolk, England during a famine period in 1555 (Miller, 1768), and as an impromptu snack from 20th century Kent (Phillips, 1983). In reality, the entire plants were probably eaten during the 16th century, as they would have been nutritious and certainly fairly palatable. The effort required to collect the seeds that are far smaller, harder and less tasty than peas would have been considerable. Other species have also been used as foodstuffs by humans and may offer potential for revival as crop species. *Lathyrus tuberosus* (Fig. 2.5) is cultivated for its edible tubers (swollen rhizomes) throughout northern Europe, albeit on a far smaller scale than in the past. The tubers were particularly popular in 19th century Holland, where they were eaten roasted (Lawson, 1852; Johnson & Sowerby, 1862; Norton, 1996).

Figure 2.5 – *Lathyrus tuberosus*

Excavations by wild boar (*Sus scrofa*) foraging for tubers of *L. tuberosus*. This species was also an important forage for domesticated swine.

Another species with edible tubers is *L. linifolius* Bässler. The rhizomes were collected from the wild in Scotland and chewed as a stimulant, particularly by crofters in the Gaelic speaking west and north of the country. A number of quasi-mystical claims were made for the effects of the plant:

- When infused in whisky [*L. linifolius*] was said to be an:
  agreeable beverage and, like the Nepenthe of the Greeks, exhilarates the mind

- Thomas Pennant, writing in 1774 (Pennant, 1998)

- *The Highlanders have great esteem for the tubercles of the roots of this plant; they dry and chew them in general to give better relish to their liquor; they also affirm them to be good against most disorders of the thorax, and that by the use of them they are able to repel hunger and thirst for a long time. In Breadalbane and Rosshire they sometimes bruise and steep them in water and make an agreeable fermented liquor with them. They have a sweet taste, something like the root of liquorice, and when boiled, we are told, are well flavoured and nutrative, and in times of scarcity have served as a substitute for bread.*

- John Lightfoot writing in 1777 (Lightfoot, 1777)

- *The plant itself is not used, but the root is eaten to expel wind and they say it prevents drunkenness by frequent chewing of it; and being so used, gives a good relish to all liquors, milk only excepted. It is aromatic and the natives prefer it to spice for brewing aquavitae* [whisky]. *The root will keep for many years; some say that it is cordial, and allays hunger.*

- Martin Martin writing in 1695 (Martin 1994)

- *The natives eat the root of the Orobus Tuberosus, or as they call it Charmelic, it is said to be aromatic and is eaten before drinking Strong Liquors to prevent intoxication.*

- From James Robertson's tour of the Highlands 1767 - 1771 (Henderson & Dickson 1994)

At the time of writing, *Lathyrus linifolius* is being investigated for its potential pharmacological activity (Brian Moffat, Soutra Hospital Archaeological Research Project, pers. comm.).

2.4.3 Lathyrus *as a model organism*

Lathyrus species have been used as model organisms for research in a broad range of areas. Many wild taxa are common in Europe and North America and are easy to cultivate. Furthermore, the widespread distribution and diverse, but manageable size of the group makes it ideal for research into generic-level evolutionary and biogeographical patterns. At the specific level, the cultivars of *L. odoratus* and *L. sativus* are readily propagated, fast-growing annuals so they can be maintained as experimental populations.

Many biomedical studies of the toxic non-protein amino acid components of *Lathyrus* seeds, roots and stems have been conducted from the 1950s to the present day (e.g. Bell, 1962a, 1962b; Simola, 1968b; Lambein et al., 1999). The group of conditions resulting from the toxicity of *Lathyrus* species is termed Lathyrism and falls into two classes – neurolathyrism causes paralysis, whilst osteolathyrism causes skeletal deformations. Both appear to be caused by metabolites of hetericyclic isoxazolin-5-one non-protein amino-acids. One of these toxins, Beta (Isoxazolin 5-on-2-yl) L Alanine has been shown to be a broad spectrum antifungal and is toxic to other eukaryotes, including plants and unicellular green algae. It is exuded from the roots of *Pisum sativum* L. and *Lathyrus odoratus*, in which it may play an allelopathic role (Bell & Foster, 1962; Lambein et al., 1999).

During the later 1960s and the 1970s, the chromatographic techniques developed for this biomedical research were applied to the seeds of a broad range of species of *Lathyrus* and the closely related genera; *Lens* Miller (lentils), *Pisum* L. (peas) and *Vicia* (vetches). These four genera are among the plant groups in which protein and amino acid chemistry has been most intensively investigated. During this period, research focussed on the phylogenetic significance of seed non-protein amino acids (e.g. Simola, 1966, 1968b; Bell, 1962a, 1962b 1971; Bell et al., 1978). These studies also suggested that non-protein amino acids might act as feeding deterrents to insect pests (e.g. Jansen, 1969; also discussed in Waterman, 1994). Simola's (1968b) paper provided a detailed comparison of the ontogenic development of amino acid pools in *L. niger* Bernhardt, *L. japonicus* and *L. sylvestris* L..

Lathyrus has also been an important genus in genetic research. Narayan and Rees colleagues (Narayan,1982; Rees & Narayan, 1989) investigated chromosome evolution; Gutiérez et al. (1994) investigated the process of polyploidy in the genus and Nandini et al. (1997) demonstrated discontinuous variation in DNA sizes across the entire genus. Karyology is generally well understood in *Lathyrus*, with chromosome counts available for the majority of species. Kenneth Wolfe's research team has investigated rates of evolution in the chloroplast genome of *L. latifolius* and have found that it possesses a highly localised gene region that is one of the fastest evolving regions thus far discovered in the Angiosperms (Ken Wolfe, Trinity College Dublin, pers. comm.).

Ecological studies also make use of *Lathyrus* species as model organisms, such as the in-depth analyses of phenological and community behaviour in *L. vernus* conducted by Ehrlen (1992, 1995a,1995b; Ehrlen & Eriksson, 1995), Ritchie & Tilman (1995). Matthias Schlee (University of Tuebingen, pers. comm.), investigated evolutionary patterns in *L. pannonicus* Garcke and *Oxytropis pilosa* De Candolle, comparing ecology with phylogeny and concluding that ancestral populations of *L. pannonicus* were reliant on regularly grazed open grasslands. On an autecological level, Bal & Khetmalas (1996) investigated seasonal behaviour of root nodules in *Lathyrus japonicus*, and suggested their importance as starch storage organs.

2.4.4 *Weeds*

Small, annual species with a weedy lifestyle are represented by *L. aphaca* and *L. clymenum* and their close relatives, as well as some of the South American species and a few members of sect. Lathyrus. These species are generally classic ruderals, doing well in a range of disturbed habitats such as cultivated fields and roadsides. Agriculturally significant weedy species include *L. aphaca* and *L. ochrus*, both of which are drought tolerant annuals (Holm et al. 1979). Species such as *L. hirsutus* and *L. pratensis* L. are often found as aliens in seed mixes, and so have a widespread temperate distribution. Both of these species are naturalised in E. Asia, Australia and N. America, and *L. hirsutus* is occasionally found in Argentina and Chile (Burkart, 1937). Escapes from cultivation include *L. tuberosus* (a former food crop) and ornamentals including *L. latifolius*, *L. odoratus* and *L. grandiflorus* Sibthorp & Smith. The latter three species are very widely cultivated and commonly escape, sometimes establishing significant populations (Figs. 2.6, 2.7)

Ornamental *Lathyrus* as garden escapes
Figure 2.6 (right) ***Lathyrus latifolius*** a perennial European species shown here as an invasive alien in the environmentally sensitive coastal mist region of Marin County, California.

Figure 2.7 (Left) ***Lathyrus grandiflorus***, (pink flowers) climbing over the native yellow-flowered *Ulex europaeus* (gorse). This Mediterranean species is shown here established in Holyrood Park in Edinburgh.

2.4.5 *Conclusion*

Perhaps because of their close connection with humans and the genus's high diversity in western Eurasia, *Lathyrus* has often been treated by taxonomists. However, these treatments have typically only considered discrete sectional or distributional groupings in isolation, making for a somewhat disjointed picture of the genus as a whole. It is therefore imperative that relationships within the genus are fully understood if resources are to be targeted effectively in the development of food and fodder crops, ornamental cultivars and sources of bioactive compounds.

2.5 Conservation status

Lathyrus neurolobus Boissier & Heldreich is an island endemic, restricted to a few valleys in western Crete. A number of continental species are known only from very limited collections. These include *L. anhuiensis* Zhu & Meng (Anhui and Hubei provinces of China), known from the type collections and two collections by *Augustine Henry 6595* (BM) and *Henry S.N.* (K); *L. lomanus* Johnstone (N. Chile), known only from the type collection and *L. nitens* Vogel (southern Brazil), only known from about five early 19th Century specimens that may represent a single collection. Wild populations of the widely cultivated *L. sativus* are completely unknown. Conversely, many *Lathyrus* species are common and significant parts of the flora in their native habitats, such as *L. pratensis* and *L. latifolius* in NW. Eurasia, *L. venosus* Butters & St John in western coastal USA and *L. pubescens* Hooker & Arnott and *L. magellanicus* Lamarck in temperate S. America.

Twenty one species, one subspecies and two varieties of *Lathyrus* are listed in the 1998 IUCN Red Data Book (Walter & Gillett, 1998). Of the species, one (*L. dominianus* Litvinov) is listed as extinct (Ex), four endangered (E), five vulnerable (V), and 11 are considered rare (R). Needless to say, this is probably an underestimate of the threats faced by *Lathyrus* species, reflecting a lack of information rather than a true picture of the conservation status of the genus. All of the taxa in the red data book are from the northern hemisphere and almost all of these are from Turkey and the USA, where relatively recent floristic and conservation studies have been conducted (Ekim et al., 1989; The Nature Conservancy, 1996).

The International Legume Database and Information Service (ILDIS) has collated taxonomy and country-level distribution data, and includes a broad-based assessment of the conservation status of *Lathyrus* species. This is a valuable reference tool for *Lathyrus* research and indeed ILDIS originally began as the Viceae Database Project, an experimental taxonomic database system focussing on *Lathyrus* and the other members of tribe Fabeae (formerly the Viceae). Again, however, lack of information precluded a definitive conservation assessment for many species in ILDIS.

2.6 Ecological and morphological diversity in *Lathyrus*

Lathyrus species grow in a great diversity of habitats. Most are mesophytes from open habitats or forest margins (Fig. 2.8), but the group also contains members with tolerances for more extreme conditions. Species such as *L. palustris* (holarctic) and members of a radiation of species from the wet chaco and near the Uruguay and Paraná rivers of South America are adapted to inundated marshlands (Fig. 2.9). Xerophytes include *L. hitchcockianus* Barneby & Reveal from Death Valley, USA and *L. tomentosus* Lamarck from arid regions of the Argentine Pampas. *Lathyrus japonicus* is a classic patch-forming littoral species with creeping, sand-catching rhizomes and semi-succulent glaucous leaves.

Figure 2.8 – *Lathyrus* habitats 1

(Below) Open woodland is a common habitat type for many species – this image shows a locality for *L. vernus* in N. central Hungary.

Figure 2.9 – *Lathyrus* habitats 2

(Right) Wet chaco of Chaco province, Argentina – typical habitat for *L. macrostachys*.

2.6.1 *Habit*

All *Lathyrus* species are herbaceous - with around 40 annuals and 120 perennials. The majority of annual *Lathyrus* species are relatively delicate. Some however, such as *L. odoratus* and *L. paranensis* Burkart are robust and can only be recognised as annuals by their feeble, non-perennating rootstocks. Perennials have creeping, or thickened rhizomes or tubers and may form extensive

Figure 2.10 – Life forms 1

(Right) A single individual of *Lathyrus venosus* climbing to 5m through *Pinus nigra*. Golden Gate Park, California.

Figure 2.11 – Life forms 2
(Right) *Lathyrus japonicus,* a sprawling perennial from littoral environments. (Kenicer 50) Sacheon beach, S. Korea.

clumps or patches, even when the above-ground stems themselves are relatively short. Because *Lathyrus* is mainly restricted to seasonal environments (cool temperate or Mediterranean), above-ground stems die back during the non-growing season. In traditional morphology-based interpretations of *Lathyrus*, habit was often interpreted as a general indication of relationships and thus many treatments used it as secondary evidence of phylogenetic groupings. Among the mesophytic members of *Lathyrus*, there are two primary life forms – sprawling, or tall-climbing generally tendrillous species (Fig. 2.10) and erect, free - standing species that often lack or have considerably reduced tendrils. There are also several small, prostrate species, as well as intermediate and phenotypically variable ones (Fig. 2.11).

Those larger species that clamber with the aid of tendrils (best represented by members of sections Lathyrus [p.38] and some of the North American members of sect. Orobus[p.40]) may either carpet scrubby hillside habitats or clamber up surrounding plants in more densely vegetated areas. The smaller tendrillous species from sections Lathyrus and Orobus and members of sect. Pratensis typically cling to surrounding vegetation (and often their own stems, forming clumped masses) for support. Such species are therefore common in areas of lower vegetation, including grasslands and ungrazed verges and meadows. More open habitats, or forest understories without a tall herb layer, tend to harbour erect, freestanding species that lack tendrils. Examples include the members of sections Lathyrostylis and Orobus.

2.6.2 *Stems*

Figure 2.12 – Stems
Stem of *L. quinqenervius*, showing wings and narrow, semisagittate stipules. (Kenicer 66)

Stems in *Lathyrus* are exclusively herbaceous. Slightly woody tissues can only be found in the oldest stem bases of *L. roseus* Steven and *L. davidii* Hance. *Lathyrus davidii* is an erect species, with cylindrical stems - it is one of the few members of the genus in which the stems become thick enough to be hollow. Stems may be terete or quadrate, with little apparent systematic correlation.

The stems in robust members of the west Eurasian sect. Lathyrus (p. 38) are often winged, with wings reaching a centimetre cross. Some species from other sections are also winged, including *L. linifolius* and *L. quinquenervius* (Miquel) Litvinov (sect. Orobus – Fig. 2.12), *L. pannonicus* and allied species (sect. Lathyrostylis), and several South American members of sect. Notolathyrus (see under sect. Orobusp.40) , such as *L. macrostachys* Vogel and *L. paranensis*. In these taxa, the wings tend to be more slender than in species from sect. Lathyrus. In all species, the stem wings are green and thus increase the photosynthetic area available to the plant.

2.6.3 *Leaves*

Leaves in *Lathyrus* are typically paripinnate, and consist of paired, sometimes large stipules (Fig. 2.12), a single or multiple pairs of leaflets and a terminal tendril that may be robust and much branched or reduced to a simple arista (Fig. 2.13). Aberrations from these patterns are fairly common within any species or population, with apical leaflets commonly found in individual leaves (Fig. 2.14).

In *L. aphaca*, the leaflets are completely absent and the leaves are reduced to a simple tendril with large, leaflet-like stipules (Fig. 2.15). In *L. nissolia* L., the leaves are simplified to phyllodes that are remarkably like the lamina of grasses. The stipules in this species are reduced to spurs. The members of sect. Clymenum also have phyllodic leaves (with winged rachises), although they also possess leaflets. Leaf characters have traditionally been given strong weighting in morphology-based classifications. Indeed, the now obsolete genus *Orobus* was based on the combination of multiple leaflets and a lack of tendrils. Most species of *Lathyrus* have reticulate veins in the leaflets, but the members of sects. Lathyrostylis (p. 40), Linearicarpus (p.36) and Pratensis (p. 34) all have parallel veins, as do some members of sects Notolathyrus (see uner sect. Orobus, p.40) and Lathyrus (p.38).

Bässler (1966, 1973, 1981), Kupicha (1976) and Simola (1968) all investigated the epidermis of the leaves, including the shape of the cell margins and the distribution of stomata on the upper and lower surfaces. Although she discerned some vague correlations between epidermal features and her sectional classifications, Kupicha's overall conclusion (1983) was that distribution of these characters in the genus is more strongly correlated with habitat than phylogeny. She noted that mesophytic species throughout the genus tend to have more even distributions of stomata than xerophytic species, in which there are more stomata on leaf undersides.

Figure 2.13 – Leaves
Leaf of *L. pratensis*.
(Kenicer 64)

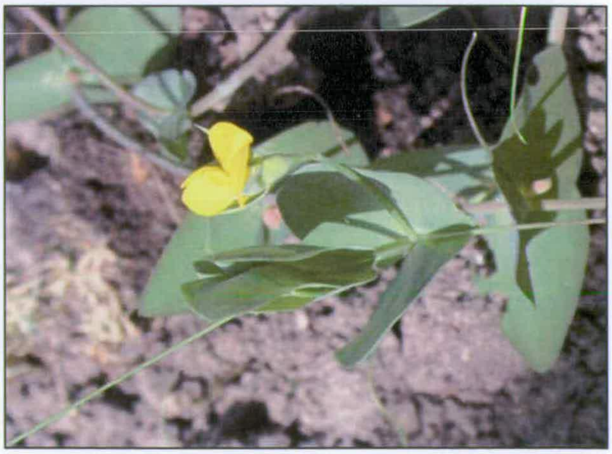
Paired leaflets showing parallel veins

Apical tendril

Paired stipules
In *L. pratensis*, the stipules are sagittate with two basal lobes.

Figure 2.14 – Imparipinnate leaves
(Below) *Lathyrus aureus*.
Arrowheads indicate aristas that have been replaced by terminal leaflets.

Figure 2.15 - Stipules
(Below) *Lathyrus aphaca*
Showing large foliolaceous stipules



2.6.4 *Inflorescences*

Inflorescences are solitary or in racemes of up to thirty flowers. Flower numbers are usually reduced in annual species, such that the members of sect Lathyrostylis are defined by their annual habit and solitary flowers. Flowers are always pedicellate, with or without a floral bract at the base. The pedicel often thickens considerably in fruit, raising the legume at 90° to the inflorescence axis or sometimes to a suberect position.

2.6.5 *Flowers*:

Lathyrus has typical papilionoid legume flowers (Fig. 2.16).

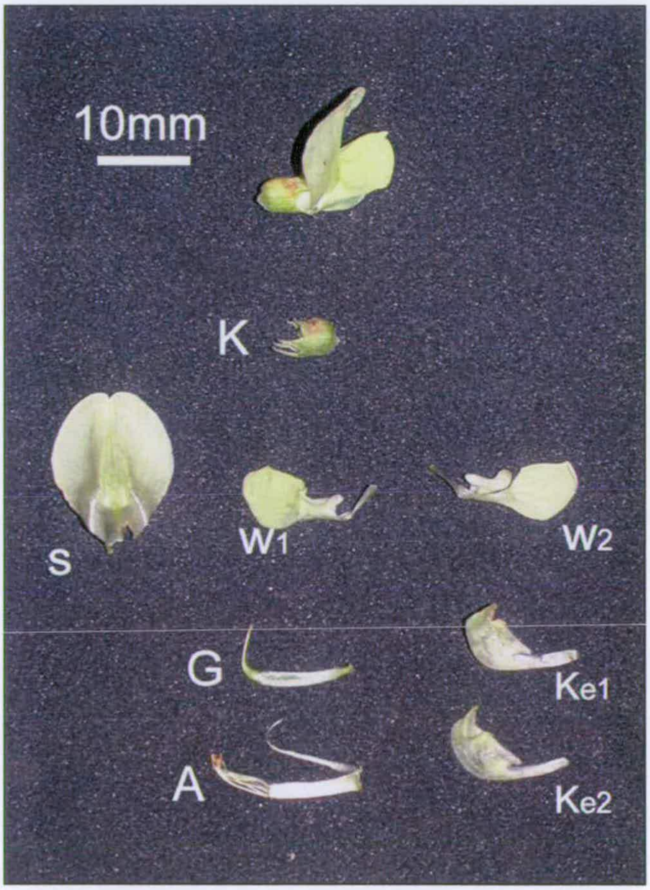
Figure 2.16 – Flowers
Flowers of *L. cabrerianus*.
(Kenicer 211).

K = Calyx

Corolla:
  S = Standard petal
  W_{1+2} = Wing petals
  Ke_{1+2} = Keel petals

A = Androecium

G = Gynoecium

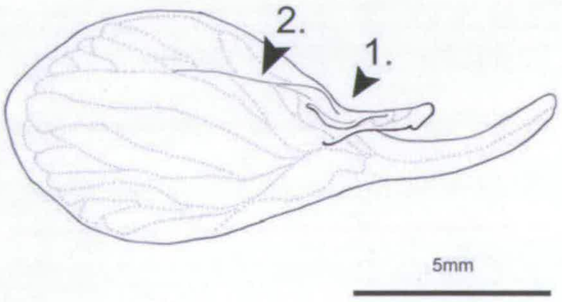


Calyces may be regular, with equal calyx teeth, or irregular, with longer lower calyx teeth, as is commonly the case in members of sects. Orobus and Notolathyrus (p. 40). Banner petals are usually stenonychoid, with a relatively narrow claw widening to a broader blade. However smaller, oblong standards are seen in some species such as *L aureus* (Steven) Brandza, *L. davidii*, *L. hasslerianus* and *L. subulatus* Lamarck. Kupicha (1983) pointed out the similarity between this standard type and those in *Vicia*.

The wing petals in *Lathyrus* are ornamented with raised processes and corresponding pouches in the keel petals (Fig 2.17). The basal part of the process on the wing hooks snugly into the corresponding basal pouch in the keel, forming a pivot against which the wings and keel are pushed when a pollinator alights on the flower, activating it. Forward of this pivot, the process may continue for some distance into the blade as a raised pleat. This leading edge of the pleat is less tightly interlocked with the keel petal and acts as a boss providing some resistance to the pollinator and preventing the wings from collapsing under the insect's weight. In some species the pleat may be discontinuous, giving the appearance of a second process.

Figure 2.17 – Wing petal architecture
Flowers of *L. nervosus*
(Gardner & Knees 6062).

1 = Basal process
('pocket' sensu Stirton, 1981)
2 = Raised pleat



Keel petals are invariably strongly fused along the basal margin.

Corolla colour varies widely across the genus and within the larger sections. Blues and purples predominate, but pinks, reds, including brick red, yellows and white are also found. Colour is variable within species and changes, usually deepening as the individual flowers age. In several species, particularly members of sects Orobus and Notolathyrus (p. 40), the banner petal is darker than the wings and keels, presumably providing a contrast between the upper and lower (landing pad) parts of the flower. The venation on the banner can often be darker than the surrounding tissue, appearing as darker traceries, which may act as nectar guides.

Several species, mainly from sect. Orobus (p. 40), have a distinctive inflorescence type with many (15-30) small, somewhat waxy flowers that begin white and darken to gold-yellow, and then orange as they mature. Perhaps in order to fit this high number of flowers into a dense display, these taxa share a relatively narrow oblong standard. These are *L. laevigatus* and allies (W. and C. Eurasia), *L. davidii* (E. Asia), and *L. sulphurous* Brewer ex Gray and *L. ochroleucus* Hooker (N. America). This same inflorescence type is seen in *L. hasslerianus* (S. America) and in *Vicia pisiformis* L. (W. Eurasia).

The androecium is diadelphous, with the single near-free stamen at the adaxial (upper) part. The nine remaining stamens form a tube which is truncate at the tip in almost all species (where the filaments become free of the tube). Some members of sect. Notolathyrus, and *L. grandiflorus* (sect. Lathyrus) have slightly oblique apices, a character more commonly seen in *Vicia*.

Ovaries are linear and laterally compressed, they may be pubescent, with simple hairs or glandular hairs, the pubescence varying within species (e.g. *L. japonicus*) or within sections (sect. Notolathyrus).

Styles are generally linear, although members of sects Clymenum (p. 33) and some members of sects Linearicarpus (p. 36) and Notolathyrus (see under sect. Orobus, p. 40) have spathulate styles, broadening towards the tip and there are many intermediate species throughout the genus. In all species, there is an introrse (adaxial) pollen brush formed from stylar trichomes (Gunn & Kluve, 1976; Lavin and Delgado 1990). This is believed to hold pollen in place in order to present it to the pollinator, although it has also been suggested that the stiff hairs play a role in breaking the anthers open (Gunn & Kluve 1976). In some species, the style is twisted - in members of sect. Lathyrus, torsion is consistently unidirectional (anti-clockwise when seen from above), and this is a good character for diagnosing the section (Fig. 2.18). Spathulate styles (as in sect. Lathyrostylis [p. 40] and some members of sect. Notolathyrus [p.40]) often appear twisted, although this is because of the lack of space in the keel (Bässler 1981).

Figure 2.18 – Stylar twisting
(Right) Flower of *L. grandiflorus*, showing the contorted style (base highlighted with an arrow). Note how the style distorts the keel petals.

Stigmas are typically simple, but sect. Clymenum is defined by a cleft stigma in which a mucro of sterile tissue separates and projects beyond the fertile portion. In some members of sect. Notolathyrus such as *L. pubescens* and allied taxa (e.g. *L. tomentosus* and *L. macropus* Gillies ex Hooker & Arnott), the stigma is divided into two separate pads or flaps (Fig. 2.19).

Figure 2.19 – Bifid stigma in *L. pubescens*
(Left) Style of *L. pubescens* showing slightly spathulate apex, and the two stigmatic flaps (pale brown tissue) highlighted with arrows.

2.6.6 *Fruits*

Fruits can be heavily ornamented, with dense pubescence (e.g. *L. macropus*) or wings along the sutures (e.g. *L. ochrus*, *L. sativus*) or on the valves of the entire pod (*L. gloeospermus* Warburg & Eig.). Kupicha's revision of the sections contains an excellent illustration of this diversity (Kupicha, 1983, p. 223, fig.5). Fruits contain between two and fifteen seeds.

2.7 The sections of *Lathyrus*

The distribution, general ecology and diagnostic characters of each of the 12 currently accepted sections (following Kupicha, 1983 as modified by Asmussen & Liston, 1998) are outlined below. Please refer to Appendix 1 for a glossary of morphological terms. The following brief sectional notes are pooled from the existing literature and field observations in Argentina, Chile, China, Hungary, Japan, South Korea, the UK and the USA.

Herbarium specimens from the following herbaria were also examined: Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires (BA); Universidad Nacional del Sur, Bahia Blanca, Argentina (BB); Universidad Nacional del Comahue, Bariloche, Argentina (BCRU); Natural History Museum, London (BM); Natural History Museum and Institute , Chiba, Japan (CBM); Royal Botanic Garden Edinburgh (E); Field Museum, Chicago (F); Royal Botanic Gardens, Kew (K); The Makino Herbarium, Tokyo Metropolitan University (MAK); Institute of Botany, Chinese Academy of Sciences (PE); Hokkaido University, Sapporo, Japan (SAP); Museo Nacional de Historia Natural, Santiago de Chile (SGO); Instituto de Botánica Darwinion, Buenos Aires (SI); New York Botanical Garden (NY); Tokyo University (TI); Universidad Nacional de Rosario, Rosario, Argentina (UNR); Smithsonian Institution (US).

SECTION CLYMENUM (Miller) De Candolle ex Seringe in (1825) *Prodromus*. **2**: 375.

No. spp. 4

Type species: *L. articulatus* L.

Distribution: Mediterranean

Section Clymenum of two core species, *L. clymenum* and *L. ochrus*.

Lathyrus articulatus is sometimes included as a variety in *L. clymenum*. The oddity of the group is *L. gloeospermus*, which has much reduced, cleistogamous flowers. The section is defined by multijugate phyllodic leaves. The first few leaves develop as simple, grass-like laminas and successive leaves produce leaflets that spring from a winged, phyllodic rachis. *Lathyrus nissolia* (sect. nissolia, p. 33) is the only other species in the genus with phyllodic leaves. *Lathyrus ochrus* is distributed widely as a seed alien.

SECTION NISSOLIA (Miller) Dumort (1827) *Flora Belgica*. p. 103

No. spp. 1

Type species: *L. nissolia* L.

Distribution: C. and S. Europe

Lathyrus nissolia (Fig. 2.20) is an annual plant of meadows and pastures and its similarity to a grass is striking. Even seasoned field botanists find it difficult to distinguish vegetative specimens from neighbouring grasses. The leaves are reduced to slender phyllodes – akin to the first few leaves of species of sect. Clymenum (p. 33). Unlike in sect. Clymenum, the leaves of *L. nissolia* are not pinnate and it is this combination of characters – phyllodic, non-pinnate leaves that defines the section.

Figure 2.20
Lathyrus nissolia

SECTION PRATENSIS Bässler (1966) *Feddes Repertorium*. **72**: p.90

No. spp. 6

Type species: *L. pratensis* L.

Distribution: *Lathyrus pratensis* is found throughout temperate Eurasia, but is possibly only an introduction to China and Japan. The remainder of the section is found in Southern Europe and Asia Minor.

The members of sect. Pratensis are pubescent perennials with several pink, purple, blue or yellow flowers per raceme (Figs. 2.13, 2.21). The section is

Figure 2.21 ***Lathyrus pratensis***

diagnosed by its sagittate stipules and bijugate leaves, a combination of characteristics otherwise only seen in some S. American species. In the northern hemisphere, the only other species with sagittate stipules are *L. japonicus* (Sect. Orobus, p. 40), which has three or more pairs of leaflets, and *L. aphaca* (sect. Aphaca) which lacks leaflets. Asmussen & Liston's (1998) RFLP analysis suggests that sect. Pratensis has a sister relationship with *L. aphaca*. The taxonomy, morphology and ecology of *L. pratensis* were extensively treated by Brunsberg (1977).

SECTION APHACA (Miller) Dumort (1827) *Flora Belgica*. p. 103

No. spp. 1

Type species: *L. aphaca* L.

Distribution: Mediterranean and northern Europe. Also known from Australia and N. America as a weed

Sect Aphaca is monotypic although *L. stenolobus*, a species distinguished from *L. aphaca* based on stipule shape, was only recently designated a syonym of *L. aphaca* (Kupicha 1983). *Lathyrus aphaca* (2.15) is an ephemeral, highly weedy plant. Unique amongst the species of *Lathyrus*, its leaves have been reduced to a pair of large, sagittate stipules and a simple tendril. Kupicha's (1974) investigations into the pattern of veins supplying the stipules in *Lathyrus* suggested a close relationship between *L. aphaca* and *L. pratensis*, a relationship supported by Asmussen & Liston's work (1998). *Lathyrus aphaca* species can be a tenacious weed of gardens once established.

SECTION NEUROLOBUS Bässler (1966) *Feddes Repertorium* **72**: p. 91.

No. spp. 1

Type species: *L. neurolobus* Boissier

Distribution: Western Crete

Lathyrus neurolobus is restricted to sheltered upland valleys of western Crete. It is a small perennial with broadly winged stems, unijugate tendrilous leaves and only one or two flowers per raceme. The leaflets are elliptic, with parallel veins. This combination of characters is unique in the genus and Bässler (1966), Kupicha (1983) and Asmussen & Liston (1998) were unable to suggest any close associations with the rest of the genus.

SECTION LINEARICARPUS Kupicha (1983) *Notes from the Royal Botanic Garden Edinburgh* **41:** 238.

No. spp. 7

Type species: *L. inconspicuus* L.

Distribution: Mediterranean, Caucasus to Pakistan

The members of sect. Linearicarpus are diagnosed by their annual life cycle, erect habit, lack of stem wings, absent or simple tendrils and solitary flowers. The annual or ephemeral life-cycle of sect. Linearicarpus is an adaptation to arid and seasonally dry habitats. Morphologically they are most similar to some of the more delicate annuals in sect. Lathyrus such as *L. cicera*, although they also superficially resemble reduced members of sect. Lathyrostylis (p. 40) in overall habit. Badr et al.'s (2002)

AFLP analysis questioned the monophyly of sect. Linearicarpus. The affinities and monophyly of this group remain open to question.

Section Orobon (1962) Tamamashjan in Takhtadjan *Flora Armenii* **4**: 316.

No. spp. 1

Type species: *L. roseus* Steven

Distribution: Black sea and Caucasus

A large clump-forming, erect perennial species with unijigate leaves, rotund leaflets and many small, rose-coloured flowers per raceme. *Lathyrus roseus* lacks tendrils and is one of the few species to become slightly woody. This combination of characters has kept it in its own separate section. In many ways, this species resembles members of sect. Orobus (p. 40). However it is distinguished based on the appearance of the leaflets, Kupicha (1983) hypothesised that it is more closely related to sect. Lathyrus (p. 38). This interpretation was borne out by the RFLP analysis of Asmussen & Liston (1998), which resolved *L. roseus* as a close ally of sect. Lathyrus.

Section Orobastrum Boissier (1872) *Flora Orientalis* **2**: 601.

No. spp. 1

Type species: *L. setifolius* L.

Distribution: Mediterranean

Lathyrus setifolius is a delicate annual that shares morphological affinities with sect. Linearicarpus (p. 36) and the delicate annuals of sect. Lathyrus (p. 38), although

Kupicha (1983) separated this species from both on the basis of its stipitate pods (i.e narrowing towards the calyx). Following their RFLP analysis, Asmussen and Liston (1998) treated *L. setifolius* as a member of sect. Lathyrus.

SECTION VICIOPSIS Kupicha (1983) *Notes from the Royal Botanic Garden Edinburgh* **41:** 237.

No. spp. 1

Type species: *L. saxatilis* (Ventenat) Visiani

Distribution: Mediterranean

Lathyrus saxatilis is the only annual species in the genus with multijugate, non-phyllodic leaves and for this reason was placed in its own section. The leaflets are obovate and apiculate with reticulate veins - characters more similar to members of *Vicia* than *Lathyrus*. However the adaxially pubescent styles confirm this species' position within *Lathyrus*, so it was treated by Kupicha (1983) as the sole member of the monotypic section Viciopsis.

SECTION LATHYRUS (1787) (c. 35 spp.) Medikus in Vorles. Churpf. Phys. Ges. **2**: 358.

No. spp. c.35

Type species: *L. sylvestris* L. (Fig. 2.22)

Distribution: Western Eurasia (Europe and the Asia Minor)

Section Lathyrus is the second largest section in the genus and is defined by its contorted styles (Fig. 2.18). Many species also have winged stems, and sometimes seeds with a rough testa – features not commonly seen in the rest of *Lathyrus*.

Kupicha recognised three groups in the section:

- Slender, but often leggy perennials with tuberculate hairs on the fruits (e.g. *L. grandiflorus*, *L. rotundifolius*, *L hirsutus*).
- Robust perennials and annuals (e.g. *L. latifolius*, *L. odoratus*, *L. sylvestris*)
- Delicate annuals (e.g. *L. sativus*, *L. cicera*)

Ecological tolerances range from mesophytes (*L. latifolius* – Figs. 2.2, 2.6) to relatively arid habitats such as the fringes of the Sahara (*L. tingitanus* and *L. sativus*). Indeed *L. sativus* is considered one of the plants with the greatest potential for widespread cultivation in arid environments and is the subject of a large body of international research. As for the entire genus, Turkey is the main centre of distribution of sect. Lathyrus, with the greatest species diversity.

Figure 2.22 – *Lathyrus sylvestris*.
Type species of sect. Lathyrus.

SECTION LATHYROSTYLIS (Grisebach) Bässler (1971) *Feddes Repertorium* **82**: 443.

No. spp. c. 20

Type species: *L. digitatus* (Bieb.) Fiori & Paoletti

Distribution: W. Eurasia

Section Lathyrostylis was treated in a very thorough revision by Bässler (1981). Its members are perennial multijugate species, usually with perennating tubers. The leaves lack tendrils and plants have an erect habit. Consequently members of this section were once placed with other etendrillous, erect species in the genus *Orobus* (e.g. Linnaeus, 1752; Alefeld, 1861). More recent classifications (Bässler 1966, Czefranova 1971, Kupicha 1983) ally this section with the members of sect. Orobus (p. 40), but keep them distinct on the basis of the spathulate styles seen in sect. Lathyrostylis.

SECTION OROBUS Godron in Grenier & Godron (1848) *Flore de France*. p. 485

Syn: *Orobus* L. (1753) *Species plantarum* p. 728; subgenus Orobus (L.) Peterm. Deutschland Flora

No. spp. c. 80 (including 26 members ascribed to sect. Notolathyrus in this thesis)[1]

Lectotype species: *L. linifolius* (Reichard) Bässler

Distribution: Temperate Eurasia, North America.

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[1] Note that the findings of the study presented here support the validity of the segregate Notolathyrus as a section. Please refer to chapter 5 for a fuller discussion of the diversity of this S. American endemic group.

The European species of sect. Orobus were revised by Bässler (1971), and the North American species by Hitchcock (1952).

At present, many of the species that are not readily assignable to other sections are lumped together in the poorly defined sect. Orobus sensu Asmussen & Liston (1998). This includes Kupicha's (1983) largely South American section Notolathyrus. Asmussen and Liston's (1998) RFLP research showed their Notolathyrus samples nested inside a clade containing members of sect. Orobus. The section is not held together by any apomorphic characters, or indeed any suites of characters, but if the South American species are excluded, the remaining Eurasian and North American species are multijugate perennials without spathulate styles, often with reticulate venation on the leaves and reduced tendrils. The exclusion of the species with spathulate styles removes the members of sect. Lathyrostylis.

As well as many species with uncertain affinities, this group contains the species that, on the grounds of morphology, appear to be closest to *Vicia* - the other large genus in tribe Fabeae (Kupicha 1983). Section Orobus has been considered basal in the genus, making it a key group for understanding fundamental relationships within *Lathyrus* and the wider Fabeae (Bässler 1966, Kupicha 1983, Asmussen & Liston 1998). In addition, sect. Orobus sensu Asmussen & Lison (1998) is by far the largest (over 75 spp.) in *Lathyrus* and covers almost the entire geographical range of the genus, spanning Eurasia, North, and South America (Bässler, 1966; Asmussen & Liston, 1998). It is an ideal candidate group for investigating the complex biogeography of temperate herbaceous plants as it is diverse and widespread enough to provide comprehensive coverage of the northern hemisphere and South American temperate regions, but small enough to make thorough sampling possible.

For these reasons, sect. Orobus is a particularly important part of chapter four in this study, where problematic infra-sectional relationships and the place of the section in the wider contexts of *Lathyrus* and the Fabeae are investigated. Particular consideration is given to the biogeography and evolutionary history of the group and to investigation of its monophyly.

A number of members of sect. Orobus show only limited similarity to any other members of the section whilst others show close morphological affinity to sect. Lathyrostylis (p. 40) and yet others to some members of *Vicia*. As a consequence the circumscription of sect. Orobus and interpretations of its relationships are continually shifting, most recently with the resurrection by Yakovlev et al (1996) and Stankevich and Roskov (1998) of the Linnaean genus Orobus.

The erect, etendrillous habit is seen in species of relatively open habitats such as grazed meadows, or as understory herbs, where low light limits the growth of other plants. These etendrillous species may grow as discrete individuals, in clumped stands forming low tussocks over time, or spreading by means of rhizomes. This group contains a number of robust alpine meadow species from the mountains of Europe, the Urals and the Himalayas (Bässler's series Lutei) as well as forest marginals (series Verni) and some seemingly unrelated species from Eurasia (e.g. *L. linifolius*, *L. niger* and *L. vaniotii*) and N. America (*L. rigidus*). The Eurasian etendrillous species are the classic 'Oroboid' taxa.

Lathyrus davidii (Fig. 2.23) is one of a number of species (including *L. humilis* and *L. palustris*) from sect. Orobus that have a habit that is intermediate between sprawling climbers and free-standers. These species have tendrils and will use surrounding vegetation for support if available. In such cases they tend to grow relatively leggy, but remain more dense and compact if growing alone - the phenotypic variation in these species can be striking and has led to the description of a number of taxa that were are now generally regarded as synonyms.

Figure 2.23 – *Lathyrus davidii*

This robust species sprawls over surrounding vegetation of any height.
At road margin under *Cryptomeria japonica*, Nikko, Tochigi Prefecture, Japan.

Lathyrus japonicus (Holarctic and Chile – Fig. 2.11) and *L. littoralis* (Oregon and California, USA) are coastal plants and whilst not true halophytes, they are typically found just above the strand line and endure extreme exposure to salt and winds. In areas where large patches are found, the root systems of these species play an important role in foreshore dune stabilization.

Lathyrus palustris is a widespread Holarctic species that is mainly found in wet meadows and dune slacks but will readily tolerate partial immersion in fresh or brackish water in reedbeds, paddy fields and ditches, where it climbs up surrounding grass and reed stems. Like *L., japonicus*, *L. palustris* spreads locally using extensive rhizomes, but unlike it, tends not to form patches, rather individual stems of a given clonal system appear scattered throughout the area. The apparently closely allied *L. quinquenervius* (from forested areas of northeast Asia – Fig. 2.12) has much the same habit. This may simply be due to the fact that *L. palustris* and *L. quinquenervius* are plants of densely vegetated habitats but *L. japonicus* seldom has any competitors for space on the beaches it inhabits.

3

Molecular phylogenetics of *Lathyrus* 1

The genus in the context of tribe Fabeae

3.1 Introduction and aims

This chapter reports an investigation of phylogenetic relationships in tribe Fabeae using the chloroplast gene *matK*. The phylogenetic analysis is the first to include representatives of all five genera in the tribe, and expands sampling of *matK* gene sequences from only five to 24 species of *Lathyrus* (Steele & Wojciechowski, 2003).

This research was developed to extend the molecular phylogenetic work of Steele and Wojciechowski (2003), and was developed in collaboration with Kelly Steele. The study concentrates primarily on *Lathyrus*, *Pisum* and *Vavilovia* - genera that were underrepresented or not represented in Steele & Wojciechowski (2003). The principal aims were to:

1. Increase sampling of *matK* gene sequences of *Lathyrus* species.
2. Provide a *matK* dataset for comparison with the data presented in chapter 4.
3. Evaluate the monophyly of *Lathyrus.*
4. Estimate the sister group to *Lathyrus.*
5. Investigate the phylogenetic positions of *Pisum* and *Vavilovia.*
6. Evaluate whether the following characters traditionally used in morphological classification diagnose monophyletic groups:
    - Adaxial stylar pubescence
    - Reflexed stylar margins
    - Leaflet vernation patterns (conduplicate vs. supervolute)

Representation of *Lathyrus* is comparable between chapters 3 and 4 in terms of breadth of morphological diversity and taxonomic sections, although species sampling was necessarily reduced for the *matK* analysis presented here given constraints of time and budget. The data presented in chapter 4 focus on *Lathyrus*, so *Vicia* is less well represented there than it is in this chapter.[1]

3.2 Tribe Fabeae

3.2.1 *Tribal diversity*

Tribe Fabeae was described by Reichenbach in 1832. Much of the recent literature uses the invalid earlier homonym Vicieae (Bronn) DC (Lock & Maxted 2005). Fabeae consists of five genera (Table 3.1). The tribe is a member of the 'temperate herbaceous' group of legumes, based on Polhill's (1981) classification. Furthermore, the tribe is nested in the Inverted Repeat Lacking Clade (IRLC) of Legumes that have lost one copy of the 25kb inverted repeat region of the chloroplast genome (Lavin et al., 1990; Wojciechowski et al., 1999; 2000, 2004; Hughes et al., 2004).

Table 3.1 genera in tribe Fabeae

Genus	No. spp	Distribution	English vernacular names/Uses
Lathyrus	c. 160	Eurasia, Temperate Americas	Sweet peas, chickling vetches • Ornamentals • Food – seeds • Fodder • Rotation crops
Lens	5-6	E. Mediterranean	Lentils • Food – seeds • Rotation crops
Pisum	3 (2-5)	E. Mediterranean, Caucasus	Peas • Food – seeds, fruits and whole plants • Fodder • Rotation crops
Vavilovia	1	Caucasus endemic	• No uses
Vicia	c. 150	Eurasia, Temperate Americas	Vetches • Fodder • Rotation crops

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[1] The results of the maximum parsimony analysis from this chapter were presented at The Botanical Society of America annual conference 'Botany 2004' in Snowbird, Utah (Appendix 1).

Many entities within Fabeae have been treated as separate genera, giving an extensive synonymy (reviewed in Gunn 1969). The most recent major taxonomic shift in the tribe has been in the removal of the genus *Cicer* L. into a separate monotypic tribe, Cicereae, by Clarke and Kupicha (1976). The delimitation and overall structure of the tribe has remained relatively stable since. The only significant exception is Roskov et al.'s (1998) floristic account of W. Eurasian legumes. These authors were working on Russian dissective principles of taxonomy (i.e. preferring 'splitting' to 'lumping') and produced a particularly wide-ranging reappraisal of the Fabeae with major implications for the relationships between *Lathyrus* and *Vicia*. These changes include the resurrection of the genera *Orobus* (including etendrillous species of *Lathyrus* and *Vicia*), *Faba* (*V. faba* and allies) and *Bona* (*V. johanis* and *V. turkestanica*) (Roskov et al., 1996; Stankevich & Roskov, 1998; Roskov et al. 1998).

All species in the tribe are herbs, generally with paripinnate leaves terminating in tendrils or apical aristas. *Lathyrus*, *Lens*, *Pisum* and *Vicia* have representatives with some of the earliest archaeological records of cultivation for any plants – all in the Fertile Crescent agricultural centre (Plitmann & Kislev, 1989). A short summary of key characteristics of each genus follows.

- *Lathyrus* L. 1753 (c. 160 species)
  See extensive discussion in chapter 2.

- *Lens* Mill. 1754 (c. 5 species)
  Annual, pubescent plants. Stems unwinged, to c. 30cm. Leaves multijugate, Flowers solitary or few on erect or nodding peduncles, with equal calyx teeth far exceeding the calyx tube. Large lenticular seeds (culinary lentils of *L. culinarius*) produced in inflated legumes.

  Wild species are distributed throughout the Mediterranean, with greatest concentrations in Turkey, Syria and surrounding countries. *Lens* *nigricans* is thought to be the closest wild relative to *L. culinarius*, a domesticated species with a history of cultivation of at least 9000 years.

- *Pisum* L. 1753 (3–5 species)

  Annual, generally glabrous plants. Stems unwinged, to 2m. Leaves terminating in a tendril, with one to three pairs of orbicular-ovate leaflets and large, foliaceous stipules. Racemes with one to three flowers. Styles inflated, with abaxial groove and reflexed margins. Legumes produce spherical to cuboid seeds – edible in *P. sativum*.

  The modern taxonomy (Kloz, 1971; Ben-Ze'ev & Zohary, 1973; Ambrose & Maxted 2000) generally accepts three species – *P. sativum*, *P. abyssinicum* and *P. fulvum*. Wild *P. sativum* or an unequivocal progenitor species are unknown, but *P. syriacum* and *P. elatius*, treated by some authors as segregates from *P. fulvum*, are hypothesised as to be the closest wild relatives (Plitmann & Kislev 1998, Ambrose & Maxted 2000; Pearce et al. 2000; Vershinin et al. 2003).

  From mesophytic areas and the summer-dry Mediterranean region. *Pisum sativum* is the most commercially significant of all the species in the tribe, with many cultivars and a worldwide distribution. It is a common garden escape.

- *Vavilovia* Al Fed. 1939 (1 species)

  Short (to 10cm), glabrous perennial with orbicular leaflets on unijugate, aristate leaves. Flowers solitary on 5-7cm peduncles. Styles as for *Pisum*. *Vavilovia* is a monotypic genus restricted to scree slopes of the Caucasus mountains, and is sometimes considered to be within *Pisum* (Gunn & Kluve 1976). This study presents the first molecular phylogenetic analysis to include *Vavilovia*

- *Vicia* L. 1753 (c. 150 species)

  Annual or perennial, glabrous or pubescent plants. Stems unwinged. Leaves usually multijugate, (although there are some unijugate species in E. Asia - e.g. *V. unijuga*), usually terminating in a tendril. Some species (e.g. *V. sativa*), with stipular nectaries – a character that defines subgenus *Vicia* (Kupicha 1976). Inflorescences axillary, diverse – from solitary, sessile flowers to many-flowered racemes. Stylar morphology very variable and apparently taxonomically significant within and beyond the genus. Styles may be terete, or laterally or adaxially compressed, with a variety of hair patterns - abaxially pubescent; pubescent around the entire circumference, or rarely with an adaxial pollen brush (Raji 1971; Gunn & Kluve 1976; Kupicha 1974, 1981; Endo & Ohashi 1995, 1996, 1997). Legumes laterally compressed, two to many seeded.

  Vicia is distributed throughout temperate Eurasia, with its centre of greatest diversity in the Eastern Mediterranean. From a wide range of habitats (predominantly mesophytic or seasonally dry).

  Many authors have addressed the taxonomy of *Vicia* and, as with *Lathyrus*, the size of the genus makes it difficult to handle on a worldwide basis. Furthermore, it is less morphologically variable than *Lathyrus*, in spite of the strong morphological, ecological and distributional parallels between the genera. Consequently most of the more recent treatments have taken Kupicha's (1976) classification as a starting point and looked at limited taxonomic or regional groupings. Morphology based classifications have resulted in varying degrees of reclassification according to the approach and range of species addressed. Examples include sectional rearrangements resulting from a phenetic reassessment of subgenus *Vicia* (Maxted 1993); descriptions of new species, and minor revisions within sections and species from East Asia and North America (e.g. Endo & Ohashi 1996, Endo et al. 2000).

3.2.2 *Karyology*

Karylogical studies on tribe Fabeae represent a considerable body of work and *Lathyrus* has been the focus of extensive studies (e.g. Narayan 1982, Yamamoto et al. 1984, Rees & Narayan 1989, Gutiérez et al. 1994, Nandini et al. 1997). The base chromosome number across the tribe is x = 7, with the vast majority of species examined proving to be diploids (2n=14). Polyploidy is rare and scattered throughout the tribe. A few species have been shown to have diploid isolates, and some N. American species of *Lathyrus* may have polyploid origins (Broich 1989), but in the main ploidy level is not thought to have any taxonomic significance (Kupicha 1976, 1981, 1983).

3.2.3 *Morphology-based classifications in tribe Fabeae*

Within tribe Fabeae, the continuous variation in many characters and high overall variability in the larger genera make identification of potentially apomorphic character states difficult (Kupicha 1974, 1983). Many of the historical classifications tended to use one or a few hypothesised synapomorphies that were later interpreted by Kupicha (1974, 1981, 1983) as homoplasious.

Most modern classifications at the tribal level distinguish the genera (and often infrageneric taxa) by suites of non-exclusive characters that overlap with the other genera. This partly reflects the fact that *Vicia* and *Lathyrus* as currently defined are particularly large genera – both are in the top 25 most species-rich legume genera (Lewis et al., 2005). Thus, within the wide range of character states seen in these two large genera, one would expect there to be more chance of homoplasious overlap with other members of the tribe.

To further compound the problem, *Vicia* and *Lathyrus* appear to have evolved and dispersed in parallel after their initial divergence, giving rise to many parallelisms throughout their range. Modern distributions, species numbers, habitat preferences and life forms are strikingly similar (Kupicha, 1976, 1983). Consequently, the interface between the two genera was a major point of debate within the tribe. This is best exemplified by the ‘Oroboid’ members of *Lathyrus* and *Vicia*. *Lathyrus* and *Vicia* were originally Linnaean genera based on classical entities, with a third genus, *Orobus*, recognised as distinct from them in its lack of tendrils and tendency towards a more erect habit. Godron (Grenier & Godron, 1848) united the majority of *Orobus* with *Lathyrus* on the basis of their adaxially pubescent styles, although several members without this character were moved into *Vicia*. In an extensive revision of tribe Fabeae, Alefeld (1861) resurrected *Orobus* again, including many members of the original Linnaean genus, as well as some South American species. Alefeld’s classification was not generally accepted, and Godron’s work was carried forward to form the basis for more modern classifications.

A considerable body of morphological and molecular work in the Fabeae has built on Godron’s work in an attempt to refine infra-generic classifications. In particular, the marvellously comprehensive and well-considered works of Kupicha attempted to take account of the seemingly homoplasious characters, and remain the basis for the classifications used today (Hanelt & Mettin, 1989; Maxted, 1993, Asmussen & Liston, 1998; Lock & Maxted, 2005). Kupicha’s work was primarily based on morphology, building on Gunn & Kluve’s (1976) investigations of reproductive morphology, but she also incorporated the biochemical research of Simola (1966, 1968b) and Bell (1971; Bell et al. 1978). Her scheme of relationships is summarized in Fig. 3.1.

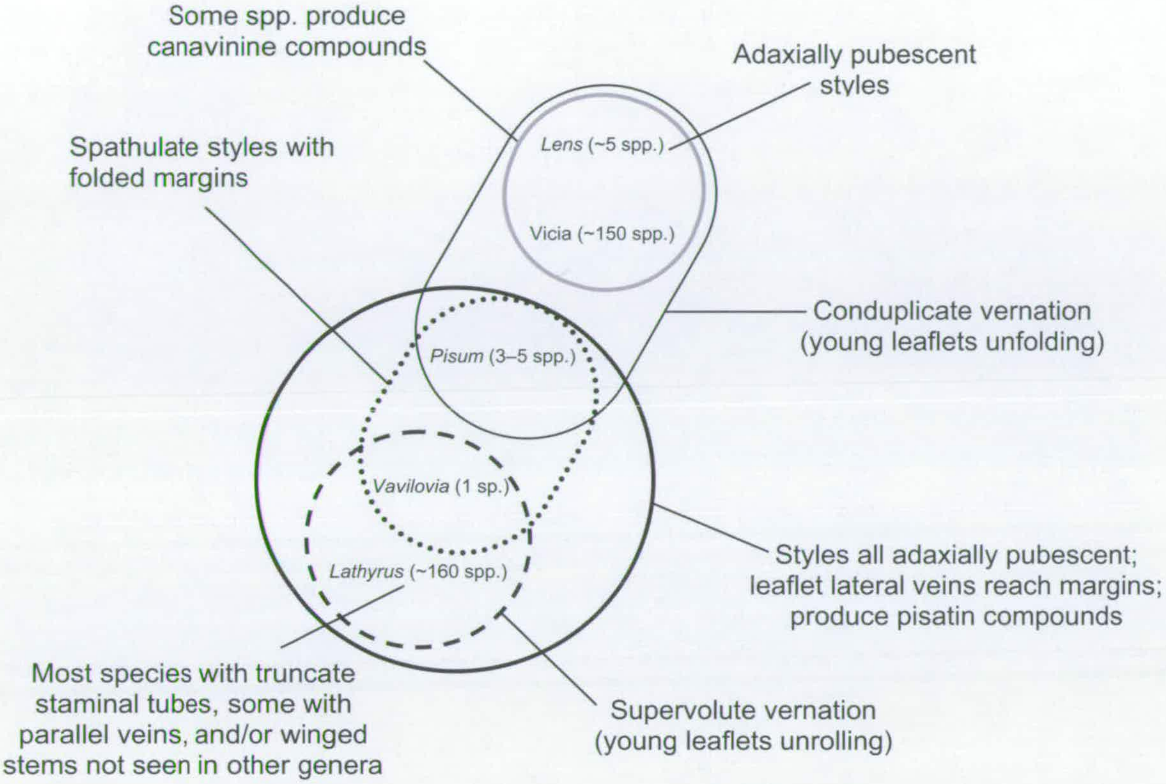

Figure 3.1 Shared and exclusive character states in tribe Fabeae
Based on Gunn & Kluve (1976) and Kupicha (1981, 1983), the diagram is congruent with recent molecular studies (Steele & Wojciechowski 2003, D.-I. Seok, University of Tokyo, personal communication) that strengthen the grouping of *Pisum* and *Lathyrus*. Neither of these analyses included *Vavilovia*. Some characters, such as the adaxially pubescent styles seen in *Vicia ervilia* (as well as *Lathyrus*, *Lens*, *Pisum* and *Vavilovia*), are more difficult to trace; they may be homoplasious or represent an ancestral character state (D.-I. Seok, personal communication).

Thus, the following *suite* of characters is currently used to distinguish *Lathyrus* within the Fabeae (Gunn & Kluve 1976, Kupicha 1983):

1. Styles pubescent only on the adaxial face
   [Shared with *Pisum*, *Lens*, *Vavilovia*, *Vicia subvillosa* and most individuals of *V. ervilia*]

2. Leaflet venation reticulate vs. camptodromous or brochidodromous
   [Shared with *Pisum*, *Lens* and *Vavilovia*, although many species of *Lathyrus* have parallel venation]

3. Truncate staminal tubes (vs. oblique) in most species
   [Oblique staminal tubes are found in some species of South American *Lathyrus*]

4. Stem winged in some species
   [Restricted to *Lathyrus*, but only found in c. 50% of *Lathyrus* species]

5. Leaflet ptyxis supervolute vs. conduplicate
   [Shared with *Vavilovia*]

6. Styles sometimes spathulate but without reflexed margins.
   [Styles are spathulate in some members of *Lathyrus* sects Clymenum, Linearicarpus and Notolathyrus. In *Pisum* and *Vavilovia* the styles are spathulate with reflexed margins.]

Critically, none of these characters are exclusive to all *Lathyrus* species.

3.2.4 *Molecular phylogenetics in tribe Fabeae*

Molecular phylogenetic analyses containing multiple genera in the Fabeae have only begun to appear relatively recently. These studies have been limited in their taxon sampling from across the tribe. In the first of these, Fennel et al.(1998) looked at a restricted dataset of *Vicia* and *Lathyrus*, based on *trn*L intron sequences. This analysis only included one species of *Lathyrus*, which was unsurprisingly found to be distant from the species of *Vicia*.

Also in 1998, Asmussen and Liston conducted a phylogenetic study of *Lathyrus* based on chloroplast DNA restriction fragment length polymorphism (RFLP) data. This study included *Vicia cracca* as an outgroup as well as *Vicia pisiformis* and produced a strongly monophyletic *Lathyrus*.

Choi et al. (2006) produced a molecular phylogeny of East Asian *Vicia* species based on nuclear internal transcribed spacer (ITS) sequences. She and collaborators included some members of *Lathyrus* (*L. latifolius* and *L. japonicus*) and their resultant phylogenetic tree suggests that *Vicia* may be polyphyletic, with *Lathyrus* and *Pisum* nested inside the *Vicia* clade. Resolution is, however, limited and firm conclusions were not drawn.

Steele and Wojciechowski's (2003) phylogeny of the Fabeae and Trifoleae (Fig. 3.2) is based on the *matK* gene and gives the most comprehensive coverage for the tribe to date, with ten species of *Vicia*, five species of *Lathyrus*, two species of *Lens* and *Pisum sativum*. This research agrees with that of Choi et al. and they suggest that *Vicia* may be paraphyletic, with the other genera nested inside it. This study places *V. articulata* and the cleistogamous *V. hirsuta* at the base of the Fabeae, albeit with very limited support. would suggest that the phylogeny of *Vicia* in particular is more complex than morphological or more limited molecular studies have been able to demonstrate. Steele and Wojciechowski (2003), however, urged a note of caution and called for further data to clarify this possible paraphyly. In spite of this lack of certainty within *Vicia*, both of these studies show the monophyly of a group containing *Pisum* and *Lathyrus*. This is well supported by their common foliar biochemistry and general patterns in stylar morphology and leaflet venation –

patterns recognised by Raji (1971) Gunn & Kluve (1976), Simola (1966), Bell et al.(1971, 1978) and Kupicha (1974, 1976, 1981, 1983).

Sampling within *Lathyrus* was limited to a few readily available species from only two sections in Choi et al.'s study (sects. Lathyrus and Orobus) and three sections in Steele and Wojciechowski's 2003 study (sects. Aphaca, Lathyrus and Orobus). Furthermore, no molecular studies have ever included *Vavilovia* (Lewis & Schrire 2002). This monotypic genus is evidently closely related to *Pisum*, and is sometimes considered to be within it (e.g. Gunn & Kluve 1976). Steele & Wojciechowski (2003) predicted that *Lathyrus* should be closer to *Vavilovia* than *Pisum*, as the two former genera share supervolute leaflet vernation.

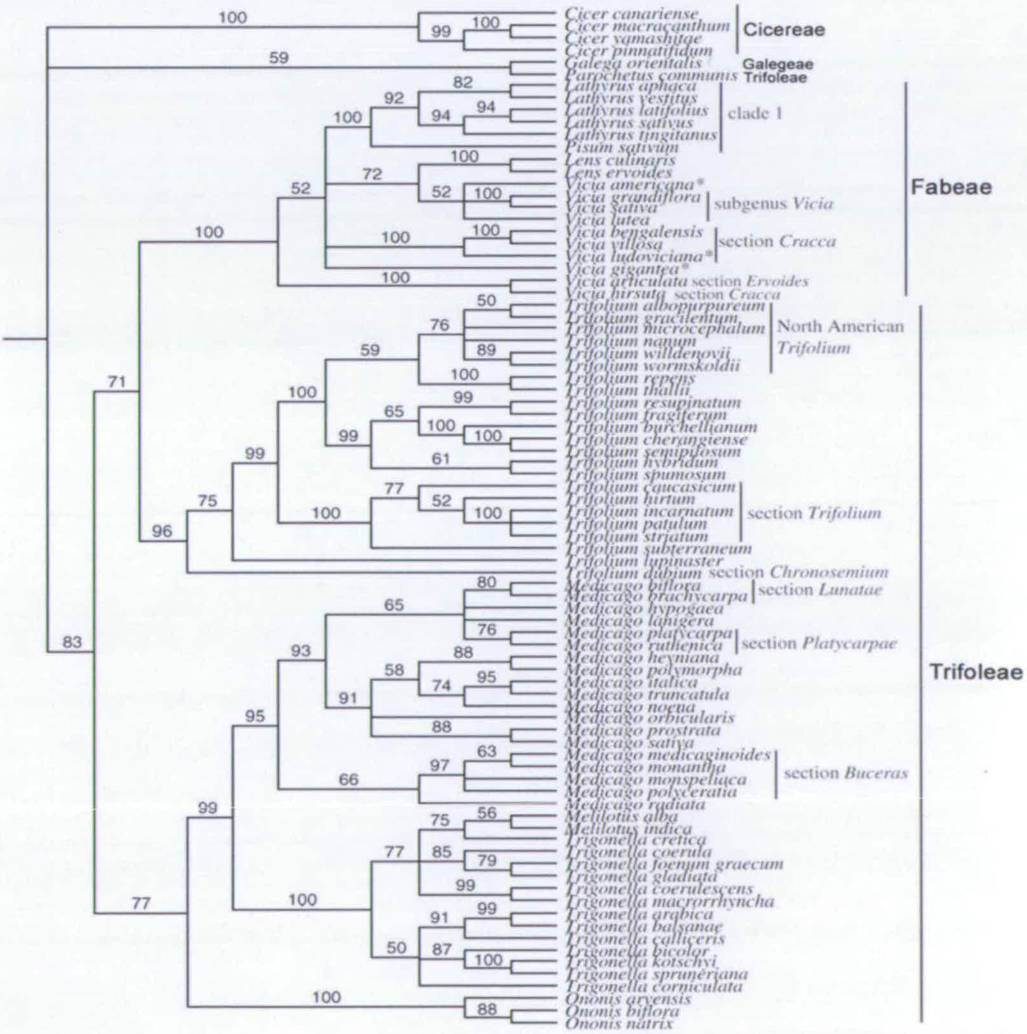

Figure 3.2 Phylogeny of tribes Fabeae and Trifoleae based on the *matK* gene
Reproduced from Steele and Wojciechowski (2003). This is a 50% majority rule consensus of 390 maximum parsimony trees of length 910 steps. Numbers above branches are bootstrap percentages. Tribes and infrageneric taxa are shown to the right.

3.3 Materials and Methods

3.3.1 *Choice of DNA region*

The chloroplast maturase K (*matK*) gene has been used extensively in phylogenetic analyses at infra-family levels Hilu & Liang (1997). Examples include Steele & Vilgalys (1994 - Polemoniaceae); Johnson & Soltis (1994 and 1995 - Saxifragaceae); Xiang et al. (1998 - Cornaceae); Stanford et al. (2000 - *Juglans*) and Hu et al. (2000 - Leguminosae tribe Millettieae). Steele and Wojciechowski's (2003) success with the gene in tribe Fabeae suggested it would be ideal for further investigations in the tribe. The *matK* gene is one of the main DNA regions used in investigations of the entire Leguminosae (e.g. Lavin et al. 2005) and it was felt that these further investigations in tribe Fabeae would be easily integrated into the wider existing Legume datasets.

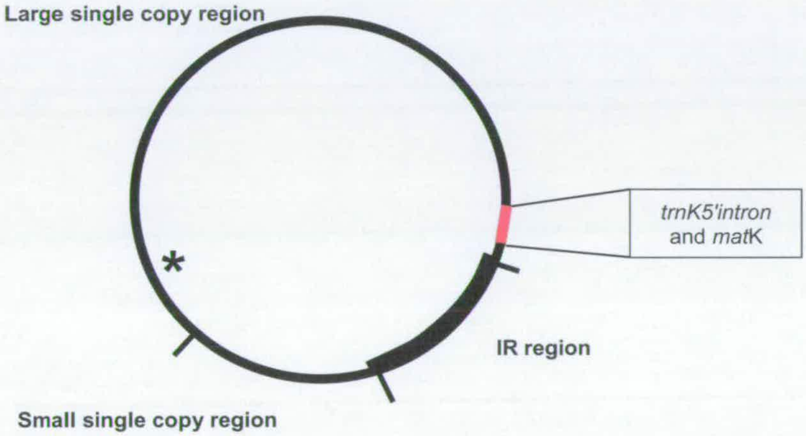

Figure 3.3 Chloroplast DNA location of the *matK* region sequenced in this study. Note that there is only one copy of the 'inverted repeat' (IR) region in *Lathyrus* and allies. The asterisk indicates the position of the other copy of the IR region in many other angiosperms.

The primers used in this analysis (Fig. 3.4, Table 3.2) were legume specific and designed by Hu et al. (2000). The *matK*10 primer is from Kato et al.(1998) designed for Betulaceae. *trnK* and *matK* code on the 'B' strand of the chloroplast genome.

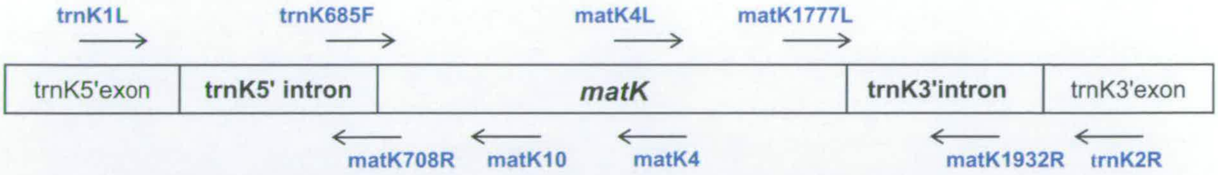

Figure 3.4 Locations of *trnK* and *matK* primers used in this study
The matK gene codes on the B strand of DNA. 'F' and 'L' primers are forward primers, 'R' primers are reverse.

Table 3.2 Primers used in the *matK* analysis

Name	Sequence (5' - 3')	Direction	Tobacco position
*trnK*1L	CTC AAT GGT AGA GTA CTC G	Forward	
*trnK*685F	GTA TCG CAC TATG TAT CAT TTG A	Forward	3724
*matK*708R	TCA AAT GAT ACA TAG TGC GAT AC	Reverse	3701
*matK*10	ATT GAT TCT GTT GAT ACA TTC	Reverse	3446
*matK*4L	CTT CGC TAC TGG GTG AAA GAT G	Forward	3157
*matK*4R	CAT CTT TCA CCC AGT ATC GAA G	Reverse	3136
*matK*1777L	TTC AGT GGT ACG DAG TCA AAT G	Forward	2603
*matK*1932	CAG ACC GGC TTA CTA ATG GG	Reverse	2468
*trnK*2R	AAC TAG TCG GAT GGA GTA	Reverse	1835

3.3.2 *Samples*

Samples of dried leaf material were collected from a variety of sources. Cultivated and wild specimens were silica-gel dried and samples taken from herbarium specimens were stored in silica-gel in zip-sealable plastic sample bags to prevent hydration and subsequent DNA degradation. My own wild collections were placed in commercially available 'make-your-own' tea bags before placing them in the silica-gel. This has the benefit of preventing the dry leaf from breaking up and becoming dispersed within the silica-gel crystals. The cuticle on *Lathyrus* species is not particularly waxy and whole leaflets dry quickly even when not in direct contact with the silica-gel. This collection method always produced well-dried samples from which DNA could readily be obtained. The accessions of *Vicia* and *Lens* used in this analysis are largely the same as for Steele & Wojciechowski, 2003 (Table 3.3).

Many specimens were provided by donation, including some of the same accessions used by Asmussen and Liston (1998). Accessions of several Eurasian and South American species come from the United Kingdom's National Council for the Conservation of Plants and Gardens (NCCPG) *Lathyrus* collection held by Sylvia Norton and come originally from collections made in the wild. Herbarium specimens for these are held in her private collection. The NCCPG collection obtained Scientific Collection status following its involvement in this research project.

Twenty taxa were chosen to represent a spread of species from within tribe Fabeae. These included *Vavilovia formosa,* new accessions of 19 species of *Lathyrus* and a new accession of *Vicia lutea*. When added to the existing tribe Fabeae sequences (Steele and Wojciechowski, 2003), this sample set represented all five genera in tribe Fabeae and eight of the twelve sections of *Lathyrus* (Table 3.3). Steele & Wojciechowski's (2003) *V. gigantea* is treated here as *V. nigricans* subsp. *gigantea*, and *V. ludoviciana*, included in their analysis, was not used here, as the sequence was not available.

3.3.3 *Ingroup delimitation and outgroup choice*

Trifolium repens was chosen as outgroup from among Steele and Wojciechowski's (2003) existing dataset as their previous analysis strongly supported *Trifolium* as sister group to a monophyletic tribe Fabeae. Given this strong monophyly of the tribe relative to *Trifolium repens*, this species was the sole outgroup used in the analyses presented here.

Table 3.3 Accessions of Fabeae sequenced for the *matK* region.

Sectional classification and species numbers for *Lathyrus* are from Kupicha (1983) with modifications based on Hara & Williams (1979), Nelson & Nelson (1983), Tsui (1984), Broich (1986), Zhu & Meng (1986), Maxted & Goyder (1988), Iseley (1992), and Asmussen & Liston (1998). Sectional classification and species numbers for *Vicia* are from Kupicha (1976)

General species distributions are shown as well as more specific localities for wild-collected specimens newly sequenced for this study.

*Accession numbers (in bold) are G. Kenicer's reference numbers. KPS, Wojciechowski and USDA are Steele & Wojciechowski's collections (s.n.=without accession numbers). Genbank accession numbers (preceded by AF) are given in brackets for accessions used in Steele & Wojciechowski (2003). New accessions have not yet been published and submitted to Genbank.

Locations of voucher specimens by source: Asmussen & Liston, University of Aarhus, Denmark; S. Norton, National Council for the Conservation of Plants and Gardens *Lathyrus* collection, West Wickham, Cambridgeshire, UK; G. Kenicer, RBGE, Herbarium, Royal Botanic Garden Edinburgh, Edinburgh, UK.

Genus Section (no. spp.)	**Species**	**Distribution** (wild origin collection locality)	**Accessions, sources and vouchers***
Lathyrus			
Aphaca (2)	*L. aphaca* L.	Europe & Mediterranean	USDA 286527 (AF522084)
Clymenum (3/4)	*L. clymenum* L.	Mediterranean	**2** Asmussen 1994 – 2
Lathyrus (34)	*L. latifolius* L.	C. Europe	Wojciechowski 543 (AF522085)
	L. sativus L.	E. Mediterranean to Iran	USDA 283562 (AF522086)
	L. sylvestris L.	Europe	**19** Asmussen 1994 – 16
	L. tingitanus L.	North Africa	USDA451858 (AF522087)
	L. tuberosus L.	Europe	**21** Asmussen 1994 – 18
Linearicarpus (7)	*L. angulatus* L.	Mediterranean	**23** Asmussen 1994 – 19
	L. sphaericus Retz.	Europe	**24** Asmussen 1994 – 20
Nissolia (1)	*L. nissolia* L.	W. and C. Europe	**26** Asmussen 1994 – 22
Pratensis (6)	*L. pratensis* L.	W. Eurasia	**30** Asmussen 1994 – 48
Orobus (~ 50; Eurasia ~ 21)	*L. davidii* Hance	E. Asia (S. Korea)	**79** Kenicer – 38 (Kangwando Province)
	L. laevigatus subsp. *laevigatus* (Waldst & Kit.) Kit.	C. Europe (Dolomites)	**101** S. Norton
	L. niger (L.) Bernh.	W. Eurasia (Hungary)	**50** Asmussen 1994 – 43
	L. palustris subsp. *pilosus*	Northern hemisphere (Japan)	**108** Kenicer – 61 (Hakone BG, from Sapporo)
	L. vaniotii Léveillé	E. Asia (S. Korea)	**117** Kenicer – 30 (Kangwando Province)
	L. vernus (L.) Bernh.	W. Eurasia	**54** Asmussen & Liston (cult. Oregon)
Orobus (N. America 29)	*L. jepsonii* E. Greene	N.W. USA	**36** Asmussen 1994 – 40
	L. littoralis (Nutt.) Endl.	N.W. USA (Oregon)	**38** Asmussen 1994 – 42
	L. polyphyllus Nutt.	N.W. USA (Oregon)	**40** Asmussen 1994 – 45
	L. vestitus Nutt.	W. USA	KPS s.n. (AF522088)
Notolathyrus (26)	*L. multiceps* D. Clos.	S. America (Chile)	**31** RBGE – 19912326 (Kirkpatrick 377)
	L. magellanicus Lam. A	S. America (Chile)	**94** S. Norton 1999 – 684
	L. magellanicus Lam. B	S. America (Chile)	**97** S. Norton 1999 – 679
Lens	*Lens culinarius* Medik.	Pantemperate crop (cultivated)	**USDA 172938 (AF522089)**
	Lens ervoides (Brign.) Grande	E. Mediterranean	**USDA 572330 (AF522090)**
Pisum	*Pisum sativum L.*	Pantemperate crop (cultivated)	**136** Kenicer – 65 (cult. Tokyo University BG)
Vavilovia	*Vavilovia formosa* Al. Fed.	Caucasus (Turkey	**130** RBGE 00158112 F. Holtz 00859
Vicia			
Cassubicae (9)	*V. nigricans* subsp. *gigantea* (Hook & Arn.)	USA	KPS s.n. (AF5220155)
Cracca (40)	*V. benghalensis* L.	Eurasia	USDA 393833 (AF 5220154)
	V. hirsuta (L.) Gray	Pantemperate weed	KPS. s.n. (AF5220157)
	V. villosa Roth	Eurasia	KPS. s.n. (AF5220161)
Americana (1)	*V. americana* Mühl ex Willd.	E. Asia (as V. bungei) / USA	KPS s.n. (AF5220153)
Vicia (6)	*V. grandiflora* Scop.	W. Eurasia	USDA 602377 (AF5220156)
	V. sativa L.	Pantemperate weed	KPS s.n. (AF5220160)
Hypechusa (12)	*V. lutea* L. A	Eurasia	USDA199226 (AF5220159)
	V. lutea L. B	Eurasia (UK)	**183** Kenicer – 54 (Nottinghamshire)
Trifolium			
	T. repens L.	Pantemperate crop/weed	KPS s.n. (AF5220117)

3.3.4 *DNA Extraction*

Total genomic DNA was isolated from dried leaf material following a modified version of the CTAB method of Doyle & Doyle (1987). 800µl of 2× CTAB solution was used with 3µl of ßmercaptoethanol added just prior to extraction. For most samples, isopropanol precipitation was overnight at -20°C, but material obtained from herbarium specimens was left for up to 3 weeks depending on the age and condition of the source specimen, following Richardson et al. (2001b).

Agarose gels (0.8%) containing 400mgl^{-1} ethidium bromide (etBr) were used to visualise the extracted DNA under UV light. PCR conditions and regimes were varied according to the region surveyed (see Materials and Methods, chapter 4 for regions other than *mat*K) and also the quality and concentration of template DNA as determined from the gels.

3.3.5 *Polymerase Chain Reaction*

The *trnK1L* / *trnK2R* primer pair was used to amplify the complete region.
The basic PCR protocol (25µl system) was as follows:

Distilled water: 18.4µl
DNTP premix (200 mM of each dNTP)*: 2.0µl
10 X PCR buffer*: 2.5µl
forward primer (5 or 10µM): 0.5 µl
reverse primer: (5 or 10µM): 0.5 µl
exTaq DNA polymerase*: 0.1µl
Template DNA: 1.0 µl

* from Takara, 3-41 Otsu city, Shiga ken Japan

Primer stock concentrations were 10µM for all *trn*K primers, resulting in final primer concentrations of 0.1 to 0.2µM. Where the template DNA was determined to be weakly concentrated, 2µl template and 0.7–1µl of each primer were used, reducing the amount of distilled water to compensate. The volume of template was reduced slightly (0.8µl) where it was particularly strongly concentrated or contained much RNA, increasing the distilled water to compensate. The full 25µl of PCR product was run on a 0.8% agarose gel.

The PCR protocol followed a standard program: (1) Initial denaturation was conducted for 90 s at 95°C. (2) Thirty cycles of denaturation were conducted for 45 s at 95°C, annealing for 60 s at 54°C, and elongation at 72°C. The elongation time began at 90 s and increased by 2 s per cycle. (3) A final elongation step of 15 min at 72°C was performed.

As a final step before cycle sequencing, the PCR product was purified using the Geneclean III kit (Bio101, Carlsbad, California, USA), using two-thirds volumes of reagents for economy but otherwise following the manufacturer's instructions.

3.3.6 *Cycle sequencing reaction*

Cycle sequencing used the primers given in table 3.2, in the combinations:

trnK1L (forward) and *matK*708R (reverse)
trnK1L (forward) and *matK*10 (reverse)
trnK685F (forward) and *matK* 4R (reverse)
*matK*4L (forward) and *matK*1932R (reverse)
*matK*1777L (forward) and trnK2R (reverse)

The reverse reaction verified each nucleotide position. The cycle sequencing reaction used the BigDye Terminator Cycle Sequencing kit, version 3.0 or 3.1 (Perkin Elmer, Foster City, California, USA) in an iCycler thermal cycler, version 1.280 (BioRad, Hercules, California, USA) with a total reaction volume of 5 µL. Initial denaturation (1 min at 96°C) was followed by 25 cycles of denaturation (10 s at 96°C), annealing (5 s at 50°C), and elongation (4 min at 60°C).

Samples were sequenced on an ABI Prism 377 automated sequencer (Perkin Elmer). Sequences were assembled using Sequence Navigator (Applied Biosystems

Division, Perkin Elmer, Foster City, CA, USA.) initially aligned using ClustalX (Thompson et al., 1997), then adjusted manually as Nexus-format text files.

Given the very high proportion of missing data for the flanking regions of the *matK* gene (including all of Steele & Wojciechowski's 2003 accessions), these regions were excluded from the analysis. Only the *matK* portion of the sequences was analysed, allowing close comparison with Steele and Wojciechowski's existing tree (2003).

3.3.7 *Phylogeny estimation*

Maximum parsimony (MP) analysis has been a widely used technique for estimating phylogenies based on molecular data for the past 15 years. Maximum parsimony is a convenient evolutionary assumption – the model can be used to aid in aligning sequences (Simmons & Ochoterena, 2000), and requires relatively little computer memory during phylogenetic analysis, allowing datasets with many operational taxonomic units to be analysed. The assumption can also readily be applied as a means of optimising any character *a posteriori*, for example morphological characters on a DNA sequence-based phylogenetic tree (figs 3.5, 3.6).

The MP assumption is one in which evolution is as conservative as possible. When treebuilding, the assumption seeks to minimise the number of character state transitions steps that have occurred in an unrooted phylogenetic tree. Thus, when estimating phylogeny from a molecular DNA dataset, MP analyses seek to minimise the number of nucleotide substitutions among taxa to give the overall shortest tree (Doyle & Davis, 1998; Page & Holmes, 1998). This is an unrealistic assumption as Maximum Parsimony estimates of phylogeny can be inaccurate when rates of substitution are high, or are unevenly distributed among lineages. In addition, reversals of point substitutions are perfectly feasible and multiple historical substitutions between lineages can be overlaid on one site. This masks previous substitutions and confounds estimates of phylogeny made by parsimony (Doyle & Davis, 1998; Huelsenbeck, 2001).

Due to the over-simplicity of the MP assumption, alternative likelihood-based analyses have also been used, incorporating more sophisticated evolutionary models.

Bayesian and other likelihood-based analyses incorporate an explicit model of DNA sequence evolution that is more parameter rich than a maximum parsimony model and are therefore regarded as more likely to estimate phylogeny accurately than parsimony methods. These methods are far more demanding of computing power and, until about 10 years ago, likelihood-based analyses were confined to use in small datasets (<15 taxa) with relatively short sequences. In recent years, Bayesian analysis has risen to prominence as a mainstream analytical technique for phylogeny estimation (Huelsenbeck et al., 2002; Douady et al., 2003). Bayesian analysis is a likelihood method that takes account of posterior probability - the probability of an evolutionary model yielding the observed data, and prior probability- an optional user-defined means of skewing the analysis towards a given preferred tree topology (Lewis, 2001; Huelsenbeck et al., 2001, 2002; Bollback, 2002; Ronquist et al. 2005). Bayesian analyses run relatively quickly and are readily applied to large datasets as they use an iterative method for estimating posterior probabilities (Markov chain Monte Carlo method). In addition, Bayesian analysis provides simultaneous estimates of tree topology, branch length and support in the form of posterior probability (PP) values. Separate estimates of topology and branch support (most commonly bootstrap values) are required for maximum parsimony analysis (Holder & Lewis, 2003).

Maximum parsimony analyses remain the most widespread basis for classification based upon phylogenetic principles in plants. Thus, for example, MP studies in angiosperms, (Angiosperm Phylogeny Group, 1998); *Centaurea* (Compositae, Garcias-Jacas, 2000; Greuter et al., 2001) and *Acacia* (Leguminosae, Luckow 2003; Maslin et al., 2003; Orchard & Maslin, 2003) have all led to major reclassifications. Bayesian and other likelihood analyses are, however, increasing in frequency (e.g. Angiosperm Phylogeny Group, 2003; Wojciechowski et al., 2004) because of the advantages outlined above. In this and the following chapter, both MP and Bayesian analyses are used to estimate phylogenies, allowing a comparison of tree topologies recovered from both approaches.

There has been considerable research into the relative merits of Bayesian and bootstrap measures of support, with some researchers suggesting that nonparametric bootstraps are overly conservative (e.g. Hillis & Bull, 1993; Leaché and Reeder, 2002; Wilcox et al., 2002) and others that Bayesian posterior probabilities are overcredible (e.g. Suzuki et al., 2002). The general consensus is that Bayesian posterior probabilities are not directly comparable to bootstrap supports (they measure different features of the dataset), but that both measures are valuable (Leaché and Reeder, 2002; Alfaro et al., 2003). In order to provide some consistency to interpretation of node supports, I use defined cut-off points for my degree of confidence in these values. Cumulative posterior probabilities (PP values) of 0.95 or greater are generally considered significant – effectively a P value of 0.05 (Huelsenbeck et al., 2001). Although PP values of 50 and greater are mapped onto the trees presented in this and the following chapter, values of less than 95 are considered relatively poor support. Maximum Parsimony bootstrap values of 50-74% are considered weak support, 75-84% are moderate and 85-100% are strongly supported (e.g. Richardson et al., 2000). If both measures of support are high, this affords us confidence in the topology. Where there is disagreement in topology, but both indices of support are high, the Bayesian tree, with its more explicit model of evolution is preferred.

3.3.8 *Maximum parsimony analysis*

PAUP*, version 4.0β10 (Swofford, 2001) was used for maximum parsimony analysis.

All characters were unordered and unweighted.

Maximum parsimony searches (following Richardson et al., 2001a) comprised two heuristic searches for each data set, using a tree-bisection-reconnection (TBR) search algorithm. An initial search of 10000 random addition sequence replicates saved one tree per replicate (MulTrees and steepest descent options off), creating a range of possible starting trees for a second search and avoiding minima of tree length that are merely local optima. The second search invoked multrees and steepest descent and saved a maximum of 10000 shortest trees, which is sufficient to capture all topological variation (e.g. Sanderson and Doyle, 1993). A fast, stepwise analysis of 100000 bootstrap replicates using a heuristic search with TBR branch-swapping algorithm, saving one tree per replicate (MulTrees off) and with one replicate per bootstrap replicate, was run in PAUP to test the support for clades.

3.3.9 *Bayesian analysis*

Modeltest version 3.7 (Posada & Crandall, 1998) was used in combination with PAUP*, version 4.0β10 (Swofford, 2001) to determine the appropriate model of evolution for the *matK* region. Modeltest applies 56 successively more parameter-rich models to the dataset, to determine which model best fits the pattern of nucleotide substitution. As models are applied, the likelihoods for successive models providing the best fit for the data asymptotically approach stationarity. Modeltest selects the model where the difference in the likelihood values for the succeeding model becomes insignificant (i.e. the P value for the pairwise comparison for the log-likelihoods between models is greater than 0.05). Modeltest estimates the optimal model based on the hierachical likelihood ratio test, the Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC). The selection based on the AIC favours a model which provides a balance between best fit to the data whilst minimising parameter richness. In addition, the AIC quantifies uncertainty in model choice, as it provides rankings for the models in question, as well as weights that can be used to weight trees in a model averaged consensus (Posada & Buckley, 2004). The hierarchical likelihood ratio test can provide false positives, as it tests successive models in a defined hierarchy (Posada & Crandall 1998) where significant differences between two models may not be recognised if the change in likelihoods between intervening models in the hierarchy is not significant. (Posada & Buckley, 2004). Consequently model choice used in this thesis is based on the AIC.

Bayesian analysis used MrBayes version 3.1 (Huelsenbeck & Ronquist, 2001), and was run on a Sharp PC-GP 10-CH Portable computer, with an Athlon 64D mobile processor. By default the PC version of MrBayes 3.1 runs two independent analyses in parallel, allowing cross correlation at the expense of longer computing time. Two separate types of search were run; one with the model determined by Modeltest input (i.e. a user defined model). A second search was run with MrBayes being left to estimate its own models of evolution.

The default settings were used for searching - four Markov chain Monte Carlo chains, with chain temperatures set at default with five million repetitions, sampling every 1000 replicates. Burnin was initially set at 10% (500,000) trees. Likelihood stationarity was then checked by plotting likelihood values against sample number (in MS Excel). The burnin could then be adjusted upwards as required.

An analysis using a codon-based model of evolution was also run, setting the parameters in MrBayes to estimate its own model. Each analysis was run at least twice in order to ensure congruent topologies and comparable branch lengths with each run.

3.4 Results

3.4.1 *Sequence characteristics*

Aligned sequence data (nexus format files) can be found on the accompanying CD-ROM. Sequence characteristics for the *matK* analysis are summarised in table 3.4

Table 3.4 Sequence characteristics for *matK* analysis

	matK
Aligned length	1552
Length range (minus gaps)	1488–1527
G and C content (%)	36.6
Gap positions	61
Constant sites	1167
Variable sites	385
Parsimony informative	174
No. of unambiguously aligned gaps	9
Parsimony informative gaps*	5

*Parsimony informative insertion-deletions included:

- Position 551-559 (9 nucleotides) shared by *Lens culinarius*, *L. ervoides*, *Vicia lutea*, *V. americana*, *V. grandiflora* and *V. sativa*. These species form a clade in the analyses. Short stretches of missing data overlap with this indel region for the following species - *Lathyrus polyphyllus*, *L. clymenum*, *L. vaniotii*, *L. niger* and *Pisum sativum*. Although it is not possible to determine the indel status for these species, they are all placed in a strongly supported clade separate from the *Vicia-Lens* clade.

- Nucleotides were not present in positions 592 – 597 (6 nucleotides) and 807 – 813 (6 nucleotides) for any taxa except both species of *Lens*.

- Two other short stretches of indel regions were potentially phylogenetically informative: 1481 – 1489 (9 nucleotides) missing in *Lathyrus vestitus* and *L. jepsonii*, and 1547 – 1550 (3 nucleotides) missing in *L. multiceps* and *L. nervosus*. However, these overlapped with longer regions of missing data in *Lathyrus magellanicus*, *L. nissolia*, *L. niger* and *Vavilovia formosa*.

Table 3.5 Missing data in the *matK* region across the taxa sampled.

Taxon	Aligned nucleotide positions missing	Total missing bases
Pisum sativum	517 – 559	42
Vavilovia formosa	518 – 542 1146 – 1552	430
Vicia americana	0 – 37	37
Lathyrus angulatus	507 – 540	33
L. clymenum	510 – 554	44
L. davidii	507 – 545	38
L. jepsonii	507 – 533	26
L. laevigatus	509 – 517	8
L. littoralis	511 – 542	31
L. magellanicus	508 – 547 1151 – 1552	440
L. multiceps	510 – 545	35
L. nervosus	518 – 546	28
L. niger	510 – 536 1165 – 1552	413
L. nissolia	0 – 48 480 - 548 1176 – 1552	492
L. palustris	507 – 545	38
L. polyphyllus	510 – 565	55
L. pratensis	518 – 538	20
L. sphaericus	1162 – 1333	171
L. sylvestris	508 – 517	9
L. tuberosus	507 – 535	28
L. vaniotii	507 – 580	73
L. vernus	480 – 543	63

In *L. nissolia*, *L. niger*, *L. magellanicus* and *Vavilovia formosa*, these stretches of missing data were caused by primer pairs that did not work in sequencing reactions. Time and budget constraints precluded new primer designs and sequencing for these species. These stretches of data missing for these species represent between one quarter and one third of the length of the region. However, this lack of data did not significantly affect the results as repeats of Maximum Parsimony and Bayesian analyses with these portions of the dataset excluded produced the same tree topologies.

3.4.2 *Maximum parsimony analysis*

A strict consensus of the 2400 equally most parsimonious trees is shown in Figure 3.5.

3.4.3 *Bayesian analyses*

Modeltest selected an F81+I+G model, with base frequencies:

A=0.3021
C=0.1920
G=0.1736
T=0.3323
Shape parameter =1.0957
Proportion of invariable sites=0.3880

This is a simple model, with substitution rates equivalent, as well as constant between mutation types. On checking the relative frequencies of substitutions – plotted on MacClade v. 4.06 (Maddison & Maddison, 2003), this model appeared valid.

When the search with the user defined model was used, computation time was considerably faster than under the second, free parameter search (i.e. with MrBayes constructing its own model). However, these two methods of searching produced identical models and tree topologies in which branch lengths varied only slightly.

The Bayesian consensus tree from the free parameter search, with averaged branch lengths is shown in figure 3.6.

Even with only a million replications, the analysis constrained to codon groups took over 30 days to run, although stationarity was reached after less than 15% of the replicates. The topology of the codon-based phylogeny was the same as that for the standard analysis.

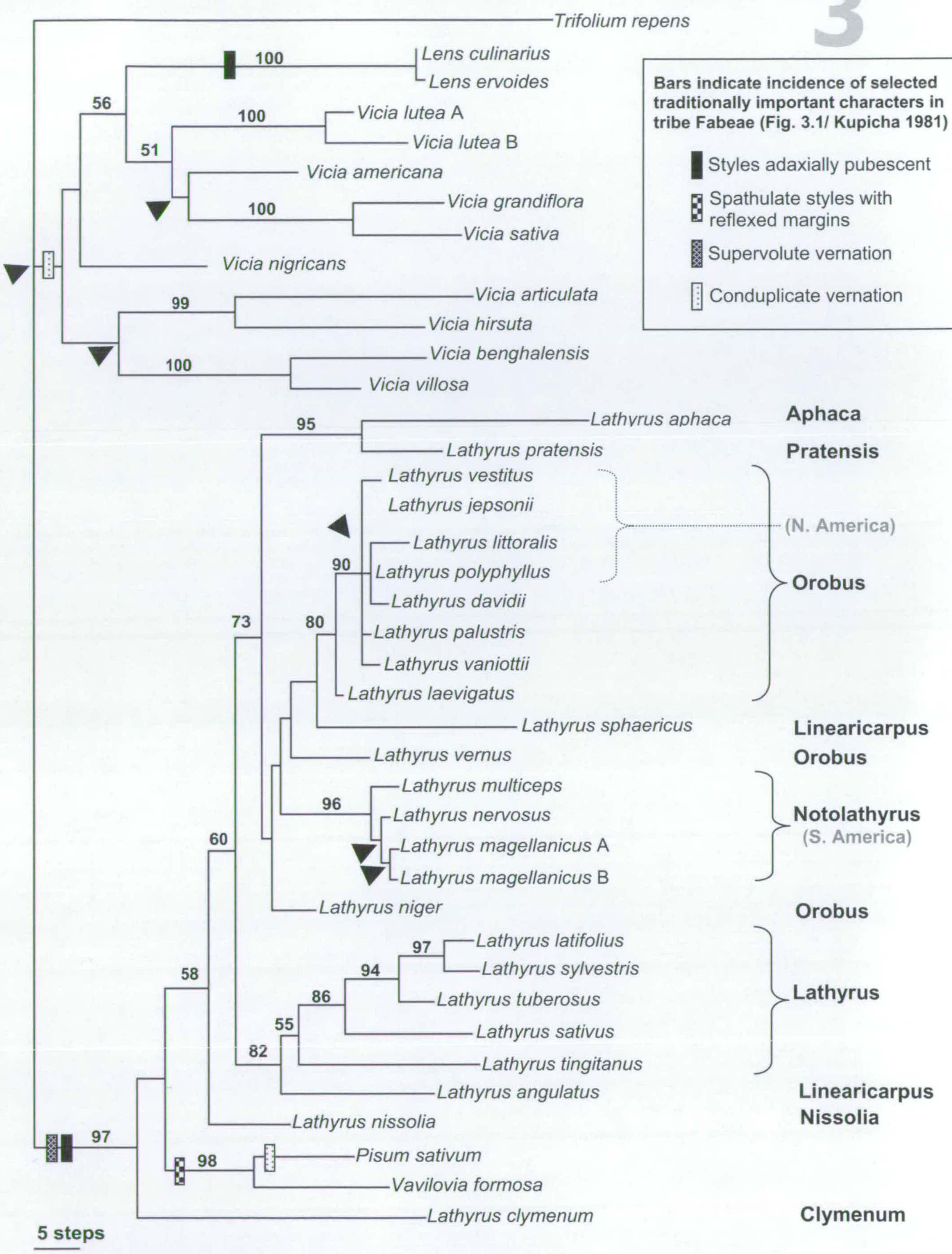

Fig 3.5 Maximum parsimony analysis of the *matK* gene
One of 2400 equally most parsimonious trees (610 steps long). Bold figures above branches are bootstrap supports. Black arrowheads indicate nodes that collapse in the strict consensus tree.
Consistency index: 0.752; Retention Index: 0.791; Rescaled consistency index: 0.595
Sections of *Lathyrus* are on the right. All *Lathyrus* taxa are Old World, except where shown.

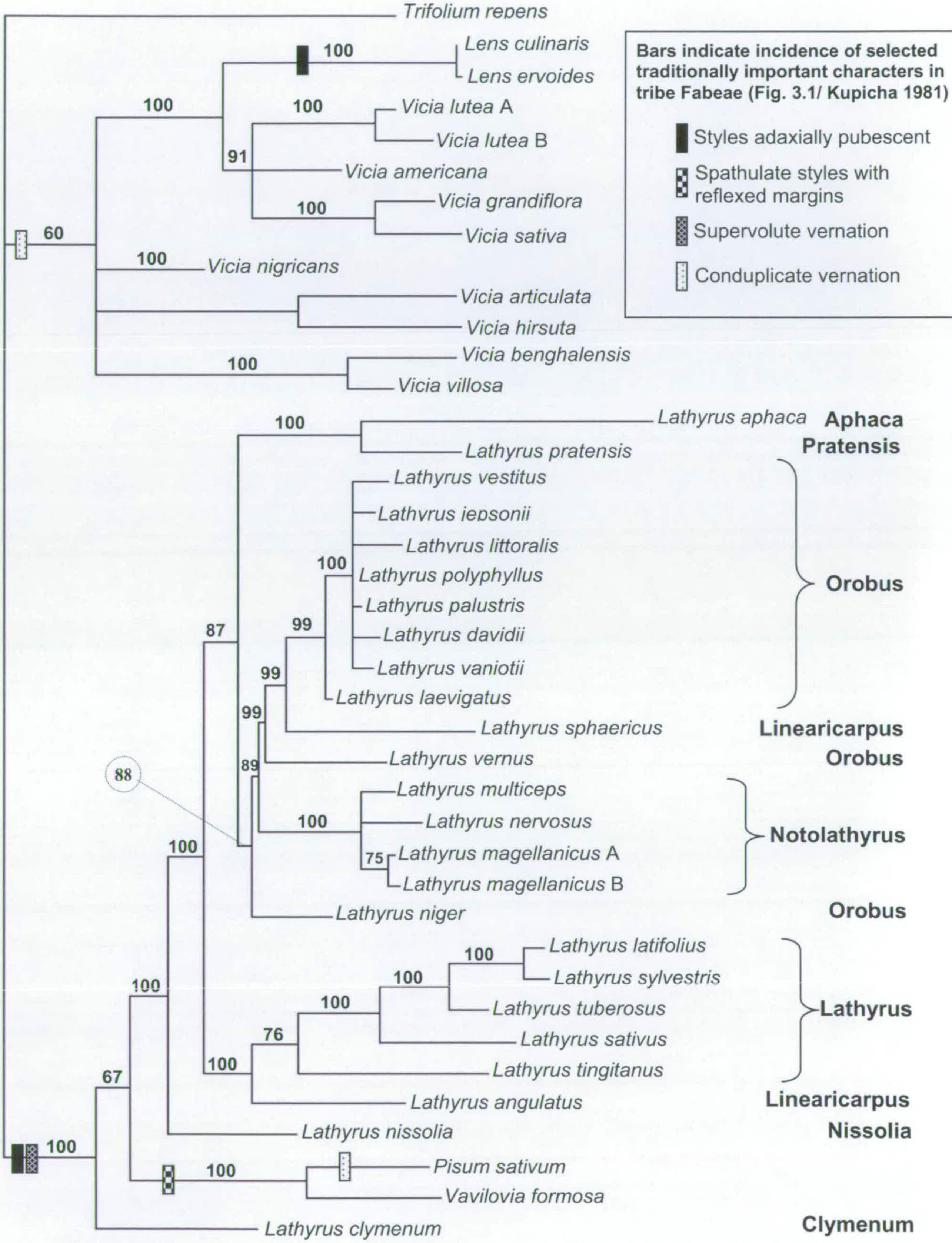

Fig 3.6 Bayesian analysis of the *matK* gene
Bold figures above branches are clade compatibility values (posterior probabilities). Sections of *Lathyrus* are indicated to the right.

3.4.4 *Phylogeny*

The Bayesian tree (Fig. 3.6) is only slightly more resolved than the strict consensus of the MP analysis (Fig. 3.5, with clades collapsed at the black arrows). The clustering of both accessions of *L. magellanicus* together is the only topological difference between the two trees. In general, the Bayesian analysis gives higher support values for each clade although the bootstraps and posterior probabilities, although strongly correlated, are not directly comparable (Huelsenbeck 2002, Douady et al. 2003).

In these analyses, (figs 3.5, 3.6) two major groups are resolved:

1) A strongly supported clade (bootstrap 97%, PP value 100) containing *Lathyrus*, *Pisum* and *Vavilovia*. The nodes closest to the root of this clade receive weak support e.g. bootstrap <50%, posterior probablility 67 for *L. clymenum* as sister to the remainder of the group.

2) The remaining accessions – from *Lens* and *Vicia* – form a clade that is very weakly supported in the Bayesian analysis (pp value 67) and collapses in the MP analysis under a 50%+ bootstrap threshold. Within this group, however, there are some well-supported clades.

3.5 Discussion

The agreement between the Bayesian and MP trees and the generally high support for clades (Figs. 3.5, 3.6) implies a robust estimate for the phylogeny.

3.5.1 *Comparison with previous* matK *analysis in tribe Fabeae*

The topology resolved in these analyses is congruent with the findings of Steele & Wojciechowski (2003). The *Lathyrus* - *Pisum* - *Vavilovia* group is monophyletic as predicted by Steele & Wojciechowski – the addition of *Vavilovia* and additional species from within *Lathyrus* did not affect relationships between *Vicia* and *Lathyrus* and there was no support for the dissective classification of Roskov and his colleagues (Roskov et al., 1996; Stankevich & Roskov, 1998; Roskov et al., 1998).

The inclusion of *L. clymenum* in the analysis produces the only disagreement with Steele & Wojciechowski's 2003 results. The monophyly of *Lathyrus* (sensu Kupicha, 1983) receives no support (Figs. 3.6, 3.7). Consequently, the question of which species or genus is sister to *Lathyrus* is unclear.

3.5.2 Vicia *and* Lens

All of the *Vicia* and both of the *Lens* accessions form a weakly supported clade. *Lens* has generally been considered to be monophyletic and distant from *Lathyrus*, and is thought to be most closely related to some of the ervoid species of *Vicia* (Czefranova, 1971a; Ladzinsky & Abbo, 1996; Mayer & Bagga, 2002). The analyses presented here support this view.

Steele and Wojciechowski's (2003, see also Fig. 3.2) *matK* analysis also indicated that *Lens* is nested within *Vicia*. *Lens* shares an adaxially pubescent style with *Lathyrus*, *Pisum* and *Vavilovia*, but has been excluded from this group on the basis of other characters (Fig. 3.1), including the production of canavanine compounds (shared with *Vicia*) (Kupicha, 1981). The addition of further *Lathyrus* species and *Vavilovia* to the analysis of Steele and Wojciechowski's data does not influence the placing of *Lens*. This argues for the independent evolution of the adaxially pubescent style in *Lens*, although the low support values separating *Lens* from the *Lathyrus-Pisum-Vavilovia* clade urge a degree of caution. This could be further investigated with data from more DNA regions, and also increased taxon sampling from within *Vicia*, which should certainly include *V. subvillosa* and *V. ervilia*, the two species for which adaxially pubescent styles have been recorded.

Vicia and *Lens* share conduplicate leaflet vernation. The only other taxon within the tribe that does so is *Pisum*. Based on the trees, it seems likely that the conduplicate leaflet vernation in *Pisum* is a homoplasy. It may be that the large stipules of *Pisum* afford developing leaflets greater space, so they do not need to be so efficiently packed and rolled up into the space available. Leaflet vernation in *L. clymenum* and other members of sect. Clymenum is obscure, as the leaves are phyllodic. Further morphological and developmental investigation in sect. Clymenum is essential in order to confirm the independence of conduplicate leaflet vernation between the *Vicia – Lens* clade and *Pisum*.

3.5.3 Pisum, Vavilovia *and* Lathyrus clymenum

Styles have long been recognised as important characters in defining genera within tribe Fabeae (e.g. Gunn & Kluve, 1976; Kupicha, 1974, 1977, 1981). The reflexed stylar margins in *Pisum* and *Vavilovia* are limited to these two genera and the tree topologies suggest this character as a synapomorphy for these genera, which are grouped with bootstrap 98% and PP value 100. This supports the relationship between *Pisum* and *Vavilovia* suggested by Gunn & Kluve (1976). *MatK* sequences for more accessions of *Pisum* are required to determine if *Pisum* is monophyletic or if *Vavilovia* is nested within it.. Ideally, at least two representative accessions of each of the three generally accepted species (Kloz, 1971; Ben-Ze'ev & Zohary, 1983; Ambrose & Maxted, 2000) in *Pisum* should be sequenced.

The relationship between *Pisum*, *Vavilovia* and *L. clymenum* in these trees is a fascinating result. The phylogenies estimated here (Figs. 3.5 and 3.6) show *Pisum* and *Vavilovia* nested inside *Lathyrus*, implying a paraphyletic *Lathyrus*. Support values are very low (<50% bootstrap and PP value 67) for the paraphyly of *Lathyrus*, however morphology suggests that the topology presented here may reflect true evolutionary relationships. *Pisum* and the species of sect. Clymenum share similar overall habits and morphologies – they are robust, solitary-flowered, annual Mediterranean taxa with spathulate styles. The phyllodic leaves of *Lathyrus* sect. Clymenum preclude direct comparison of leaf morphologies with *Pisum*, but ontogenic observations of styles amongst these taxa may provide further clues as to their relationships. Such detailed observations of styles have proven effective in identifying groups in *Vicia* (Endo & Ohashi, 1995, 1997). The other members of *Lathyrus* sect. Clymenum, *L. ochrus*, *L. gloeospermus* and *L. articulatus* (often considered a variety of *L. clymenum*), should certainly be included in future morphological and molecular studies, including sequencing of the *matK* gene.

The styles are broadly spathulate in *Pisum* and *Vavilovia*, most taxa in *Lathyrus* sect. Clymenum (except the small-flowered, cleistogamous *L. gloeospermus*), and some members of sects. Lathyrus and Lathyrostylis and the Notolathyrus group. In the trees presented here, taxa with a spathulate style are not well enough represented to make any conclusions as to the systematic significance of this character state, although its presence in the Notolathyrus group is probably secondarily derived. Given the topology of the trees resolved here, the spathulate styles common to *L. clymenum*, *Pisum* and *Vavilovia* may have been retained from a common ancestor and may be a synapomorphic character state for the *Lathyrus – Pisum – Vavilovia* clade.

Given its long history as one of the most important non-cereal crop plants, it is not surprising that Linnaeus treated *Pisum* as a genus distinct from *Lathyrus* (Linnaeus, 1753). *Pisum*'s long history of cultivation and selection by humans has led to highly desirable morphological traits being overselected for and has overemphasised some traits whilst reducing or getting rid of others (Ambrose & Maxted, 2000). This pattern tends to result in morphology-based classifications that carve out economically important taxa as genera distinct from broader 'parent' genera. This appears to be the case in genera such *Lycopersicon* Miller, now treated as *Solanum*, (Olmstead & Palmer, 1997; Bohs & Olmstead, 1999), and *Pastinaca* L. (Parsnips) which from ITS sequence data appears to be nested deep inside *Heracleum* L. (Jin Hyub-Paik, RBGE, personal communication).

3.5.4 Lathyrus

Most of the clades resolved in *Lathyrus* approximate to recognised sections. It should be stressed that taxon sampling was not sufficient in this analysis to determine monophyly of sections with any great degree of confidence. The analyses presented in chapter 4 focus on sectional relationships in the genus and further discussion of sectional level classifications appears in that chapter.

All members of sect. Lathyrus form a clade. The species represented here are a mix of perennial N. European taxa (*L. latifolius*, *L. sylvestris* and *L. tuberosus*) and annual Mediterranean taxa (*L. sativus* and *L. tingitanus*). This sampling was led somewhat by availability of the taxa and the fact that each of these species has some economic significance, so it does not represent an ideal spread of the diversity of the section. *Lathyrus angulatus* (Sect. Linearicarpus) is sister to this group in the analysis.

Lathyrus nissolia has an unique morphology within the genus. The leaves are completely phyllodic – appearing almost like grass blades. Most modern authors cannot suggest an alliance with any other taxa in the genus. This isolated position is supported here.

A large, poorly supported clade (bootstrap 73%, PP value 87) was resolved in both analyses. This clade consists of a core group of species from sect. Orobus as well as *L. aphaca* (sect. Aphaca); *L. pratensis* (sect. Pratensis); *L. sphaericus* (sect. Linearicarpus) and the members of Kupicha's predominantly South American sect. Notolathyrus. This clade does not correspond to any taxonomically recognised group. However, it does contain predominantly N. Eurasian mesophytic taxa, as well as all of the New World taxa. It therefore probably represents an important radiation in the genus into more mesophytic habitats. Within this group, *L. aphaca* and *L. pratensis* cluster together (bootstrap 95%, PP value 100). Both of these species share sagittate stipules, a relatively rare character in *Lathyrus*. The RFLP study of Asmussen & Liston, as well as Kupicha's (1974) morphological studies on vascular supply to the stipules also suggested a close affinity between the two species.

The oddity within this clade is *Lathyrus sphaericus*, which is a delicate annual plant with a morphology and habit quite unlike the taxa of sect. Orobus among which it is nested in the trees (Figs. 3.5, 3.6). *Lathyrus sphaericus* has been placed in sect. Linearicarpus based on its morphology. Although its position is well supported in the Bayesian analysis, support for *Lathyrus sphaericus* in this position in the MP analysis is very low, and it is borne on a long branch. In order to confirm the possibly erroneous placing of this taxon in the *matK* trees, the accession was sequenced twice from separate extractions. The same topology was resolved in both analyses. Sequence data from further accessions and from more genome regions would potentially help resolve its phylogenetic placement.

The South American Notolathyrus group is well supported as monophyletic in both trees (bootstrap 98%, PP value 100), and is placed on long branches in both cases. Combined with its geographical isolation from the remainder of the genus, this may be enough to warrant its reinstatement as a section, disagreeing with Asmussen & Liston (1998) who placed it inside sect. Orobus. Although there is no single synapomorphy that defines sect. Notolathyrus, all except for *L. macropus* have unijugate leaves, a condition not otherwise seen in sect. Orobus sensu Asmussen & Liston. If Notolathyrus is reinstated as a section, then the classification of *L. niger* may need to be reassessed if a recircumscribed sect. Orobus is to be monophyletic. *Lathyrus niger* and *L. venetus* (not sampled here) are both etendrillous species with dense racemes of more than 10 lilac-purple flowers and leaflets without 3 parallel veins, a combination of characters that sets them apart from other members of sect. Orobus. Given the size of sect. Orobus, its broad geographical distribution and wide morphological variation, it is perhaps not surprising that as currently circumscribed, sect. Orobus may be paraphyletic. These results are supported by the findings presented in chapter 4 and are discussed in further detail there.

3.6 Conclusions

This study has proven valuable in our understanding of the structure of tribe Fabeae. Maximum parsimony and Bayesian analyses yield largely congruent tree topologies.

The increased sampling of *Lathyrus matK* gene sequences supports the monophyly of a *Lathyrus* – *Pisum* – *Vavilovia* clade and the close relationship between *Pisum* and *Vavilovia*. *Lens* and *Vicia* are distinct from the *Lathyrus* – *Pisum* – *Vavilovia* clade, with *Lens* nested inside *Vicia*. The adaxially pubescent style found in *Lathyrus*, *Lens*, *Pisum*, *Vavilovia*, and two species of *Vicia* (*V. subvillosa* and *V. ervilia*) may be a homoplasy with at least two separate origins.

The *Vicia* – *Lens* clade is sister group to the *Lathyrus* – *Pisum* – *Vavilovia* clade. Inclusion of sequence data from more genome regions, and increased sampling in *Vicia* would help to resolve whether these are nested inside the *Vicia* – *Lens* clade or sister to the *Lathyrus* - *Pisum* – *Vavilovia* clade. Such a study should certainly include *V. subvillosa* and *V. ervilia*, as their adaxially pubescent styles suggest an affinity with the *Lathyrus* - *Pisum* – *Vavilovia* clade.

Pisum sativum and *Vavilovia* are resolved as sisters. The evidence that suggests they are nested inside *Lathyrus*, with *L. clymenum* being the most basally divergent species in the *Lathyrus* – *Pisum* – *Vavilovia* clade, is very poorly supported. Further data (particularly from other genomic regions) is evidently required before generic delimitations in tribe Fabeae can confidently be recircumscribed. If *Pisum* and *Vavilovia* are indeed nested within *Lathyrus*, a nomenclatural reappraisal would be required. The potential implications of this are discussed further in chapter 4. The results also confirm the reflexed stylar margin common to *Pisum* and *Vavilovia* – a character that has traditionally been used to diagnose this pair of genera – as a synapomorphy.

Within *Lathyrus*, clades corresponding to sects. Lathyrus sensu Asmussen & Liston (1998) and Notolathyrus sensu Kupicha (1983) are resolved. An alliance between sects Aphaca and Pratensis is supported, as is the isolated position of *L. nissolia*. The two members of sect. Linearicarpus sequenced here are very distant from each other.

A mesophytic, predominantly 'oroboid' clade is also resolved within *Lathyrus*, hinting at a split between a wide Eurasian / New World group and a Mediterranean / European group. However, support for this clade is low (bootstrap 73%, PP value 87). This pattern is investigated further in chapter 4. The position of *L. sphaericus* (sect. Linearicarpus) is surprising. This delicate annual species is nested within the robust, perennial oroboid members of *Lathyrus* sect. Orobus, and needs further investigation. The oroboid group consists predominantly of members of sect. Orobus and sits in the large, poorly supported mesophytic clade with *L. aphaca* (sect. Aphaca) and *L. pratensis* (sect. Pratensis), as well as members of Kupicha's predominantly South American sect. Notolathyrus. If sect. Notolathyrus is treated as a section (as in Kupicha, 1983), then sect. Orobus sensu Bässler becomes paraphyletic, with *L. niger* isolated from the remainder of the section.

Resolving such issues of sectional classification and the relationships among the basal lineages in the *Lathyrus – Pisum – Vavilovia* clade requires far better sampling of *Lathyrus* species, including data from further genome regions, and a better resolved phylogenetic tree. The following chapter presents a phylogenetic analysis sampling more *Lathyrus* species, and using multiple, more rapidly evolving genome regions than *matK*.

4

Molecular phylogenetics of *Lathyrus* 2

Biogeography and systematics of the genus

4.1 Introduction and aims

This chapter presents phylogenetic analyses of *Lathyrus* and uses them to study sectional classifications and biogeography.[1] DNA sequence data from accessions representing 55 species, for the internal transcribed spacer plus 5.8S-coding region of nuclear ribosomal DNA as well as the *trnL-F* and *trnS-G* regions of chloroplast DNA, are used in this chapter to:

1. Evaluate the findings of the phylogenetic analysis of *matK* presented in chapter 3, particularly whether *Lathyrus* is monophyletic.
2. Evaluate the monophyly of the sections in *Lathyrus* proposed by Kupicha (1983) and modified by Asmussen and Liston (1998).
3. Answer biogeographical questions:
    - Is the Mediterranean region the centre of origin for the genus?
    - From where are the North American taxa derived?
    - What is the origin of the South American species?

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[1] The Maximum parsimony analysis presented in this chapter was published in:

Kenicer G.J., Kajita T., Pennington R.T. & Murata J. (2005) Systematics and biogeography of *Lathyrus* (Leguminosae) based on internal transcribed spacer and cpDNA sequence data. *American Journal of Botany* **92**: 1199-1209.

4.2 *Lathyrus*

4.2.1 Lathyrus *classifications past and present*

Lathyrus has traditionally been divided into sections as a reflection of putative natural groupings and for ease of reference (Fig. 4.1; de Candolle, 1825; Godron 1848). As in the wider tribe Fabeae, circumscription of these sections has shifted considerably over the years primarily due to the lack of clear-cut morphological characters available for classification in the genus.

Godron (1848)	**Boissier (1872)**	**Czefranova (1971b)**	**Kupicha (1983)**	**Asmussen & Liston (1998)**	**This study**
▨	▨	▨	Notolathyrus	Orobus	Notolathyrus
Orobus	Orobus	Lathyrobus	Orobus		Orobus
	Orobastrum	Orobus	Lathyrostylis	Lathyrostylis	Lathyrostylis
		Pratensis	Pratensis	Pratensis	Pratensis
		Eurytrichon			
Aphaca	Aphaca	Aphaca	Aphaca	Aphaca	Aphaca
Orobus	Orobastrum	Neurolobus	Neurolobus	Neurolobus	Neurolobus*
		Orobon	Orobon	Lathyrus	▨
Eulathyrus	Eulathyrus	Lathyrus	Lathyrus		Lathyrus
Cicercula	Cicercula	Cicercula			
				Cicercula	
Orobus	Orobastrum	Orobastrum	Orobastrum	Orobastrum	
			Linearicarpus	*L. sphaericus*	*L. sphaericus*
				L. angulatus	*L. angulatus*
			Viciopsis	▨	▨
Nissolia	Nissolia	Nissolia	Nissolia	Nissolia	Nissolia*
Clymenum	Clymenum	Clymenum	Clymenum	Clymenum	Clymenum*
				L. gloeospermus	L. gloeospermus
					Pisum*
					Vavilovia*

Figure 4.1 Selected sectional classifications of *Lathyrus*

Key sectional classifications in the history of *Lathyrus*. Hatched boxes represent species groups not treated by the respective authors. The only authors to treat the Notolathyrus group were Kupicha (1983); Asmussen & Liston (1998) and myself. My study did not include either of the monotypic sects. Viciopsis (*L. saxatilis*) or Orobon (*L. roseus*), as good quality leaf material was not available for DNA extraction.
Grey shaded box (Boissier's Orobus) is a genus. Dashed lines represent equivocal separations.
*The results presented in this thesis (chapter 3 and this chapter) imply that *Pisum* and *Vavilovia* could be treated within *Lathyrus*, or that sects Clymenum, Neurolobus and Nissolia could be treated as separate genera.

Bässler (1966), Simola (1968) and Kupicha (1983) discussed the difficulties of morphology-based classifications. Many traditional characters, such as habit and growth form, size, the degree of development of tendrils, and broadening of the styles show continuous variation both among and within species. Discontinuous characters, such as parallel leaflet venation and bifid stigmas had previously proven useful for defining some groups within Eurasia. However, when Simola (1968) and Kupicha (1983) considered the genus in its entirety (including S. American species), it became apparent that these characters were shared by apparently distantly related groups. At present (based on Kupicha's classification), the only section defined by an unequivocal diagnostic apomorphy is the monotypic sect. Nissolia, which has phyllodic leaves without leaflets.

4.2.2 *Recent classifications - morphology*

Almost all recent classifications of *Lathyrus* have differing approaches to hierarchical subclassifications. The general trend is to recognize twelve or thirteen sections or their equivalents (Czefranova, 1971b; Kupicha, 1983; Asmussen & Liston, 1998; ILDIS World Database of Legumes ver. 6.05 2002). Kupicha's classification was in part developed from Simola (1967), Bässler (1966, 1973, 1981), and Czefranova (1971b).

The sectional classifications of *Lathyrus* by Bässler (1966, 1971, 1973, 1981), Czefranova (1971b), and Kupicha (1983) attempted to account for convergence in morphological characters and possible reversal of character states across the Fabeae. The groups defined by these authors are based on combinations of character states in which one or more states may be absent for some taxa within a group. Such reliance on a preponderance of shared characters rather than on diagnostic potential synapomorphies hinders the demonstration of sectional monophyly based on morphology. One aim of this paper is to assess the monophyly of *Lathyrus* sections based on phylogenetic analysis of DNA sequence data.

4.2.3 *Recent classifications – molecular research*

Five molecular phylogenetic studies of *Lathyrus* species have been published: Asmussen and Liston (1998), Croft et al. (1999), Chtourou-Ghorbel et al. (2001), Badr et al. (2002), and Ben Brahim et al. (2002). All except that of Asmussen and Liston are of limited geographic or taxonomic scope; they focus on Mediterranean taxa, particularly within sect. Lathyrus, a group containing many economically and ecologically important species.

Asmussen and Liston's (1998) study which mapped cpDNA restriction fragment length polymorphism (RFLP) data, is the largest molecular investigation to date. They sampled 42 western Eurasian and New World species, and their study included representatives of all but one section (Fig. 4.2). Asmussen and Liston's results generally agreed with the sectional classifications of Kupicha (1983), but they suggested merging some groups: the monotypic sects. Orobon and Orobastrum with sect. Lathyrus, and the South American sect. Notolathyrus with the Holarctic sect. Orobus (Fig. 4.2). Their results supported the close relationship between sects. Pratensis and Aphaca proposed by Kupicha (1974, 1983) but were inconclusive about the relationships between other sections.

Section Orobus sensu Asmussen and Liston (1998) is a key taxon in our understanding of systematic and biogeographic relationships within *Lathyrus* and the wider Fabeae (Bässler, 1973; Kupicha, 1983; Asmussen and Liston, 1998). With over 75 species, Orobus is the largest section in *Lathyrus*. Its members are distributed across the entire geographic range of the genus in Eurasia (Bässler, 1966, 1973; Czefranova, 1971b; Kupicha, 1974, 1983; Allkin et al., 1985; Roskov et al., 1998), and it is the only section native to the New World (Asmussen and Liston, 1998). As a poorly delimited "dustbin" group, Orobus contains many species with uncertain affinities and is traditionally thought of as basal in the genus (Kupicha 1983).

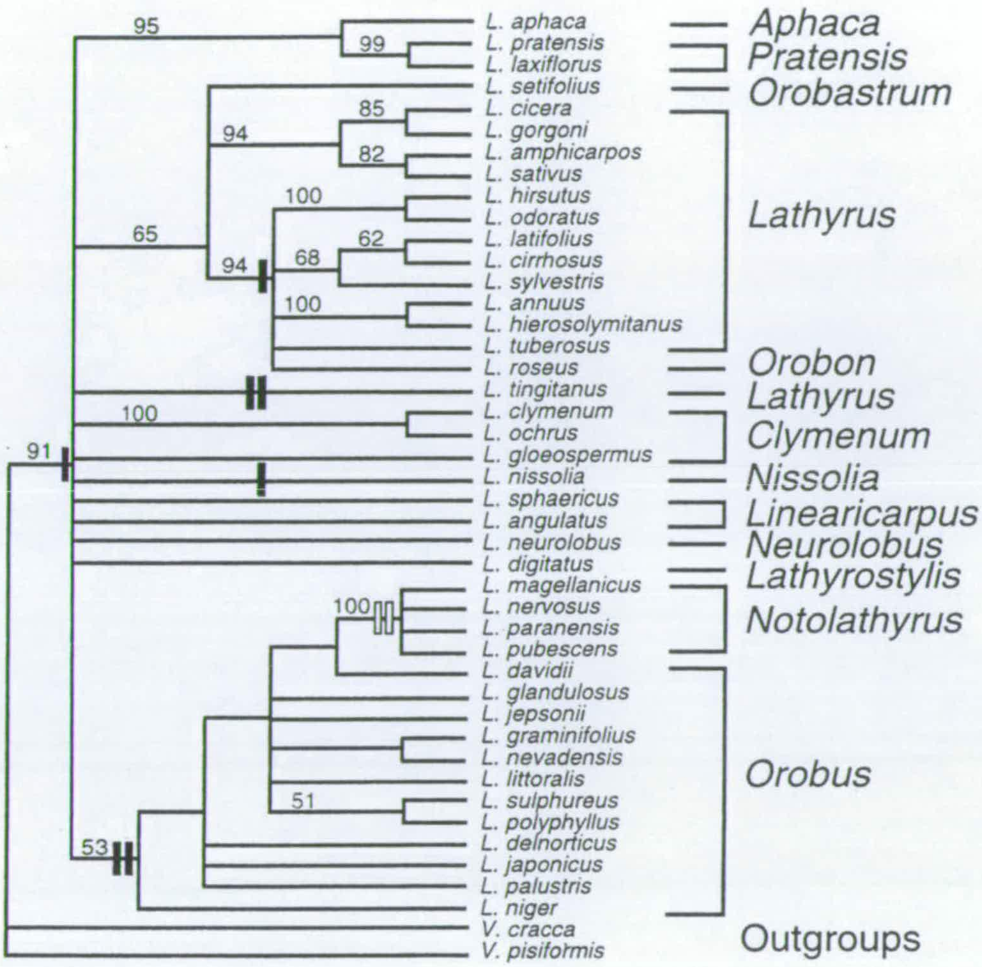


Fig. 4.2 Asmussen and Liston's strict consensus of 18500 equally parsimonious trees Based on *rpo*C and cpDNA RFLP data. Filled bars represent major length mutations. Open bars (in Notolathyrus) represent reversals of the same mutations at the base of the Orobus clade. The numbers above branches are percentage bootstrap values. Reproduced from Fig. 5 of Asmussen and Liston (1998).

4.3 Biogeography of *Lathyrus*

For an introduction to the distribution of *Lathyrus*, see chapter 2.

Intercontinental relationships between *Lathyrus* taxa have only been addressed by a few authors (Simola, 1968a; Kupicha, 1983; Asmussen & Liston, 1998). The patterns of diversity and dispersal within and between continents and when and how the key dispersal events occurred in *Lathyrus* are the principal areas investigated in this thesis. In order to clarify my approach, the current perspective on these questions in *Lathyrus* in the wider context of the biogeography of north-temperate plants is outlined in the following two sections.

4.3.1 *Origins and dispersal - development of biogeographic patterns in Lathyrus*

Simola's (1968a) detailed work on leaflet anatomy and venation is the earliest to consider the genus in a worldwide context. She looked to the strong morphological similarities between Turco-Iranian members of sect. Lathyrostylis and the South American species to suggest a link through Africa in the late Cretaceous.

Following on from Simola, Kupicha (1983) produced the next significant worldwide treatment and had the benefit of 15 years more research into the specifics of plate tectonics. A number of lines of evidence suggested a different pattern to Kupicha from that proposed by Simola. *Vicia* shows a strikingly similar distribution pattern to that of *Lathyrus*, with a far larger number of Eurasian species than New World ones and similar centres of diversity, indicating that the two genera share a parallel history. In addition, all of the smaller genera of the Fabeae are predominantly found in the Eastern Mediterranean - Turco-Iranian region. Kupicha's interpretation of this pattern was that the Tribe as a whole has had a far longer time to diversify in that area. In both *Lathyrus* and *Vicia*, the North American species are morphologically relatively uniform compared to the Eurasian group. She considered the similarities between S. American and Eurasian *Lathyrus* to be the result of parallel evolution between the two lineages. Kupicha proposed that Eurasia must have been the site of origin of the group from a common vicioid stock with dispersal through North America and then into South America. She suggested that a "primitive ancestral stock having characteristics of Sect. Orobus" made the crossing between Eurasia and North America with the circumboreal *L. palustris* as a possible linking species.

Kupicha's conclusion was supported by Asmussen and Liston (1998) in the most recent worldwide treatment. Their cpDNA study (Fig. 4.2) resolved the South American species as a well supported monophyletic group with predominantly North American sister groups, although this relationship was not strongly supported. This New World clade was most closely related to a poorly resolved group of Eurasian sect. Orobus. Asmussen and Liston therefore concurred with Kupicha's interpretation of the sequence of colonisation from Eurasia, via North America to South America. They did not make any explicit revision of timings of these events, but saw the northern hemisphere groups as part of the temperate element of the boreotropical flora and the South American species as part of the holarctic element of the modern Andean flora. As a critical cautionary note, Asmussen and Liston highlighted the lack of any bootstrap support at the key nodes representing the intercontinental disjunctions. They also emphasized the need for further research on sect. Orobus. Their study included only two exclusively Eurasian species from this section, of which the East Asian *L. davidii* was placed inside the North American clade, as sister to the South American group, implying more complex geographic interchange than Kupicha (1974, 1983) suggested. Wider sampling of Eurasian species from sect. Orobus and a better supported phylogenetic tree are necessary before any more robust biogeographic conclusions can be made.

Unfortunately, confirmation of the biogeographical scenario suggested above is further confounded by lack of any direct fossil evidence for the Fabeae. However, fossil pollen assemblages from other groups suggest a suite of major radiations of herbaceous angiosperms during the mid and later Miocene (Graham 1993). Recent molecular clock estimates have been attempted across the whole of the temperate herbaceous legume clade which agree with this timing, placing the origin of the Fabeae crown clade at 17.5±1.9 Mya (Lavin et al. 2005). This provides further evidence against geologically earlier biogeographic hypotheses such as that of Simola (1968).

The following section discusses how the scenario outlined above for *Lathyrus* fits into the wider context of north temperate and American intercontinental floristics.

4.3.2 *Plant migration in the Cenozoic - Lathyrus in the bigger picture*

Disjunctions apparent in taxa between Eurasia and North America have drawn at least as much attention over the years as Huxley's and Wallace's Lines and the South American-Antipodean legacy of the Gondwanan breakup. The presence of common Eurasian and American floristic elements was first highlighted by European botanists such as Halenius, Kalm and Thunberg in the mid 1700s but were not really developed until almost a century later when Nuttal and particularly Asa Gray had the opportunity to look at many specimens from both continents (reviewed in Boufford & Spongberg 1983). These observations introduced the concept of a once common forest structure covering the northern hemisphere. Mid 20th century observations of a temperate 'arcto-tertiary geoflora' across the fossil record led to the further development of the idea (Axelrod, 1952). Modern north-temperate elements were believed to have shared a common, continuous, very high latitude distribution during the warm Eocene and Oligocene (e.g. Axelrod, 1948, 1952). The warmer temperate elements then became isolated from one another as climates deteriorated through the Miocene, pushing the communities (in their entirety) south (Axelrod 1966). By extension of this, much of the continental landmass to the south of this thin temperate band was covered by a near continuous forest of megathermal plants (i.e. those that require a mean annual temperature over 20°C) during the late Cretaceous and early Eocene (Axelrod 1948). The gradual breakup of this megathermal flora was thought to have given rise to many of the commonalities seen between floras today in the Old and New Worlds from the tropics northwards (Axelrod, 1948, 1966; Chaney, 1940, 1947). However, this view was considered a gross oversimplification and refinements were made in the light of reassessments of fossil ages and the timings of intercontinental land connections (e.g. Wolfe, 1975; McKenna, 1983; Tiffney, 1985a, 1985b). These revisions, which constitute the 'Boreotropical hypothesis' stem primarily from a more detailed understanding of what was happening tectonically and climatically in the Northern Hemisphere during the Cenozoic.

4.3.3 *Eurasia*

In the Paleocene and Eocene, the modern Eurasian landmass was not continuous. Until at least the Oligocene, Western and Eastern Eurasia were held in isolation from each other by the Turgai straits, a seaway to the east of the Urals which acted as a barrier to floristic interchange (e.g. Tiffney 1985). By the time of the putative origin of tribe Fabeae according to Lavin et al. (2005) (c. 17.5 Mya), however, the Turgai Straits had long since disappeared (by around 30Mya McKenna 1975). The overall pattern of habitat zonation in Northern Eurasia is east-west, following the climatic zones and enhanced by the Himalayas (Qian & Ricklefs 2000). The Caucasus and Ural mountains may have also promoted vicariant speciation during colder periods when they presented greater barriers to dispersal than today. In addition, the extreme continentality of climate in the central Eurasian plain means it is subject to cyclical desertification and 'regreening' according to climatic fluctuations. During particularly dry periods, species ranges of mesophytes might be split, affording West and East Eurasian groups periods in which to develop in isolation from one another.

Interchange of taxa between Eurasia and America was facilitated by two major connections both during and after the existence of the Turgai straits:

1) The North Atlantic Land bridge(s) are believed to have been open as a route for exchange of fauna and possibly temperate to megathermic floristic elements- through the 'Thulean' Greenland-Scotland ridge route (45-50°N) and the more Northerly 'De Geer' route (around 68°) (McKenna 1975 Tiffney 1985). Both these routes would have been available during the Early Eocene and there are some suggestions that megathermal species reached latitudes as high as 70°N (Wolfe 1997), allowing them free passage via either connection. Debate remains as to when this land connection was finally severed – with estimates ranging from the late Paleocene to mid or even late Miocene (Tiffney 1985, Tiffney & Manchester 2001). If the current age estimates for the origin of *Lathyrus* are correct, then it is probable that only the most recent of these dates that would have afforded intercontinental exchange by these routes.

2) The Bering Land Bridge is thought to have been available for species interchange since at least the Paleocene. It may have been severed in the mid Eocene and then resumed in the late Eocene (Tiffney 1985b) but this is uncertain and the earliest stratigraphic evidence for the Bering Strait comes from 4.3 - 7.4 million years ago when arctic mollusc species are first recorded from the Pacific (Marincovich & Gladenkov 1999, Sher 1999). Beringia thus allowed exchange of flora and fauna between Eurasia and North America until far later than the North Atlantic

connections and long after the closure of the Turgai straits so it would seem to be a far better candidate as the dispersal route for *Lathyrus*. This is perhaps borne out by the placing of the East Asian *L. davidii* within the N. American clade in Asmussen & Liston's (1998) molecular phylogeny. Throughout the Eocene, Beringia was north of its current position of 68°N although there is disagreement as to quite how far north. Some researchers (e.g. Tiffney 1985, Graham 1993, Tiffney & Manchester 2001) suggest a maximum of 75° N in the early Eocene such that only species that could cope with (or adapt to) very short winter days could have survived in Beringia at that time.

As the climate cooled from the Oligocene onwards, progressively more cool-tolerant floras established themselves across Beringia. If tribe Fabeae did indeed arise during the mid- or late- Miocene as proposed by Lavin et al. (2005), suitable temperate conditions appear to have been present to allow trans Beringian interchange for much of its existence.

As each floristic assemblage was driven south of the land bridges connecting the two continental landmasses, it can be assumed that interchange and geneflow stopped for many taxa, and isolation began. Although the general trend was towards a cooler and wetter environment, a general increase in the range of climatic fluctuations (Graham 1993) makes it difficult to say when any particular taxon would be excluded from making the crossing. Taxa might have had the opportunity to make the crossing multiple times in either direction through multiple representatives (Manchester & Tiffney 2001, Donoghue & Smith, 2004). Most modern East Asian and North American members of *Lathyrus* sect. Orobus (including *L. davidii*) are found in open mixed-forest or forest margins. The group might be expected to have colonized when such habitats were established across the intercontinental connections. When more open habitats were dominant, species with tolerances similar to the modern *L. palustris* (found in wet meadows and marshland) would have been the main contenders for interchange.

As intercontinental areas cooled during any fluctuation, the extent to which taxa moved by dispersal or adaptated to new conditions is also difficult to assess. Whilst reference is typically made in the literature to 'crossing the land bridges' (e.g. Hopkins, 1967; Tiffney, 1985b;) there is no reason why taxa might not have arisen on the land bridges and then dispersed in both directions as the floras were driven south. Thus the northern hemisphere intercontinental land bridges might themselves have been major sources of diversity.

4.3.4 *North America*

Graham (1993) reviewed the paleofloristics of North America, emphasising the importance of the Rocky Mountain uplift, and the development of different climates on either side from the Paleoene onwards. Extensive wet forests predominated (as they do today) on the west coast whilst the Great Plains were subjected to the drying effects of the rain shadow cast by the Rockies, most significantly during the late Miocene. Further east still, the Appalachians formed a third north-south barrier. Consequently, the North American flora developed the longitudinal patterning that persists today.

The major radiations in North American *Lathyrus* are overwhelmingly western in distribution - perhaps another argument in favour of colonisation from adjacent East Eurasia. One species group follows the forests of the west coast and mountains, one group is adapted to the arid areas of Southern, inland California, Colorado and New Mexico and a smaller, more diffuse group inhabits the area from the Great Plains to the East Coast (Broich, 1987, 1989 and S. Broich, Oregon State Department of Health personal communication).

4.3.5 *Across the Isthmus of Panama*

As well as the high latitude disjunction between Eurasia and the Americas, *Lathyrus* also straddles the Isthmus of Panama. In contrast to the Bering and North Atlantic land bridges, the Isthmus of Panama is oriented North-South. A continuous land connection formed only relatively recently (c. 3.5Mya, Burnham & Graham 1999). The current vegetation across the Isthmus of Panama is predominantly lowland and megathermal in character. Rather than a corridor, it is thought that the Isthmus actually represents a barrier to interchange of temperate taxa (e.g. Simpson & Neff

1985). *Lathyrus* is not found in Mesoamerica, reaching only as far south as Chihuahua in Mexico. In northern S. America (Venezuela, Colombia, Ecuador, Peru and Bolivia), the genus is restricted to temperate, upland areas, typically sub-Páramo and higher (over 2200m altitude). Further south, the genus becomes more diverse and descends to sea level by about 25°S.

4.3.6 *Antitropical distribution of Lathyrus*

Lathyrus has a continental double disjunctive distribution – between Eurasia and N. America and between N. and S. America. As Beringia is seen as an extant intercontinental bridge, it is generally assumed to explain the Eurasia-N. America disjunction and the northern distribution of *Lathyrus* is typically classed as holarctic. The disjunct presence of the group in temperate S. America means that the distribution of the whole of *Lathyrus* is termed antitropical. The antitropical pattern is sometimes referred to as amphitropical, extratropical or trans-tropical, none of which are entirely satisfactory terms. Amphitropical is ambiguous, implying an organism is found either in both tropics or on either side of the tropics; trans-tropical implies it is found in both the northern and southern tropics, while extratropical merely implies that an organism is found (somewhere) outside the tropics (Raven 1963, Humphries & Parenti 1999).

The antitropical pattern is shared by many temperate taxa (reviewed in Raven 1963, 1972). Raven's (1963) review paper lists 160 temperate taxa, mainly species or species pairs, that show this disjunction. Around 30 of these are bipolar disjuncts (Arctic/Antarctic-alpines), and the remainder are more temperate species, most of which have a Holarctic northern hemisphere distribution. The same pattern is also seen at the generic level (Table 4.1). The vast majority of these disjuncts are herbaceous plants, but with some woody groups (van der Hammen & Cleef 1985,Takhtajan 1986, Cleef 1979).

Table 4.1 Some example angiosperm genera with an antitropical and Holarctic distribution. Examples from Raven, 1963, 1972; Cleef, 1979; van der Hammen & Cleef, 1985,Takhtajan, 1986)

Genera	Family
Sambucus	Adoxaceae
Berberis	Berberidaceae
Hackelia, Lappula	Boraginaceae
Cerastium	Caryophyllaceae
Erigeron, Hypochaeris	Compositae
Cornus	Cornaceae
Draba	Cruciferae
Gaylussacia, Empetrum, Vaccinium	Ericaceae
Muehlenbergia, Cinna	Gramineae
Salvia, Satureja, Stachys	Labiateae
Tofieldia	Melanthiaceae
Oenothera	Onagraceae
Castilleja, Bartsia	Orobanchaceae
Sibthorpia	Plantaginaceae
Primula	Primulaceae
Potentilla, Spiranthes	Rosaceae
Gleditsia, Lathyrus, Lupinus, Trifolium, Vicia	Leguminosae
Anemone, Thalictrum	Ranunculaceae
Ribes	Grossulariaceae
Chrysosplenium	Saxifragaceae
Verbena	Verbenaceae

Most notable among the antitropical taxa from the perspective of *Lathyrus* are *Trifolium* and *Vicia*, genera that are closely related members of the 'Vicioid clade' (Wojciechowski et al. 2000). North American members of *Trifolium* are a monophyletic group derived from Eurasian species (Wojciechowski et al. 1999), a finding that invites comparison with *Lathyrus* and other genera.

Some phylogenetic studies of antitropical groups already exist that may offer comparison with *Lathyrus*. Recent molecular systematic research by Hughes and

Eastwood (2006) suggests that South American *Lupinus* is paraphyletic. One lineage of high altitude species is derived from a western North American lineage, and is distinct from a Mississippi/lowland South American (S.E. Brazil/N.E. Argentina) lineage. In *Hypochaeris* (a wind-dispersed composite), the S. American taxa form a monophyletic group, with Eurasian species as sister taxa (Samuel et al. 2003). *Chrysosplenium valdivicum* (Saxifragaceae) from Chile has its sister taxa in Eastern Asia (Soltis et al. 2001). Its diaspores that may variously be dispersed by wind, water or on the surface of animals (Savile, 1953; Rozzi & Armesto 1989).

One of the aims of this chapter is to determine the pattern of radiations in *Lathyrus* and establish whether the genus might have achieved its antitropical distribution through:

1. Long distance dispersal as has been inferred for *Lupinus*, *Chrysosplenium* and *Hypochaeris*.
2. Passing over the Isthmus of Panama at a time when the ecological tolerance of some representative(s) of the genus allowed them to cross by stepping-stone migrations from North America, as suggested by Kupicha (1974, 1983) and Asmussen & Liston (1998).

4.4 Materials and Methods

4.4.1 *Choice of regions*

By providing a test that is relatively independent of morphological classifications, DNA sequence data may help us to understand the systematics of this genus. Investigating independent genomes (e.g., nuclear and chloroplast) facilitates recognition of patterns and processes such as hybridization events (e.g. Francisco-Ortega et al., 1996; Doyle & Doyle, 1998). Following investigation of several nuclear and cpDNA regions, I used sequence data from the nuclear ribosomal internal transcribed spacer (ITS) plus 5.8S-coding regions of nuclear ribosomal DNA, as well as the *trnL* intron plus flanking spacer (*trnL-F*) and *trnS* (GCU)–*trnG* (UCC) intergenic spacer (*trnS-G*) regions of cpDNA (figs. 4.3, 4.4), to estimate the phylogeny of *Lathyrus* worldwide. The second intron of the single copy nuclear Unifoliata (Uni) gene region and low-copy number GA20 Oxidase gene were surveyed, but rejected as they showed too little variation amongst taxa.

ITS has been used to reconstruct phylogenies at the species level in *Lupinus* L. (Aïnouche and Bayer, 1999), *Lotus* L. (Allan and Porter, 2000), and *Lens* L. (Mayer and Bagga, 2002); *trnL-F* has been used in *Vicia* L. (Fennell et al., 1998), *Astragalus* L. (Wojciechowski et al., 1999), and *Genista* L. (de Castro et al., 2002). The *trnS-G* region is less widely used but has proved informative in a sample set of *Glycine* subgenus Soja (Xu et al., 2001). This implies that the *trnS-G* region can resolve relationships in closely related taxa of legumes; the initial pilot survey in *Lathyrus* proved encouraging, showing similar levels of variation to ITS.

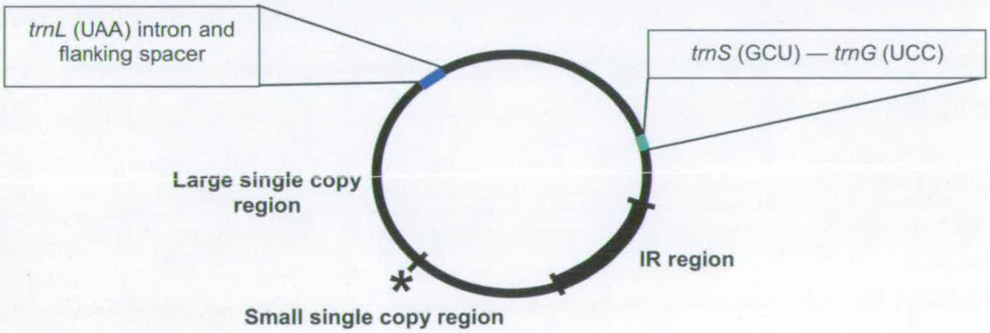


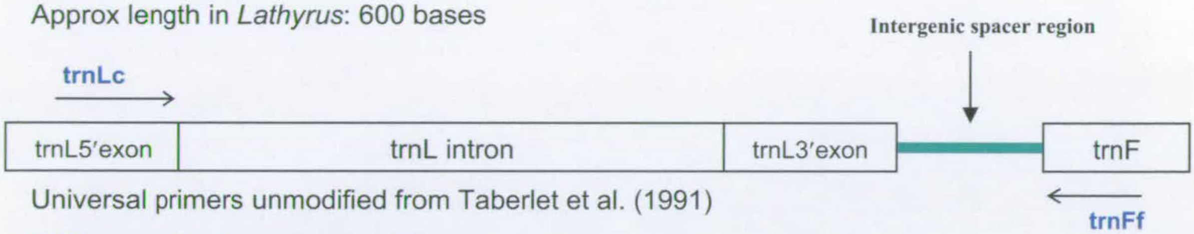
Figure 4.3 Locations of cpDNA regions sequenced in this study.
Note that there is only one copy of the 'inverted repeat' (IR) region in *Lathyrus* and allies. The asterisk indicates the position of the other copy of the IR region in other Angiosperms.

Figure 4.4 Structures of DNA regions used in this study

Maps indicate delimitation of regions, with spacer regions in green, and positions of primers (in blue). Approximate lengths, tobacco annealing temperatures for PCR and primer sequences are given. Positions of primers on the Tobacco chloroplast are given for cpDNA.

4.4a) *trnL (UAA) intron and flanking spacer* (*trnLF*)

Approx length in *Lathyrus*: 600 bases



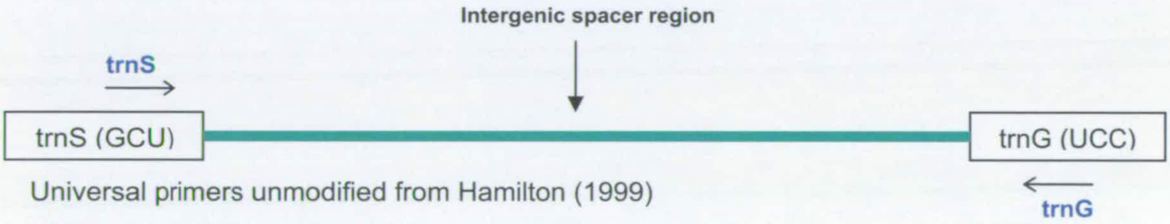
Universal primers unmodified from Taberlet et al. (1991)

PCR annealing temperature 54°C

- **trnLc** (forward): 5′ CGAAATCGGTAGACGCTACG 3′ (Tobacco cp position: 49306)
- **trnFf** (reverse): 5′ ATTTGAACTGGTGACACGAG 3′ (Tobacco cp position: 50280)

4.4b) *trnS (GCU) — trnG (UCC)*

Approx length in *Lathyrus*: 720 bases (but very variable, with many indels)



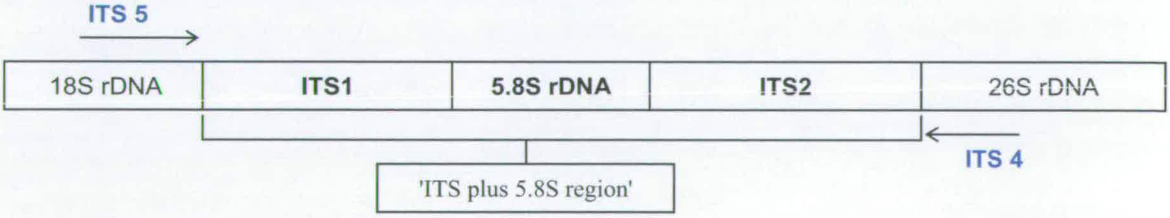
Universal primers unmodified from Hamilton (1999)

PCR annealing temperature 54° up to 60°C if multiple bands were produced at lower temperatures.

- **trnS (GCU)** (forward): 5'GCCGCTTTAGTCCACTCAGC 3' (Tobacco cp location: 8691)
- **trnG (UCC)** (reverse): 5' GAACGAATCACACTTTTACCAC 3' (Tobacco cp location: 9531)

4.4c) Nuclear Internal Transcribed Spacers 1 & 2 (plus 5.8S coding region)

Approx. combined length in *Lathyrus*: 650 bases



Universal primers unmodified from White et al (1990)

PCR annealing temperature 51°C

- **ITS 5** (forward): 5' GGAAGTAAAAGTCGTAACAAGG 3'
- **ITS4** (reverse): 5' TCCTCCGCTTATTGATATGC 3'

4.4.2 *Samples*

I obtained total genomic DNA from fresh or silica gel-dried leaf material from wild, cultivated, and herbarium specimens. Many of these specimens were donations, including most of the accessions used by Asmussen and Liston (1998). Accessions representing 53 species of *Lathyrus* and four other members of tribe Fabeae (*Vicia cracca* L., *V. nipponica* J. Matsumura, *V. unijuga* A. Braun, and *Pisum sativum* L. 'Tōmyo') were used. The herbarium specimen of *Vavilovia* used for the *matK* analysis presented in chapter 3 was of poor quality, and the *trnL–F* and *trnS–G* regions would not amplify. This was the only sample available and given time and budget constraints, it was not possible to obtain another for comparison. Sampling from within sect. Orobus received particular attention because of the group's wide distribution, morphological diversity, and important position within the genus.

Where possible, I sequenced multiple accessions of the same species for each region to verify identification and to investigate potential intraspecific variation, especially in wide-ranging and morphologically variable species. Although two accessions were sequenced for ITS and *trnL-F* from *L. angulatus* L. and *L. sphaericus* Retz., the *trnS-G* region was only obtained from one accession from each of these species.

4.4.3 *Ingroup delimitation and outgroup choice*

The combination of an adaxial pollen brush on the style and non-brochiododromous leaflet venation (i.e., veins reaching the margins) is considered synapomorphic for the *Lathyrus-Pisum* group, distinguishing it from *Vicia* (Kupicha, 1974, 1981; Gunn & Kluve, 1976). Data from the *matK* gene support this arrangement (Steele & Wojciechowski, 2003, chapter 3). I included three *Vicia* species in the analysis as multiple outgroups to test the hypothesis that the *Lathyrus-Pisum* group is monophyletic.

Genus Section (no. spp.)	Operational Taxonomic Unit	Distribution (wild origin collection locality)	Sources, accessions and vouchers	ITS	trnL-F	*trn*S-G
Lathyrus						
Aphaca (2)	*L. aphaca* L.	Europe & Mediterranean (Turkey)	**118** Norton 1991 – 008	AY839345	AY839413	AY839489
Clymenum (3/4)	*L. 'articulatus'* L. = *clymenum*?	Mediterranean	**1** Asmussen & Liston	AY839346	AY839414	AY839528
	L. clymenum L.	Mediterranean	**2** Asmussen 1994 – 2	AY839349	AY839417	AY839529
	L. gloeospermus Warb. & Eig.	Mediterranean	**3** Asmussen 1994 – 3	AY839356	AY839424	AY839527
	L. ochrus (L.) DC	Mediterranean	**4** Asmussen 1994 – 4	AY839376	AY839444	–
Lathyrostylis (20)	*L. digitatus* (M. Bieb.) Fior.	S.E. Europe (Crimea)	**6** Asmussen 1994 – 5	AY839352	AY839420	AY839514
	L. pallescens (M. Bieb.) K. Koch	N.E. Mediterranean (Turkey)	**124** RBGE D.M. Brown 572	AY839378	AY839445	AY839515
	L. filiformis (Lam.) Gay	S.W. Europe (Spain)	**133** RBGE Brummit, Gibbs & Ratter 670	AY839354	AY839422	AY839536
	L. spathulatus Celak.	Turkey (Turkey)	**125** RBGE Coode & Jones 1200	AY839392	AY839459	AY839513
Lathyrus (34)	*L. annuus* L.	Mediterranean	**8** Asmussen 1994 – 07	AY839344	AY839412	AY839525
	L. cicera L.	Mediterranean	**9** Asmussen 1994 – 08	AY839348	AY839416	AY839518
	L. latifolius	C. Europe	**12** Asmussen & Liston (cult. Oregon)	AY839358	AY839425	AY839532
	L. odoratus L.	Sicily (Garden origin)	**16** Asmussen 1994 – 14	AY839377	AY839474	AY839533
	L. rotundifolius Willd.	W. Asia (Turkey)	**89** Norton 2000 – 443	AY839388	AY839455	AY839535
	L. sativus L.	E. Mediterranean to Iran	**18** Asmussen 1994 – 15	AY839389	AY839456	AY839517
	L. setifolius L.	S. Europe	**27** Asmussen 1994 – 27	AY839391	AY839458	AY839516
	L. sylvestris L.	Europe	**19** Asmussen 1994 – 16	AY839398	AY839465	AY839523
	L. tingitanus L.	North Africa	**20** Asmussen 1994 – 17	AY839399	AY839466	AY839519
	L. tuberosus L.	Europe	**21** Asmussen 1994 – 18	AY839401	AY839468	AY839524
Linearicarpus (7)	*L. angulatus* L.	Mediterranean	**23** Asmussen 1994 – 19	AY839342	AY839410	AY839522
	L. sphaericus Retz.	Europe (Cyprus)	**122** RBGE Edmondson & McClintock 2847	AY839394	AY839461	AY839512
Neurolous (1)	*L. neurolobus* Boiss. & Heldr.	(Endemic to Crete)	**25** Asmussen 1994 – 21	AY839373	AY839440	AY839521
Nissolia (1)	*L. nissolia* L.	W. and C. Europe	**26** Asmussen 1994 – 22	AY839375	AY839443	AY839520
Pratensis (6)	*L. laxiflorus* (Desf.) Kuntze	S. and E. Europe	**29** Asmussen 1994 – 47	AY839367	AY839434	AY839482
	L. pratensis L.	W. Eurasia	**30** Asmussen 1994 – 48	AY839384	AY839451	–
Orobus (~ 50; Eurasia ~ 21)	*L. alpestris* (Waldst. & Kit.) Kit.	Balkans (Slovenia)	**99** Norton 2001	AY839341	AY839409	AY839476
	L. aureus (Steven) Brandza	E. Europe	**100** Norton 1992 – 122 (cult. Cambridge)	AY839347	AY839415	AY839481
	L. davidii Hance	E. Asia (S. Korea)	**79** Kenicer – 38 (Kangwando Province)	AY839350	AY839418	AY839492
	L. gmelinii Fritsch	C. Asia (SW Siberia)	**113** RBGE Elias, Shetler & Murray 7468	AY839357	AY839475	AY839537
	L. humilis (Ser.) Sprengel	C. and E. Asia (Mongolia)	**128** RBGE R.J. Allen 1008	AY839360	AY839427	AY839494
	L. incurvus (Roth) Willd.	Caucasus / Caspian (Armenia)	**134** RBGE B. Abemucen 00158109	N.S.	N.S	N.S.
	L. japonicus Willd.	Worldwide (Korea)	**135** Kenicer – 52 (Kangwando Province)	AY839361	AY839428	AY839495
	L. komarovii Ohwi	C. and E Asia (Altai)	**120** RBGE Elias, Shetler & Murray 7091	AY839363	AY839430	AY839478
	L. laevigatus subsp. *laevigatus* (Waldst & Kit.) Kit.	C. Europe (Dolomites)	**101** Norton	AY839364	AY839431	AY839497
	L. laevigatus subsp. *laevigatus* (Waldst & Kit.) Kit.	C. Europe (Slovenia)	**102** Norton 1997 – 583	AY839365	AY839432	AY839498
	L. linifolius (Reich.) Bässler	N. Europe	**48** Asmussen & Liston (cult. Oregon)	AY839368	AY839435	AY839477
	L. niger (L.) Bernh.	W. Eurasia (Hungary)	**50** Asmussen 1994 – 43	–	AY839442	AY839488
	L. palustris L.	Northern hemisphere	**51** Asmussen 1994 - 44	AY839379	AY839446	AY839502
	L. palustris subsp. *pilosus*	Northern hemisphere (S. Korea)	**107** Lee (Kangwando Province)	AY839380	AY839447	AY839503
	L. palustris subsp. *pilosus*	Northern hemisphere (Japan)	**108** Kenicer – 61 (Hakone BG, from Sapporo)	AY839381	AY839448	AY839504
	L. pisiformis L.	W. Eurasia (Kirgizistan)	**116** RBGE Maxted & Sperling 8251	AY839382	AY839450	AY839491
	L. quinquenervius (Miq.) Litv.	E. Asia (S. Korea)	**109** Lee (Inha University)	AY839386	AY839453	–
	L. transsylvanicus (Sprengel) Reichenb. f.	E. Europe	**110** Norton 1992 – 212	AY839400	AY839467	AY839509
	L. vaniotii Léveillé	E. Asia (S. Korea)	**117** Kenicer – 30 (Kangwando Province)	AY839402	AY839469	AY839511
	L. venetus (Miller) Wohlf.	S. / E. Europe	**53** Asmussen & Liston (cult. Oregon)	N.S.	N.S.	N.S.
	L. vernus (L.) Bernh.	W. Eurasia	**54** Asmussen & Liston (cult. Oregon)	AY839403	AY839470	AY839479
	L. vernus (L.) Bernh.	W. Eurasia	**85** RBGE living collection (19881239)	AY839404	AY839471	AY839480
Orobus (N. America 29)	*L. delnorticus* C. Hitchc.	Oregon	**33** Asmussen 1994 - 29	AY839351	AY839419	–
	L. glandulosus Broich	N. California	**34** Asmussen & Liston	AY839355	AY839423	AY839493
	L. holochlorus (Piper) C. Hitchc.	(Oregon)	**35** Asmussen & Liston	AY839359	AY839426	AY839490
	L. jepsonii E. Greene	N.W. USA	**36** Asmussen 1994 – 40	AY839362	AY839429	AY839496
	L. lanszwertii Kellogg	N.W. USA (Oregon)	**37** Asmussen & Liston	AY839366	AY839433	AY839499
	L. littoralis (Nutt.) Endl.	N.W. USA (Oregon)	**38** Asmussen 1994 – 42	AY839369	AY839436	AY839500
	L. nevadensis S. Watson	N.W. USA (Oregon)	**39** Asmussen 1994 – 41	AY839374	AY839441	AY839501
	L. polyphyllus Nutt.	N.W. USA (Oregon)	**40** Asmussen 1994 – 45	AY839383	AY839449	AY839505
	L. rigidus T. White	N.W. USA	**41** Asmussen & Liston	AY839387	AY839454	AY839506
	L. splendens Kellogg	S. Californian endemic	**98** Norton 1992 - 245 (cult. Cambridge)	AY839395	AY839462	AY839507
	L. sulphureus Brewer	N.W. USA	**43** Asmussen 1994 – 46	AY839397	AY839464	AY839508
	L. vestitus Nutt.	N.W. USA	**44** Asmussen & Liston	AY839405	AY839472	AY839510
Notolathyrus (23)	*L. multiceps* D. Clos.	S. America (Chile)	**31** RBGE - 19912326 (Kirkpatrick 377)	AY839370	AY839437	AY839484
	L. magellanicus Lam.	S. America (Chile)	**94** Norton 1999 – 684	AY839371	AY839438	AY839485
	L. subandinus Philippi	S. America (Chile)	**95** Norton 1999 – 676	AY839396	AY839463	AY839483
	L. nervosus Lam.	S. America (Uruguay)	**32** Asmussen 1994 – 24	AY839372	AY839439	AY839486
	L. pubescens Hook. & Arn.	S. America (Chile)	**96** Norton 1992 – 247	AY839385	AY839452	–
	L. magellanicus G. Don	S. America (Chile)	**97** Norton 1999 – 679	AY839390	AY839457	AY839487
Pisum						
Pisum	*Pisum sativum L.*	Pantemperate crop (cultivated)	**136** Kenicer – 65 (cult. Tokyo University BG)	AY839340	AY839473	AY839526
Vicia						
Cracca (40)	*V. cracca* L.	Eurasia (Denmark)	**57** Asmussen 1994 – 49	AY839339	AY839406	AY839530
Vicilla (15)	*V. nipponica* J. Matsumura	E. Asia (Japan)	**81** Kenicer – 23 (Yamanashi Prefecture)	AY839338	AY839407	AY839534
	V. unijuga A. Braun	E. Asia (Japan)	**82** Kenicer – 27(Yamanashi Prefecture)	AY839337	AY839408	AY839531

Table 4.2: Accessions of Fabeae sequenced for nuclear internal transcribed spacer and chloroplast *trnL-F* and *trnS-G* regions

Sectional classification and species numbers are from Kupicha (1983) with modifications based on Hara & Williams (1979), Nelson & Nelson (1983), Tsui (1984), Broich (1986), Zhu & Meng (1986), Maxted & Goyder (1988), Iseley (1992), and Asmussen & Liston (1998). General species distributions are shown as well as more specific localities for wild-collected specimens.

Locations of voucher specimens by source: Asmussen & Liston, University of Aarhus, Denmark; J.-Y. Lee, Inha University, Incheon, South Korea; S. Norton, National Council for the Conservation of Plants and Gardens *Lathyrus* collection, West Wickham, Cambridgeshire, UK; G. Kenicer, RBGE, Herbarium, Royal Botanic Garden Edinburgh, Edinburgh, UK.

Genbank accession numbers are given under each of the regions; – designates a region unable to be sequenced or not alignable; N.S. indicates sequences not yet submitted.

4.4.4 *Polymerase Chain Reaction*

The basic protocol for PCR was the same as for the *matK* analysis (chapter 3). Primer pairs were universal (Fig. 4.4).

The PCR protocol followed a standard program, adjusted only for annealing temperatures. (1) Initial denaturation was conducted for 90 s at 95°C. (2) Thirty cycles of denaturation for 45 s at 95°C, annealing for 60 s at a temperature depending on the region, and elongation at 72°C. The elongation time began at 90 s and increased by 2 s per cycle. (3) A final elongation step of 15 min at 72°C was performed. Annealing temperatures were 51°C for ITS, 53--54°C for *trnL-F*, and 61°C for *trnS-G*. Some herbarium specimens produced low initial yields for the *trnS-G* region, in which case I did a second round of PCR using the same protocol as above, and 1.0 μl of template DNA.

4.4.5 *Cycle sequencing*

Cycle sequencing used the same primers as those for PCR and the same protocol as for the *matK* analysis (chapter 3). The reverse reaction verified each nucleotide position. *Lathyrus gmelinii* Fritsch, *L. littoralis* (Nutt.) Endl., *L. rigidus* T. White, and *L. setifolius* L. needed internal primers, ITS2g and ITS3p (White et al., 1990). Thus the 5.8S-coding region was not completely sequenced for these three species.

4.4.6 *Alignment and gap coding*

Sequences were initially aligned using ClustalX (Thompson et al., 1997), then alignments were adjusted manually in Nexus-format text files. I used PAUP*, version 4.0b10 (Swofford, 2001) for phylogenetic analysis. The sequences were lodged with GenBank (Table 4.2).

Where insertion–deletions (‘gaps or ‘indels’) were shared by two or more taxa and could be aligned unequivocally, they were treated as additional potentially phylogenetically informative characters to maximize phylogenetic information in the MP analysis. Such indels were coded as a binary ‘1’ or ‘0’ state for all data matrices, following Simmons and Ochoterena (2000) and Simmons et al. (2001). Each putative event was treated as independent of overlapping gaps (see Fig. 1 of Eriksson et al., 2003). Once indels were coded, all gap regions were excluded using the "exclude gapped" command in PAUP. Long indels sometimes spanned areas containing potentially phylogenetically informative nucleotide or indel sites in other sequences. In such cases, "N" coding was used in the gap-containing sequence to ensure the inclusion of that site in the analysis. Consequently, it is possible for the number of parsimony-informative sites to exceed the total number of sites minus gap-containing sites (Table 4.3). To eliminate the primer site and areas of poor read at the start and end of each sequence, I excluded these portions from the matrices. In the combined matrix, this corresponded to positions 1-49 (beginning of ITS), 687-803 (between ITS and *trnL-F*), 1521-1595 (between *trnL-F* and *trnS-G*), and 2708-2797 (end of *trnS-G*). Where two accessions of the same species showed identical sequence data, I used only one in the sequence analysis.

4.4.7 *Analytical strategies*

Trees were generated following three different combinations of data, as follows:

Maximum Parsimony analyses:

(1) The three separate (ITS1 plus ITS2; *trnL-F* and *trnS-G*) data sets, both with and without coded gaps (this allowed a visual comparison of congruence between data sets and also an indication of the influence of including gap characters on topologies).

(2) A combined data set including only the *trnL-F* and ITS regions to determine possible phylogenetic positions of some taxa that would not amplify or align satisfactorily for the *trnS-G* region (*L. delnorticus L. ochrus*, *L. pratensis*, *L. pubescens* and *L. quinquenervius*).

Maximum Parsimony and Bayesian analyses:

(3) A combined analysis of all three regions, including only those species where the ITS, *trnL–F* and *trnS–G* regions were available and could be aligned with confidence. The results of these analyses are presented in figures 4.5 and 4.6.

In order to support the visual comparison between the separate trees generated in (1) the incongruence length difference test of Farris et al. (1995), a partition homogeneity test, was implemented on a combined three-region data set (3) above, using PAUP. This acted as a second test for congruence between the three separate data sets (ITS, *trnL–F* and *trnS–G*).

Maximum parsimony searches followed the same protocol as for the *matK* analysis (chapter 3).

The Bayesian analysis followed the protocol outlined in chapter 3, with two separate types of search - one with the model determined by Modeltest (i.e. a user defined model), and a second search with MrBayes being left to estimate its own models of evolution.

For the Bayesian analysis with user defined models of evolution, the data set was divided into three partitions, with the model for each partition specified separately:

- ITS (combined ITS1, ITS2 and 5.8S); *trnL–F* (complete region), and *trnS–G* (complete spacer region)

For the combined Bayesian analysis, without a user-defined model, the data set was divided into seven partitions:

- ITS1; 5.8S; ITS2; *trnL* intron, *trnL*3'exon; *trnL*3' spacer and *trnS–G*.

4.4.8 *Character mapping and alternative topologies*

A simple visual comparison between trees and assignment of bars to indicate character states were used to map characters on to the trees in the analyses presented here and in chapter 4. More refined methods include mapping discrete character states for each operational taxonomic unit on to trees under maximum parsimony criteria. This can be implemented in MacClade v. 4.06 (Maddison & Maddison, 2003), by including morphological, biogeographical area, or other character state data in the data matrix to be analyzed. MacClade will then optimize the data on a given tree topology under a parimony criterion. As this method of character mapping makes use of a user-defined tree topology, it does not take into account the possibility that suboptimal trees may have different topologies. Likelihood and Bayesian approaches have been developed to estimate the evolution of characters at specific nodes. Unlike character optimization methods, the methods outlined by Pagel et al. (2004; Lutzoni et al., 2001) allow estimates of confidence in alternative hypotheses by estimating the spread of posterior probabilities for competing hypotheses across a given node. These then give a measure of confidence for a given character state at a given node.

Decay analyses (Bremer 1994) in which parsimony is relaxed, allow investigators to explore how well clades are retained in suboptimal parsimony trees. Two simple decay analyses, following the same search criteria as for the parsimony analyses above, but retaining 10,000 trees of lengths 3 and 5 steps longer than the shortest tree were run. The retention of key clades in the analysis under these relaxed parsimony conditions gives an indication of their robustness (see 4.6.10 Biogeography: South America). The retention of all major clades in the analysis under these relaxed parsimony conditions suggests that the biogegraphic conclusions drawn here are robust, though it is acknowledged that quantitiative character optimisation techniques would be preferable in future studies.

4.5 Results

4.5.1 *Sequence characteristics*

Aligned sequence data (nexus format files) can be found on the accompanying CD-ROM. Table 4.3 summarizes sequence characteristics. The ITS and *trnL-F* sequences aligned readily, with insertion of a few gaps, while the *trnS-G* region contained more extensive indels.

Table 4.3 Sequence characteristics for the 63 accessions of Fabeae sampled

	ITS1	ITS2	ITS1 and 2	*trn*L-F	*trn*S-G	Total
Aligned length	247	223	472	694	1061	2227
Range (minus gaps)	235–239	181–217	418–453	542–602	457–717	–
G and C content (%)	51.7	47.3	49.6	34.0	25.5	–
Gap positions*	61	66	127	344	972	1443
Constant sites	99	111	210	344	941	1495
Variable sites	87	46	133	103	243	479
Parsimony informative	57	21	78	46	115	239
No. of unambiguously aligned gaps	7	14	22	33	67	122
Parsimony informative gaps	2	4	6	11	43	60
Sequence divergence (all species)	0.059	0.026	0.044	0.021	0.024	–

*In some taxa, parsimony-informative nucleotides may be present at these sites.

4.5.2 *Maximum Parsimony analysis*

Visual inspection of the strict consensus trees derived from individual MP analyses of ITS, *trnL-F*, and *trnS-G* (trees not shown) indicated many common clades, with differences reflecting lack of resolution rather than conflicting groupings with strong bootstrap support. The *trnL-F* and ITS phylogenies resolved few major clades, but several smaller groups such as the taxa generally corresponding to sect. Lathyrus and

Bässler's series Verni (1973) were consistently resolved in each of the single-region trees (ITS, *trnL-F*, and *trnS-G*). Inclusion of gap characters generally bolstered support for clades present in analyses without gaps (data not shown).
The incongruence length difference test result ($P = 0.1$) indicated an acceptable degree of congruence among the three components of the combined data set. A P value of 0.05 or lower suggests significant incongruence (Farris et al., 1995; Johnson et al., 2001). These lines of evidence justified the combined analysis including coded gaps.

The combined parsimony analysis, with gaps included, produced 8640 equally most parsimonious trees of 1223 steps, with a consistency index of 0.676 (homoplasy index 0.324), retention index of 0.776, and rescaled consistency index of 0.52. Figure 4.5 shows one of the most parsimonious phylograms. The Bayesian consensus tree from the seven partition, free parameter search is shown in Fig. 4.6.

For *L. delnorticus L. ochrus*, *L. pratensis*, *L. pubescens* and *L. quinquenervius*, the *trnS-G* region could not be aligned due to major indels. The ITS region would not sequence successfully for *L. niger*.

4.5.3 *Bayesian analysis*

Topologies generated by the two separate Bayesian analyses (with and without user-defined models) were completely congruent. User defined models, as derived from Modeltest version 3.7 (Posada & Crandall 1998) and PAUP*, version 4.0β10 (Swofford, 2001) are as shown in table 4.4:

TABLE 4.4 Model parameters for Bayesian analysis of combined regions

Region	ITS[1]	*trnL-F*[2]	*trnS-G*[3]
Model	TVM+I+G	TVM+G	TVM+G
A	0.2401	0.3684	0.3734
C	0.2120	0.1672	0.1295
G	0.2444	0.1624	0.1057
T	0.3035	0.302	0.3914
Shape parameter	0.9126	0.4994	0.6070
Proportion of invariable sites	0.4286	0	0

Rates:

1. ITS (A-C=2.0681; A-G=5.4911; A-T=2.1413; C-G=0.6247; C-T=5.4911; G-T=1.0000)
2. *trnL-F* (A-C=0.7445; A-G=0.3945; A-T=0.2143; C-G=1.0765 C-T=0.3945; G-T=1.000)
3. *trnS-G* (A-C=0.5741;A-G=0.3386 A-T=0.1087; C-G=1.2495; C-T=0.3386; G-T=1.000)

4.5.4 *Phylogeny*

The MP tree (Fig. 4.5) is more resolved than that derived from the cpDNA RFLP analysis of Asmussen and Liston (1998) (Fig. 4.2). The Bayesian tree is more resolved still and with stronger support values throughout for the clades. The MP and Bayesian analyses yielded trees that were topologically very similar. In both trees, the *Lathyrus-Pisum* clade is well supported as distinct from the species of *Vicia* included in the analysis - 100% bootstrap for MP analysis and posterior probability value (PPV) 100 for the Bayesian analysis.

The MP analysis places *P. sativum* as sister to all *Lathyrus* species, albeit with bootstrap values less than 50%. In the Bayesian tree, *Pisum* sits inside a grade of four *Lathyrus* species representing three sections (Clymenum, Neurolobus and Nissolia), and is sister to the remainder of *Lathyrus*. However, this topology is poorly supported, with PP values of 59 and 83 for the two branches separating *Pisum* from the *L. articulatus- L. clymenum* clade. Further sequence (i.e. from additional genome regions) is required to clarify this relationship.

In *Lathyrus,* clades corresponding to Kupicha's (1983) sect. Notolathyrus, Bässler's (1971) sect. Lathyrostylis and Fritsch's series Verni minus *L. venetus* (Fritsch 1900) all received 100% bootstrap support and PP value 100. Further clades correspond to groups that agree with the findings of Asmussen & Liston (1998), as outlined in the Discussion below. A number of other clades were also resolved, with more limited support. Among these are two large clades (labeled A and B in Figs. 4.5 and 4.6) that are important in the interpretation of systematics and biogeography in sect. Orobus and allied taxa but do not correspond to any taxonomically recognized entities in the genus.

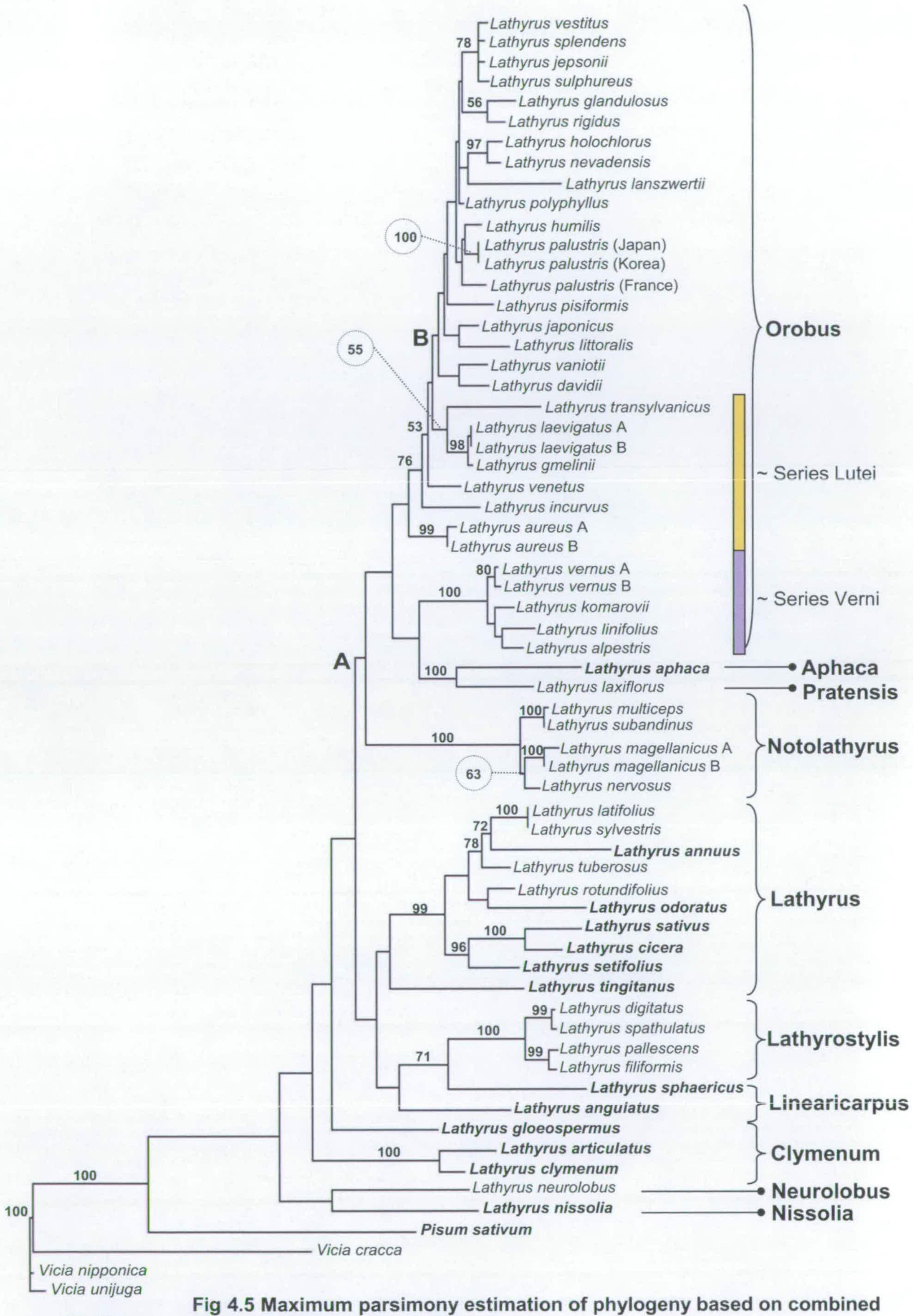


Fig 4.5 Maximum parsimony estimation of phylogeny based on combined ITS, trnLF and trnSG regions.
One of 8640 equally most parsimonious trees (1223 steps long). This analysis includes only those accessions for which all three regions were sequenced. Figures above branches are bootstrap supports. Clades designated 'A' and 'B' are discussed in the text, taxon names in bold are annuals. Consistency index: 0.676; Retention Index: 0.766; Rescaled consistency index: 0.52. All clades with bootstrap are retained in the strict consensus of the 8640 trees.

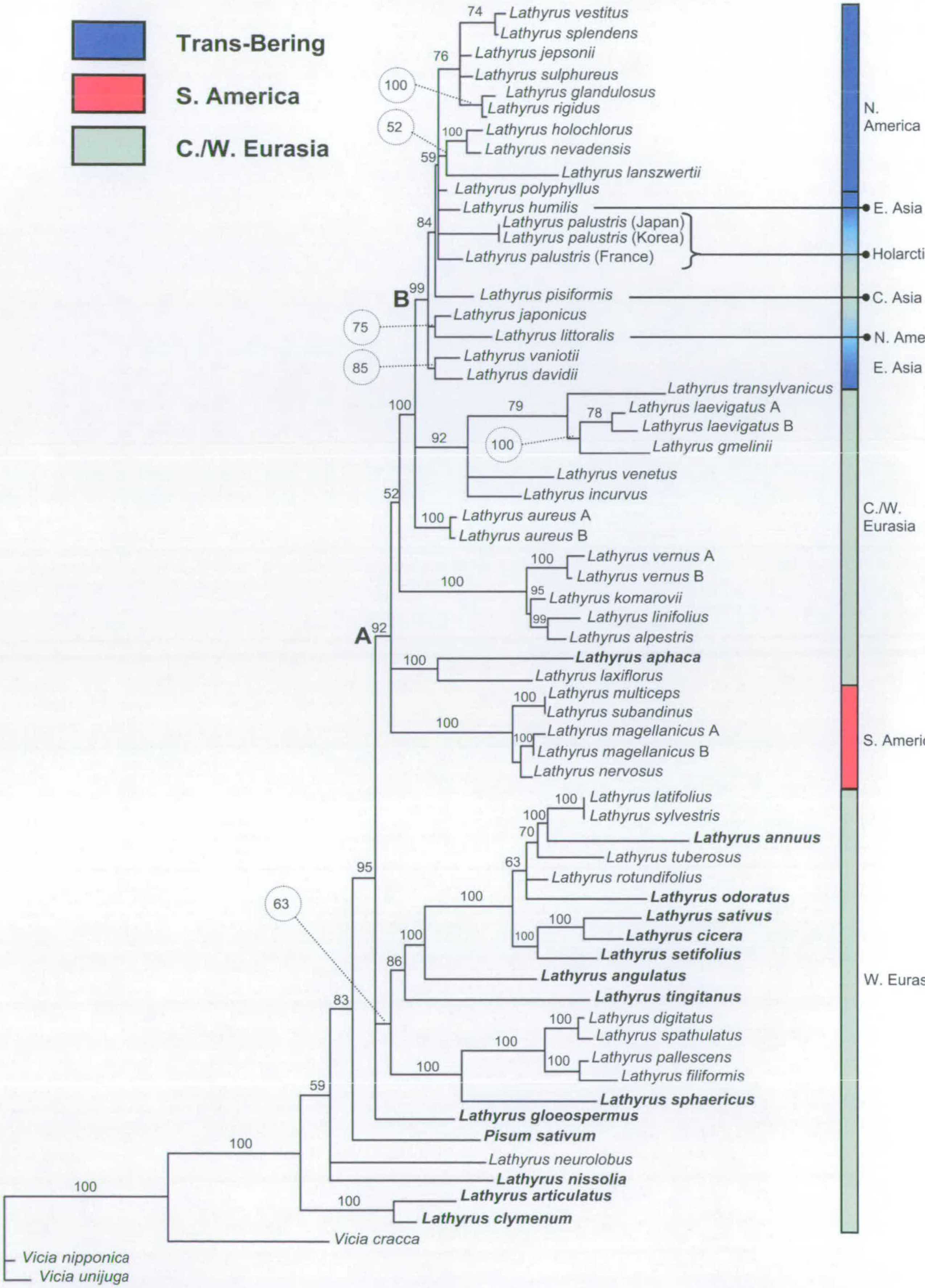


Fig 4.6 Bayesian estimation of phylogeny based on combined ITS, trnLF and trnSG regions
50% Majority rule consensus tree based on the components of the combined ITS, *trnL-F* and trnS-G gene regions – partitions: ITS1, 5.8S, ITS2, *trnL* intron, *trnL*3'exon, *trnL* 3' spacer and *trnS-G* Numbers above branches are posterior probability values. Coloured bars to the right indicate general distributions; clades designated 'A' and 'B' are discussed in the text; taxon names in bold are annuals.

4.6 Discussion

4.6.1 *Phylogeny and generic classification*

This analysis agrees with the findings of the *matK* study reported in chapter 3, that strongly support the generally accepted view that *Lathyrus* and *Vicia* are distinct (Kupicha, 1974, 1983; Gunn and Kluve, 1976; Steele and Wojciechowski, 2003). Early classifications, including *Species Plantarum*, and a recent revision by Roskov et al. (1998), treated the etendrillous species of these two genera as a third, intermediate genus, *Orobus*. The data presented here clearly refute this view.

The multi-region Bayesian analysis (Fig. 4.6) and the analyses of the *matK* gene (chapter 3) also both suggest that *Lathyrus* is paraphyletic, with *Pisum* nested within it. Although it was not possible to sample *Vavilovia* for this analysis, the *matK* analysis and morphology (chapter 3) strongly supports it as sister to *Pisum*. *Lathyrus* and *Pisum* have been separated on the basis of stylar characters and leaflet ptyxis (Gunn & Kluve 1976, Kupicha, 1981). However, morphological comparisons between *Pisum* and the phyllodic-leaved members of *Lathyrus* (*L. nissolia*, *L. clymenum*, *L. articulatus* and *L. gloeospermus*) to which the analyses described here show it is related, are more difficult than for the remainder of the genus. Leaflet ptyxis is not directly comparable between these and other taxa with true leaflets - detailed ontogenetic observations are required. The genes regulating leaf development are fairly well understood in *Pisum* (e.g. Hofer & Ellis, 1998; Gourlay et al., 2000) and there is excellent scope for expanding developmental genetic studies into *L. clymenum* and *L. nissolia*. The *Unifoliata* gene which, as a *uni* mutant, causes leaves to be expressed as a single leaflet in *Pisum* (Hofer et al., 1997) would be an interesting first starting point for such investigations.

Although the *matK* and the multi-region Bayesian analyses agree that *L. clymenum* sits outside *Pisum*, support is very weak in both analyses, and they disagree in arrangement of the basally branching lineages in the *Lathyrus – Pisum* (and *Vavilovia*) clade. This discrepancy between the two analyses may be due to the differences in sampling between the datasets presented for chapters 3 (*matK*) and 4 (multi-region). The analyses presented in chapter 4 used more accessions (representing 53 species) of *Lathyrus*, including *L. neurolobus*, and does not include

Vavilovia. Time and budgetary constraints precluded more complete reciprocal sampling for both of the studies.

Although further research is necessary to establish firmer conclusions, it is likely that the generic level taxonomy of the basally divergent lineages of annual Mediterranean species in the *Lathyrus* - *Pisum* – *Vavilovia* clade will need to be redefined. Some writers support classifications accepting paraphyletic groups above species level (e.g. Sosef, 1997; Brumitt & Sosef, 1998; Brummitt, 2002; Brummitt 2003). However, such groups are generally considered impractical and irrelevant from an evolutionary viewpoint (e.g. Nelson et al., 2003), with the general consensus being that taxonomic groups should be both monophyletic and morphologically diagnosable (e.g. Stevens, 2006). Although the evidence remains inconclusive, there are two most obvious ways to recircumscribe *Lathyrus*, *Pisum* and *Vavilovia* based on a criterion of monophyly. The simplest would be a broad generic definition, with *Lathyrus* incorporating both *Pisum* and *Vavilovia*, as all the taxa share an introrse (adaxial) pollen brush. However, given their economic significance, it could be argued that *Pisum* and *Lathyrus* should be retained as distinct entities. If this narrower definition of *Lathyrus* were used, further generic names would be required in order to maintain monophyly of the groups within the grade of basally diverging Mediterranean lineages. Thus, Tournefort's *Clymenum* could be used for a genus corresponding to sect. Clymenum excluding *L. gloeospermus* (Gunn 1969). Further generic names may be required for monotypic genera containing *L. neurolobus* and *L. nissolia* depending on whether the topology indicated by the *matK* trees or the multi-region Bayesian tree is accepted. In order to clarify these relationships, all representatives of the current sects. Nissolia, Clymenum, and Neurolobus, should certainly be included in any future analyses of intergeneric relationships within tribe Fabeae. *Lathyrus ochrus* is the only species from this group that is not included in the trees reported here (Figs. 4.5, 4.6), although this species formed a clade with *L. clymenum* in the analysis of ITS and *trnL–F* sequences alone (analysis strategy 2 in the materials and methods section). The monotypic sect. Viciopsis (*L. saxatilis*) is the only section that has not been represented in any phylogenetic analyses of *Lathyrus*, so this species should also be included in future investigations.

Sectional classifications

4.6.2 *Sections Clymenum, Neurolobus, and Nissolia*

Kupicha (1983) placed *L. neurolobus* and *L. nissolia* in monotypic sections based on morphology and habit and suggested that they both occupy isolated positions within the genus. The sequence data support this view (Figs. 4.5, 4.6). The long branches leading to each of the two taxa, combined with their distinctive morphologies argue for their recognition at sectional level at least.

Lathyrus articulatus L. is often considered to be synonymous with *L. clymenum* but the sampling of single accessions of both species in this study precludes any definite decision as to their distinctness. However, they each have many morphological and molecular autapomorphies that indicate they may be separate. In the MP analysis, this pair is closely related to *L. gloeospermus* Warb. et. Eig. (Fig. 4.5), and all of these species are traditionally placed in sect. Clymenum on the basis of their phyllodic leaves. The results of the MP analysis contrast with the weighted RFLP data analysis of Asmussen and Liston (1998), which placed *L. gloeospermus* distant from other members of sect. Clymenum. The Bayesian analysis (Fig. 4.6) also suggests that sect. Clymenum is a non-monophyletic group with three nodes (PP values 59, 83 and 95) separating *L. gloeospermus* from the other two species. In Kenicer et al. (2005), *L. gloeospermus* was provisionally retained in sect. Clymenum because of nomenclatural stability and ease of diagnosis, although this does not reflect monophyly. If the remaining members of sect. Clymenum were to be reinstated as the genus Clymenum, *L. gloeospermus* might best be treated as a monotypic section within *Lathyrus*, or a genus in its own right.

4.6.3 *Section Lathyrus*

The multi-region trees place *L. tingitanus* in a weakly supported (bootstrap < 50%, PP value 86) position as sister to the rest of a well-supported (bootstrap 99%, PP value 100) clade comprised mainly of sect. Lathyrus species (Figs. 4.5, 4.6). This is a similar topology to that retrieved by Badr et al. (2002) from amplified fragment length polymorphism (AFLP) data.

There is some disagreement in this clade between the MP and Bayesian analyses, and the *matK* analysis (chapter 3). In the Bayesian analysis (Fig. 4.6), *L. tingitanus* is sister to a clade containing members of sect. Lathyrus, and *L. angulatus* (sect. Linearicarpus) (PP value 100). The *matK* analysis shows a reversal of this pattern, with *L. angulatus* as sister to a clade containing *L. tingitanus* although the support for the overall clade is strong (bootstrap 82%, PP value 100). In the MP tree (Fig. 4.5), *L. angulatus* is sister to the *L. sphaericus*-sect. Lathyrostylis clade, although there is little support for this relationship (Fig. 4.5).

Lathyrus setifolius, formerly Kupicha's monotypic sect. Orobastrum, is sister in both the MP and Bayesian trees to the delicate annual members of sect. Lathyrus, represented here by *L. sativus* L. and *L. cicera* L. This clade is sister to a second clade that receives no credible support (<50% bootstrap, PP value 63). It is composed of perennials and a few robust annuals such as *L. odoratus* (Fig. 4.6). These results support those of Asmussen and Liston (1998) (Fig. 4.2), who were unable to decide whether to treat these two groups as separate sections. The multi-region sequence data draw together the results of previous RFLP and AFLP analyses, and morphological data, providing some support for a circumscription of sect. Lathyrus in Asmussen and Liston's broader sense, containing both *L. setifolius* and *L. tingitanus* (Fig. 3).

Dogan et al's (1992) morphometric analysis split Kupicha's (1983) circumscription of sect. Lathyrus into six separate sections, which included the members of sects. Clymenum, Orobon and Orobastrum. There is no support for their classification from this molecular study.

4.6.4 *Sections Lathyrostylis and Linearicarpus*

Bässler's sect. Lathyrostylis is a morphologically uniform group of approximately 20 erect, perennial species. Members of Lathyrostylis share many characters with some species in sect. Orobus, which prompted Czefranova (1971b) and many authors before her to treat them as part of a broader section (or subgenus, or genus) Orobus. Bässler recognised the two sections as distinct, describing sect. Platystylis in 1966 (later renamed Lathyrostylis in 1971 and 1981). Kupicha (1983) agreed with his circumscription, although both authors suggested a close affinity between sects. Lathyrostylis and Orobus. The species of sect. Lathyrostylis sampled form a clade (100% bootstrap, PP value 100) distinct from sect. Orobus, supporting Bässler's (1981) and Kupicha's (1983) interpretations (Figs. 4.5, 4.6). There is no evidence to suggest a recircumscription of the section is required, although complete sampling of species would help to confirm this.

Lathyrus sphaericus Retz. of Kupicha's (1983) sect. Linearicarpus, is sister to the sect. Lathyrostylis clade in both trees (71% bootstrap and PP value 100). The other member of this section, *L. angulatus*, is placed as sister to the *L. sphaericus* – sect. Lathyrostylis clade in the MP tree, albeit with low support (bootstrap <50%). In the Bayesian tree, this taxon is placed inside the sect. Lathyrus clade (PP value 100) The morphometric analysis of Dogan et al. (1992), as well as molecular data from Asmussen and Liston (1998) and Badr et al. (2002), questioned the monophyly of sect. Linearicarpus. Members of sect. Linearicarpus are small, single-flowered, paucijugate annuals that share no distinctive synapomorphies. Indeed, they appear morphologically intermediate between species of sect. Lathyrostylis and the small, annual members of sect. Lathyrus – a relationship supported by the phylogeny. It may be that diagnostic convenience justifies Kupicha's sectional delimitation, although this is hardly satisfactory in a strict phylogenetic taxonomic context where taxa should correspond to clades. In the *matK* analysis presented in chapter 3, *L. sphaericus* is placed inside the members of sect. Orobus, a result that disagrees with the topologies retrieved from the multiregion analysis (Figs 4.5, 4.6). Further data are required for the other five species of sect. Linearicarpus before any firm systematic decisions can be made.

4.6.5 *The Notolathyrus group*

The South American Notolathyrus group forms a well-supported (100% bootstrap, PP value 100) clade, agreeing with morphological (Kupicha, 1983), cpDNA RFLP (Asmussen and Liston, 1998), and karyological (Senn, 1938; Seijo and Fernandez, 2003) data. In this study, the group's position is not resolved with any appreciable level of support, appearing as a very poorly supported (bootstrap <50%) sister to the remainder of the A clade in the MP analysis (Fig.4.5), and a part of the clade A polytomy in the Bayesian analysis (Fig.4.6). This placement contradicts that in Asmussen and Liston's 1998 study, in which Notolathyrus is nested deep within sect. Orobus, but bootstrap support for their arrangement was low and two reversals of large cpDNA structural mutations had to be invoked (Asmussen and Liston, 1998) (Fig. 4.2). The *trnS-G* region of the South American *L. pubescens* Hooker et Arnott contained deletions that made it unalignable with the other taxa. However, analysis of the combined ITS and *trnL-F* regions placed this species within the Notolathyrus group. A broad analysis of ITS data alone for 111 species of tribe Fabeae included six further Notolathyrus species sequenced by Rhonda Ridley for an MSc project at RBGE (Ridley 2004 and see introduction, chapter 5). This gave a total of 12 species representing the complete morphological variation for the section and confirmed the monophyly of the Notolathyrus group. Although species of Notolathyrus display almost as much morphological variation as the entire remainder of *Lathyrus*, their well supported monophyly and separation from sect. Orobus indicates that Kupicha's sect. Notolathyrus should be reinstated.

4.6.6 *Section Orobus*

The trees place all members of sect. Orobus in a clade with sect. Notolathyrus, *L. aphaca* L. and *L. laxiflorus* Desf. (Fig. 4.5, 4.6, clade A), albeit with weak support (bootstrap <50%, PP value 92). This corresponds approximately to Bässler and Czefranova's interpretations of subgenus Orobus, although neither of these authors included sect. Aphaca or considered sect. Notolathyrus, and both included groups corresponding to sects. Lathyrostylis, and Neurolobus. If clade A were to be treated as a subgenus Orobus, then the clade containing sects. Lathyrus, Lathyrostylis and Linearicarpus might usefully be interpreted as subgenus Lathyrus, with outlying species (*L. nissolia*, *L. neurolobus* and the members of sect. Clymenum) as other subgenera or even genera.

The monophyly of sect. Orobus sensu Kupicha (1983) is equivocal, and the members of sects. Aphaca and Pratensis may be included among them. However, some clades within sect. Orobus were strongly resolved.

One group of Eurasian species forms a well-supported clade (bootstrap 100% and PP value 100) comprising most of Fritsch's (1900) series Verni plus Bassler's monotypic series Tuberosi (*L. linifolius*) (Bässler, 1966). This group is equivalent to Czefranova's subsection Tuberosi plus *L. alpestris* (Czefranova, 1971b) and is indicated with a purple bar on Fig 4.5. All species in this clade share similar, purple-flowered inflorescences; broad-deltoid lower calyx teeth; semisagittate, foliacious stipules; aristate rachises; and three prominent, parallel primary leaflet veins. These characters are also common in sect. Lathyrostylis, which made it difficult for Czefranova (1971b) to separate the members of the series Verni plus Tuberosi clade from sect. Lathyrostylis. *Lathyrus venetus* was also included in the series by Bässler, but is distant in the analysis presented here. *Lathyrus venetus* lacks the three prominent veins characteristic of the species of series Verni and Tuberosi, and the flowers are smaller, more numerous, and pale lilac with purple veins.

The remaining Eurasian members of sect. Orobus form a "core Orobus group" (bootstrap 76%, PP value 100) with the North American species (Fig. 4.5). Within this group, clade B is composed of species that lack any clear putative morphological synapomorphies suggesting subgroups. Because of this difficulty, Czefranova (1971b) and Bässler (1973) were unable to suggest how the Eurasian members of this clade may be interrelated. The results of this analysis show the same problem: the taxa in clade B form a polytomy in the MP tree, and are only retained in the Bayesian tree because of the low threshold for node collapse (PP value 50+). Inclusion of the North American species further compounds this lack of resolution, although all members of clade B are eastern Eurasian/North American (i.e. transberingian), or Holarctic (Fig. 4.6). The sister group to clade B (orange bar Fig. 4.5), contains a morphologically uniform group of stocky, erect, yellow or white-flowered species from western and central Eurasia. This group forms a grade that corresponds closely to Bässler's (1973) series Lutei, although his series included the East Asian, purple-flowered *L. vaniotii* which is nested in clade B. He excluded *L. venetus* (a species with pale lilac flowers veined with purple) from series Lutei, placing it in series Verni, but the analyses presented here place it among the members of series Lutei.

Major gaps and inversions between the primers precluded satisfactory alignment of the *trnS-G* region for *L. quinquenervius* (Miq.) Litv. (East Asia) and *L. delnorticus* C. Hitchc. (North America). When they were included in analyses, the results were as predicted from morphological and geographic affinities, as well as from the molecular data of Asmussen and Liston (1998). *Lathyrus quinquenervius* formed a clade with the East Asian accessions of *L. palustris*, and *L. delnorticus* was in clade B.

4.6.7 *Sections Aphaca and Pratensis*

In the combined analysis, sect. Aphaca (one or sometimes two species) is represented by *L. aphaca* and sect. Pratensis (approximately six species) by *L. laxiflorus*. Members of these two sections share a distinctive wing-petal architecture and sagittate stipules supplied by an unusual vascular arrangement. Such clear putative synapomorphies are rare in *Lathyrus* and prompted Kupicha (1974, 1975, 1983) to suggest that the two sections are closely related. The sister relationship between these two section is strongly supported by both cpDNA RFLP data (Asmussen and Liston, 1998) (Fig. 4.2) and the sequence data presented here (Figs. 4.5 and 4.6). I agree with the conclusion of Kupicha and of Asmussen and Liston: these sections should be retained as separate because of their morphological distinctiveness (sect. Aphaca is annual and lacks leaves while sect. Pratensis is perennial with unijugate leaves); and the long branch lengths separating the taxa. In fact, *L. aphaca* is the only annual species in clade A.

4.6.8 *Unrepresented sections*

Lathyrus saxatilis, the sole member of sect. Viciopsis, was not sampled. It would certainly be important to include this species in future studies – it is difficult to speculate where this plant would resolve phylogenetically. It has a gross morphology reminiscent of *Vicia* or a very delicate member of sect. Orobus. Yet it is almost certainly annual, and is distributed throughout the Mediterranean, characteristics associated with species outside clade A (Figs 4.5, 4.6).

The other monotypic sect., Orobon (*L. roseus*) was not sampled as good quality specimens were not available. Although it is morphologically akin to members of sect. Orobus, Asmussen & Liston's (1998) analysis placed this species inside sect. *Lathyrus* (Fig. 4.2). This relationship was suspected by Kupicha (1983) based on floral characters, so there is no reason to doubt the placing given by the RFLP data. Needless to say, it would be valuable to have confirmation from sequence data.

4.6.9 *Biogeography: Northern Hemisphere*

Section Orobus had been thought of as the most unspecialized group in *Lathyrus* because of its perennial life cycle, the relative complexity of leaves (multijugate and often tendrillous), several or many-flowered inflorescences, and northern Eurasian (i.e., mesophytic) distribution (Simola 1968a, Bässler 1973, Kupicha, 1974, 1983). Kupicha proposed that *Lathyrus* arose from perennial taxa similar to sect. Orobus in northern Eurasia during the early Tertiary (Kupicha 1974, 1983).

The tree topologies contradict Kupicha's hypothesis because the Mediterranean taxa (*L. neurolobus*, *L. nissolia*, sect. Clymenum, and *Pisum*) appear at the base of the trees (Fig. 4.5, 4.6). Except for *L. neurolobus*, these species are annuals adapted to a seasonally dry climate. This pattern repeats in the predominantly Mediterranean clade containing sections Lathyrostylis, Linearicarpus, and Lathyrus (sensu Kupicha 1983). In this clade, the modern perennial lineages occupy derived positions because they are nested within groups of annual species. Morphometric (Dogan et al. 1992), RFLP (Asmussen and Liston, 1998), and AFLP (Badr et al., 2002) studies showed similar results, with perennial species nested inside annual clades.

Using dated phylogenies based on *rbcL* and *matK* data, Lavin and colleagues recently estimated the origin of the Fabeae crown clade to be approximately 17.5 million years ago (Mya; mid Miocene) (Lavin et al. 2005). This estimate disagrees with Kupicha's early Tertiary origin for *Lathyrus* (Kupicha, 1983). The ITS sequence data gathered for *Lathyrus* provide independent support for Lavin and co-workers' more recent origin. I calculated mean substitutions per site across the *Lathyrus-Pisum* clade (Fig 4.5) using the program DNAsp 3.53 (Rozas and Rozas, 2001), and in the absence of any fossil data for calibration, used absolute substitution rates for ITS from previously published studies of herbaceous legumes with similar life histories. Based on the rates given for the combined ITS1 and ITS2 regions in *Astragalus* (Wojciechowski et al., 1999), the *Lathyrus-Pisum* crown group is estimated at 5.4--6.3 My old, while the rates for *Lupinus* (Käss and Wink, 1997) give an estimate of 6.4–8.2 My (ITS1) and 3.5–4.3 My (ITS2). It thus seems highly likely that the modern diversity of *Lathyrus* stems from relatively recent radiations.

In the light of this timing, the results require a different biogeographic explanation from that proposed by Kupicha (1974, 1983). One scenario might be that the *Lathyrus* lineage diverged from the *Vicia-Lens* lineage in the eastern Mediterranean region during the mid- to late Miocene rather than dispersing into this area from northern Eurasian Eocene or Oligocene lineages, as Kupicha proposed. From the late Miocene, the establishment of the modern, seasonally xeric climatic rhythm (Suc, 1984) - coupled with major tectonic upheavals, including the Alpine, Caucasus, and Zagros mountain orogenies (Meulencamp and Sissingh, 2003) - would have acted as major engines for evolution, with xerophytic annuals being selected in the eastern Mediterranean and mesophytic perennial lineages in the incipient mountains and northern forests of the Euro-Siberian region (Ramstein et al., 1997). In both trees, at least four independent transitions from annuality to perenniality are inferred: in *L. neurolobus*, sect. Lathyrus, sect. Lathyrostylis, and the clade A lineages (Figs. 4.5, 4.6). Accompanying increases in complexity of leaf form and inflorescence also occurred. Alternatively, following Kupicha's scenario (1974, 1983) with revised timings, *Lathyrus* may have originated as mesophytic perennials in the Mediterranean with extensive extinctions of perennial lineages and establishment of annual lineages among the basal groups required to explain the tree topologies.

The North American–East Asian polytomy (clade B, Fig. 4.5 bootstrap <50%, Fig. 4.6 PP value 99) shows no evidence for monophyly of the North American species. The Bayesian analysis shows a grade from Eurasian to N. American taxa, but the structure within this is based on very low or negligible support values. In spite of this, clade B itself receives support in the Bayesian analysis, and Kupicha's proposal that modern North American taxa derived from a "primitive ancestral stock [from Eurasia] having characteristics of sect. Orobus" (Kupicha, 1983, p. 242) is feasible. However, her estimate of a Cretaceous or early Tertiary colonization of the New World (Kupicha, 1974) is clearly awry. The transberingian distribution of this complex reflects its probable center of diversification and suggests that the Bering land bridge was the main route by which taxa have been exchanged between the two continents. Although the pairing receives negligible support in the phylogenetic analyses (bootstrap <50%, PP value 75), the morphological similarities between *L. littoralis* and *L. japonicus* suggest close ties. Both species are sea dispersed, mat-forming species with semisagittate stipules. *Lathyrus japonicus* is the most widespread species in the genus and has a chromosome number 2n=14, which is usual in *Lathyrus*. *Lathyrus littoralis* is restricted to the west coast of N. America, from British Columbia to N. California and is one of the rare polyploid taxa in the genus (2n=28) (Broich 1989). It seems feasible that *L. littoralis* is derived from a local population of the *L. japonicus* lineage – possibly through polyploidy. However, more fine-resolution techniques such as AFLPs may be required to draw stronger conclusions.

4.6.10 *Biogeography: South America*

Burkart (1966) and Kupicha (1983) suggested that the South American species of *Lathyrus* dispersed into the region from North America via the Andes, a scenario supported by Asmussen and Liston (1998). The sequence data place the South American Notolathyrus clade clearly outside the transberingian clade B, which contains all the extant North American species sampled (Fig. 4.6). Decay analysis with parsimony relaxed by 3 and 5 steps (i.e. to 1226, and 1228 steps respectively) retained the transbering and notlathyrus clades as distinct. A Maximum Parsimony analysis of ITS sequences including 70 species of *Lathyrus* and 12 from sect. Notolathyrus (Ridley 2004) supports this view. The Notolathyrus taxa form a strongly supported monophyletic group with *L. pusillus*, the sole N. American species in the group, nested deep inside. All this evidence suggests scenarios other than those of Burkart (1966), Kupicha (1983) and Asmussen & Liston (1998) for the colonization of the continent:

4.6.11 *Transoceanic dispersal*

The tree topology (Figs. 4.5, 4.6) and age estimates for *Lathyrus* suggest that the most likely scenario is direct, long-distance dispersal of taxa to South America from Eurasia, most probably as sea-drifted seeds. Long distance dispersal is gaining increasing support to explain plant geographical patterns – particularly transoceanic disjunctions (e.g. Davis et al. 2002, Pennington et al., 2004; Renner, 2004; de Queiroz 2005a). Burkart (1937) claimed that the coastal Chilean populations of *L. japonicus* are relatively recent seaborne arrivals. Although *L. japonicus* is distant from the Notolathyrus group in these trees, it illustrates that such dispersal between the Northern and Southern hemispheres is possible. The sea-dispersal potential of seeds from species in sect. Notolathyrus is untested but coastal, fore-dune populations of *L. nervosus* are well known.

A relationship between the South American clade and Eurasian species is also suggested by morphology. The South American taxa are morphologically more similar to taxa outside sect. Orobus than they are to those in clade B (Kupicha, 1974, 1983), most notably the members of sect. Pratensis. Indeed, *L. pusillus* shares striking similarities in stipule and leaf vasculature with *L. pratensis* and *L. laxiflorus*, although this may be a parallelism (Kupicha, 1974). Interestingly, the South American species of *Vicia* are also thought to be morphologically closer to western Eurasian species than they are to most North American ones, although *V. americana* Muhl. may provide a link (Kupicha, 1974, 1976). This relationship is corroborated by stylar morphology (Endo and Ohashi, 1997) and *matK* data (Steele and Wojciechowski, 2003), but such evidence is still patchy and a targeted study of the phenomenon remains to be undertaken. Given the striking similarities in evolutionary history between *Vicia* and *Lathyrus*, this is an intriguing area for future investigation of the two genera.

4.6.12 *Extinction of North American lineages*

An alternative hypothesis close to that of Kupicha (1983) necessitates extra inferences of extinction. Under this scenario, an early lineage dispersed from

Eurasia into North America, with subsequent dispersal into South America (possibly via the temperate Andes), followed by extinction of the lineage in North America.

4.6.13 *Sampling artefact*

Although the North American species not sequenced in this study may prove to contain relatives of sect. Notolathyrus, this seems unlikely based on morphology. The North American taxa form a morphologically uniform group of taxa similar to those in clade B (Fig. 4.5). They have multiple leaflets with reticulate venation and foliolaceous, semisagittate stipules. Although the South American species show a greater range of morphological variation, almost all are unijugate with parallel veins and many species have sagittate stipules. In addition, the broad styles with sometimes bifid stigmas and the lanceolate lower calyx teeth found in some South American taxa are not found in North American taxa, but are characteristic of some west Eurasian species. *Lathyrus pusillus* subsp. *pusillus* is a North American taxon that is nested within sect. Notolathyrus (Ridley 2004). The other subspecies of *L. pusillus*, subsp. *crassipes*, is endemic to South America.

Similar scenarios, invoking long distance or iterative, short dispersals have been proposed for the Eurasian–South American disjunction in *Chrysosplenium* (Saxifragaceae), again, with no clear evidence for either hypothesis (Soltis et al., 2001). Testing this possibility in the absence of *Lathyrus* fossils is difficult.

4.7 Conclusions and further research

4.7.1 Generic delimitations

The sequence data analysis for these three regions generally agrees with the results for the *matK* analysis (chapter 3). Further data (i.e. for more genome regions) is required in order to determine if *Lathyrus* is rendered paraphyletic by *Pisum* (and *Vavilovia*) nesting inside it.

Although more conclusive data are required, it seems that *Vavilovia* and *Pisum* could be included in a broader *Lathyrus*, following a criterion of monophyly. However, if there is a strong call for retention of *Pisum* as a distinct genus (i.e. from the commercial sector), an alternative reclassification of the *Lathyrus – Pisum - Vavilovia* group might include the following names:

Genus *Clymenum*

Genus *Neurolobus*

Genus *Nissolia*

Genus *Pisum*

Genus *Vavilovia*

Genus *Lathyrus*

Subgenus Orobus
- Section Verni
- Section Niger
- Section Orobus
- Section Pratensis
- Section Aphaca
- Section Notolathyrus

Subgenus Lathyrus
- Section Lathyrus
- Section Lathyrostylis
- Section Linearicarpus

Subgenus Gloeospermus
- Section Gloeolathyrus

Position unknown

- Section Viciopsis
  (monotypic – *L. saxatilis*)

The sections and genera above might not necessarily contain all of their current members.

In order to address the remaining systematic uncertainties among the genera of tribe Fabeae, phylogenetic analysis using complete sampling of the three genome regions presented in this chapter, as well as the *matK* gene would be desirable. Sampling should include at least the following additional species:

- *Vicia ervilia* and *Vicia subvillosa*, the two members of *Vicia* that show the same stylar characteristics (laterally compressed and adaxially pubescent) as the members of the *Lathyrus – Pisum – Vavilovia* clade.
- The remaining unsampled species of *Pisum* (*P. fulvum a*nd *P. abyssinicum*) and *Vavilovia formosa* in order to determine the monophyly of *Pisum* and confirm the placement of the *Pisum – Vavilovia* clade relative to *Lathyrus*.
- *Lathyrus saxatilis* (Sect. Viciopsis) and *L. ochrus* (Sect. Clymenum), which morphology suggests may be allied to the basally diverged lineages of the *Lathyrus – Pisum – Vavilovia* clade.
- The remaining members of Sect. Linearicarpus (*L. hygrophilus*, *L. inconspicuous*, *L. tauricola*, *L. vinealis* and *L. woronowii*), given the significant disagreements in placing of *L. angulatus* and *L. sphaericus* (both Sect. Linearicarpus) among the trees presented in these studies (Figs. 3.5, 3.6, 4.5, 4.6).

4.7.2 *Sectional classifications*

Current sectional classifications of *Lathyrus* are generally well supported by the phylogenetic analysis. Most sections in Kupicha's genus-wide classification, as modified by Asmussen and Liston (1998), are monophyletic or nearly so. In most cases, Kupicha and her contemporaries' sectional classification based on character suites remains the most satisfactory and convenient way to treat the patterns of diversity in *Lathyrus*. Further sequence data for the three regions sampled here would help to clarify the relationships amongst the difficult annual Mediterranean grades (particularly the members of Kupicha's Lathyrostylis).

Studies based on chloroplast RFLP (Asmussen and Liston, 1998) and AFLP data (Badr et al., 2002), and the sequence data presented here (Figs. 4.5, 4.6) differ on the relative positions of *L. nissolia*, *L. neurolobus*, and sects. Clymenum and

Linearicarpus. In contrast to the conclusions of Asmussen and Liston (1998), the results suggest that the South American Notolathyrus group should be retained as the section proposed by Kupicha (1983).

The DNA sequence data resolve the discrepancies in classification of sect. Orobus between Czefranova (1971b) and Bässler (1966, 1973). The lineages within sect. Orobus show suggest several patterns of dispersal and diversification and include monophyletic groups corresponding to Fritsch's series Verni (if *L. linifolius* is included, and *L. venetus* is excluded – purple bar Fig 4.5), and a transberingian group of North American–East Asian species. The position of sect. Notolathyrus relative to sect. Orobus remains uncertain but appears to be derived from Eurasian rather than from North American lineages. A better resolution of the placing of *L. niger* is critical to our understanding of the North-temperate / S. American clade A group.

4.7.3 *Biogeography*

The results of these analyses agree with the generally accepted scenario that *Lathyrus* originated in the Mediterranean region. In contrast to these previous hypotheses, however (Kupicha 1974, 1983) it seems that the annual habit is the plesiomorphc condition in *Lathyrus*, with most of the perennial species occupying derived positions on the tree. The Bering Land Bridge appears to have played a major role in the colonisation of North America by *Lathyrus*. However, the importance of the Isthmus of Panama in the genus's colonisation of South America is not well supported, and South America may have been colonised directly by species from Eurasia.

The Mediterranean annual taxa appear to be fundamental in our understanding of the relationships between *Lathyrus* and *Pisum*, as well as those among the difficult sects. Lathyrus and Lathyrostylis. Section Orobus and the Pratensis–Aphaca group may represent a northern, mesophytic lineage distinct from the Mediterranean species and with a complex biogeographic history. Future studies should certainly aim to use broad sampling from both these geographical groups whenever possible.

Further investigation of the poorly resolved nodes within the sect. Orobus clade will provide important insights into the interrelationships of each of these lineages and consequently the intercontinental biogeography of the genus.

This scenario is a synthesis of current hypotheses and remains open to testing. A greater understanding of the relationships across the intercontinental divides, and indeed within Eurasia, is critical before the various elements of this hypothesis can be accepted or alternatives offered. It is clear that long distance dispersal events must be taken into consideration. Such events are feasible for at least some *Lathyrus* species. Seeds of *L. japonicus* have been shown to germinate readily after ten months in fresh water and remain viable in seawater for up to five years. Furthermore, the availability of *L. japonicus* seeds late on in autumn makes them an attractive food for Columbid birds (pigeons and doves) which are classic long distance dispersal agents (Brightmore & White 1963).

Lavin et al. (2004) and Schrire et al. (2005) hypothesised that phylogenetic patterns in Leguminosae reflect underlying ecological preferences and dispersal events rather than tectonic history - hence groups such as such as the 'temperate herbaceous clade' (e.g. Wojciechowski et al. 2000) have been recognised, whose members are collectively geographically widespread, but share the same habitat. Within Schrire et al.'s (2005) informal classification of these ecological groups, *Lathyrus* appears to display a representative pattern for the 'T' (temperate) group within the inverted repeat lacking clade (Palmer 1987, Lavin 1990 – the IRLC of Wojciechowski et al. 1999). The preponderance of species in the Mediterranean region, with further groups in the Holarctic and southern temperate regions is typical of the wider pattern in the IRLC as a whole. This implies a predisposition in *Lathyrus* for temperate habitats and that its current antitropical distribution is determined by its ecology and success at colonising new temperate areas.

5

Taxonomic treatment

Lathyrus section Notolathyrus Kupicha

5.1 Introduction

This chapter presents research into the systematics and taxonomy of Notolathyrus, the predominantly South American section in the genus. Although many researchers have treated taxa in section Notolathyrus on a local, or country-wide level, a revision of the group as a whole had not yet been attempted. Researchers based at the Royal Botanic Gardens Edinburgh and Kew, and Cambridge Botanic Garden, as well as their South American collaborators, and a number of interested horticulturists had all expressed a keen interest in seeing this group revised because this is a widespread, little known group, the members of which are notoriously difficult to identify.

Chapters 3 and 4 have demonstrated the monophyly of sect. Notolathyrus. Further evidence comes from an MSc research project done by Rhonda Ridley, at the Royal Botanic Garden Edinburgh (Ridley 2004). Adding sequences to existing accessions on Genbank, and those produced for my research, Ridley sequenced the ITS region for a further 16 accessions of S. American taxa. These included samples of six species that had not yet been sequenced. As part of her project, Ridley ran a Maximum Parsimony analysis including a total of 149 accessions from tribe Fabeae and with *Trifolium pratense* and *T. repens* as outgroups. Ridley's results showed a strongly monophyletic sect. Notolathyrus (bootstrap 99%).

The synoptic revision of section Notolathyrus presented in this chapter includes full descriptions for twenty six species native to South America. Of these, one has a disjunct subspecies in the southeastern states of the USA (*L. pusillus* subsp. *pusillus*). In S. America this species is represented by subsp. *crassipes*. Other infraspecific taxa in this study are four varieties in *Lathyrus magellanicus*, and two varieties in *L. pubescens*. Many more names have been applied to the S. American taxa than the thirty one used here. Some particularly widespread and variable species, such as *L. magellanicus* and *L. pusillus* include extensive synonymies. These are mainly synonyms used by researchers such as Philippi (1856, 1862, 1864, 1872) and Reiche

(1898) in the mid- and late 1800s working on the plants of different regions, unaware that contemporaries were describing and naming similar specimens elsewhere in the plants' range.

5.2 History of *Lathyrus* research in South America

The earliest known specimens of S. American *Lathyrus* to reach Europe were brought back by natural history or naval expeditions in the mid 1700s. The first of these were seeds of *L. nervosus* introduced to the UK in 1744. It is thought that the seeds came back on the sole surviving ship of Commodore Lord Anson's disastrous circumnavigation of the globe (1740 – 1744; Gorer et. al., 1991). By the following decade, the plants were in cultivation at Chelsea Physick Garden and it is from these specimens that Miller (*Gardener's Dictionary* 7th edition, 1758) described the plant under *Pisum*. His 1763 edition gives it the epithet *americanum* but as the plant is not a *Pisum* and Miller had already used *Lathyrus americanum* (for a Mexican *Rhynchosia*), Kupicha's (1983) combination *Lathyrus americanus* is unfortunately invalid.

Another decade after the Chelsea plants had been discovered, Phillipe Commerson collected plants of *L. subulatus*, *L. magellanicus*, *L. nervosus* and *L. tomentosus* around 1767, near Montevideo, Uruguay and further south, in Argentina. Using these collections, Lamarck (1788) described each of these species, as well as *L. sericeus* (based on a short-petioled specimen of *L. tomentosus*). These represent the first validly published members of *Lathyrus* from S. America. As is typical for many of these early collections, very little information on dates and localities was recorded. By the early 19th century, several other species were being brought back, both as dried specimens and seeds. In this respect, the thick testa and large cotyledons of *Lathyrus* seeds ensured that they remained viable for the journey back to Europe. Sello collected several species from southern Brazil and Uruguay, which were later described by Vogel (1839). William Hooker was also receiving specimens from many collectors. These included Baird, Cuming, Bridges & MacRae and Lay &

Collie in central Chile, and Gillies in Argentina. Tweedie, a nurseryman based in Buenos Aires also sent specimens to Hooker and Arnott.

In the years following these expeditions, and certainly by the middle of the century, more botanists based in South America began working on the plants. Many of these were first generation immigrants from war-ravaged Europe, settling in the newly liberated countries of South America, where climates could be found to match those of home.

One of the last major European works of this period was Alefeld's *Ueber Vicieen* (1861). Working in Germany, he treated *Lathyrus*, *Lens* and *Vicia* in a major revision. Although he transferred many species of *Lathyrus* into *Orobus* (including four from S. America), and placed these into a subgeneric framework, Alefeld's work was not widely accepted.

From this period onwards, only relatively little work has been done on these members of the genus by researchers in Europe. From a Northern-hemisphere perspective, the South American species remained on the periphery of the rest of the genus, until Kupicha (1983) placed them in her sectional classification as sect. Notolathyrus. Kupicha was building on the evidence of several authors, whose research into the morphology (Burkart, 1937; Bässler, 1966, 1973), karyolgy (Senn, 1938), and biochemistry (Simola, 1968) hinted that the S. American species were indeed a cohesive group.

5.2.1 *Argentina*

Lathyrus research in Argentina (indeed in all of S. America) is dominated by the work of Arturo Burkart. His extensive and considered revision (1937) formed the primary reference work for the initial stages of the revision presented here. Indeed, it has been the standard reference work on the genus in South America since its initial publication. Although Burkart covered mainly the Argentine species, he did discuss those from neighbouring areas of Bolivia, Brazil and Chile. This work contains the most extensive key to the genus – the only one that is known to have been translated into English. His 1942 follow up to the revision expanded on this and provided fuller notes on R.A. Philippi's Chilean taxa.

5.2.2 *Bolivia*

No works focussing on *Lathyrus* are known from Bolivia and the majority of collections are fairly recent. The earlier collections include *L. tropicalandinus* (e.g. *Mandon 726*, from 1860) and *L. woodii* (*Kuntze s.n.*). This latter species is described in the present revision. Several collections of this new species have been made by John Wood, one of the most active current collectors in the country.

5.2.3 *Brazil*

Sello was one of several plant collectors and nurserymen based in Montevideo and Buenos Aires, who collected in southern Brazil, as well as Argentina and Uruguay. All of Sello's collections were sent to Vogel in Berlin, who published *De Vicieis Brasiliensibus* in 1839. Although the Berlin originals were destroyed during the Second World War, many duplicates had been distributed among more than 40 herbaria across Europe and North America. Unfortunately, this wide disbursement of specimens means that some of Vogel's types are difficult to locate and may no longer exist. Future investigations of continental European herbaria will hopefully uncover potential lectotypes, for example of *L. macrostachys* and *L. elegans*. In total, Vogel described nine species, of which I accept five in the present revision. The most recent major taxonomic work on Brazilian *Lathyrus* is an excellent revision of the genus in Brazil by Neubert & Miotto (2001).

5.2.4 *Chile*

Relatively early collections from Chile include those of Bridges and MacRae, amongst others, who sent material to Hooker for description in the early 1830s (Hooker & Arnott, 1831, 1833; Hooker 1837).

Several collections are mentioned (effectively as syntypes) in the protologues of Hooker & Arnott's *L. pubescens*. In reality, these collections also include members of *L. cabrerianus* and *L. subandinus*. Hooker and Arnott also described *L. macropus*, based on Gillies' collections from the Andes of Mendoza, again mistakenly including some specimens of *L. subandinus* (collected by Cruickshanks) in the protologue for this species.

Meanwhile, Bertero was sending specimens to Colla in Turin (who described *L. berterianus*) and Claude Gay's massive work on the cultural and natural history of Chile includes the protologue of *L. multiceps* Clos (Clos in Gay 1847). The German-Chilean taxonomist Rodulfo Amando Philippi worked on the Flora of Chile over many years, describing many new species and several new combinations in *Lathyrus* among his works (Philippi, 1856, 1862, 1864, 1872, 1893). One of his sons, Frederico, listed 29 species in his *Catalogus Plantarum Vascularium Chilensium* (Philippi 1881). Karl Reiche's *Flora de Chile* (1898) lists seventeen species including sixteen natives. Only five of these are considered valid in the following treatment. Many specimens since then have reached northern hemisphere herbaria, especially Edinburgh (E), for which Chile is a key research area. Major collections in Edinburgh include those of Comber and Elliott (1920s) and Gardner and Knees (1990s – present).

5.2.5 *Colombia, Ecuador, Venezuela*

Collections from the 19th Century from these three countries are relatively limited in northern hemisphere herbaria. There are several collections of *L. magellanicus* var. *gladiatus* and *L. meridensis* from throughout the 1800s, including those of Linden (1842 – Venezuela), Fosberg & Prieto 22815 (1845 – Ecuador), Triana (1853 - Colombia), Jameson (1859 - Ecuador), André (1875/1876 – Ecuador and Colombia) and Lehmann (1884 – Colombia). Collections increased from the turn of the century, as more botanists regularly visited the Páramo and sub-Páramo vegetation where *Lathyrus* grows in these tropical countries. Until now, little taxonomic research has been done on *Lathyrus* of these countries. The exception is the description of *L. meridensis* from Venezuela by Pittier (1938) – a taxon accepted in this account.

5.2.6 *Paraguay*

The Swiss botanist Emile Hassler, who collected extensively in Paraguay, passed many of his specimens on to Arturo Burkart in neighbouring Argentina. The work of these two botanists represents the vast majority of work on *Lathyrus* in Paraguay. Hassler's (1919) work reporting his collections from the country included three new species, one new variety and two new forms. Paraguay remains perhaps the most under collected country in South America for *Lathyrus*.

5.2.7 *Peru*

As with Bolivia, both research and collection is limited from Peru. A few early collections (e.g. *Matthews 1572* E) stem from the 1820s when many specimens were being sent to Europe from Chile and Argentina. The great drive for collection from Peru came with the work of the Field Museum, Chicago in the 1920s – 1940s when the *Flora of Peru* was being written. Extensive collections lodged in northern hemisphere herbaria date from this time, particularly in Chicago (F). At this time, Burkart had just produced his comprehensive revision of Argentine *Lathyrus* (1937), and had included species from neighbouring countries. Consequently, relatively few new species were described for the *Flora of Peru*. MacBride collected and described *Lathyrus longipes* var. *peruvianus* J.F. MacBride (1943), although this was later sunk into Burkart's *L. tropicalandinus* (Burkart 1942).

5.2.8 *Uruguay*

Although many of the early collectors were based in Montevideo, their specimens were sent to Europe for description. Arechavelata's (1901) *Flora Uruguaya* included ten species, including *Lathyrus laevigatus* Arechevalata which was described as new. Not only is this a homonym of *L. laevigatus* (Waldst & Kit.) Kit. (a European species) but the species is based on specimens of *L. latifolius* L., an introduction from Europe. The major work on the Leguminosae of Uruguay by Izaguirre & Beyhaut (1998) covers seventeen species of *Lathyrus* and includes both superb illustrations and a key to the species.

Synoptic revision of *Lathyrus* L. sect. Notolathyrus Kupicha

5.3 Morphological diversity in *Lathyrus* sect. Notolathyrus

The following section presents a brief overview of the morphological diversity in sect. Notolathyrus. It should be stressed at this point that the section presents almost as much morphological and ecological diversity as the entire remainder of the genus combined (Kupicha 1983). It is tempting to draw comparisons between species in S. America and their ecological and morphological equivalents in the northern hemisphere and I have done this throughout the species accounts presented here. Twenty six species are recognised, ranging from the montane tropics of Venezuela to coastal Tierra del Fuego. This pantemperate S. American distribution is similar to that seen in genera such as *Calceolaria* (Calceolariaceae) and *Alstroemeria* (Alstroemeriaceae).

5.3.1 *Habitats, life cycles and rhizomes*

Section Notolathyrus, as circumscribed here, contains species with the following life cycles:

- ANNUAL: *L. campestris*, *L. berterianus*, *L. paranensis*, *L. pusillus*.
- BIENNIAL: *L. nigrivalvis*.

Of these, *L. paranensis* and *L. nigrivalvis* are relatively tall, climbing up neighbouring vegetation to 1m (exceptionally 2m) high. This habit is similar in many ways to the medium to large Eurasian annuals such as *L. hirsutus* and *L. odoratus*. The remaining annuals are more delicate, and often with more branched stems. These species are comparable in habit to species such as *L. cicera* and the members of sect. *Lathyrostylis* (W. Eurasia).

- PERENNIAL: The remaining twenty one species are perennials.

Of the perennials, there is a group that has long-creeping rhizomes, forming clumps or spreading stands comprised of scattered aerial stems. This group includes: *L. acutifolius*, *L. linearifolius*, *L. nitens*, *L. subulatus* and *L. tomentosus*. They are further characterised by their small size, dense pubescence throughout (including the ovary) and seasonally arid habitat.

The remaining perennial species in the section usually have rhizomes thickened for storage. These rhizomes give rise to many stems and the aerial parts of the plants have a clambering habit, using surrounding vegetation or other stems of the same plant as support.

5.3.2 *Stems*

Stems in sect. Notolathyrus may branch under or above ground, although most branching occurs at the base of the plant.

In species throughout the section, the stems are often ornamented with pairs of opposite wings. These provide an increase in surface area available for photosynthesis. The *Lathyrus nervosus*, *L. elegans*, *L. paraguariensis* species group can often be identified based on the absence of wings. In *L. hasslerianus* and *L. cabrerianus*, the stems are terete, but with slight wings only in the extreme upper parts of some plants.

5.3.3 *Drying colour*

In the Old World, the sole member of the genus to consistently dry black is *L. niger*. The phenomenon is more common in section Notolathyrus, with several species blackening to varying degrees. In conjunction with semisagittate stipules, linear lower calyx teeth and glabrous ovaries, this blackening or the absence of it has been seen as a taxonomically significant character (Burkart 1937, Kupicha 1983). Both of Burkart and Kupicha saw the following species as a related group, although neither formalised them into a series.

- *L. parodii* (not drying black, but other characters as for group)
- *L. magellanicus* var. *glaucescens* (entire plant becoming slightly grey)
- *L. nigrivalvis* (calyces and fruits drying black)
- *L. paranensis* (entire plant darkening to grey)
- *L. magellanicus* vars. *magellanicus* and *gladiatus* (entire plant often drying completely black)
- *L. macrostachys* (entire plant often drying completely black)

5.3.4 *Stipules*

Stipules in sect. Notolathyrus show the full range of diversity seen elsewhere in the genus. They have a large upper lobe and one (semisagittate) or two (sagittate, hastate) basal lobes or spurs. These basal lobes may be directed downwards (semisagittate, sagittate), or sideways (hastate). In either case the upper lobe may be symmetrical or somewhat curved (falcate). In *L. linearifolius* and *L. nitens*, there is no basal spur and the stipules are simple and acute-triangular.

5.3.5 *Leaves*

The length of the petiole has been of particular importance in the classification of the *magellanicus* group – giving rise to names such as *L. sessilifolius* and *L. epetiolaris*. However, this is never a consistent trait when large numbers of specimens are compared.

The majority of Section Notolathyrus has unijugate leaves. *Lathyrus macropus* is the only consistently multijugate member of sect. Notolathyrus, with three or more pairs of leaflets per leaf. A single specimen of *L. multiceps* is known with a number of leaves terminating in leaflet-like structures. This specimen has been debated for many years and known variously as *L. multiceps* Clos *var. pastorei* Burkart (Burkart 1942) and *L. pastorei* (Burkart) Rossow (Rossow 1982). Substitution of the terminal tendril with a leaflet is a common aberration in individual leaves of many species of *Lathyrus*, so I do not consider this a valid taxon at either rank.

In most members of Notolathyrus the primary veins in the leaflets are parallel, with reticulate veins among them. In *L. elegans*, *L. nervosus* and *L. paraguariensis* the reticulate veins are particularly apparent and the leaflets often have a single prominent vein running around the margin.

Tendrils are very variable in sect. Notolathyrus. As in the wider genus, they may be strong and many-branched, or reduced to an arista. Smaller plants (including those from smaller species) usually have more simple tendrils. Even in larger species, within individual specimens, tendrils lower down, on older parts of the plant tend to be simple, with those in the younger parts branching more. Terminology for leaf architecture follows Hcikey (1974)

5.3.6 *Inflorescence*

Flowers are sessile in *L. campestris* and in some individuals of both *L. berterianus* and *L. pusillus*, all of which have solitary or very few flowers. Peduncles are held erect in most species and are tipped with an apical arista. Many members of *L. pusillus* subsp. *crassipes* have a swollen peduncle, a feature seen in occasional individuals of other species (e.g. *L. magellanicus Gardner & Knees 6129* E). This character is often associated with congested flowers and appears as if two peduncles have fused together.

Pedicels often swell and lengthen following fertilisation, raising the flowers or pods to a horizontal or semi-erect position in some species. The relatively large, pendulous flowers of *L. tropicalandinus* are quite distinctive in this regard.

5.3.7 *Calyx*

The calyx in *Lathyrus* is always campanulate. It is quite blunt (i.e. the tube is short and the base truncate) in some members of sect. Notolathyrus. This is a good spot character for identifying *L. pubescens* in the herbarium. Calyces are typically grass green when fresh, although often with a faint purple tinge, or occasionally with a deep purple colour (as in *L. tropicalandinus*). In some species, the calyces blacken within a few days of the plant being picked. This is certainly the case in

L. magellanicus and *L macrostachys*. Blackening is present, but sometimes less pronounced in the calyces *L. nigrivalvis* and *L. paranensis*.

In other species of *Lathyrus* calyx pubescence can be a useful character for species delimitation, but the degree and type of calyx pubescence varies widely in section Notolathyrus. Calyces may be glabrous, sparsely pubescent to densely lanate, or lanulose-hairy, and with both simple and glandular hairs.

5.3.8 *Corolla*

Flowers in section Notolathyrus are predominantly shades of blues and purples. Petals may be a uniform colour or, more commonly, with wings and keel lighter than the standard petal. There is a great degree of variation even within species, and individual flowers tend to darken after anthesis. As with many angiosperms, several taxa (often at forma rank) have been proposed based on one or a few individuals with white flowers. Only a few species have flowers of other colours:

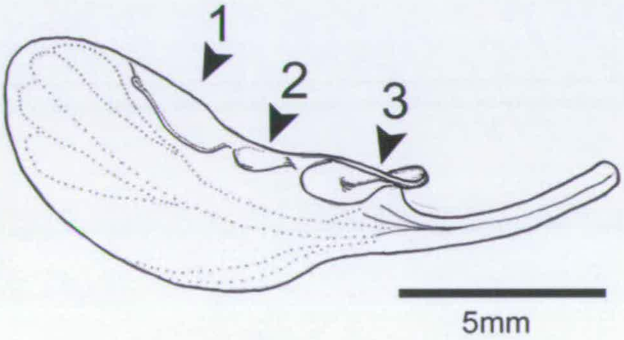
Lathyrus tomentosus has dirty white or cream-coloured petals with purple veins, whilst *L. cabrerianus* has white flowers maturing to primrose yellow.

Lathyrus hasslerianus is unique amongst the group, with inflorescences composed of many (up to 30) relatively small, waxy flowers that begin white and mature to golden yellow and then orange. Almost identical inflorescences are seen in *L. davidii* (N.E. Asia), *L. laevigatus* and allies (N.W. Eurasia), *L. sulphureus* and *L. ochroleucus* (N. America), and in *Vicia pisiformis* (Europe). The Eurasian – N. American species all belong to the core Orobus group but *V. pisiformis* is only very distantly related suggesting parallel, independent evolution. When dry, the petals of blue and purple-flowered species usually retain at least some patches of colour for thirty years or more.

Banners (standard petals) are diverse in the genus, with the larger-flowered species having a rotund or orbiculate blade above a distinct claw. In smaller-flowered species (e.g. *L. hasslerianus* and *L. nigrivalvis*), the entire banner appears continuous, with the claw the same size and shape as the blade. The two are separated by a waist, giving the whole a panduriform appearance.

As with all other members of tribe Fabeae, and many other evolutionarily recent genera of papilionoid legumes, the wing petals are ornamented with pleated processes on the upper (adaxial) edge, at the base of the blade – these correspond to the 'pockets' referred to in Stirton (1981). The pleats allow the wings to interlock with corresponding pockets on the keel petals. In most species in the genus, these processes are formed from a single infolding of the wing petal, but in *L. macrostachys*, the pleat is not continuous, and so forms two processes. In the related *L. magellanicus*, there is a small boss, followed by a pleat. The upper margin of the pleat continues into a short spur that sits above the claw (fig. 5.1).

Figure 5.1 Wing petal structures
Wing petal of *Lathyrus macrostachys*
1.+2. pleat
3. pocket and short spur
In this species, the pleat is discontinuous.



The outer surfaces of the blades of the wing petals in all species are ornamented with fine sculpturing in the apical parts. These are thought to act as footholds for alighting insect pollinators (Stirton 1981).

As mentioned above, the keel petals have a pocket that grips the wing, holding it in place. The keel petals are firmly fused together along the entire lower (abaxial) margin in all species of *Lathyrus*. At the apex, most of the keels have a slight kink that encloses the apex of the style in vivo. This acts as a pollen pouch, with pollen held ready for presentation by the pubescent style. When insect visitors activate the flower, all four wing and keel petals are depressed, the style pushes through the pollen pouch, picking up pollen on the hairs and presenting it to the underside of the pollinator.

5.3.9 *Androecium*

As in all *Lathyrus* species, the androecium is diadelphous, with 9+1 stamens. The vexillary stamen is free almost to its base, although it can sometimes be difficult to pull it free of the staminal tube in dried specimens after boiling. The staminal tube is usually truncate at the apex, although it can be somewhat rounded or oblique in many species – a feature more commonly seen in *Vicia*. Although shape of the androecium varies among species, it does also vary within species, making it an inappropriate character for species delimitations.

5.3.10 *Gynoecium*

Styles in all species of Notolathyrus are adaxially pubescent, as is the case with the rest of the genus. The style of *L. tomentosus* coils, often through a full revolution, when the petals have been shed.

Stigmas in section Notolathyrus show as much variation as the rest of the genus combined (Kupicha 1983). As the stigma matures, the tissue dries and folds back on itself adaxially towards the pollen brush, encouraging self-pollination.

Some species have a double stigma, with the style tipped by two separate stigmatic flaps or discs. These include *L. acutifolius L. macropus*, *L. pubescens* and *L. tomentosus*, all of which also have pubescent ovaries and appear to be closely related.

5.3.11 *Fruits*

The valves on legumes of sect. Notolathyrus are unornamented. The only species that may be encountered in S. America with wings on the sutures is *L. sativus* (sect. *Lathyrus*), in cultivation or as an escape. Valves may be covered with varying degrees of pubescence and, in sect. Notolathyrus, pubescent ovaries retain their hairs through to maturity. In some species (e.g. *L. hasslerianus L. pubescens*), the valves follow the contour of the seeds closely, giving a nodose appearance.

In some species, spongy or woolly tissues form around the seeds, giving the appearance of septation within the pod. Within section Notolathyrus, such woolly false septa are found in a number of species including *Lathyrus pubescens* and *Lathyrus nervosus*. *Lathyrus davidii* Hance (sect. Orobus) from northeast Asia often has similar woolly partitions between the seeds. However, this is a less constant character than in section Notolathyrus.

5.4 Insect visitors

I have observed *Bombus* species visiting all members of sect. Notolathyrus that have been seen in the field. Coleopterans feed on pollen held in the apex of the keel after anthesis, and large vespids (hornets) were seen biting through the calyx in *L. pubescens* (Fig. 5.2).

Figure 5.2 Insect visitors
Hornets and a coleopteran thieving nectar and pollen respectively from *L. pubescens*. Cerro Bahia Blanca, Buenos Aires Argentina.

5.5 Chromosome numbers

2n=14; polyploids: 2n=28 (tetraploid); 2n=42 (hexaploid). Polyploids are relatively rare in *Lathyrus*. Of the c. 100 species thus far surveyed, only a few Eurasian species such as *L. odoratus*, *L. palustris* and *L. pratensis* have been shown to contain polyploids. Polyploidy is more common in N. America with four recorded polyploids from the US (Broich 1989).

5.6 Species concept

Throughout this revision I have used a pattern-based species concept based on morphological diagnosability - one that aims to be as functional as possible for end users in the herbarium and in the field who are observing snapshots in evolutionary time (Luckow 1995). Diagnosability is at the heart of recently proposed species concepts including those of Platnick (1979), Nelson & Platnick (1981) Cracraft (1997), Nixon & Wheeler (1990), and Donoghue (1985).

Alternative, process-based concepts such as the biological species concept (e.g. Mayr, 1982; reviewed in de Quieroz, 2005b) are altogether impractical for the taxonomist- they rely on demonstrating actual or potential genetic exchange between the members of the species in question (e.g. Bunge, 1981). The vast majority of practising taxonomists will not have access to the time, expertise or expensive resources required to evaluate genetic markers necessary to infer breeding patterns. (Seberg et al., 2003; Will & Rubinoff, 2004).

The diagnosability criterion is a useful one, and one that can be applied readily with the aid of a key to almost any specimen encountered in the field or herbarium. Consequently, I follow a traditional morphology-based, essentially phenetic species concept, assessing the morphology of all specimens to determine diagnostic characters. Characters used for species delimitation in this account are discontinuous, or non-overlapping and I consider the species I have defined to be equivalent to phylogenetic species sensu Nixon & Wheeler (1990):

> "The smallest aggregation of populations . . .diagnosable by a unique combination of character states."

In common with other plant species defined using these traditional morphological approaches, I suspect that the morphological discontinuities observed reflect reproductive isolation (Ortiz-Barrientos & Rieseberg, 2006), and in this sense, I have defined entities corresponding to biological species.

My species delimitations are broader than those of previous workers. Where species or infraspecific taxa have been based on dimensions of organs, measurements have been taken in order to determine the extent of discontinuous variation. In most cases, there is no apparent support for the taxa in question. Thus, for example, leaflet length in *L. subulatus* shows a continuum which argues against the use of Hassler's (1919) *L. subulatus* var. *longifolius*. Similarly, my particularly broad view of the diverse *L. magellanicus* stems from the fact that characters show continuous variation throughout their range. Thus the plants accepted by Burkart (1937) as *L. sessilifolius* and later (Burkart, 1942) as *L. hookeri* were distinguished based on their sessile leaflets alone. However, petiole length shows a continuum in *L. magellanicus* and there is no justification for separation of species.

5.7 Materials

This revision is based on four years of study of around 2000 herbarium specimens, and field observations of wild populations of *Lathyrus*.

5.7.1 *Living material*

Field work was conducted in subtropical, Mediterranean, and temperate Andean areas of Argentina and Chile. Specimens collected on these expeditions (c. 200 collection numbers for 13 species) are lodged with the herbarium of the Royal Botanic Garden Edinburgh.

Living specimens were cultivated in the Royal Botanic Garden Edinburgh, and in the UK's National Council for the Conservation of Plants and Gardens (NCCPG) *Lathyrus* collection held by Sylvia Norton, West Wickham, Cambridgeshire.

5.7.2 *Herbarium material*

During the course of this research, I was based in the Royal Botanic Garden Edinburgh (E, E-GL), and in Tokyo University (TI).

In addition, loans of all available material were received from:

The Natural History Museum, UK (BM); Field Museum, Chicago (F); Royal Botanic Gardens Kew (K); New York Botanical Garden (NY); The Smithsonian Institution (US)

The following herbaria were visited for specimen observations:

Museo Argentino de Ciencias Naturales Bernardino Rivadavia (BA); Universidad Nacional del Sur, Bahia Blanca, Argentina (BB); Universidad Nacional del Comahue, Bariloche, Argentina (BCRU); Museo Nacional de Historia Natural, Santiago de Chile, Chile (SGO); Instituto de Botánica Darwinion, Argentina (SI) and Universidad Nacional de Rosario, Rosario, Argentina (UNR).

Additional information, including photographs of type material was kindly provided by Muséum National d'Histoire Naturelle, Paris (P) and Charleston Museum, South Carolina USA (ChM). All specimens have been seen unless otherwise stated.

5.7.3 *Specimen localities*

In the following accounts, specimen localities cited as latitude and longitude coordinates follow the available label information on the sheet – typically in 'Degrees (°) minutes (') and seconds (") format. The remainder are presented in decimal degrees format (xx.yyy°). The maps that are included for most species in the accounts below show only the specimens for which latitude and longitudes could confidently be identified. The maps were generated in the DIVA-GIS mapping program (Hijmans et al. 2005)

Lathyrus L.

Linnaeus, C. (1753) *Species Plantarum*, Vol. 2, Impensis Laurentii Salvii, Stockholm.

Annual and perennial herbs, some species drying black. Stems erect or climbing, winged or wingless. Stipules semisagittate or sagittate, sometimes large and leaf-like. Leaves paripinnate, with 1-many pairs of leaflets, rarely phyllodic or reduced to modified stipules, terminating in branched or simple tendrils or aristate; leaflets elliptic, ovate, ovate-oblong, lanceolate or linear; veins parallel, pinnate or reticulate. Racemes axillary, pedunculate with 1 to many flowers; flowers purple, pink, yellow or white, sometimes crimson, brick red or orange; calyx campanulate, unequally or equally toothed; style dorsally compressed, linear or spathulate, pubescent on adaxial (inner) surface. Legume laterally compressed, dehiscent. Seeds 2 to many.
TYPE SPECIES *Lathyrus sylvestris* L.

Lathyrus Section Notolathyrus Kupicha

Kupicha F. (1983) The infrageneric structure of *Lathyrus*. *Notes from the Royal Botanic Garden Edinburgh* 41: 209–244.

Perennial and annual herbs; perennials with creeping or thickened rhizomes, annuals with fine roots. Stems decumbent to erect, herbaceous throughout, 5cm – 5m high; grass green when fresh tinged purple in some species, often glaucous throughout, blackening when dry on vegetative organs, calyces and/or ovaries in some species; plants glabrous, sparsely pubescent to lanulose- or tomentose-hairy.
Stipules small, subulate to large and foliose, semisagittate, semihastate, sagittate or hastate, often pubescent in the axils. **Leaves** paripinnate, usually with one pair of leaflets (3–5 in *L. macropus*); petioles to 8cm long; tendrils branching, simple or reduced to an arista; leaflets 1cm long and 0.7-40mm wide, upper surfaces often bright green when fresh and glaucous underneath, or glaucous on both surfaces. Primary veins parallel, prominent or with prominent reticulate venation, sometimes with a reinforcing vein around the margin.

Inflorescence a raceme (to 30cm total length) with 2–30 flowers, or solitary and sessile. **Flowers** 1.2–2.5cm long. Calyx campanulate, pubescent or glabrous, often tinged purple, calyx teeth shorter or longer than the tube, equal, subequal or unequal (in which case with the lower teeth longer than the upper) sometimes fringed with simple and glandular hairs; corolla sky blue, violet, lilac or primrose- to golden-yellow, sometimes white or with white wings and keel only; banner petal stenonychoid to oblong, androecium diadelphous (9+1 stamens), staminal tube truncate or slightly oblique at apex. Ovary glabrous or pubescent, styles linear to broadly spathulate, stigmas simple or bifid with two stigmatic flaps. **Fruits** linear to trapezoid, chestnut brown (in which case often pubescent); or black (usually glabrous).

26 species: Argentina, S. Brazil, Bolivia, Chile, Colombia, Ecuador, Paraguay, Peru, Uruguay, Venezuela. S.E. USA

TYPE SPECIES: *Lathyrus magellanicus* Lamarck

CHROMOSOME NUMBERS:

2n=14, polyploidy not recorded.

5

Key to the species of *Lathyrus* in South America

This key includes all species of sect. Notolathyrus, as well as *L. japonicus* and the introduced and escaped Eurasian species that may be encountered in the field in S. America. Non-native species appear in regular font, natives in bold. Only the members of sect. Notolathyrus are included in the descriptions that follow. *Flora Europaea* includes information on all of the Eurasian species mentioned here, as well as *L. japonicus*. The latter is a coastal species from the cold-temperate northern hemisphere, with disjunct populations in Chile.

USER NOTES:

- It is important to dissect flowers where possible, because the pubescence of the ovary is a particularly significant character.
- Colour on drying is a difficult character to interpret for both the vegetative and reproductive parts of the plant. Please refer to the notes on stem and flower drying colour above for further information.

1a) Fruit two-winged on the upper (adaxial) suture, ovoid, 1–2cm wide. Racemes 1-flowered. Seeds angular, trapezoid, large. Ovary glabrous. Leaflets linear. Stipules semisagittate. 29. *L. sativus*

1b) Fruit unwinged on the upper (adaxial) suture, linear, 0.3–1.2cm wide. Racemes 1–12 - flowered. Seeds spherical, globose-cuboid or lenticular 2

2a) Most leaves 3- or more-jugate, only the lower leaves unijugate 3

2b) Leaves unijugate, only very rarely bijugate on the upper leaves 4

3a) Stipules sagittate, large-foliose (>5mm wide). Racemes with 4–9 flowers. Plant glabrous or glabrescent, leaflets elliptic to ovate. Generally from coastal habitats in Chile. 27. ***L. japonicus***

3b) Stipules semisagittate, 2–4mm wide. Racemes with 8–17 flowers. Plant pubescent or puberulent, leaflets linear or lanceolate. Plant of montane habitats 10. ***L. macropus***

4a) Ovary and mature fruit densely pubescent, hirsute, lanulose or tomentose-hairy. Stipules semisagittate. 5

4b) Ovary glabrous or with only a very few scattered hairs. Stipules semisagittate or sagittate to hastate. 18

5a) Flowers primrose yellow *in vivo* in a dense terminal head. Plants very robust, tendrilous vines with stems to 5m, pubescent throughout. From temperate Chilean deciduous forests and neighbouring Argentina. 4. ***L. cabrerianus***

5b) Flowers with blue or violet markings on the banners at least, wings and keel violet or white. Plants less than 3m, if more, then from subtropical and tropical areas (*L. tropicalandinus* and *L. pubescens*). 6

6a) Racemes with 6–20 flowers, habitats diverse, corolla sky blue, lilac or violet (pink, red or maroon in *L. odoratus*). Only wings and keel white in some species. 7

6b) Racemes with 1–6(–8) flowers. If more than six flowers, then plants of seasonally dry pampa with all petals creamy white, veined purple (*L. tomentosus*). 13

7a) Stipules simple, acute-triangular (i.e. without a basal spur). 8

7b) Stipules sagittate or semisagittate (i.e. with a basal spur or spurs). 9

8a) Leaflets linear, 7–14cm long, 1–3(–5)mm wide, apices acute. 7 ***L. linearifolius***

8b) Leaflets narrow elliptic, 3.5–5.3cm long, 5–6(–9)mm wide, apices rounded-mucronate. 16. ***L. nitens***

9a) Stems winged, leaflets to 0.7cm wide. 1. ***L. acutifolius***

9b) Stems unwinged, leaflets (0.5–)1–2(–2.9)cm wide. 10

10a) Stigmas bipartite (with two stigmatic flaps). Fruits usually with woolly false septa between seeds. Stipules semisagittate. 20. ***L. pubescens***

10b) Stigmas simple. Fruits usually without woolly false septa between seeds. At least the upper stipules sagittate. 11

11a) Inflorescence a loose raceme, flowers pendent. Leaves and stems glabrous to densely pubescent, with golden or brown hairs, sometimes only the ovary, calyx and buds pubescent. From tropical and subtropical mountains (Bolivian Andes and northwards). 25 ***L. tropicalandinus***

11b) Inflorescence a dense raceme, sometimes pseudo - verticillate, flowers held at 90° to the inflorescence axis or suberect. Entire plant densely pubescent. From Chilean mountains (Regións II: Antofagasta – VI: O'Higgins). 12

12a) Stipules hastate, 13–20mm broad. Lower calyx teeth linear >5mm long. Chile, Región II Antofagasta. 8. ***L. lomanus***

12b) Stipules sagittate or semisagittate, 3–8mm broad. Lower calyx teeth deltoid <4mm long. Chile, Regións IV: Coquimbo – VI: O'Higgins. 22. ***L. subandinus***

13a) Fruits covered with tuberculate hairs, usually pendulous, stems broadly winged (wings >1mm), plants non- native. 14

13b) Hairs on fruits without basal swelling, fruits usually held erect, stems unwinged, plants of Pampas and other dry grassland habitats in Argentina and temperate regions of Chile. 15

14b) Flowers 1.8–2.5cm long. Plant robust, 1–2.5m tall. Leaflets ovate, apices rounded-mucronate. 29. *L. odoratus*

14b) Flowers 1.5cm long or less. Plant small, 10–50cm tall. Leaflets linear to lanceolate, apices acute. 30. *L. hirsutus*

15a) Inflorescence (including peduncle) shorter than leaflets of the subtending leaf. Very delicate annuals with fine roots. Chile, lowlands of Regións IV to X (Coquimbo to Los Lagos). 4. ***L campestris***

15b) Inflorescence (including peduncle) longer than the leaflets of the subtending leaf. Delicate perennials with running rhizomes or woody, thickened tap-roots.

Plants of dry, open grasslands, in Argentina, Brazil and Uruguay or mountains of central and southern Chile and neighbouring Argentina. 16

16a) Style a little expanded above, stigma simple. Mature fruits 7–8mm wide, without woolly false septa between the seeds. Calyx hairs somewhat curly and not appressed. Plants of open forests and forest margins in the temperate Andes of Chile and Argentina. 13. ***L. multiceps***

16b) Style broadly spathulate, stigma bipartite. Mature fruit 3–6mm wide with woolly false septa between the seeds. Calyx hairs straight, appressed. Plants of the Argentine Pampas, and similar seasonally dry grassland and rocky habitats in Uruguay and S. Brazil. 17

17a) Flowers 1.2–1.6cm long, lilac to violet. Leaflets 1–3mm wide. Style 3–4mm long, not coiling at the base when dry. Racemes with 1–4 flowers. 23 ***L. subulatus***

17b) Flowers 2.2–2.8cm long, creamy white with dark purple veins. Leaflets >3mm wide. Style 7–10mm long, frequently coiling at the base when dry. Racemes with 2–6 flowers. 24. ***L. tomentosus***

18a) Corolla golden yellow, maturing to orange-brown. Plants of subtropical Brazil and Argentina 6. ***L. hasslerianus***

18b) Corolla pink, sky blue, lilac, or violet, sometimes with white wings and/or keel 19

19a) Ovaries and fruits not typically blackening or greying on drying, mature fruits chestnut to dark brown (if plants from mountains of Ecuador, Venezuela and Colombia then see also *L. meridensis*). 20

19b) Ovaries and fruits blackening; at least the calyces and buds, often the whole plant darkening quickly when picked. 28

20a) Plants delicate annual ruderals 21

20b) Plants robust with thickened rhizomes 22

21a) Stipules sagittate. Racemes 1–3-flowered, generally paired. A delicate, widespread meadow herb or ruderal. 21. ***L pusillus***

21b) Stipules semisagittate. Racemes 1-flowered, very rarely with 2 flowers. Regións IV to X (Coquimbo to Los Lagos), Chile 2. ***L. berterianus***

22a) Leaflets and stipules with many reticulate veins, and sometimes with a stiff reinforcing vein at the margin. Plant completely glabrous, drying hard and not blackening except in poorly dried specimens. Petioles very short (to 7mm), stipules sagittate, large (1.5–4.1cm long and (0.7–)1.5–2.5 cm broad). Stems not winged 23

22b) Leaflets and stipules with thin margins, not reinforced with a continuous vein. Plants variously pubescent or glabrous, blackening or not on drying. Leaves petiolate or not, stipules sagittate or semisagittate. Stems winged or not, but never the same combination of characters as in 22a) above 25

23a) Leaflets 9–15cm long, racemes with 16–30 flowers 17. ***L. paraguariensis***

23b) Leaflets to 8.5cm long, racemes with 3–20 flowers 24

24a) Racemes with 3–7(–9) flowers, these 15–20mm long. Leaflet apices acute. Lowest calyx tooth exceeding length of calyx tube 14. ***L. nervosus***

24b) Racemes with 11–20 flowers, these 15mm long. Leaflet apices rounded. Lowest calyx tooth subequal to the length of the tube 5. ***L. elegans***

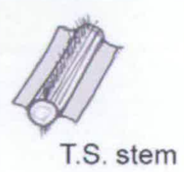
25a) Stipules semisagittate, upper lobe very narrowly elliptic to lanceolate. Style contorted, twisting through 90° to appear laterally compressed with pubescent stylar surface at 90° to the main axis of the plant 26

25b) Stipules sagittate, if semisagittate then upper lobe ovate or rotund. Styles not contorted 27

26a) Stems unwinged. Rhizomes with large (>1cm long) lacrimoid storage tubers. 30. *L. tuberosus*

26b) Petioles and stems very strongly winged (stem wings>3mm). Tubers absent. 28. *L. latifolius*

27a) Lower calyx teeth 2–3 times longer than the tube and longer than the upper teeth. Stems winged, with two lines of pilose-pubescent



hairs at right angles to the wings. Plants of inundated lowland forests. 19. ***L. parodii***

27b) Lower calyx teeth subequal to the tube. Stem unwinged or with very slight (<1mm) wings only in upper parts, but without opposite lines of hairs on the stems. Plants of upland forest margins. Bolivia >2000m altitude 26. ***L. woodii***

28a) Annual or biennial plants of wet chaco swamps and inundated forests near the Paraná and Uruguay rivers. 29

28b) Perennial plants with creeping or thickened rhizomes 30

29a) Style c 5mm long. Racemes 3–11cm long with (1–)2–3(–5) flowers. Leaflets 3–6(–9)cm long, with rounded, mucronate apices. Only the ovaries, fruits, buds and calyces blackening in herbarium specimens 15. ***L. nigrivalvis***

29b) Style 8-12mm long. Racemes 14–25(–45)cm long with 3-12 uncrowded flowers. Leaflets 5-13.5 cm long, apices acute. The whole plant greying on drying, the calyces and base of the stipules blackening 18. ***L. paranensis***

30a) Wing petals with two distinct basal processes interlocking with the corresponding pouch on the keel petal. Calyx glabrous. Flowers (5–)7–17 in a loose raceme. Plants of wet chaco swamps. 10. ***L. macrostachys***

30b) Wing petals with a basal raised boss and one basal process interlocking with the corresponding pouch on the keel petal. Calyx glabrous or pubescent. Flowers (2–)4–10(–12) in a dense raceme. Plants from Tierra del Fuego to the Venezuelan Páramo in a wide range of habitats, but never in wet chaco swamp (if apparently found in wet chaco or other marshland near the Uruguay and Paraná rivers then see the annual/biennials *L. nigrivalvis* and *L. paranensis*) 31

31a) Calyces lanulose-pubescent. Leaflet apices rounded. Only the fruits drying black. Plants of Colombia, Ecuador and Venezuelan Páramo 12. ***L. meridensis***

31b) Calyces usually glabrous (except in central Chilean specimens). Leaflet apices variously acute or rounded. Entire plant usually drying black, if not, then specimens from Southern Argentina and Chile 11. ***L. magellanicus***

5

Species descriptions

1. Lathyrus acutifolius Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 27
TYPE: URUGUAY *Sello s.n.* (lectotype, here designated: K!; isolectotypes K! – two specimens, one attached to lectotype; E!).

Perennial herb not blackening on drying. Rhizomes woody, filiform, creeping, branching underground. Stems erect to 40 (–80)cm, quadrate, with distinct wings c. 1.5mm wide, broader in the upper parts of the plant (to 2mm). Pubescent throughout, with simple white and dark orange-red glandular hairs.

Stipules semisagittate, the upper lobe linear, acute, (6–)8–15mm long and 2–3mm broad (broadest at point of attachment), with lower lobe an acute basal spur to 5mm long, smaller in the upper portions of the plant. **Leaves** unijugate, rarely bijugate terminating in a simple or branched tendril, petioles dorsally compressed 6–8(–15)mm long, pubescent, with simple and glandular hairs; leaflets borne on densely pubescent, prominent, articulated pulvini; upper surface grass green when fresh, glabrous or nearly so, lower surface somewhat grey-green when fresh, with long silky white or golden simple hairs and red glandular hairs; primary veins parallel, conspicuous on the undersides of the leaflets, narrow – to very narrow elliptic or lanceolate, apex acute with a short mucro, 51–70(–93)mm long and 4–7mm broad. **Inflorescence** a somewhat one-sided raceme of 8–14 flowers borne on an erect peduncle, typically twice as long as the leaflets of the subtending leaf (to 19cm, but usually shorter). Floral bracts absent. **Flowers** 10–13mm long, borne on c.2mm, pubescent pedicels, held slightly erect. Calyx campanulate, tube 2–4mm long, densely pubescent, tube c. 4mm long, lowest and second calyx teeth acute-triangular, the upper teeth shorter, deltoid. Corolla blue; banner blade held erect, 9mm long, 11mm wide, deeply notched (to 3mm) at the apex, claw 6mm long; wing blade 11mm long, 4mm wide with a strong pleated basal process, claw 6mm long; keel blade 7mm long, 3mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube truncate or very slightly oblique at apex. Ovary densely tomentose hairy with silky white, or golden hairs; style c. 3mm long, broadly spathulate, with bipartite stigma, the two fertile portions separated by a strip of translucent white stylar tissue. **Immature fruits** densely pubescent, drying red-brown, linear. Mature fruits not seen.

PHENOLOGY:

Flowering: November and December
Fruiting: late December
Plants die back in the dry season.

DISTRIBUTION (FIG. 5.3):

Brazil – Paraná, Santa Catarina; **Uruguay**.
In dry, open grassland and grassland amongst patches of remnant forest.

DIAGNOSTIC NOTES:

Lathyrus acutifolius is closely allied to *L. nitens* and *L. linearifolius*. In particular, small specimens of *L. acutifolius* may be mistaken for *L. nitens*. However, they can be distinguished by the following characters:

L. acutifolius	***L. nitens***	***L. linearifolius***
Stems winged	Stems not winged	Stems not winged
Stipules semisagittate (with basal spur)	Stipules simple acute-triangular (without basal spur)	Stipules simple acute-triangular (without basal spur)
Leaflets narrow – to very narrow elliptic or lanceolate. < 15 times as long as broad	Leaflets narrow elliptic. < 15 times as long as broad	Leaflets linear > 15 times as long as broad
Leaflet apices acute	Leaflet apices rounded	Leaflet apices acute

Most herbarium collections of *L. acutifolius* have mistakenly been identified as *L. nitens*. Grisebach (1879) precipitated this confusion when he placed *L. acutifolius* as a variety under *L. pubescens*.

TYPES:

Three sheets, two held in Kew and the other in Edinburgh, represent the surviving Sello collections from which Vogel described this species. None are numbered and collection information is limited to the printed 'Brasilia' on the label. The original description cites the collections as being from Montevideo. Two of the Kew specimens that have been combined onto the same sheet bear an amendment in pencil: 'Uruguay'. The larger of these two specimens was chosen as the lectotype as the flowers are in better condition.

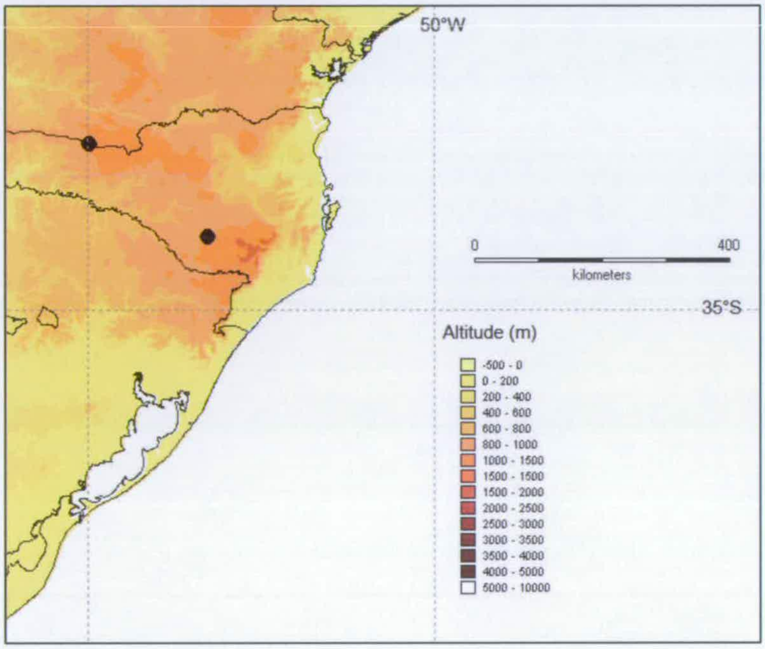


Figure 5.3 *L. acutifolius*
This species is distributed in Santa Catarina and Paraná, Brazil.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Brazil

PARANÁ: Mun. Palmas, Morro da Baliza *Hatschbach 30719* (NY)

SANTA CATARINA: Mun. Lajes: Campo along the Estrada de Rodagem Federal, South of Lajes alt. 900m, *Smith & Klein 8132* (US); São Joaquim, outskirts of São Joaquim, rd towards Bom Jardim da Serra (28°22'42"S, 49°56'12"W) alt. 1450m, *Miotto 2224* (E – duplicates in FHO, ICN not seen).

2. Lathyrus berterianus Colla (1832) *Plantae Raiores in Regionibus Chilensibus*. A. Clarissimo M.D. Bertero, Nuper detectae et Ab. A. Colla in Lucem editae, **2**: 61, Tab. XI. *Lathyrus debilis* Clos var. *berterianus* (Colla) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p.200. TYPE: CHILE: In fruticetis saxosis Prope la Punta de Cortez Sept. 1828, *Bertero 359* (holotype: P!; isotypes: F! K!)

Lathyrus debilis Clos (1847) in Gay C. (ed.) *Historia Fiscia y Politica de Chile* (*Flora Chilena II*), (non Vogel). Claudio Gay, Paris. p.142. TYPE: CHILE: in pratis montuosus Hiago. aout 1829, *Gay 490* (holotype: P!)

Lathyrus gracilis Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 627. *Lathyrus debilis* Clos. *var. gracilis* (Colla) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 200. TYPE: CHILE: Valparaiso Novembri 1854 *Germain 484* (holotype: SGO!, isotype SGO!; photograph: F!, NY!)

Annual herb not blackening on drying. Roots delicate and rhizomes absent. Stems few-branched, slender, to 25(–40)cm, unwinged, or very rarely with slight (0.5mm broad) stem wings in exceptionally large specimens. Fringed with pilose hairs throughout except on the ovaries, smaller plants and younger organs often pilose-pubescent, becoming less so with age.

Stipules semihastate to broadly semihastate, the upper lobe 5–12(–18)mm long, 1–5(–7)mm wide, lower lobe 2–3(–6)mm long, fringed with simple white and golden hairs and glandular hairs, stipules lower down the plant much smaller. **Leaves** unijugate, petiole 5–15(–28)mm terminating in a simple or branched tendril; leaflets lanceolate to very narrowly elliptic, 12–50(–75)mm long and 1–4mm broad; grass green throughout when fresh, pilose-pubescent in young plants and young leaves of older plants, becoming sparsely pubescent with age.

Inflorescence solitary, or very rarely a 2-flowered raceme, with a slender peduncle subequal to twice as long as the leaflets of the subtending leaf. Floral bracts absent. **Flower(s)** c. 15mm long, borne on a 2–3mm terminal pedicel. Calyx campanulate, tube 2–4mm long, glabrous, pubescent or fringed with long hairs; calyx teeth equal, acute linear – lorate, 2–5mm long. Corolla pale lilac; banner darker (purple-red, with dark purple veins), obcordate, blade held erect, 10–12mm long, 13mm wide, with a deep apical notch, claw 3mm long; wings far exceeding the keel, blade 11mm long, 4mm wide with a basal pleated process, claw c. 3mm long; keel blade 6mm long, 4mm wide, claw 4mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube slightly oblique. Ovary glabrous; style spathulate, margins occasionally inrolling when dry, giving appearance of pubescence encircling the style; c.4mm long, with a simple stigma. **Fruits** 6–8-seeded, glabrous, with reticulate venation, red-brown, linear, 4–6 cm long and 4–5mm wide. Seeds not seen.

PHENOLOGY:

Flowering: August to November
Fruiting: November

DISTRIBUTION (FIG. 5.4):

Chile: from Región IV (Coquimbo); Región VII (Maule); to Concepción, Región VIII (Bío- Bío). In coastal mist forests and inland, as a reuderal in Mediterranean central Chile.

VERNACULAR NAMES:

Clarincito (Spanish).

DIAGNOSTIC NOTES:

This species is evidently morphologically similar to *L. pusillus*, but can be readily distinguished by its:

- Flowers almost always solitary, borne on a slender peduncle (generally paired flowers on crassulate peduncles in *L. pusillus*).
- Semihastate stipules
- Dense pubescence (larger specimens less so)

In northern Hemisphere herbaria, this species is known mostly from older collections. The much smaller *L. campestris* may be confused with small specimens of *L. berterianus*, but the latter has a glabous ovary, in contrast to the densely pubescent ovary of *L. campestris*. Nevertheless, these two species may prove to be closely allied.

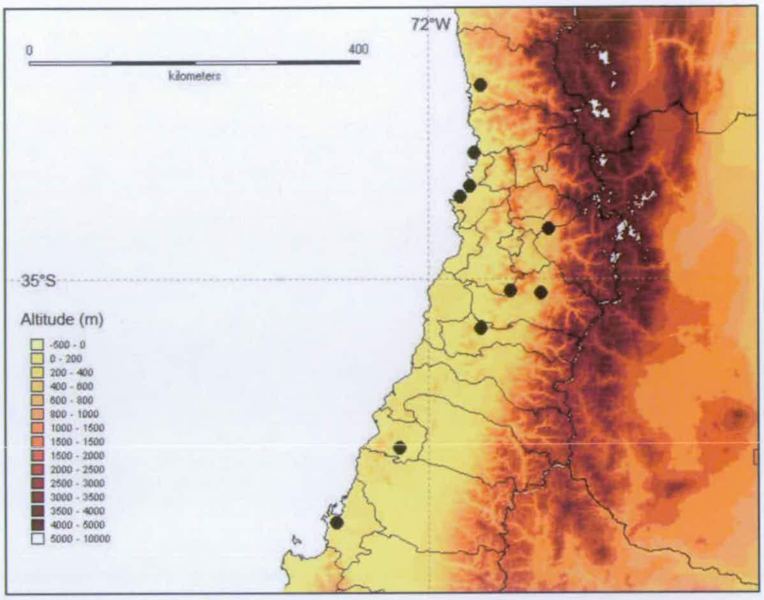


Figure 5.4 *L. berterianus*
This species is found in Chile, from Concepción north to Coquimbo.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Chile

REGIÓN IV (COQUIMBO): Prov. Petorca 1.3km north of the first (northernmost) road into Zapallar, on the road from Papudo, *Lammers 7704* (F); Depto. Illapel Cuesta de Cavilolen ca. 30km from Illapel to Los Vilos *Worth & Morrison 16459* (K)

REGIÓN V (VALPARAISO): Mont. La Leona, *Bertero 559* (BM, E, NY); Near Caucon, *Bridges 247* (E-GL); Prov. De Petorca Quebradas Aguas Claro 2km south of Cachagua, *Gardner & Knees 5961* (E); Concon, *Pöppig 193* (BM); El Saltio, *Skottsberg & Skottsberg 943* (F, NY)

REGIÓN (METROPOLITANA DE SANTIAGO): Santiago, Joséph *3415* (US).

REGIÓN VI (O'HIGGINS): Rancagua, Joséph *4374* (US).

REGIÓN VII (MAULE): Baths of Cauquenes, *Reed s.n.* (K).

REGIÓN VIII (BÍO-BÍO): Propè Concepción, *Macrae s.n.* (K).

UNKNOWN: *Cuming s.n.* (E); *Ex. Herb. Jullivant* (NY).

3. Lathyrus cabrerianus Burkart (1942), Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6:** 14. TYPE: ARGENTINA en la costa de Lago N.H. entre Bariloche y Pto. Moreno *Burkart 6253* (holotype SI!).

Perennial herb, not blackening on drying. Rhizomes woody, thickened, giving rise to many stems. Stems very vigorous, clambering over surrounding vegetation, to 5m, terete slightly ridged, without wings, or slightly winged (to 1.5mm) in the upper parts.

Sparsely lanulose-pubescent with white hairs interspersed with glandular hairs, more densely hairy on younger vegetative organs.

Stipules semisagittate, upper (primary) lobe ovate (6–)7–12(–18)mm long and 4–7(–11)mm broad, with acute lower lobe to 6mm long, broader in the upper portions of the plant. **Leaves** unijugate, terminating in a simple or branched tendril; leaflets with a pubescent petiolule; lanceolate to narrow ovate (4.5–)5–5.7(–7.5)cm long and 1–2(–2.9)cm broad. Rich dark green on both surfaces, upper surface glabrous or with very few hairs; undersides with prominent, parallel primary veins and sparse to dense pubescence.

Inflorescence a compact, domed raceme of 7–13 pleasantly scented flowers borne on a 7–15(–19)cm peduncle, the flower-bearing portion of the inflorescence rachis always shorter than the peduncle. Floral bracts absent. **Flowers** 25–30mm long, borne on 3–6mm pubescent pedicels. Calyx campanulate, tube c. 5–6mm long, densely lanulose-pubescent, often with many glandular hairs; teeth triangular-acuminate, lower calyx teeth 2–5mm, the upper slightly shorter. Corolla white when young, maturing to primrose yellow; banner blade orbiculate, held erect, 18mm long and 18mm wide, notched (to 1mm) at the apex, claw 6mm long; wing blade 14mm long, 8mm wide, with a basal pleated process, claw 11mm long; keel blade 11mm long, 6.5mm wide, claw 7mm long, fused along the entire length (including the claw) of the lower margin. Androecium diadelphous (9+1 stamens); staminal tube truncate. Ovary densely pubescent; style linear, 5–7mm long with simple stigma, pubescent on adaxial face. **Fruit** densely pubescent, rich red-brown, without woolly false septa, linear and slightly laterally compressed, 6–7 cm long and 7–9mm wide. Seeds 7–11 per pod, smooth, dark brown-black, subspherical, 3–4mm across, with hilum c. one fifth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Senn 1938 (as *L. dumetorum*); Seijo & Fernández, 2003)

PHENOLOGY:

Flowering: October to December.

Fruiting: Late December to January, dying back over winter.

DISTRIBUTION (FIG. 5.5):

Argentina – Neuquen, Río Negro. **Chile** – Región VIII (Bío-Bío), Región IX (Araucanía), Región X (Los Lagos).

In deciduous and mixed woodland – climbing over shrubs in light shade under, or at the edges of mixed forests.

DIAGNOSTIC NOTES:

Lathyrus cabrerianus is a distinct species, readily identified by its primrose yellow corollas. Where flowers are dried to yellow in older herbarium specimens confusion may be possible with *L. pubescens*. However, *L. cabrerianus* is generally a larger and more robust plant than *L. pubescens*; it has a simple (rather than bipartite) stigma and lacks woolly false septa between the seeds. In addition, *L. cabrerianus* has a more restricted distribution – it is found in Chile's Región VIII and southwards, and in neighbouring areas of Argentina. *Lathyrus pubescens* has a more northerly and easterly distribution in Mediterranean climates of Región V and northwards in Chile, and in Buenos Aires province and northwards in Argentina.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

NEUQUEN: Dep. Los Lagos. Lago Correntoso. Bajo bosque de Austrocedrus chilensis, *Seijo 1604* (F, NY).

RÍO NEGRO: Los Lagos Loc. Villa La Angostura, Camino de acceso a Lago chilensis, *Seijo 2107* (K, NY).

Chile

REGIÓN VIII (BÍO-BÍO): Lota, *Brooke 6961* (BM); Concepción, *Cuming 136* [BM – on same sheet as Cuming 484 (*L. pubescens*); K – on same sheet as *Cuming 268* (*L. subandinus*)], Near Concepción alt. 400ft., *Elliott 572* (E, K).

REGIÓN IX (ARAUCANÍA): Woods near Valdivia, *Bridges 673* (BM, E - 2 sheets); Lallauquén [Calafquén] alt. 1500ft., *Comber 1009* (E); Maquehue [Maquegua] Temuco, *Collector unknown* (BM).

REGIÓN X (LOS LAGOS): Panguipulli, Jos*éph 2417* (US); Corral, *Reed 68* (BM); Chiloe, *Reed s.n.* (K – on same sheet as *Williams Andrews s.n.*)

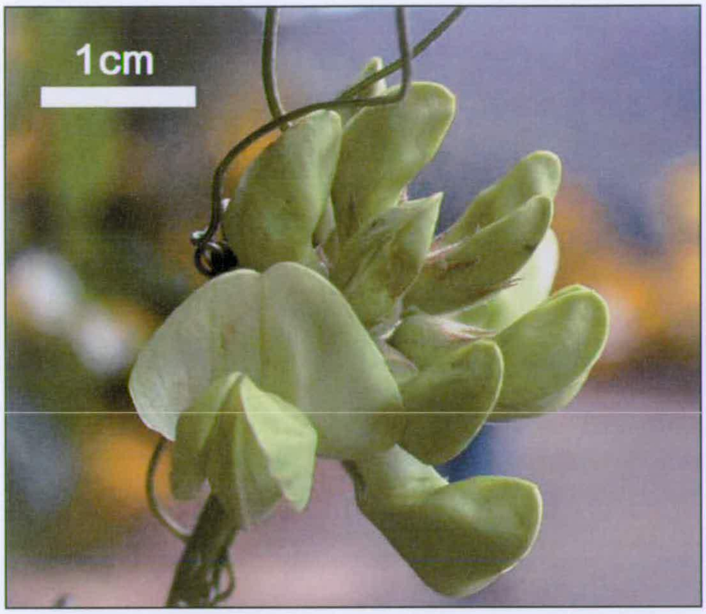
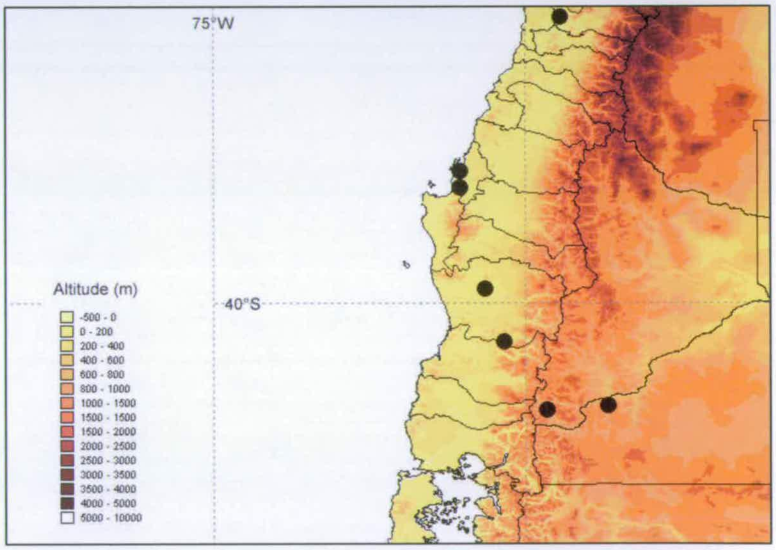


Figure 5.5 *L. cabrerianus*

(Above) Inflorescence

(Top right) Habit (to 5m)

(Right) This species is found in the Valdivian forest zone and other temperate woodlands of Chile and Argentina



4. Lathyrus campestris Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 626. *Lathyrus debilis Clos* var. *campestris* (Philippi) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 201 TYPE: CHILE: Valdivia in Pascuis prope. Valdivia *Philippi 1134* (lectotype, here designated: SGO!; isolectotype: SI!; Photograph: F!, NY!)

Lathyrus gracillimus Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. P.198 TYPE: CHILE: Constitución X 94 *Reiche s.n.* (lectotype, here designated: SGO!, isolectotype SI!)

Lathyrus lancifolius Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 198. TYPE: CHILE: Concepción *Reiche s.n.* (type not present in SGO or SI – may be housed in Concepción de Chile CONC)

Annual herb, not blackening on drying. Roots delicate. Stems very slender, to 10(–30)cm, unwinged. Lanulose-pubescent throughout, with white and golden hairs. Smaller plants and younger organs more densely pubescent than larger (or older) ones.

Stipules semihastate, upper lobe 3–7(–12)mm long, 1–3(–5)mm wide, lower lobe 2–4mm long, fringed with simple white and golden hairs and glandular hairs. **Leaves** unijugate, petiole 1–5mm terminating in an arista or feeble, simple tendril; leaflets linear to lorate, 9–17(–28)mm long and 1–3mm broad.

Inflorescence with a slender peduncle shorter than the leaflet of the subtending leaf (<3cm), with a single flower. Floral bracts absent. **Flowers** small, c. 10mm long, borne on a 2–3mm terminal pedicel. Calyx campanulate, tube 2–3mm long, densely pubescent; calyx teeth equal, lorate-acute, 2–4mm long. Corolla blue, material for dissection not available. Androecium diadelphous (9+1 stamens); staminal tube truncate at apex. Ovary pubescent; style not seen. **Fruits** not seen at full maturity.

PHENOLOGY:

Flowering: November

Fruiting: November to December? (fully mature fruits not seen)

DISTRIBUTION:

Chile: from Región V (Valparaíso) to Región VI (O'Higgins).

In areas of coastal mist forest – habitats similar to *L. berterianus*.

DIAGNOSTIC NOTES:

Lathyrus campestris shares a similar distribution and many characters with *L. berterianus* (e.g. annual habit, solitary flowers, equal calyx teeth). However, *L. campestris* can be readily distinguished by its pubescent ovary. In addition, it is generally more densely pubescent and smaller in habit (5-10cm high, although see the note on types below). Its range appears to be more limited than that of *L. berterianus*. *Lathyrus campestris* is restricted to Regións V and VI of Chile, while *L. berterianus* spreads further south.

Most collections in Chilean and northern hemisphere herbaria are old. The current conservation status of the species is uncertain and the plant may be severely endangered, extinct, or merely overlooked by collectors.

TYPES:

Philippi's syntype collections in SGO consist of two specimens – one is c. 30cm in length (height) and the other is less than 10cm in height. The Darwinion (SI) duplicate and the photographs of the Berlin specimens (in F and NY) agree with the taller specimen and the protologue describes the plant as having a c. 30cm stem (*caulis pedalis*). Consequently this specimen was selected as the lectotype. It should be noted that this collection appears to be an exceptionally tall specimen because others commonly seen in herbaria are less than 10 cm in height.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Chile

REGIÓN V (VALPARÁISO): Near Caucon *Bridges 250* (E-GL, K); Propè Valparaiso, *Cuming 726* (E-GL, K); Valparaiso, *King s.n.* (K)
REGIÓN VI (O'HIGGINS): Prov. Colchagua, *Bridges 178* (NY)
UNKNOWN: *Bridges s.n.* (K); *Cruickshanks 31* (K); *Philippi s.n.* (BM)

5. Lathyrus elegans Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 30.
TYPE: Uruguay? Montevideo, *Sello s.n.* (Type not seen)

Perennial vine-like herb, not drying black. Rhizomes woody, thickened, giving rise to several unwingesd stems, seldom branching above ground. Stems robust to very robust and near-woody to 8mm diameter, clambering, to 4m. Glabrous and somewhat glaucous throughout.

Stipules large, semisagittate to unequal hastate-auriculate, the upper lobe lanceolate to ovate, 2–3.8cm long and 1.2–1.9cm broad, primary lower lobe deltoid, rounded to acute at the apex, secondary lower lobe an acute tooth. **Leaves** unijugate, sessile or with petioles to 4(–7)mm long terminating in a robust, branched tendril; leaflets borne on a short (1mm), pubescent petiolule; upper surface grass green when fresh, drying dull khaki, lower surface grey-green when dry, thickly glaucous and greasy to the touch, both surfaces glabrous; reticulate venation conspicuous on the undersides of the leaflets between primary veins, and with a prominent reinforcing vein running round the margin; elliptic-lanceolate to ovate, (5.3–)6–8.5cm long and 1.4–3(–4)cm broad, (length:width ratio c. 1.2–4).

Inflorescence at least as long as the leaflet of the subtending leaf, with a raceme of 11–20 flowers borne on a robust, erect or slender, curved peduncle. Floral bracts absent. **Flowers** 11–15mm long, somewhat pendent, borne on glabrous pedicels to 10mm long. Calyx campanulate, tube c. 5mm long; totally glabrous, upper teeth bluntly deltoid, c.1mm long, the lower teeth longer (to 4mm), but seldom longer than the calyx tube, linear-acute. Corolla probably blue *in vivo* (based on dried specimens, which retain blue petals), banner broadly obovate, blade 10mm long and 11mm wide, with slight apical notch, claw 5mm long; wing blade 9mm long, 6mm wide with a basal pleated process, claw c. 5mm long; keel blade 10mm long, 5mm wide, claw 7mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube rounded-oblique at apex. Ovary glabrous; style, 5–7mm long, with simple stigma. **Fruits** glabrous, chestnut-brown, linear, 6–7cm long and 6–8mm wide. Seeds 10–14 per pod, smooth, mottled dark brown, 2–3mm across, hilum not seen.

PHENOLOGY:

Flowering: September to November

Fruiting: October to December

DISTRIBUTION (FIG. 5.6):

Brazil – PARANÁ.

Climbing over vegetation at the margins of subtropical forests, in moist clay soils.

DIAGNOSTIC NOTES:

Lathyrus elegans is morphologically similar to *L. nervosus* and *L. paraguariensis*, Differences are summarised in the following table:

	L. nervosus	***L. elegans***	***L. paraguariensis***
Leaflet shape	Suborbiculate to wide-elliptic (L:W ratio 1.2–4)	Lanceolate (L:W ratio 1.4–4)	Very narrow elliptic-lanceolate (L:W ratio 10+)
Leaflet apex	Acute	Rounded	Acute
No. flowers	Flowers 3–7(–9)	Flowers 11–20	Flowers 16–30
Lowest calyx tooth	Subulate, exceeding length of calyx tube	Deltoid – acuminate deltoid subequal to calyx tube	Deltoid, equal to calyx tube
Fruit septation	Often with woolly false septa	Without woolly false septa	Without woolly false septa
Habitat & Distribution	Widespread - from Mediterranean scrub and coastal dune slacks from S. Brazil, Uruguay, Argentina to Tierra del Fuego, and extreme S. Chile.	Moist subtropical forests and forest margins, Brazil, N. Argentina & N. Uruguay.	Open subtropical forests and forest margins in Argentina (Misiones province), Paraguay and S. Brazil.

Lathyrus elegans might also be confused with *L. hasslerianus* and *L. woodii*, but both of the latter are relatively delicate, with slender stems, more or less petiolate leaves and thin leaflets that become membranaceous when dried. *Lathyrus elegans* is far more robust, with near-sessile leaves and thick, slightly succulent leaflets. They can be further distinguished as *L. hasslerianus* has yellow-orange corollas (blue in *L. elegans*) and *L. woodii* is pubescent on at least the calyces (*L. elegans* is glabrous throughout).

TYPES:

I have not seen any Sello collections of *L. elegans*, the Berlin type having been destroyed in Berlin during the Second World War. A potential lectotype specimen may exist in another herbarium, but was not located for this account.

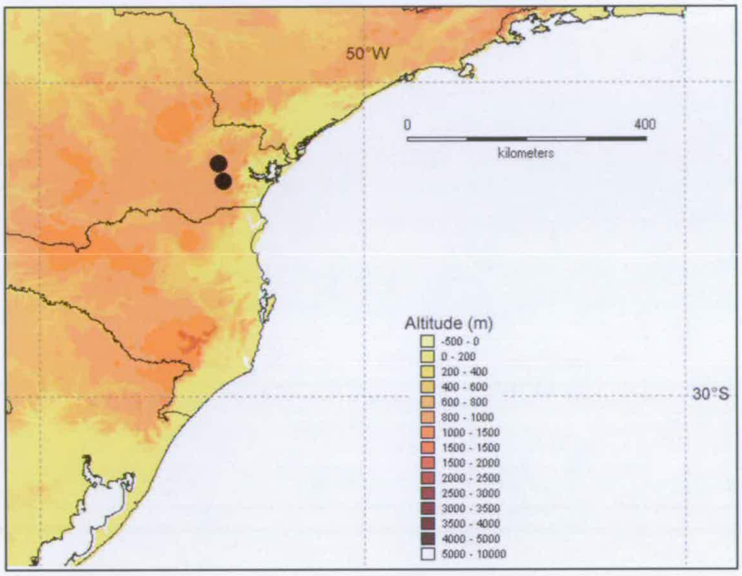


Figure 5.6 ***L. elegans***
This species is found in Paraná, Brazil.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Brazil

PARANÁ:

Pinhães, *Dusén 936a* (F); Pinhães, *Dusén 13360* (BM, K); Pinhães, alt. 885m, *Dusén 15815* (F); Pinhães, *Dusén 7081* (E, NY); San José do Pinhães, Roseira, *Hatschbach 8553* (US).

6. Lathyrus hasslerianus Burkart (1937) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p. 100. TYPE: ARGENTINA Misiones, Arroyo Macaco, San Pedro, en rozadas de los Indios en las cabeceras del Río Yabotí-Guazú, *Niederlein 750* (holotype BA!, isotype SI!)

Perennial herbaceous vine, not blackening on drying. Rhizomes woody, perennating, with several stems arising from the rhizome. Stems slender, branching, climbing, to 3m, quadrangular, unwinged, with prominent ridges on the angles, glabrous throughout

Stipules semisagittate, rarely sagittate (in which case with only a very short second lower lobe), rotund to ovate with entire margin, upper lobe 9–15(–18)mm long and 7–15mm broad, lower lobe deltoid, 2–4(–9)mm long. **Leaves** unijugate, terminating in a branched, very fine tendril; petioles unwinged, 6–15(–25)mm long; leaflets borne on a 1–2mm, glabrous petiolule; upper surface bright green when fresh, underside grey-green (glaucous) and remaining so on drying, both surfaces usually glabrous, but undersides sometimes villous, reticulate-veined, with parallel primary veins on the underside, oval to elliptic-lanceolate, 3–5.5cm long and 1–2.5(–3.3)cm broad.

Inflorescence a raceme of 10–17 flowers, at least twice as long as the leaflets of the subtending leaf (peduncle and rachis 3–5cm each, usually equal). Floral bracts absent, or reduced to a minute raised area of tissue. **Flowers** small, 14–17mm long, borne on 3–6mm, slender pedicels, readily caducous (e.g. in rain), somewhat pendulous. Calyx campanulate, tube 5–7mm long, glabrous; calyx teeth acute, slightly unequal; lower teeth ca. 2–3mm long, the upper shorter. Corolla white when young, maturing through golden yellow to orange-brown, somewhat waxy when fresh; banner obovate, blade held erect, 8mm long and 9mm wide, with no apical notch, claw 7mm long; wing blade 8mm long, 4mm wide with a shallow basal pleated process, claw c. 7mm long; keel blade 7mm long, 3.5mm wide, claw 6mm, keel fused along the entire length of the lower margin (including the claw); wings and keel strongly upcurved towards the blade of the banner. Androecium diadelphous (9+1 stamens), staminal tube truncate at apex. Ovary glabrous, or very rarely with very few scattered hairs; style linear 4–6mm, with a simple, domed stigma. **Fruits** 7–9-seeded, glabrous, red-brown, appearing stipitate when calyces senesce, 6–7cm long and 7–8mm wide, with prominent veins on the surface. Valves contracting around seeds when dry, giving a nodose appearance. Interior of fruits with woolly false septa. Seeds dull brown, drying black, lenticular, c. 4mm across.

CHROMOSOME NUMBER: 2n=14. (Seijo & Fernández, 2003)

PHENOLOGY:

Flowering October to December

Fruiting late December to January

DISTRIBUTION (FIG. 5.7):

Argentina – Misiones; **Brazil** – Minas Gerais, Paraná, São Paulo

At the margins of dense subtropical forest, by creek banks and roadsides.

DIAGNOSTIC NOTES:

This species is readily distinguished from all other members of sect. Notolathyrus by the inflorescences with many (10 – 17) relatively small (14 –17mm total length) flowers that are white, maturing through yellow to orange-brown.

Non-flowering specimens may be confused with *Lathyrus elegans*, but *L. hasslerianus* is less robust, and can also be distinguished by the consistently petiolate leaves (petioles >5mm), and more feeble leaflets. This species is also similar to *L. woodii*, although the latter species has blue flowers.

The inflorescence type is unique in South American species of *Lathyrus*, but is very similar to that seen in *Lathyrus sulphureus* and *Lathyrus ochroleucus*, from North America, *Lathyrus davidii* (East Asia) and the West Eurasian members of Bässler's (1966) *Lathyrus* series *Lutei*. These species are evidently only distantly related (chapter 4, this thesis), suggesting that the profuse, yellow flowered inflorescence structure has evolved independently many times, perhaps in response to selection pressure from pollinators.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

MISIONES: Dep. San Pedro, Ruta Provincial No 15. Arroyo Tambero, en borde arroyo, *Seijo 2000* (NY); Dep. Guarani Predio IPS, cabacera norte, arroyo "Tambero", puente sobre ruta 15, borde de arroyo, *Keller 91* (F, NY).

Brazil

MINAS GERAÏS: Ad Caldas in Minas Geraes *Ex. herb. Regnelli Ser. III Ino. 435* (K, US).

PARANÁ: Río Despedida (Mun. Laranjeiras do Sul), *Hatschbach 19854* (NY); Rod. Do Xisto, Río Barigui (Mun. Curitiba) Paraná, *Hatschbach 18232* (F); Bank of Río dos Indios 15km NW. of Ivaí, *Lindeman & Haas 2718* (K, NY, US); S.E. of Campo Novo, ca. 50km W. of Laranjeiras do Sul. Creek Bank, *Lindeman & Haas 2910* (F).
SAO PAULO: Rodovia Piedade-Tapirai. Km 114, *Leitão Filho 1083* (NY).

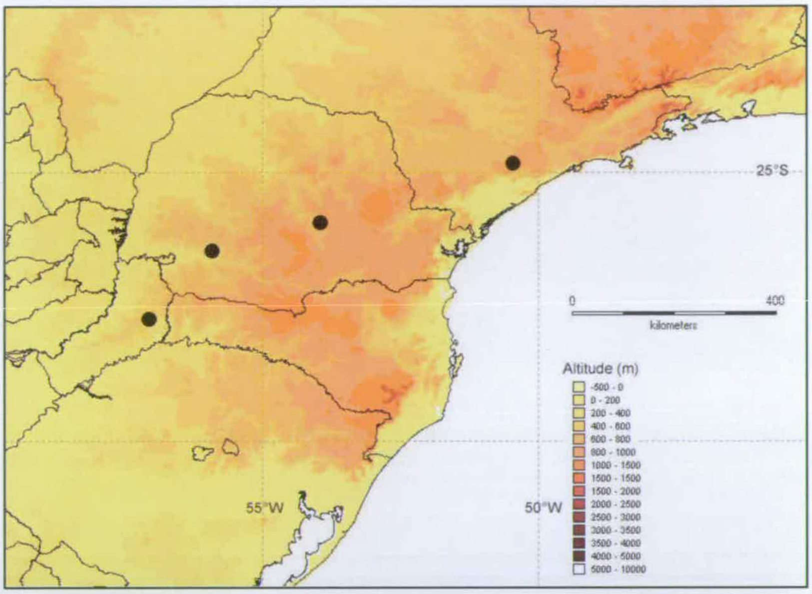
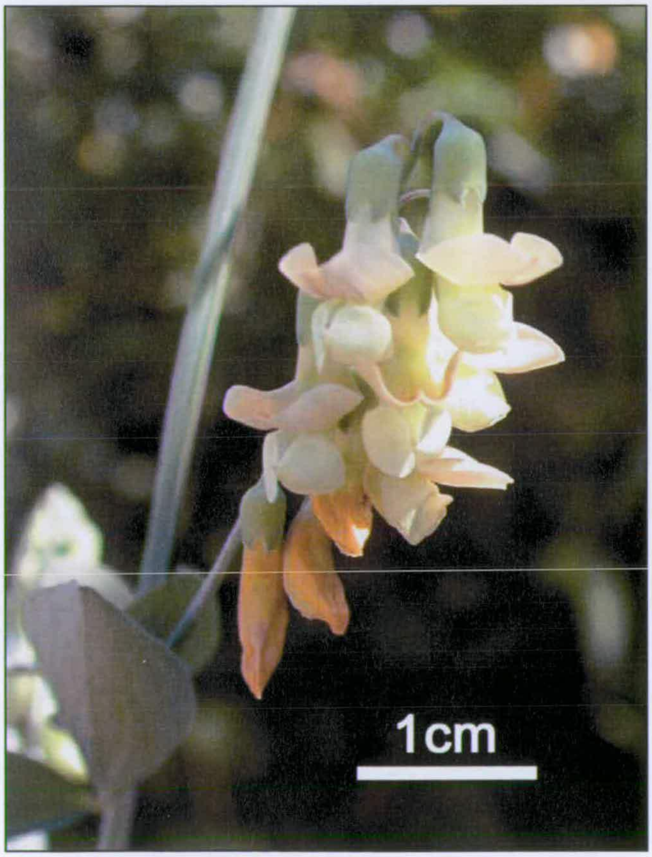


Figure 5.7 ***L. hasslerianus*** This species is found in Misones province, Argentina and in Minas Geraïs, Paraná and Sao Paulo states, Brazil.

(Below) Inflorescence

(Below right) Glaucescent foliage and scrambling habit.



7. Lathyrus linearifolius Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 28.
TYPE: URUGUAY. Sello s.n. (lectotype, here designated: K!; isolectotypes E!, F!)

Perennial herb, not blackening on drying. Rhizomes woody, running, bearing numerous stems. Stems branching at the base (often underground), erect, to 90cm, terete, without wings. Glabrous on lower portions of the plant, becoming more pubescent towards the top of the plant and younger vegetative tissues; hairs both simple and glandular.

Stipules small, linear-subulate, simple without lower lobe (i.e. not semisagittate or sagittate), 5–7mm long and 1–2mm wide. **Leaves** unijugate, terminating in an arista or rarely a short (c. 3cm), simple tendril; leaflets borne on short 2–5mm petiole, sparsely pubescent on both surfaces, linear, (7–)8.8–14cm long and 1–3(–5)mm broad.

Inflorescence longer than the leaflets of the subtending leaf, with a raceme of 8–20 lilac coloured flowers borne on a robust, erect peduncle 8–14cm long, pubescent throughout. Floral bracts absent. **Flowers** 10–14mm long, borne on c. 2mm, pubescent pedicels, held somewhat erect. Calyx blunt-campanulate, tube 3–4mm long, pubescent with simple and glandular hairs; lower calyx teeth acute, 2–3mm long, the upper deltoid, to 2mm long. Corolla pale lilac-blue, banner blade held erect, orbicular, 8mm long and 10mm wide, with no apical notch, claw 3mm long; wing blade 7mm long, 4mm wide with a basal pleated process, claw c. 5mm long; keel blade 8mm long, 4mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube truncate at apex. Ovary densely appressed-tomentose with golden hairs; style c. 5mm long, slightly spathulate at apex, with a bipartite stigma, the fertile portions of the stigma held apart from one another on short flaps. **Fruits** pubescent, c. 5–7-seeded chestnut-brown, linear, c. 5.5cm long and 4–7mm broad, with woolly false septa between the seeds. Seeds smooth, dark brown to black, 2–3mm across, ellipsoid, with hilum c. one eighth to one tenth of the circumference.

PHENOLOGY:

Flowering: November to January
Fruiting: December to January
Dying back in the dry season.

DISTRIBUTION (FIG. 5.8):

Brazil – Paraná, Río Grande do Sul; **Uruguay**.
In meadows dominated by tall grasses.

DIAGNOSTIC NOTES:

Lathyrus linearifolius is readily distinguished from all other taxa of sect. Notolathyrus by its slender, linear leaflets, reduced tendrils and simple, subulate stipules (i.e. not sagittate, and thus without a basal lobe). It appears most closely allied to *L. nitens* and *L. acutifolius*, particularly in the running habit and all characters of the inflorescence. However, *L. nitens* can be distinguished by its shorter and broader leaflets, with a rounded apex. In *L. acutifolius* the stems are at least slightly winged, the stipules have a basal spur (i.e. are semisagittate) and leaflets are typically greater than 5mm wide. Differences are summarised under the description for *L. acutifolius*.

Some specimens of the linear-leafleted form of *L. macropus* have been mistakenly determined as *L. linearifolius* but these are sprawling plants of the Argentinean and Chilean Andes and Cordillera de Córdoba, that consistently have multiple (usually three or more) pairs of leaflets per leaf.

TYPES:

At least three of Sello's original collections remain, despite the loss of the complete Berlin collection in World War II. Those held in Kew and Edinburgh are poor quality stems, although both retain leaves, stipules and the wingless stems necessary for diagnosis. The Kew specimen bears a later amendment in pencil: 'Uruguay'. This is probably taken from the original description, in which Vogel (1839) suggests the plant was collected: *in Montevideo*? The third remaining Sello duplicate is held in

Chicago (F) and is a capsule containing a few flowers accompanied by an early 20th century photograph of a Berlin Sello specimen. New York (NY!) also holds a photograph of the same Berlin specimen.

I have selected the Kew specimen as the lectotype as it is in marginally better condition (the capsule contains more complete flowers). In addition, the lectotypes of *L. nitens* and *L. acutifolius* are held at Kew, perhaps affording a more convenient comparison for future researchers. Other potential isolectotype specimens may exist in other herbaria, as Sello's collections were widely distributed.

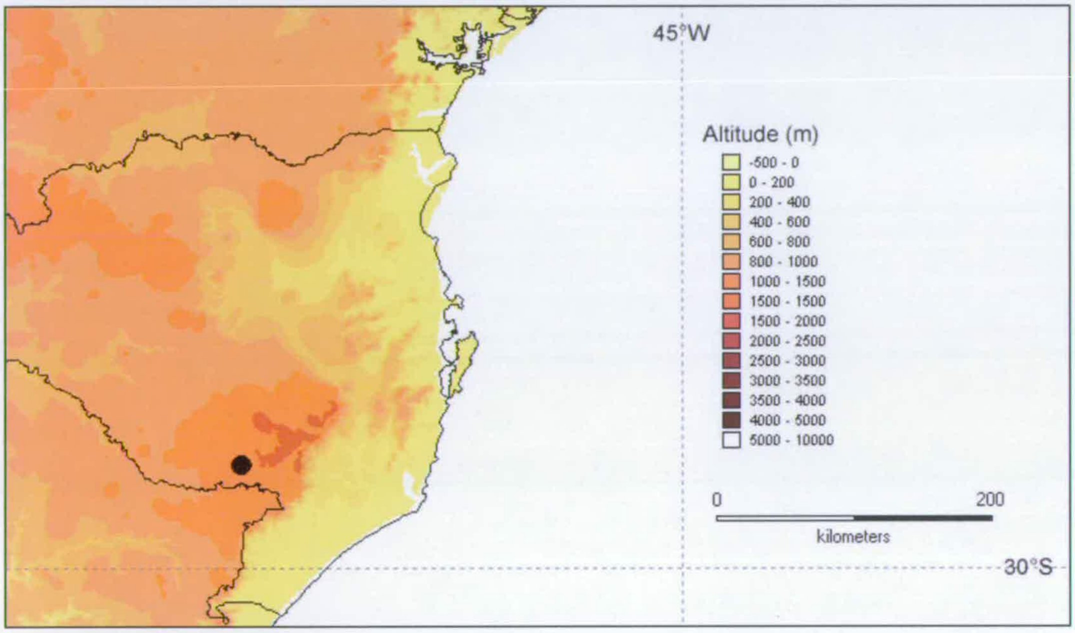


Figure 5.8 ***L. Linearifolius*** This species is found in Paraná, Río Grande do Sul and Santa Catarina states in Brazil.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Brazil

PARANÁ: S. Agostinho (mun. Palmas), *Hatschbach 15423* (F – 2 sheets, K, NY, US).
RÍO GRANDE DO SUL: Mun. Bom Jesus, Rodovia Bom Jesus - São Joaquim, descida ao Río Pelotas alt. 850-900m, *Hatschbach et al., 72660* (K); Entre Taimbezinho e Cambará do Sul-a 2km de Cambará, *Oliveira 458* (F!); Fazenda, B. Velho, Bom Jesus, *Rambo 35029* (NY!).
SANTA CATARINA: Fazenda, B. Velho, Bom Jesus (28°22'42"S, 49°56'12"W) alt. 1450m *Miotto 2223* (E).

8. Lathyrus lomanus Johnston (1938) *Journal of the Arnold Arboretum*. **19**: 250.
Type: Chile: Aguada de Panul, dept. Taltal, trailing over the rocks in steep gulch quebrada above water hole, ca. lat 24°47′S Dec. 4 1925, *Ivan M. Johnston 5430* (holotype NY!).

Perennial herb not blackening on drying. Rhizomes slightly thickened (c.7mm diameter), woody, running. Stems prostrate, to c.1m long, unwinged. Plant sparsely pubescent on mature vegetative organs, lanulose pubescent on young structures, and reproductive organs.

Stipules large, hastate, the upper lobe broadly deltoid, 1.8–2.7cm long and 1.3–2cm broad, lower lobes deltoid, deeply incised, making the base of the stipule appear deeply, dentate 0.8–1.2cm long and 0.6–0.9cm broad.

Leaves unijugate, petioles 20-30mm long, terminating in a short, branching tendril; leaflets borne on a short (1mm), pubescent petiolule, green, tinged with purple, upper surface glabrous, drying dark olive, lower surface lanulose-pubescent on young leaves, less so on older ones, drying brown; primary veins and reticulating veinlets conspicuous on the undersides of the leaflets, ovate to narrow-ovate, pinnately veined, 5–6.5cm long and 2.5–3.5cm broad, apex rounded, shortly-mucronate.

Inflorescence a raceme of 7–11 flowers borne on a robust, erect peduncle at least three times as long as the leaflets of the subtending leaf. Floral bracts absent.

Flowers c. 18mm long, borne on c. 5mm, pubescent pedicels, held horizontally (at 90° to the main inflorescence axis). Calyx campanulate, tube c. 3mm long, densely lanulose-pubescent, teeth linear, the lower teeth c. 6mm long, the upper slightly shorter. Corolla purple, dissected flowers not seen. Androecium diadelphous (9+1 stamens), fused into a tube, the uppermost free from the remainder; staminal tube oblique.

Ovary densely pubescent, except at the tip; style broadening towards the tip, 4-5mm long with a simple stigma. **Fruits** not seen at maturity, submature fruits pubescent, rich brown, broadening slightly at the apex, to 5.5 cm long and 6mm wide, c. 10-seeded, seeds not seen.

PHENOLOGY:

Flowering: November to December.

Fruiting: late December to January?

DISTRIBUTION:

Chile Región II Antofagasta: Aguada de Panul.

DIAGNOSTIC NOTES:

Known only from the type collection, *Lathyrus lomanus* is perhaps most similar to *L. cabrerianus* in overall appearance, but can be distinguished on the basis of its purple corollas (primrose yellow in *L. cabrerianus*) and its more northerly distribution. Johnston indicates in the protologue that the leaflets are tinged purple – a character never seen in *L. cabrerianus*. This species also shows similarities to *L. tropicalandinus* although the flowers are held more erect and the whole plant is more robust, but compact. *Lathyrus lomanus* is evidently a handsome plant and further investigations of the type locality would be very welcome. If new collections could be made, molecular investigation would also be very helpful to determine its affinities with other taxa in the section.

9. Lathyrus macropus Gillies in Hooker W.J. & Arnott G.A.W (1833) Contributions towards a flora of South America and the islands of the Pacific. Botanical Miscellany III John Murray, London. p.198. TYPE: ARGENTINA: On the Andes of Mendoza, *Gillies s.n.* (lectoype, designated here K!, isolectotypes E! – 3 sheets).

Perennial herb, not blackening on drying. Rhizomes woody, thickened, giving rise to many robust, decumbent stems. Stems zig-zagging, erecto-patent, to 120cm, terete, with 2 prominent ridges, sparsely pubescent or occasionally glabrous lower down the plant.

Stipules semisagittate, the upper lobe linear, acute (6–)11–19mm long and 2–4mm wide, the lower lobe subulate, 3–7mm long; narrower in the upper portions of the plant and in plants with narrow leaflets. **Leaves** (2–)3–5 jugate with robust petiole, dorsally compressed triangular in cross section and slightly winged rachis, terminating in a simple or branching tendril; leaflets borne on a short (1mm), pubescent petiolule; upper surface grass green when fresh, glabrous or rarely sparsely pubescent, lower surface grey-green, glaucous, sparsely to densely pubescent with simple, straight or crinkled white hairs; primary veins parallel, conspicuous on the undersides of the leaflets, and also on the upper sides in dry specimens, lanceolate to linear, apex rounded, with a 2mm mucro, (5.5–)6–10(–13)cm long and (1.5–)5–13(–16)mm broad.

Inflorescence at least as long as the leaflets of the subtending leaf, with a raceme of 7–15(–20) flowers, sometimes arranged in pseudo-verticils up the infloresence rachis, borne on a robust, erect peduncle to 25cm; peduncles pubescent, with simple, straight or crinkled white hairs, often interspersed with glandular hairs; floral bracts absent. **Flowers** fragrant, 15–18(–22)mm long, borne on 2–3(–5)mm pubescent pedicels, held horizontally, or somewhat erect. Calyx bluntly campanulate, tube 4–6mm long, lanulose-pubescent; calyx teeth unequal: the lower acute, 4–5mm long, the upper bluntly triangular, incurved c. 2mm long. Corolla lilac to violet, often with lighter, sometimes white, wings and keel; banner blade held erect, orbicular, 15mm long and 18mm wide, with an apical notch (c.2mm), claw 6mm long; wing blade 11mm long, 6mm wide with a basal pleated process, claw c. 11mm long, slightly curved; keel blade 9mm long, 5mm wide, claw 7mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube truncate or slightly oblique at apex. Ovary densely pubescent; style c. 4-5mm long, spathulate, with a bipartite stigma, the two stigmatic lobes often curling inwards when dry. **Fruits** pubescent, red-brown, c. 10–13-seeded, linear-trapezoid, broadening towards the apex, 5–6.5cm long and c. 5–8mm wide, with or without woolly false septa between seeds. Seeds smooth, dark brown, somewhat ellipsoid, c. 4mm long and 2–3mm wide, with hilum less than one tenth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Senn 1938; Seijo & Fernández, 2003)

PHENOLOGY:

Flowering: (October) November to January (April)
Fruiting: December to February.

DISTRIBUTION (FIG. 5.9):

Argentina – Central and southern Andes of Argentina and associated outlying mountain ranges (Sierras de Córdoba). Catamarca, La Ríoja, Mendoza, Córdoba, San Luis and Tucuman provinces. One specimen seen from Salta province; **Chile** – A single record from Maule region.

On mountain slopes at 1500 – 3000m, on gravely soil in full sun. *Lathyrus macropus* can grow in extensive stands, but is very susceptible to grazing by livestock, so when growing near habitation it is often found only in relatively inaccessible areas such as gulleys.

VERNACULAR NAMES:

Agua de nieve (Spanish)

DIAGNOSTIC NOTES (FIG. 5.10):

This species is readily identified by the lanceolate to linear leaflets on multijugate leaves, and by its southern montane distribution (typically above 1500m).

There is considerable variation in leaflet width and a plant may have narrow, broad, intermediate or a combination of leaflet types. In plants with extremely narrow leaflets (<5mm wide), the calyx teeth are often relatively long and fine (>10mm long, <1mm wide) and the upper surfaces of the leaflets are consistently glabrous. The majority of the narrow-leafleted specimens come from the area around the Sierra de Córdoba (Córdoba and San Luis Provinces). Andean specimens from Mendoza, San Juan, Catamarca and Tucumán provinces typically have broader leaflets.

Some herbarium specimens with narrow leaflets previously have been identified as *L. linearifolius* Vogel, a misidentification perpetuated by Grisebach (1874). *Lathyrus linearifolius* is a lowland species from southern Brazil and Uruguay and has only one pair of leaflets per leaf.

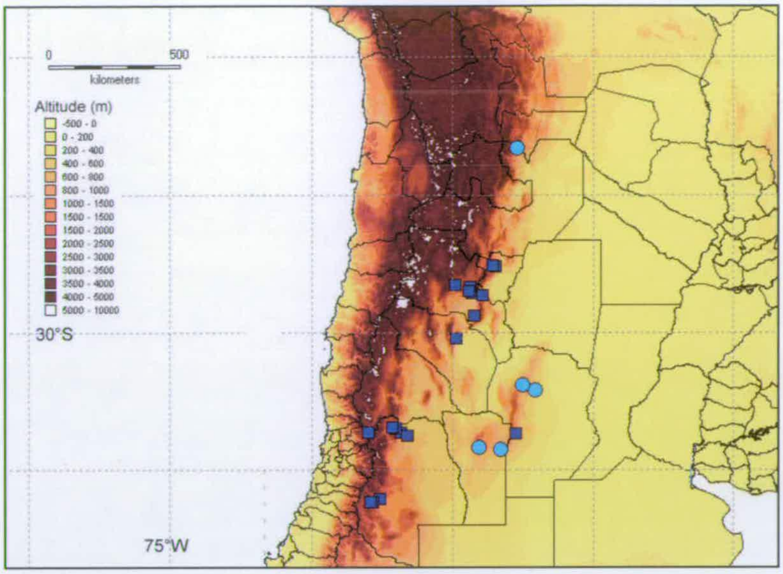


Figure 5.9 ***L. macropus***

(Above) The species is distributed in the Southern Andes, in central western Argentina.

Squares show localities for specimens with broad leaflets.

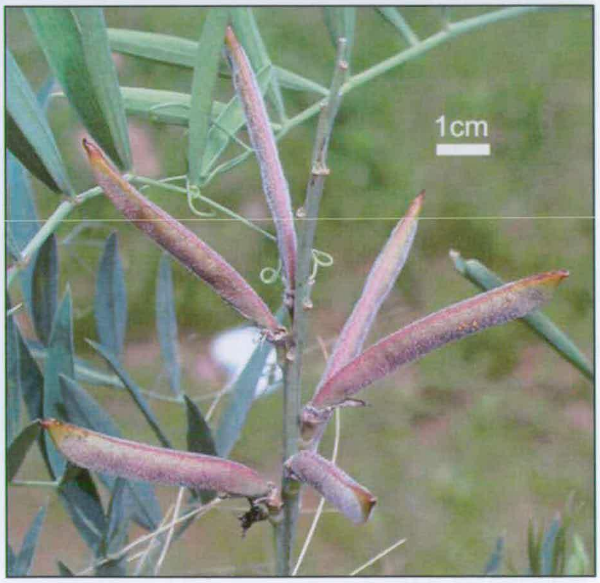
Circles show localities for specimens with narrow leaflets.

Figure 5.10 ***L. macropus***

(Right) Multijugate leaves

(Below right) Fruits

(Below) Raceme



SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

CATAMARCA: Pomán Sierra de Ambato (Falda O.): Subiendo desde El Rincón hacia Las Casitas, Rumbo al Cerro Manchado, *Hunziker & Ariza 20539* (F); Andalgala, *Jörgensen 1124* (NY) Río Alumbrara, *Riggs 104* (F); Sierras de Narvaez: Los Narvaes, *Kiesling 1105* (F, US); Belén, Las Mansas, *Schreiter 68580* (F); Belén, Las Faldas (Sierra de Belén), *Schreiter 68528* (F); Andalgala Alto de las Juntas, en la barranca del camino, *Sleumer 2117* (US); Andalgala Choya - El Tofo, submont., *Sparre 1005* (K); Andalgala Capillatas, Cerro La Negrilla, dry slopes, *Wall s.n.* (NY) Andalgala Choya - El Tofo, *Wipipi? 1085* (K).
CÓRDOBA: Punilla, Sierra Chica: Cerro Uritorco, frente a Capilla del Monte, *Hunziker 8546* (NY); Punilla Sierra Chica: Cerro Uritorco, falda occidental, *Hunziker & Cocucci 17705* (F, NY); Río Cuarto Entre Alpa Corral y Gigena, *Hunziker, Subils & Anton 24457* (F); In der Ungebung der Cuesta de Arjel, Sierra Grande (Arhala) de Córdoba, *Hieronymus 327* (K); *Lossen 20* (F); Punilla Near Los Cocos, *Pedersen 9956* (K).
LA RÍOJA: Capital Mina el Cantadero, *Meyer 3961* (F).
MENDOZA: Neighbourhood of Lago El Sosneado at the Hotel, Estancia El Sosneado, *Bartlett 19491* (F); Quebrada del Toro between Mendoza and Upsallata, *Beetle 584* (NY); Las Heras, Quebra de Bueyes, *King 98* (BM); Cordillera de Mendoza (Río salado sup.) Arroyo Alverja, *Kurtz 7134* (NY); Cord. De Mendoza (Río Salado sup.) Los Molles, *Kurtz 7494* (NY); Cordillera of Mendoza Villa Vicencio, *Miers s.n.* (BM); Malargüe 5km antes de Los Molles, camino de tierra sobre costa N. del arroyo Salado. En ladera de montaña, sobre curso de agua, *Seijo 1732* (F, K, NY); Bet. Villavicencia and Upsallata. Dry shaly rocks, *Senn 4450* (NY).
SALTA: Candado *Bruch s.n.* (NY).
SAN LUIS: [Las] Barranquitas, *Presented by Mr John Miers s.n.* (K); Colonel Pringles Cerro Inti Huasi. En cascada sobre ladera norte, *Seijo 1820* (K, NY).
TUCUMÁN Tafi Ancajulio: Las Arquitas, *Olea 48* (NY); Sauce Yacu, *White 26* (BM).

Chile

REGIÓN VII MAULE: Below Hornillas, *Cruickshanks 91* (K).

10. Lathyrus macrostachys Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 23. TYPE: Uruguay? Montevideo, *Sello s.n.* – Berlin type destroyed, potential lectotype not located (See notes below).

Lathyrus magellanicus Lamarck β var. *subsessilifolius* Kuntze (1898) *Revisio Generum Plantarum III*. London, Dulaud & Co. p.65 TYPE: PARAGUAY: Süd Paraguay, IX 92 *Kuntze s.n.* (holotype: NY)

Perennial herb, blackening on drying, often to jet black. Rhizomes woody, creeping. Stems prostrate to ascending to 150cm, winged, with wings to 3mm broad. Glabrous throughout.

Stipules large, unequal-sagittate, occasionally auriculate, the primary (upper) lobe lanceolate, 25–38mm long and 8–11mm wide, larger in the upper portions of the plant; the larger lower lobe deltoid to falcate, 4–9mm long, the smaller lobe to 5mm long, deltoid. **Leaves** unijugate, terminating in an often stout, branched or very rarely simple tendril; almost sessile, petiole 1–10mm long; leaflets borne on a short (1mm), glabrous petiolule; somewhat glaucous green above and below, both surfaces glabrous; parallel veined, with primary veins conspicuous on the undersides of the leaflets, linear to lorate, (6.8–)10–15(–17)cm long and 0.3–1.1(–1.8)cm broad. **Inflorescence** at least as long as the leaflets of the subtending leaf (12–30cm), with (5–)7–17 flowers borne on a robust, erect peduncle. Flowers densely packed, held erect in bud, with calyx teeth forming an erect fringe, peduncle and raceme rachis elongating and flowers drooping to form a loose raceme at maturity. Floral bracts short (0.5–2mm), linear-acute. **Flowers** 13–19mm long, slightly pendulous, borne on 2–3mm, glabrous pedicels. Calyx campanulate, tube 8–11mm long, glabrous; lower teeth linear, c. 8mm long, middle teeth linear, c.6mm long, the upper teeth shorter. Corolla pale rose, through sky blue to deep purple, or white (cf. Burkart's f. *albiflora*), sometimes with darker veins; banner blade held erect, orbicular, 15mm long and 19mm wide, with very slight (<0.5mm) apical notch, claw 6mm long; wing blade 15mm long, 8mm wide with a double basal pleated process (two flaps engaging the corresponding single flap in the keel petals), claw c. 6mm long; keel blade 9mm long, 5.5mm wide, claw 6mm long, straight, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube oblique. Ovary glabrous; style linear to slightly spathulate, 5–7mm long, with simple stigma. **Fruits** glabrous, black, linear, 5.5–7cm long and 3–4mm wide, with c. 18 seeds separated by woolly false septa. Seeds smooth, spherical, or spherical with a single flattened face, very dark brown-black with olive-grey mottling, 2–3mm across, with hilum c. one sixth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Battistin & Fernández, 1994; Seijo & Fernández, 2003).

PHENOLOGY:
Flowering: September to November
Fruiting: October to December

DISTRIBUTION (FIG. 5.11):
Argentina – Buenos Aires, Chaco, Corrientes, Formosa and Santa Fé. **Paraguay** – Paraguari, San Pedro. **Uruguay** – Río Negro.
An uncommon member of the herb community in wet chaco swamps

DIAGNOSTIC NOTES (FIG. 5.12):
Lathyrus macrostachys is most likely to be confused with *L. magellanicus*, although habitat is a good first point on which to distinguish the species – *L. magellanicus* is found in relatively dry areas, while *L. macrostachys* is endemic to wet chaco swamps. *L. macrostachys* also tends to dry very black and has relatively long, very acute leaflets. Several other species may also be confused with *L. macrostachys*. The differences among them are summarised in the table on the following page:

	L. macrostachys	**L. nigrivalvis**	**L. paranensis**	**L. parodii**
Habit	Perennial	Annual / Biennial?	Annual / Biennial	Perennial
Colour on drying	Blackening/ darkening throughout	Blackening on ovaries/mature fruits, buds, slightly on vegetative organs	Greying / darkening	Not darkening
Pubescence	None	None or rarely sparse on vegetative organs	None, or sparsely at base of stipules / between calyx teeth	2 lines of hairs on stems leading away from nodes
Style	Linear to slightly spathulate 5–7mm long	Spathulate 3–5mm long	Linear 9–12mm long	Linear c. 4mm long

TYPE:

Vogel's Berlin specimen of *L. macrostachys* is unknown, the original having been lost to fire. As Sello's collections were widely distributed, a potential lectotype specimen may exist in other herbaria, but was not discovered and examined for this account. Future investigations in Continental European herbaria may yield an appropriate specimen for designation as lectotype, and if not, a neotype should be described

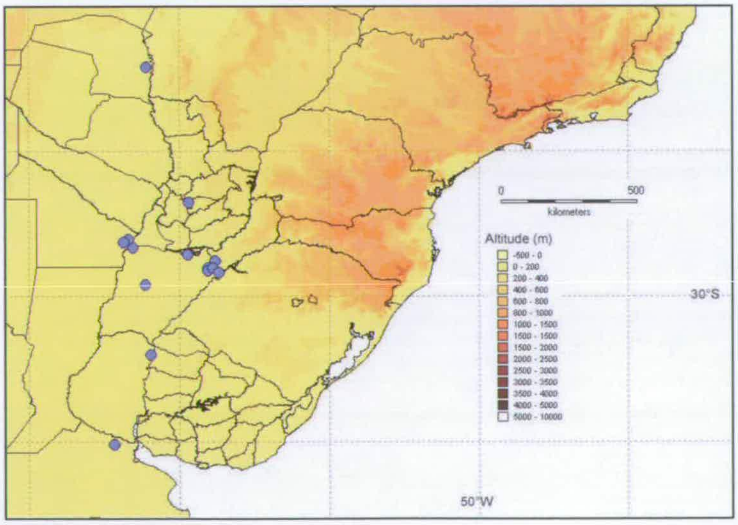


Figure 5.11 ***L. macrostachys***
This species is distributed throughout the watershed of the Paraná river.

Figure 5.12 ***L. macrostachys*** Mature black fruits containing many relatively small seeds.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Pampas of Buenos Aires, *Gillies s.n.* (E).

CHACO: Las Palmas Camino Margarita Belén a Las Palmas, orilla Río Guaycurú (27.135°S, 58.849°W), *Schulz 2.918* (F); Campo Velaz, ruta 11, *Schulz 15.765* (F); Puente Zapirán ruta 11 (salida del camino a Gral.Vedia) 27.04°S, 58.704°W *Schulz 17.901* (F).

CORRIENTES: Dep. Santo Tomé Garruchos, Estancia San Juan Battista Costa del Río Uruguay (28.18°S, 55.69°W), *Krapovickas et al. 25853* (NY); Dep. Ituzaingó Isla Apipé Grande Panco cué, (27.561°S, 56.722°W), *Schinini & Vanni 15791* (F); Dep. Santo Tomé Gdor. Virasoro. Por vía ferrocarril, 4 Km SW, (28.109°S, 56.043°W), *Seijo 1253* (NY); Dep. Santo Tomé Gdor. Virasoro, 10Km W por camino a Garruchos (28.031°S, 55.872°W), *Seijo 1263* (NY); Dep. San Cosme Desvío a Pto. González 9 Km del cruce con camino a Paso de la Patria, (27.311°S, 58.555°W), *Tressens et al. 193* (F); Dep. Santo Tomé 38km N de Santo Tomé, ruta 40E a "Timbó". Proximidades de selva marginal del Río Uruguay. 28.019°S, 56.032°W, *Vanni & Maruñak 3717* (F, NY).

ENTRE RÍOS: Federación Estancia "Buena Esperanza" 31.008°S, 57.924°W, *Pedersen 6239* (K, US).

MISIONES: Apostoles San José, Escuela Agrotecnico Don Bosco 27.776°S, 55.7830°W, *Renvoise 3116* (K, NY, US).

SANTA FÉ: Villa Guillermina, *Meyer 3289* (F); Mocoví, *Venturi 4* (K).

Paraguay

PARAGUARI: Plaine de Pirayu entre Paraguari et Villa-Rica 25.77°S, 56.684°W, *Balansa s.n.* (K).

SAN PEDRO: alto Paraguay, Primavera 21.083°S, 58.099°W, *Woolston 1423* (K).

UNKNOWN: *Jorgensen 4401* (NY); Süd Paraguay, *Kuntze s.n.* (F, NY).

Uruguay

RÍO NEGRO: Cero Largo Palleros *Gallinal et al. B-410* (NY).

11. Lathyrus magellanicus Lamarck M. (1788) *Encyclopédie méthodique ou par ordre de materieres*. **II (Cic. – Gor.)** Panckouke, Paris. p. 708 (holotype: P!)

Perennial herb. Rhizomes woody, thickened or running. Rich green and somewhat glaucous on all the vegetative organs, often tinged purple-red when fresh, particularly in individuals growing in exposed sites, often drying jet black, or with at least the fruits and buds drying black. Stems clambering, to 80(–180)cm, unwinged or winged (wings to c.3mm). Plants glabrous, sometimes sparsely, or rarely densely pubescent on stems, leaf axils and undersides of leaves and calyx.

Stipules large, saggitate to nearly semihastate (second lower lobe sometimes <2mm long in var. *gladiatus*), often with a few crinkled hairs in the axis, primary lobe suborbiculate to lanceolate, 0.9–3.5cm long and 0.4–1.8cm broad, the lower lobes 1–8(–13)mm long, acute to deltoid. **Leaves** unijugate, very rarely bijugate, terminating in a branched or simple tendril. Petioles 0–38mm long; leaflets with both surfaces typically glabrous, or pubescent with simple curled hairs, somewhat glaucous; primary veins parallel, apparent on the undersides of the leaflets, rotund, elliptic to lanceolate (0.9–)2–15cm long and 2.5–30(–35)mm broad.

Inflorescence usually twice as long as the leaflets of the subtending leaf (c. 1.5 times in var. *gladiatus*), with a raceme of (2–)4–10(–12) flowers borne on an erect peduncle, 3–18(–21)cm long. Floral bracts absent, but pedicel bases appearing articulated as they are protected by a cusp of peduncle tissue. **Flowers** 14–18(–26)mm long, borne on 2–5mm, usually glabrous, pedicels. Calyx campanulate tube 2–5mm long, often glabrous (sometimes hirsute or sparsely lanulose); calyx teeth subequal to unequal; lower teeth linear-acute, 4 – 8mm long; upper teeth shorter, deltoid to linear, 1–3mm long. Corolla varicoloured, banner pale pink, fuchsia to violet coloured, wings and keel often lighter (pale pink to white); banner blade held erect, rotund to orbicular, 14–18mm long and 14–20mm wide, usually with an apical notch, claw 4–7mm long; wing blade 10–12mm long, 6–8mm wide with a basal boss and pleated process, claw c. 7–10mm long, usually strongly curved; keel blade 10–14mm long, 5–7mm wide, claw c. 6mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens);

staminal tube truncate to slightly oblique at apex. Ovary glabrous; style linear or slightly broadening towards the apex, 5–7mm long, with simple stigma. **Fruits** glabrous, grey-brown to black, linear, 3.5–7cm long and 5–8mm wide, sometimes with woolly false septa or woolly tissue running along the inside of the upper suture, 9–15-seeded. Seeds smooth, subspherical, chestnut brown to olive-grey, often with dark brown or black flecks, 3–6mm across, with hilum c. a quarter of the circumference.

INTRASPECIFIC VARIATION:

The species is extremely diverse, with a pan-Andean distribution, from sea level at Tierra del Fuego to the Páramo of Colombia at 3500m. Morphological trends are distinguishable from certain areas of the species' range. The discussion under each variety attempts to describe trends in morphological diversity, focussing on petiole length, leaflet and stipule shape, flower size and pubescence. These characters were treated as significant in many descriptions of new infraspecific taxa and species allied to *L. magellanicus* Lam. However, there is not enough consistency in these characters to justify many of the taxa, which I treat as synonyms here. I recognise four varieties that represent plants from the extremes of the species' geographical range. This morphological and ecological diversity within *Lathyrus magellanicus* makes it the most difficult species in the genus worldwide, and it may perhaps better be treated as a complex ochlospecies (Cronk 1998).

Key to the varieties of *Lathyrus magellanicus*:

1a) Plants < 20cm tall, vegetative organs pilose-pubescent, entire plant greying (i.e. not blackening) in herbarium, plants of Southern Patagonia 11c) **var. *glaucescens***

1b) Plants >20cm tall, vegetative organs glabrous, or rarely sparsely pubescent, mature fruits and often the rest of the plant blackening in herbarium, rarely remaining green (var. *pterocaulos*). Plants of Central Patagonia and northwards. 2

2a) Plants very robust (150–180cm tall), wings >2mm broad, flowers 25–31mm long. Chile, Cordillera de Nahualbuta and surrounding areas. 11b) **var. *pterocaulos***

2b) Plants to 120cm tall, wings <1.5mm broad, flowers< 20(very rarely to 23mm long) Central and northern Chile and Argentina, and northwards 3

3a) Stipules unequal sagittate (one lower lobe much shorter than the other). Calyx glabrous. Andes of Córdoba, Argentina to Venezuela. 11d) **var. *gladiatus***

3b) Stipules symmetrically sagittate. Calyx sometimes pubescent. Central Chile, Patagonia, Buenos Aires Province of Argentina 11a) **var. *magellanicus***

11a) var. magellanicus

Lathyrus sessilifolius Hooker et Arnott (1831) *Botany of Captain Beechey's Voyage*. London, Henry G. Bohn. p.20. *Lathyrus hookeri* G. Don (1832) *A General System of Gardening and Botany* 2, London. p.332. *Lathyrus epetiolaris* Clos (1847) in Gay C. (ed.) *Historia Fiscia y Politica de Chile* (Flora Chilena II). Claudio Gay, Paris. p. 146.
TYPE: CHILE: Valparaiso 1831 *Cuming 628* (lectotype, here designated E-GL!, isotypes: E-GL! – on same sheet as Bridges 243; K! – on same sheet as *Macrae s.n.*)

Lathyrus chilensis Steudel (1841) *Nomenclator Botanicus* 2nd edition. J.G. Cotta, Stuttgart. p. 13. TYPE: CHILE: Quillota, 'la Campagna chico' *Steudel s.n.* (lectotype here designated: BM!)

Lathyrus litoralis R.A. Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 625. *Lathyrus epetiolaris* Clos en Gay var. *litoralis* (Philippi) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p 202. TYPE: CHILE: San Antonio de las Bodegas. Sept. 1853 *Germain s.n.* (lectotype, here designated: SGO!, isolectotype: SI!)

Lathyrus roseus R.A. Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 626. TYPE: CHILE: Cordillera de la Compañia. Nov. 1853 *R.A. Philippi s.n.* (lectotype here designated: SGO!).

Lathyrus longipes R.A. Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). Linnaea **28**: 625. *Lathyrus dumetorum* var. *longipes* (R.A. Philippi) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 207. *Lathyrus. magellanicus* var. *longipes* (Philippi) Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de Lathyrus. *Darwiniana* **6**: 23. TYPE: CHILE: Cordillera de S. Fernando. Feb 1843. *R.A. Philippi s.n.* (lectotype, here designated: SGO!, isolectotype SI!, photograph of W isolectotype F!)

Orobus philippi Alefeld (1861) Ueber Vicieen. *Bonplandia* **9**: 144; *Lathyrus philippi* (Alefeld) R.A. Philippi (1872) Descripción de las nuevas plantas incorporadas últimamente en el Herbario Chileno. *Anales de la Universidad de Chile*. **41**: 694; *Lathyrus berteroi* R.A. Philippi (1872) Descripción de las nuevas plantas incorporadas últimamente en el HerbaRío Chileno. *Anales de la Universidad de Chile*. **41**: 694. TYPE: CHILE: Rancagua in sylvaticis petrosis Monte la Leona. *Bertero 360* (lectotype, here designated: BM!, isolectotype: NY!)

Lathyrus trichocalyx R.A. Philippi (1872) Descripción de las nuevas plantas incorporadas últimamente en el Herbario Chileno. *Anales de la Universidad de Chile*. **41**: 695. *Lathyrus sessilifolius* forma *trichocalyx* (Philippi) Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p. 117. *Lathyrus hookeri* var. *trichocalyx* (Philippi) Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6**: 23. TYPE: CHILE: Tomé November 1855 *Germain s.n.* (lectotype, here designated: SGO!)

Lathyrus ovalifolius R.A. Philippi (1872) Descripción de las nuevas plantas incorporadas últimamente en el Herbario Chileno. *Anales de la Universidad de Chile*. **41**: 694. *Lathyrus magellanicus* var. *ovalifolius* Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 203. TYPE: CHILE: Baños de Cauquenes *Volkmann s.n.* (lectotype, here designated: SGO! isolectotypes: K!, SGO!, SI!)

Lathyrus heterocirrus R.A. Philippi (1893) Plantas nuevas chilenas. *Anales de la Universidad de Santiago de Chile*. **84**: 279. *Lathyrus magellanicus* var. *heterocirrus* (R.A. Philippi) Reiche (1898) *Estudios Críticos Sobre la Flore de Chile*. Vol.2. Imprente Cervantes, Santiago de Chile. p. 204. TYPE: CHILE: Baños de Cauquenes October 1869 *Philippi s.n.* (lectotype, here designated: SGO!, isolectotype: SI!)

Lathyrus magellanicus var. *araucanus*? Philippi. (1893) Plantas nuevas Chilenas. Anales de la Universidad de Santiago **84:** 279. (Type not present in Philippi's collections in SGO, the question mark in the name is Philippi's)

Lathyrus magellanicus α *normalis* O. Kuntze (1898) *Revisio Generum Plantarum III*. London, Dulaud & Co. p. 65. TYPE: ARGENTINA: Patagonia. *Moreno & Tonini 736* (lectotype, here designated: NY!)

Lathyrus magellanicus var. *subsessilifolius* O. Kuntze (1898) *Revisio Generum Plantarum III*. London, Dulaud & Co. p. 65. TYPE: ARGENTINA: Patagonia. 50°3'S *Moreno & Tonini 442* (lectotype, here designated: NY!)

Lathyrus philippianus Spegazzini (1902) Nova addenda ad floram Patagonicam IV. *Anales del Museo Nacional de Hist. Nat. de Buenos Aires* **7:** 280. TYPE: not seen

Lathyrus magellanicus forma *longipetiolatus* Hassler (1919) ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum* **16**: 226. TYPE: PARAGUAY: Gran Chaco: Nueva Pompeya. *Flossdorf 93*. TYPE: not seen

DIAGNOSTIC NOTES:
Plants 20–120cm high, usually darkening or drying black throughout. Glabrous save for very sparse pubescence along the ridges of the wingless stems and in the axils at the base of the stipules. Leaflets typically with rounded apex. Flowers usually 4–6, exceptionally 9–(15–20mm) long.

CHROMOSOME NUMBER: 2n=14. (Senn 1938 – as *L. sessilifolius*; Seijo & Fernández, 2003 – as var. *magellanicus*)

PHENOLOGY:
Flowering November–February
Fruiting: November–March

DISTRIBUTION:
Throughout central S. America. **Argentina** – Buenos Aires, Chubut, La Pampa, Neuquen, Río Negro, Santa Cruz, Tierra del Fuego. **Chile** – Región IV (Coquimbo), Región Metropolitana de Santiago; Región V (Valparaiso); Región VII (Maule); Región VIII (Bío Bío); Región IX (Araucanía)Region X (Los Lagos)Región XII (Magellanes).

In a wide range of mesophytic habitats, forest margins and in open woodland on clays, sandy and gravely soils. In grassland, scrub or forest marginal vegetation. Sometimes seen as a coloniser on lava flows on volcanic sands.

VERNACULAR NAMES: Arvejilla (Spanish), Clarincillo (Spanish), Ichivudu (Mapudungun), Ñilpe (Mapudungun)

INTRAVARIETAL VARIATION (FIG. 5.13):
Lathyrus magellanicus var. *magellanicus* is a widespread and diverse variety. The geographical trends in morphology are outlined below:

- *Southern Argentina and Chile*
  From Tierra del Fuego (Argentina and Chile) to southern Chubut province, (Argentina) *L. magellanicus* var. *magellanicus* is most like the type, with petiolate leaves, ovate stipules and leaflets.

- *Central Argentina and Chile* (Fig. 5.13)

Northwards from the type area, through Chubut and Neuquen provinces in Argentina and regions X, IX and VIII of Chile, plants become typically more robust and the following changes occur:

  - Petiole lengths reduce (until leaves are sessile)
  - Leaflets become longer, tending towards a more lanceolate overall form, and stipules become more deltoid, with apices more acute.

Plants with sessile leaves from throughout this region have been referred to *L. hookeri* or *L. sessilifolius* and more recently *L. magellanicus* var. *hookeri*. However, there appears to be no clear distinction between 'var. *magellanicus*' and 'var. *hookeri*' type plants, with many intermediates between the two extremes. Consequently, I treat all these specimens as *L. magellanicus* var *magellanicus* Lam. Particularly large plants (>120cm tall) from central Chile (near Sierra de Nahualbuta and Concepción) that remain green when dry can be referred to 12b) *L. magellanicus* var. *pterocaulos*.

- *North-central Argentina and Chile*
  Plants from Regions VI and V in Chile, the area around Valparaiso and the Santiago Metropolitan area, and from Mendoza, Córdoba and San Juan provinces of Argentina, typically show reduced flower sizes and variable petiole lengths between individuals. Two further morphological subgroups become apparent in these areas:

  1: Individuals with relatively broad leaflets and stipules – similar to those seen in *L. magellanicus* from the type area. These have been referred to *L. ovalifolius* Philippi (1872).

  2: Individuals with generally slender leaflets and often with pubescence on the calyx (particularly the abaxial parts of the tube), as well as the stems and undersides of the leaves. Higher altitude specimens were referred by R.A. Philippi to *L. trichocalyx* Philippi (1872), and lower altitude specimens to *L. litoralis* Philippi (1856). Specimens from Valparaíso, Chile and occasionally Mendoza, Córdoba and San Juan in Argentina.

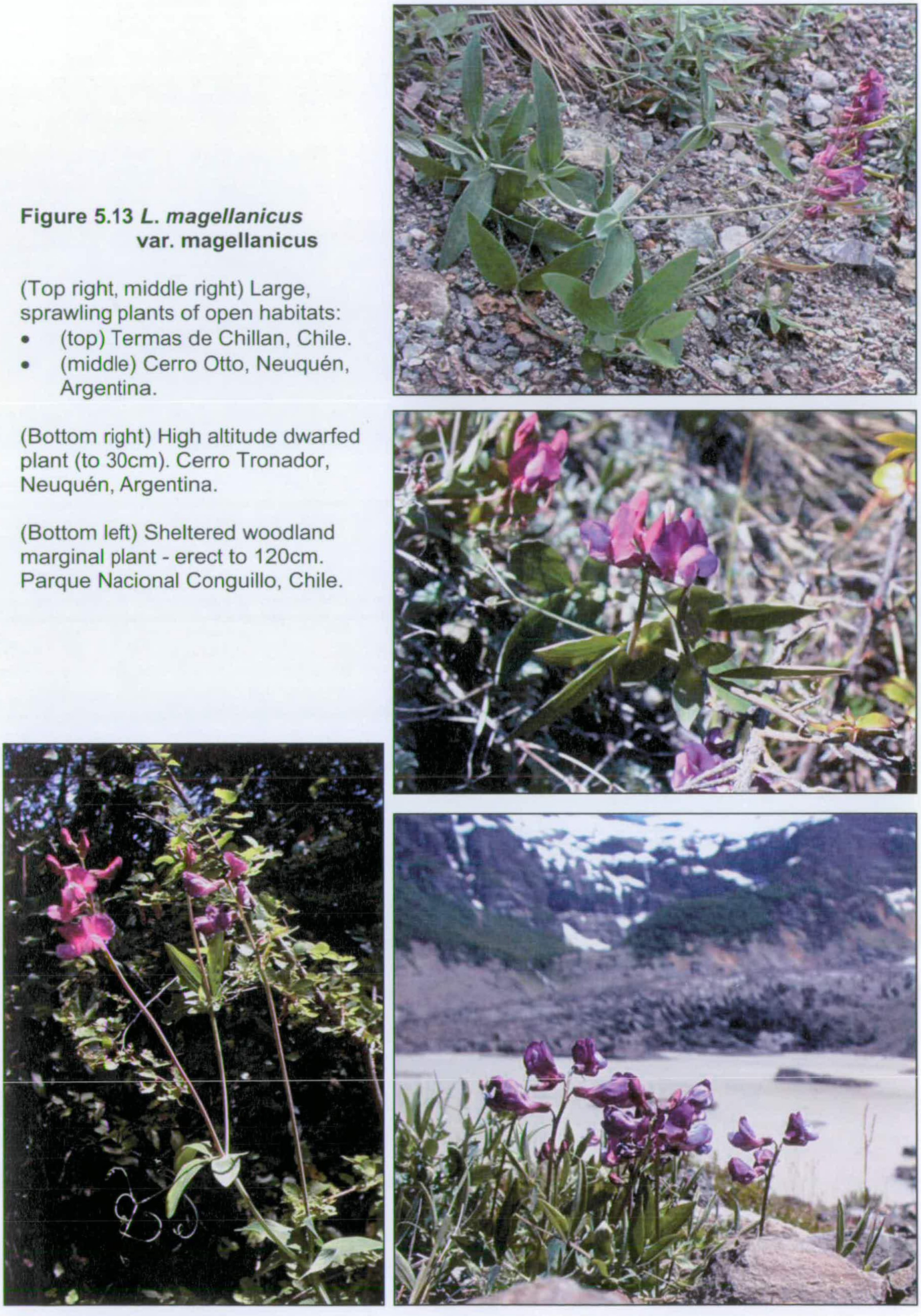
Figure 5.13 ***L. magellanicus*** **var. magellanicus**

(Top right, middle right) Large, sprawling plants of open habitats:

- (top) Termas de Chillan, Chile.
- (middle) Cerro Otto, Neuquén, Argentina.

(Bottom right) High altitude dwarfed plant (to 30cm). Cerro Tronador, Neuquén, Argentina.

(Bottom left) Sheltered woodland marginal plant - erect to 120cm. Parque Nacional Conguillo, Chile.



SELECTED ADDITIONAL SPECIMENS EXAMINED:
^{T} denotes petiolate specimens similar to the type of the species.
* Denotes specimens with pubescent calyces and other vegetative organs.

Argentina

BUENOS AIRES: Junin Agustina, *Cabrera 6569* (NY); Zárate Las Palmas, *Hunziker 1683* (K); *Commerson s.n.* (F); Pampas of Buenos Aires, *Gillies s.n.* (E-GL); *Tweedie s.n.* (E-GL)
CHUBUT: Pico Pico (*Det.*), *Rodriguez* (NY)^{T} ; Villa de la Laguna Blanca *Koslowsky 184* (BM)^{T} ; Valle de la Laguna Blanca (45°52'S, 71°15' W) *Koslowsky 186* (K - 2 sheets)^{T} ; Lago Puelo, *Meyer 9286* (K)^{T} ; Dep. Fataleufú A 3km W del Balneario de Corcovado (43°30'59" S, 71°36'24" W), *Seijo 1530* (NY); Dep. Futaleufú Villa Futalaufquen, arroyo Cascada, *Seijo 1577* (F)^{T} .
NEUQUEN: San Martin de los Andes 2400ft., *Comber 713* (E, K); Paso Perez Rozales, *Moreau 287* (F)^{T} ; Nahual Huapi National Park 700m, *Archer 5* (K); River Limay district 300m, *Archer 9* (K); Dep Lácar San Martin de los Andes, camino a Hua Hum., *Seijo 1193* (K); Dep Lácar San Martin de los Andes, camino a Hua Hum., *Seijo 1199* (NY).
RÍO NEGRO: Dept. Bariloche: Cerro Tronador, East side, 1,200m *Archibald 14303* (E)^{T} ; Lago Nahuel Huapi, *Cordini 70* (F); Parque N. Huapi Psicicuttung, *Disarbro*? *774* (F); Cordillera de los Andes: southern end of Lago Correntoso (40.74°S, 71.67°W), *Gardner & Knees 6149* (E); Lago Nahuelhuapi East End of Lago Moreno, *Ljungren 135* (NY); Lago Nahuel Huapi Portezuelo 775 m, *Ljunger 435* (BM, NY); Bariloche Cerro Otto, *Seijo 1161* (NY); Dep. Bariloche Bariloche, camino a circuito chico, mirador al lago Moreno, Costa SE. Vista al cerro Capilla, sobre falda del cerro., *Seijo 1167* (NY)^{T} ; Bariloche Ruta Bariloche-El Bolsón, *Seijo 1173* (K); Bariloche Camino de tierra desde cerro Catedral a Lago Gutierrez, *Seijo 1182* (F, NY); Bariloche Cerro Catedral a Lago Gutierrez (41°10'37"S, 71°25'09"W), *Seijo 1600* (NY); Bariloche Camino de Cerro Catedral a Lago Gutierrez, *Seijo 2098* (F); Bariloche Camino de Cerro Catedral al Lago Gutierrez, *Seijo 2307* (NY); San Carlos de Bariloche (71°19'S, 41°09'W, *Senn 4266* (NY); Bariloche, *Shannon & Shannon 1* (US)^{T}
SANTA CRUZ: Depto. Lago Argentino Bosque de raulí cerca de la entrada a Reserva del Parque Nac. Los Glaciares (50°31'S, 72°46'W) 120 m, *Fortunato 4933* (NY)^{T} ; Parque Nacional Los Glaciares: collina in facia alla fronte del ghiacciaio Perito Moreno (lago Argentino), *Mares7443* (K)^{T} ; Río Gallegos Estancia Stag River 270 ft, *Tweedie 243* (K)^{T}
TIERRA DEL FUEGO: Port Famine (*Herb. Asa Gray*) (NY)^{T} ; Río Grande Cabo Peñas (Estancia José Mendez). To east of hills and cliffs, from road to beach. 0-30ft. *Goodall 526* (NY, US)^{T} .
UNKNOWN: Cohunco (38.53°S,70.251°W) 2500ft., *Comber 868* (E); Patagonia 50°3', *Moreno & Tonini 442* (NY).

Chile

REGIÓN IV (COQUIMBO): Upsallata-pass der chilenischen Hochcordillere, Juncal Am Juncalflusse (32.865°S, 70.17°W) 2200m *Buchtien s.n.* (E)*; Prov. de Choapa 1 km inland at Pichidangui. 10m *Gardner & Knees 5926* (E)*; Depto. Illapel Caren, Quebrada los Buitres 1000m *Johnston 16492* (K)*; Ovalle Quebrada la Embarrado, 9km east of Hurtado, Hacienda El Bosque; near the stream in quebrada. 1600m *Wagenknecht 18487* (F)*; Depto. Illapel Caren, Quebrada los Buitres, tributary of Illapel river. (31.55°S, 70.87°W) 1000m *Worth & Morrison 16492* (K)*.
REGIÓN V (VALPARAÍSO): Quillota *Bertero 1076* (BM); Quintero, *Bertero 1760* (E) *; *Borchers s.n.* (BM); *Bridges 243* (E, K) *; *Cuming 628* (BM, E-GL, K) ***;** Prov. de Petorca Zapallar: Quebrada Aguas claro, 2km south of Cachagua and 3km inland from coast. (32°35'S, 71°55'W) 70m *Gardner & Matthews 15* (E) *; Hills above Valparaiso, *Gourlay*

s.n. (E)*; Algarrobo Punta sur *Kausel 4229* (F) * Casablanca Cuesta Lo Orozco 400m *Kausel 4293* (F, NY); Valparaíso *King s.n.* (E-GL) *; Sierra above Villa Alemana 800ft., *Leaudenau 248* (K) O*; Valparaíso *Pöppig 192* (BM) *; Montemar (32.9650°S, 71.485°W) *Skottsberg 1043* (NY) *; El Salto (33.05°S, 71.52°W) *Skottsberg 921* (F, NY) * Cerro Campana *Solbrig 3613b* (NY); Quintero 10m *Werdermann 2* (BM, E, F, US)*; In Puertas Negras *Zollner 8332* (NY)*.

REGIÓN METROPOLITANA DE SANTIAGO: Provincia de Melipilla (34.12°S -70.87°W) 1398m *Baxter et al. DCI 1453* (E); *Claude-Joséph 533* (US) O*; Near Río Colorado 4000ft. *Hastings 436* (US)*; San José de Maipo (33.645°S, 70.345°W), *Holway 97* (NY) O*; Santiago 4000ft. *Leaudenau 314* (BM, K) O*; *Philippi s.n.* (K).

REGIÓN VII (MAULE): Prov. De Talca Cordillera de los Andes: Valle de Maule. (35°56'43"S, 70°30'29"W) 1750 m, *Baxter et al. UCEXC 89* (E)*; Provincia de Talca San Clemente: Cordillera de Los Andes: Valle de Maule. Just before Lauguna del Maule (36.005°S, 70.56°W) 2260 m, *Brownless et al. DCI 1220* (E)*; Provincia de Talca Radal: Parque Nacional Radal Siete Tazas, Sector Parque Inglés, Quebrada La Leona (35.465°S, 70.962°W) 1593 m, *Gardner et al. DCI 106* (E)*; Provincia de Talca Radal: Parque Nacional Radal Siete Tazas, Sector Parque Inglés, Sendero Los Chiquillanes (35.46°S, 70.98°W) 1412 m, *Gardner et al. DCI 98* (E); Curicó Cordillera Petroa-Planchon; along Río Planchon 2500m *Mexia 7889* (BM, F, K)*.

REGIÓN VI (LIBERTADOR): Rancagua montis La Leona, *Bertero 360* (BM, NY); Provincia de Colchagua San Fernando: Cordillera de los Andes: Sector La Rufina. Pasando Unión between Río Clarillo and Río Tinguiririca. Quebrada el Avellano. (34.75°S, 70.7°W) 963m, *Baxter et al. DCI 1414* (E); Cardenal Caro 1.5km south of Cahuil on the road to Bucalemu 5m, *Lammers et al. 7914* (F); Talcareque (34.633°S, 70.92°W), *Reed Herbarium s.n.* (K).

REGIÓN VIII (BÍO BÍO): Provincia de Ñuble Chillán: Road to Termas Chillán. (36°55'05"S, 71°26'33.5"W) 1,328m, *Gardner & Knees 6772* (E); Provincia de Ñuble Chillán: Cordillera de los Andes: road to Shangrila (36°53'1"S, 71°28'01.5"W), 1461m, *Gardner & Knees 6805* (E); Baños de Chillan *King T.* (E-GL); Concepción Environ Cerro Caracol *Junge 1940* (F)*; Propè la Concepción, *Macrae s.n.* (K)*.

REGIÓN IX (ARAUCANÍA): Pucón, *Behn s.n.* (F); P.N. Villarica 1000 m, *Billiet 3698* (BM)^{T}; Island in Lake Villa Rica (39.25°S, 72.1°W) 700ft., *Eliott 618* (E, K); Provincia de Malleco Los Alpes, Cordillera de Nahuelbuta; Near southern boundary, Fundo Solano 1,200m *Eyerdam 10237* (US); Provincia de Malleco Angol: Parque Nacional Nahuelbuta. Near to main camping area. (37.82°S, 73°W) 1074m, *Gardner et al. DCI 582* (E); Provincia de Malleco Curacautín: Cordillera de los Andes: Parque Nacional Conguillío, Puente Conguillío Roadside on volcanic ash slopes. (38°38'48"S, 70°38'37.2"W) 1153m, *Gardner - DCI 945* (E); Provincia de Malleco: Angol: Cordillera de Nahuelbuta: Parque Nacional Nahuelbuta: Below Piedra El Aguila. 1060m, *Gardner & Knees 6129* (E); Temuco, *Scott Elliot 291* (BM).

REGION X (LOS LAGOS): Valdivia, *Bridges 674* (E-GL); Valdivia, *Buchtien s.n.* (E)

REGIÓN XII (MAGELLANES): Punta Arenas Río Seco, *Brooke 7013* (BM, NY)^{T}; 15km south of Punta Arenas 20 m, *Eyerdam et al. 24122* (K)^{T}; Punta Arenas, *Huthwaite s.n.* (E); Ultima Esperanza Parque Nacional Torres del Paine. Path between Lago Pehoe (Refugio at western end of L. Pehoe) and Ventisquero Grey (Glacier) 500 m, *Sobel & Strudwick 2617* (NY)^{T}; Ultima Esperanza Parque Nacional Torres del Paine, 3hrs. By car north of Puerto Natales, southern Chile, southern extremes of the Andes, *Sobel & Strudwick 2630* (NY)^{T}; Ultima Esperanza Parque Nacional Torres del Paine. Trip from Guarderia Laguna Azul along boundary of park to Nothofagus forest. 600 m, *Sobel & Strudwick 2643* (NY)^{T}.

UNKNOWN: [East?] side of Andes of Chile El Valle de las Cuevas, *Bridges 1130* (E-GL)*; *Bridges s.n.* (K); Suangulo 5000ft., *Comber 483A* (K).

11b) var. pterocaulos (Philippi) Kenicer comb. and stat. nov.
Lathyrus pterocaulos R.A. Philippi (1872) Descripción de las nuevas plantas incorporadas últimamente en el Herbario Chileno. *Anales de la Univesidad de Chile* **41**: 694 – 695. TYPE: Chile San Lorenzo, Araucanía. *Volkmann s.n.* (holotype: SGO, isotype SI).

Plants very robust (120–180cm tall), wings >1.5mm broad, flowers 25–31mm long.

PHENOLOGY:

Flowering November to December

Fruiting: December and January

DISTRIBUTION:

Chile – Araucanía, Bío Bío. An area centered on Cordillera de Nahualbuta, between approximately 38°4'S and 76°3'W in the triangle described by Concepción, Chillan and Temuco.

At forest margins, clambering up neighbouring vegetation.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Chile:

REGIÓN IX (ARAUCANÍA): Provincia de Cautín Temuco: Predio Rucamanque, Universidad de la Frontera (UFRO) (38.687°S, 72.685°W) alt. 323m, *Baxter et al. DCI 1303* (E); Temuco, *Elliott 594* (E, K); Provincia de Malleco Road from Victoria to Termas de Tolhuaca before Parque Nacional Tolhuaca near to Puente Tacadero. (38°13'37"S, 71°49'46"W) alt. 942m, *Gardner & Knees 6887* (E).
REGIÓN VIII (BÍO BÍO): Environs de Chillan, *Germain s.n.* (BM, K); Concepción *Elliott 573* (E, K).

11c) var. gladiatus (Hooker) O. Kuntze. (1898) Revisio Generum Plantarum III. London, Dulaud & Co. p.65. *Lathyrus gladiatus* Hooker (1837) Icones Plantarum 1. Longman, Rees, Orne, Brown Green & Longman, London. Tab. 72. TYPE: ECUADOR: Pichincha in the region of Páramos, *Jameson s.n.* (holotype: K!).

Lathyrus magellanicus var. *tucumanensis* Burkart. (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. Revista de la Facultad de Agronomía y Veterinaria 8, Universidad de Buenos Aires, Buenos Aires.p. 108. Type: Dept. Tafí Sierras Calchaquíes Río San José a 2200m January 1933, *Burkart 5437* (holotype: SI!, isotype: K!).

Stems decumbent or prostrate. Stipules unequal sagittate (one lower lobe much shorter than the other). Calyx glabrous.

CHROMOSOME NUMBER: 2n=14. (Seijo & Fernández, 2003 – as var. *tucumanensis*)

PHENOLOGY:
Flowering: year round
Fruiting: year round

DISTRIBUTION:
Argentina – Córdoba, Jujuy, Mendoza, Salta, San Luis, Tucuman. **Bolivia** – Chuquisaca, Cochabamba, Santa Cruz, Sorata. **Peru** – Departments of Amazonas, Ayaraca, Cajamarca, Huánuco, San Martin. **Ecuador** – Bolivar, Cañar, Carchi, Chimborazo, Cotopaxi, Imbabura, Napo, Pichincha, Quito, Tusa. **Colombia** Bogotá, Boyacá Cauca, Nariño.
Upland rain-and cloud-forest (>2400m) and in Jalca and Páramo rangeland, above the treeline.

VERNACULAR NAMES: Alberjilla grande (Spanish)

INTRAVARIETAL VARIATION:
Given the wide distribution and range of habitats in which var. *gladiatus* is found, it is a variable taxon. Above the treeline, specimens tend to have a prostrate creeping habit; whilst specimens from forest margins have longer internodes and clamber over neighbouring vegetation. There is evidently some variation between local populations as well – some Peruvian plants have relatively long petioles (to 1.5cm) and rounded apices to the leaflets. Although these individuals may be confused with *L. meridensis*, they consistently dry black and have glabrous calyces. In the south of the range (Argentina), flowers are typically very small (<1cm long) – such specimens were referred to *L. magellanicus* var. *tucumanensis* by Burkart (1937).

Argentina

CORDOBA: Sierra Grande Copina (31.566°S, 64.704°W), alt. 1400m, *Burkart 7376* (F); Sierra Achala, *Kurtz 8376* (NY).
JUJUY Sep. Capital Camino a Tiraxi 1.6km antes de Escuela, *Seijo 1109* (NY).
MENDOZA: Dep. Malargüe camino a Paso Pehuenches km 50, alt. 1800m, *Cabrera 22830* (F).
SALTA: Oran San Andres alt. 1800m, *Pierotti 289* (NY).
SAN LUIS: Dep. Chacabuco Chorro de San Francisco, *Seijo 1865* (NY - 2 sheets).
TUCUMAN: Dept. Tafí Sierras Calchaques: San José, alt. 2200m, *Burkart 5439* (K).
UNKNOWN: Chicligasta N. of La Alvaresada, alt. 1400m, *Sparre 936* (K) alt. 1100m, *Venturi 1359* (US).

Bolivia

CHUQUISACA: Tomina c. 10km N of Sopachuy on road to Tarabuquillo (19.414°S, 64.516°W) alt. 2400m, *Wood 14438* (K)
COCHABAMBA: Carrasco c. 3km from Monte Puncu towards Sehuencas alt. 2800m, *Wood 10314* (K); Ayopaya Independencia, 28km from Independencia along road north to Sailapata and La Mina. (16°56'78"S, 66°50'08"W) alt. 3406m, *Wood 18723* (K); Colomi alt. 12000ft., *Brooke 5059* (BM, F, NY); About 100 miles N.W. of Cochabamba Choro alt. 11000ft., *Brooke 6034* (BM, F, NY)
SANTA CRUZ: Prov. Vallegrande 3km (by air) S of Khasa Monte onm road to Los Sitanos, ca. 2km N. of Los Hornos. (18.705°S, 64.035°W) 2400, *Nee 38412* (NY)
SORATA: Tusuhuaya 3600m, *Cardenas 1363* (NY)
UNKNOWN: *Bang s.n.* (NY); Padcaya (21.886°S, 71.413°W), *Fiebrig 3451* (E); *Mandon 725* (NY).

Colombia

BOGOTÁ: Facataliva in alta planite Bogotensis alt. 2630m, *André 648* (K);
Pasto a bogotá Andes de Tuquey alt. 3000m, *Triana s.n.* (E)
BOYACÁ: Valle de Cocuy, southwest slopes alt. 3100m, *Cuatrecasas 1277* (F);
CAUCA: Paletara Bushy bank near Río Cauca alt. 2950m, *Pennell 7074* (NY, US) alt. 2950m, *Lehmann 3505* (BM); Páramo de Palacio flanco W. km 6 de la carretera alt. 3100m, *Cleef 3715* (US); Marizo de Bogotá eastern slopes of Páramo de Chisacá: Quebrada de Santa Rosa, subpáramo. Eastern slopes of Páramo de Chisacá: Quebrada de Santa Rosa, subpáramo. alt. 3300m, *Cuatrecasas & Jaramillos 26001* (NY); Páramo de Sumapaz cerc al Río Santa Rosa alt. 3700m *Uribe 4512* (NY); hillside Bogotá alt. 8900ft., *Tracey 387* (K); near Bogotá, Monserrate, Valley of the Río San Francisco alt. 2900m, *Hawkes & Garcia-Barrgia 86* (K); Salto de Tequendamama al Lado norte de La Planta, *Cuatrecasas 176* (F).
NARIÑO: al norte de Yacuanquer, *de Garganta 469* (F); Mpio. De Pasto. SE de la Población de Jamondino alt. 2900m, *Ramírez 5.357* (NY); Yanuanguer Pasto alt. 2500-3000m, *Lehmann 6336* (K - 2sheets).

Ecuador

BOLIVAR: Simiatug Hacienda Talahua alt. 3300m, *Penland & Summers 606* (F).
CAÑAR: Río Paute drainage Headwaters of Río Mangán 20-22km e.n.e. of Azogues, alt. 3300m, *Fosberg & Prieto 22815* (US); Asorgues alt. 13000ft., *Balls 7325* (F, K, US).
CARCHI: Above Tulc'an towards Páramo del Angel, alt. 3250m, *Asplund 17060* (NY); Near La Rinconada, alt. 3200m, *Asplund 7183* (US); Maldonado-Tulc'an road ca km40. alt. 3500m, *Werling & Leth-Nissen 023* (F, NY); along road from Tulcan to El Pun alt. 11000ft., *Wiggins 10651* (NY).

CHIMBORAZO: Mt. Chimborazo, nr. Urbina (1.5°S, 78.735°W) alt. 11700ft., *Balls 7319* (F); Daldal Valley 10Km E of Licto (1.48'S 78.32'W) alt. 3700m, *Ramsay & Merrow-Smith 47* (K); Cord. Oriental. Bosque Andino de Cubullín alt. 3300m, *Solís 7561* (F).
COTOPAXI: Zumbagua alt. 12000ft., *Bell 913* (BM).
IMBABURA: Shanshipamba Macholoma alt. 2900m, *Solís 14329* (F); Canton Otovalo Hcda. "Rosa Pamba" alt. 2850m, *Solís 8061* (F); Faldas Occ. Del Cotacachi Urcusique alt. 3000m, *Solís 8198* (F).
NAPO: aldaredores de Los Llanganati entre Ainchilibí y Río Portero, al este de Roma Páramo. alt. 3600m, *Barclay & Juajibioy 9200* (US).
PICHINCHA: Mt. Pichuncha alt. 3500m *Firmin 39* (F, NY); In the region of Páramos, alt. 13000ft., *Jameson 111* (K, NY); El Corazon alt. 10500ft., *Prescott 919* (NY); N Slope of Volcan Cayambe, on road to Lag. San Marco km12. alt. 3500m, *Sparre 17808* (US).
QUITO: Andium Quitensium alt. 13000ft., *Jameson 462* (BM, E-GL); Andium Quitensium alt. 13000ft., *Jameson 81* (K); Andes of Quito, *Jameson s.n.* (NY).
TUSA: *Shumann 5353* (F).
UNKNOWN: In monte ignivomo Pastensi "La Galena", *André 3152* (K, NY); Moscofio alt. 2028m, *André 1134* (F, K, NY); UNKNOWN: Hubabura? alt. 3200m, *Hirsch E69* (NY).

Peru

AMAZONAS: Province of Chachapoyas Cerros Calla Calla 25km above Leimebamba on road to Balsas alt. 3300m, *Hutchison & Wright 6964* (F, NY, US); Chachapoyas, *Mathews 1572* (E-GL, K, NY).
AYARACA: *Weberbauer 6405* (F).
CAJAMARCA: on road to Celendin alt. 3600m, *Dillon & Turner 1627* (F); Jalca de Kamulca close to the summit of the rd ENE from Cajamarca to Celendin (7°02'13"S, 78°15'W) alt. 3700m *Hughes 2008* (E, K); Prov. Celendín alt. 3500m *López & Aldave-8449* (NY); Prov. Celendin Chaluallaco, carretera Celendin-Cajamarca alt. 3350m, *Sanchez- Vega 571* (F); Prov. Cajamarca Jalca de Kumullca entre La Encanada y Celendin alt. 3350m, *Sanchez-Vega 1701* (F); Prov. Cajamarca Coymolache ruta Cajamarca-Hualgalloc alt. 3850m, *Sanchez- Vega 2051* (F); Hualgayoc Prov Cajamarca-Bambamarca road (6°47'S 78°36'W) alt. 3900m, *Smith & Rodolfo Vasquez 3503* (NY).
HUÁNUCO: 15 miles N.E. of Huanuco alt. 13000ft., *MacBride & Featherstone 2158* (F).
SAN MARTÍN: Prov. Mariscal Caceres Río Abiseo National Park (7°S 77°W) alt. 3300m, *Young 2011* (F).

11d) var. glaucescens Spegazzini (1902) Nova addenda ad floram Patagonicam IV. Anales del Museo Nacional de Hist. Nat. de Buenos Aires **7**: 279. (Type not seen)

Lathyrus magellanicus var. oxyphylla Spegazzini (1902) Nova addenda ad floram Patagonicam IV. *Anales del Museo Nacional de Hist. Nat. de Buenos Aires* **7**: 280. (Type not seen)

Lathyrus magellanicus var. *campestris* Dusén (1914) in MacKloskie and Dusen P. Revision of Flora Patagonica Reports Princeton Expedition 1896 - 1899 Vol. 8[3] Supplement: p. 162 tab. III Scwheizerbart'sche Verlagshandlung, Stuttgart. (Type not seen)

Small plants, to 20cm high, much-branched from creeping rhizomes with a prostrate habit and short internodes; small, mucronate, lanceolate leaflets 11–44mm long, 3–8(–10)mm broad; stipules approximately the same size as the leaflets, oblique at the base. Plants are glaucous throughout and do not usually dry completely black, giving a lustreless olive-grey appearance in the herbarium. Vegetative organs, particularly younger ones often pilose-pubescent. Flowers small (c. 15mm long) (2–)3 – 6, with upper calyx teeth only slightly subequal to the lower.
On sandy soils, including littoral environments.

PHENOLOGY:

Flowering: (November) January to February

Fruiting: January to April

DISTRIBUTION:

Argentina – Chubut, Santa Cruz, Tierra del Fuego. **Chile** - Region XII (Magellanes y Antarctica Chilena)

This variety is sympatric with southern specimens of var. *magellanicus*. Several individuals appear intermediate in form and it may be that var. *glaucescens* represents a response to growing in exposed conditions (cf. discussion on *L. multiceps* var. *setiger* (Philippi) Acevedo under *L. multiceps* Clos).

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

CHUBUT:

Ruta 15, 3km al oeste de intersección de Ruta 15 y Ruta 40. (42°23'37.1"S, 71° 09'54.3"W), *Bonifacio 396* (US).

SANTA CRUZ: Puerto San Julian (49.303°S, 67.712°W), *Blake 4* (BM, K, NY); Puerto San Julian, *Blake 189* (K); Río Gallegos Killik-Aike (51.578°S, 69.219°W), *Brown 29* (NY); Guar. Aiken Road to Punta Arenas (Magellanes) c. 8km west of town of Río Gallegos (51.623°S, 69.43°W) alt. 20m, *Eyerdam et al. 24076* (K).

TIERRA DEL FUEGO:

Lago Arg. 50deg. (50.344°S, 72.282°W), *Burmeister 87* (NY); Depto. Río Grande San Sebastían, borde de playa sobre la Bahía San Sebastían., (53°17'S, 68°26'W) alt. 0m, *Fortunato 4889* (K, NY); Port Famine Strait of Magellan (53.621°S, 70.939°W), *Expedition of Capt. King* (BM); Estancia Los Flamencos 46km W. of Río Grande. (53°42'S, 68°09'W), *Moore & Goodall 272* (K).
UNKNOWN:
Andes Barda las Lajitas alt. 7000ft., *Comber 330* (E, K); PATAGONIA: Bories alt. 500ft. *Elliot 336* (E); Patagonia 50°3'S *Moreno & Tonini 456* (NY – 2 sheets).

12. Lathyrus meridensis Pittier (1938) Boletin Sociedad Venozelana de Ciencias Naturales **4**: 345. TYPE: VENEZUELA: Mucurubá 2700–2800m.Quebrada del pueblo. Junio 27 1930 *Gehriger 264* (holotype: F!, isotypes: NY! US!)

Perennial herb. Rhizomes not seen. Aerial parts (except fruits) not usually blackening on drying. Stems clambering, to 120cm, robust, with very slight wings on the angles. Densely pubescent throughout, with long white hairs and sometimes orange glandular hairs.

Stipules large, semisagittate to very unequally sagittate, the upper lobe lanceolate, 14–35mm long and 7–10mm wide, lower lobe to 7mm. **Leaves** unijugate, terminating in branching tendril. Petioles 10–25mm; leaflets drying to rich brown in the herbarium, with prominent parallel primary veins and densely pubescent with curled hairs on the underside, narrow elliptic to oblanceolate with rounded, slightly aristate apex, 6–10.5cm long and 16–32mm wide.

Inflorescence at least as long as the leaflet of the subtending leaf, with a raceme of 9–11 flowers borne on a robust, erect peduncle 10–12(–26)cm long, floral bracts absent. **Flowers** 14–17mm long, borne on 3–6mm, pubescent pedicels, somewhat pendulous, but becoming more vertical as the pedicels thicken after anthesis. Calyx campanulate tube to 5mm long, pubescent; calyx teeth unequal, the lower linear-acute, 5–10mm long, the upper shorter. Dissected flower not seen. Androecium diadelphous (9+1 stamens), staminal tube oblique. Ovary glabrous, usually drying to black; style c. 5mm long, linear with simple stigma. **Fruits** broadening somewhat towards the apex. glabrous, red-brown, or often blackening, with prominent reticulate veins, 5–6.5cm long and c.0.8 cm wide. Seeds 8–11 per pod, without woolly false septa between the seeds.

PHENOLOGY:

Flowering: December to February (April)

Fruiting: January to March

DISTRIBUTION:

Colombia – Bogotá, Cauca, Norte de Santander, Santander. **Venezuela** – Caracas, Mérida

In sheltered areas among Páramo vegetation.

VERNACULAR NAMES: Arveja macha (Spanish), Arvejo de monte (Spanish).

DIAGNOSTIC NOTES:

This species shares similarities with *L. tropicalandinus* in the petiolate leaves and somewhat pendent flowers. However, the ovaries of *L. meridensis* are consistently glabrous (pubescent in *L. tropicalandinus*).

The complex and variable *L. magellanicus* tends to dry black throughout and plants are less commonly pubescent on the calyces, but individuals in N. Peru do approach *L. meridensis* and there may be a close affinity between the two species.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Colombia

CAUCA: Cordillera Central, Palatera near Río Cauca alt. 2950m, *Penell 7074* (US).
NORTE DE SANTANDER: Pamplona Santa Cecilia alt. 2300m, *Alston 7276* (BM, NY, US).
SANTANDER: Vicinity of Vetas alt. 3100m, *Killip & Smith 17899* (F, NY).
BOGOTÁ: Andes de Bogotá Pasto Tuqhemes alt. 3200m, *Triana s.n.* (K).

Venezuela

CARACAS: *Linden 367* (K, NY).
MÉRIDA: Near Mucuchies alt. 3000m *Alston 6704* (BM, US); Páramos between Sta Domingo and Chachopo alt. 3000m *Jahn 1117* (US); Arriba de El Valle alt. 2400m, *López-Palacios 1791* (NY).

13. Lathyrus multiceps Clos (1847) in Gay C. (ed.) *Historia Fiscia y Politica de Chile* (Flora Chilena II). Claudio Gay, Paris. p.149. - TYPE: CHILE. (P? – not seen)

Lathyrus setiger Philippi (1864) Plantarum novarum Chilensium *Linnaea* **33**: 53. *Lathyrus multiceps* Philippi var. *setiger* (Philippi) Acevedo (1928) Sobre el género *Lathyrus* L. en Chile. *Revista Chiulena de Historia Natural* **31**: 126. TYPE: CHILE, Prov. Colchagua 5-7000ft. *Landbeck s.n.* (holotype SGO!).

Lathyrus eurypetalus Philippi (1893). *Anales Universidad de Santiago* **84**: 278 – 281. *Lathyrus multiceps* Clos forma *eurypetalus* (Philippi) Acevedo (1928) Sobre el género *Lathyrus* L. en Chile. *Revista Chilena de Historia Natural* **31**: 126. TYPE: CHILE, Baños de Chillan Februar 1878 *Collector unknown s.n.* (lectotype, here designated SGO!).

Lathyrus multiceps Clos var. *pastorei* Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6**: 20 *Lathyrus pastorei* (Burkart) Rossow (1982) Notas sobre el género *Lathyrus* (Leguminosae) *Darwiniana* **24**: 492. TYPE: ARGENTINA Neuquén. *Pastore 44* (holotype SI!).

Lathyrus multiceps Clos var. *normalis* Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6**: 20. TYPE: ARGENTINA Neuquén, San Martín de los Andes, *Rasp 91* (holotype SI!).

Prostrate or ascending to erect perennial herb to 60cm high. Not blackening on drying. Rhizomes woody, slender to thickened, creeping, with caudex giving rise to many stems with strongly branching basal nodes. Stems unwinged, but strongly ridged, giving a square cross section to the stem. Sparsely pilose-pubescent throughout.

Stipules semisagittate, the upper lobe very narrow-elliptic to lanceolate, often somewhat curving (falcate), 13–18mm long and 2–6mm across at the base, lower lobe a basal spur c. 2mm long and 1mm broad, somewhat smaller and lanceolate in the lower portions of the plant. **Leaves** unijugate, petiole flattened, 12–18mm long, c. 1mm wide terminating in a small, leaflet-like arista in the lower portions of the plant, in a curling, feeble, simple or rarely few-branched tendril in the upper portions; leaflets borne on small pulvini at tips of petioles, often oriented with the axis of the petiole (i.e. somewhat forward-pointing); upper surface grass green when fresh, lower surface grey-green, glaucous, both surfaces sparse- to densely pilose-pubescent (usually denser on undersides), with prominent, parallel primary veins on the undersides; lorate to very narrow-elliptic, rarely lanceolate (2.5–)3–6.5(–7)cm long and 0.3–10(–12)mm broad.

Inflorescence longer than the leaflets of the subtending leaf, with a raceme of 3–4(–6) flowers borne on a slender to robust, erect peduncle longer than the leaflets of the subtending leaf. Floral bracts present, persistent, minute (0.5mm long), deltoid, rarely longer (to 2mm, linear). **Flowers** borne on slender, 3–5mm long pedicels, pedicels with scattered glandular hairs and sparse to dense pilose-pubescence, becoming more robust at fruiting. Flowers medium to large and showy (12–)16–18(–22)mm long. Calyx campanulate, tube c.4mm long, pilose-pubescent, with some glandular hairs, Calyx teeth fringed with pilose and glandular hairs, lower calyx teeth deltoid to linear, (2–8mm) slightly longer to more than twice as long as the upper teeth, middle and upper teeth deltoid to acute-deltoid, the upper shorter (c. 2mm long). Corolla varicoloured; banner royal blue to lilac or deep purple, often with darker purple veins, blade held erect, orbicular, 15mm long and 15mm wide, with an apical notch, claw c. 6mm long; wings usually paler than banner, sometimes white, blade 15mm long, 8mm wide with a basal pleated process, claw c. 8mm long, curved; keel paler than banner, often same as, or lighter than the wings, blade 11mm long, 6mm wide, claw 8mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1); staminal tube oblique. Ovary densely pubescent; style broadening slightly towards the apex, 5–7mm long, with simple stigma. **Fruits** pilose-pubescent, orange-brown, linear, (5.3–)6–7cm long and 6–8mm wide, upper suture thickened, often lanulose on the inside of the pod near the apex and upper suture, but not enough between the seeds to constitute false septa. Seeds 8–10 per pod, smooth, ellipsoid to cuboid, dark brown, c.4 × 3mm, with hilum c. one twelfth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Seijo & Fernández, 2003)

PHENOLOGY:

Flowering: November to January

Fruiting in January and February

DISTRIBUTION (FIG. 5.14):

Argentina – Chubut, Neuquén, Río Negro. **Chile** – Región VII (Maule), Región VIII (Bío-Bío), Región IX (Araucanía).

On sand and gravel, and volcanic soils, in open forest, at forest margins (and roadsides), and on open sunny slopes.

VERNACULAR NAMES:

Arvejilla

DIAGNOSTIC NOTES (FIG. 5.15):

Lathyrus multiceps is a variable species, showing distinct suites of morphological character states probably in response to the local environment. In light shade, under forest canopies, plants have long internodes and relatively long, sometimes branching tendrils with which they clasp surrounding vegetation. In more exposed, sunny slopes, at the margins of forests, plants are low-growing, forming a compact sometimes cushion-like growth and with tendrils reduced to a simple arista. Specimens showing this latter suite of characters were those described as *L. setiger* by Philippi. These two morphological extremes are sometimes apparent in a single individual where it spreads from under the shade of neighbouring shrubs into a more open site.

The species shows strong morphological affinities to *L. subandinus*. The two can be distinguished by the more slender stipules and leaflets in *L. multiceps* (leaflets lorate to narrow-elliptic in *L. multiceps* versus lanceolate to elliptic in *L. subandinus*), and fewer (3–4), larger flowers in *L. multiceps* ((4–)5–10 in *L. subandinus*). In addition, *L. subandinus* is more densely sericeous-hairy throughout, with a glaucescent indumentum on the entire plant giving an overall more silvery appearance than in *L. multiceps*. Their distribution ranges do not contact. *Lathyrus* *multiceps* is found at lower altitudes (<2000m), in temperate, forested areas of Argentina and Chile, while *L. subandinus* is found in higher altitudes, in the more arid areas around Región Metropolitan, Chile. Some specimens from the more northerly populations of *L. multiceps* (e.g. around Termas de Chillán, in Región VIII, Chile) approach *L. subandinus* in having relatively large, lanceolate leaflets with a very glaucous indumentum, but these can be distinguished on the basis of flower numbers.

Lathyrus multiceps Clos *var. pastorei* Burkart was described on the basis of its imparipinnate leaves - terminating in a leaflet rather than a tendril or arista. This is a common enough aberration in many species of *Lathyrus*, and is of no taxonomic significance.

Gardner & Page 4997 (E) is a specimen noteworthy for its oblanceolate leaflets, very small stipules (upper lobe c. 4mm long, lower lobe c. 1mm), pseudo- verticillate racemes with 5-6 small flowers per inflorescence and very late flowering time (February). It is not clear if this specimen fits into *L. multiceps* or warrants treatment as a new species. Further collections from this area would be highly desirable.

Figure 5.14 ***L. multiceps***
This species is distributed in the southern Andes.

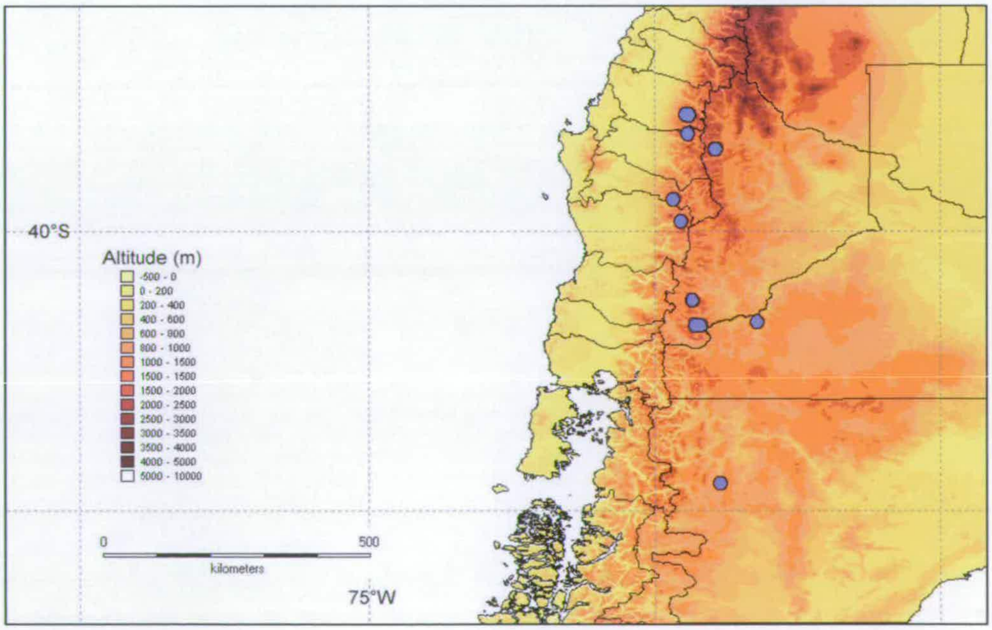
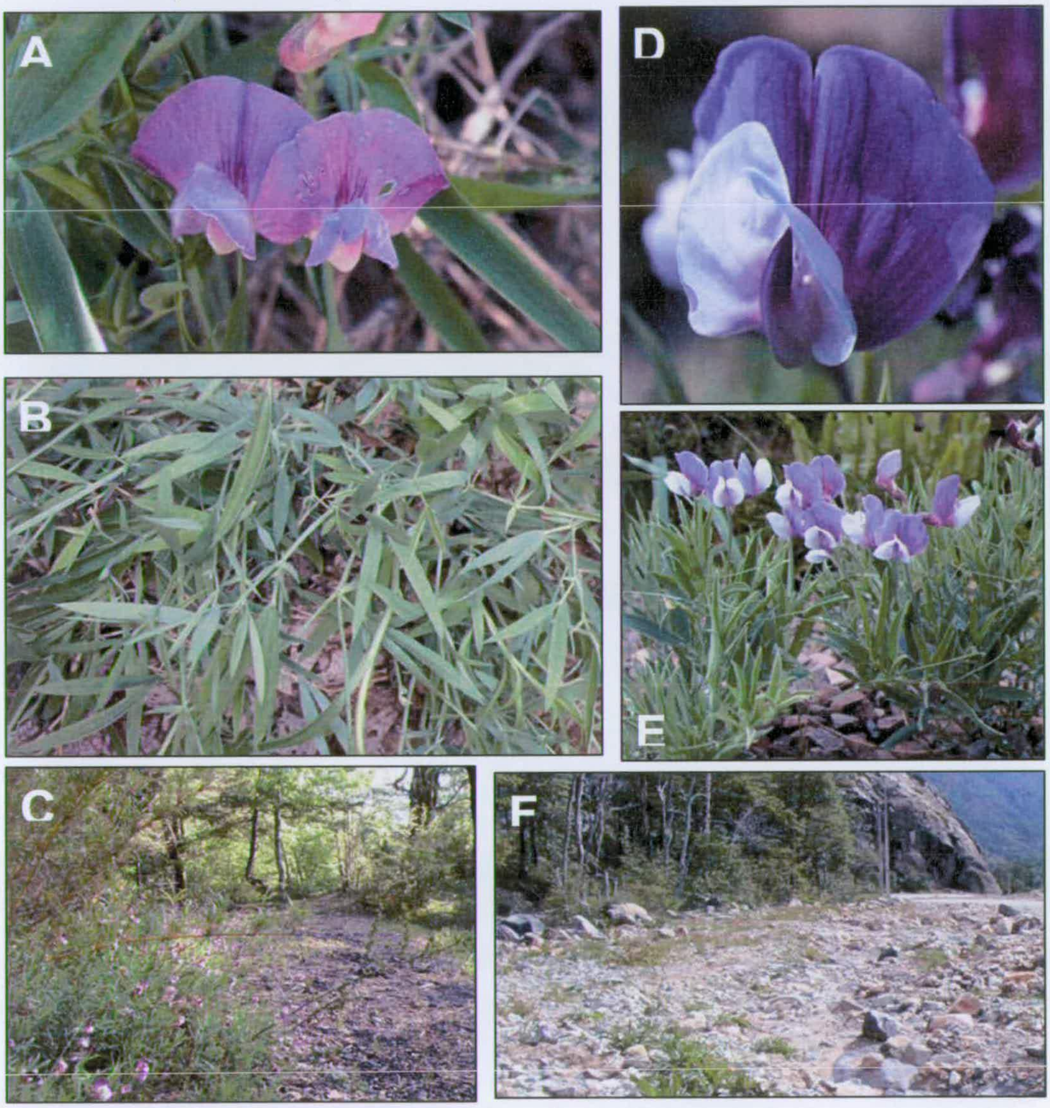


Figure 5.15 ***L. multiceps***
Images on the left show leggy plants from open forest (c. 900m alt.), those on the right are 'setiger' like, compact plants.

A Flowers. Cerro Otto, Neuquen, Argentina.
B Sprawling habit. Termas de Chillan, Chile.
C Habitat. Open forest. Road to Shangri-la, Termas de Chillan, Chile.
D Flower. Specimen cultivated at RBGE (accession number 19912326).
E Plants showing compact form. Specimen cultivated at RBGE (19912326).
F Habitat. Exposed, upland site typical of 'setiger' like plants. Termas de Chillan, Chile (c. 1300m alt.).



SELECTED ADDITIONAL MATERIAL EXAMINED:
Specimens marked * are those showing the 'setiger'-like facies (see diagnostic notes for further information).

Argentina
CHUBUT: Valle Río Foyel *Meyer 9350* (BM).

NEUQUÉN: Nahual Huapi Nt. Park River Traful c. 700 - 1200m *Archer 2* (K); Suangulo (Pulmari) 5000ft., *Comber 483** (E - 2 sheets); San Martin de los Andes, Cerro Colohuincul 2400 – 5000ft., *Comber 712** (E - 3 sheets, NY); Depto. Lacar: 32km al SW de San Martin de Los Andes por Ruta Nac. 234, (40°15', 71°22'W). 850m, *Fortunato 5766** (K, NY); Neuquén, Río Negro Border Altergillas, Lago Traful, Bariloche, *Miles 1* (K); Dep. Lácar Camino de Los Siete Lagos. Arroyo Pichi Traful. 3 Km S del Hotel Pichi Traful, *Seijo 1192* (K); Dep. Lácar Lago Hermoso. En todo el camino sobre cuesta soleado del cerro, *Seijo 1194* (K); Dep. Los Lagos Arroyo Pichitraful, bajada 3km antes de Villa Pichitraful. En borde del camino, *Seijo 1607* (F); Dep. Minas. Lagunas de Epu-lafquen. En estepa graminosa, arriba de bosque de lengas, *Seijo 1700* (NY).

RÍO NEGRO: Cordillera Dep. Bariloche Bariloche, Cerro Otto. Picada por lado SE del Cerro. En cima de cerro, en terreno arrenoso, bajo bosqlue de lengas, semiaberto, *Seijo 1164* (NY).

Chile

REGION VII (MAULE): Jalcareque 1600m, *Philippi s.n** (BM); Prov. Curicó Hacienda Monte grande 1600m, *Werdermann 50** (E, F, NY, US).

REGION VIII (BIO-BIO): Antuco: Cordillera de Los Andes. Fundo Los Ciervos, passing into El Toro hydroelectric central, and crossing the Río Polcura. 823m, *Gardner 1049* (E); Provincia de Ñuble Chillán: Road to Termas Chillán at Puente Torrealba. 1328m, *Gardner & Knees 6774** (E); Provincia de Ñuble Chillán, Cordillera de los Andes: Road to Shangrila. 1461m, *Gardner & Knees 6811** (E); Provincia de Ñuble Chillán, Cordillera de los Andes: Termas de Chillán. Slopes below thermal springs. 907m, *Gardner & Knees 6849** (E); Cordilieres de Chillan, *Germain s.n.* (F); Antuco. Lava zwischen dem Refugio und Los Barros, *Grau 3224** (BM); Ñuble Baños de Chillán 1800 – 1900m, *Pennell 12386** (F, NY).

REGIÓN IX (ARAUCANÍA): Prov. Malleco Lonquimay; Parque Nacional Malalcahuello, Estero de la Plancha. Close to water course in deep volcanic ash ravine dominated by lush herbaceous vegetation and *Escallonia virgata*. Alt. 1500m, (38°48'S, 71°33'W), *Gardner & Page 4997* (E); Sierra Mamuil Malal 5000ft., *Comber 928** (K - 2 sheets); Provincia de Malleco Cordillera de Los Andes, Parque Nacional Tolhuaca. Laguna Verde. *Araucaria araucana* forest. Margin of lake. 1392m, *Gardner & Knees 6894* (E).

14. Lathyrus nervosus Lamarck (1788) Encyclopédie méthodique ou par ordre de materieres. II (Cic. – Gor.) Panckouke, Paris. p. 708. TYPE: URUGUAY. Montevideo *Commerson s.n.* (holotype: P!)

Pisum americanum Miller (1758) *Pisum* in The Gardeners Dictionary. Frances Rivington, London. TYPE: UNITED KINGDOM, cultivated in Chelsea Physick Garden, *collector unknown, s.n.* (holotype: BM!)

Lathyrus armitageanus Knowles & Westcott (1839) *The Floral Cabinet and Magazine of Exotic Botany* **3**: 81. William Smith, London. TYPE: picture tab. 110 in protologue (lectotype, here designated: picture, tab. 110 in Knowles & Westcott, 1839).

Lathyrus trigonus Vogel (1839) De Vicieis Braziliensibus. *Linnaea* **13**: 31. TYPE: URUGUAY *Sellow s.n.* (lectotype – here designated: E!)

Lathyrus ovalifolius Philippi var. *mucronatus* Philippi (1893) Plantas nuevas chilenas. *Anales de la Universidad de Santiago* **84**: 280. TYPE: CHILE Río Palena Jan. Feb. 1887 F. Dèlphín 474 (holotype SGO!, isotype SI!)

Perennial herb, not blackening on drying. Rhizomes woody, with deep tap root, producing many stems. Stems prostrate to scandent, to 80cm, terete, branching at base. Slightly to very glaucous on vegetative organs, glabrous throughout. **Stipules** large, leaflet-like, hastate to ovate-hastate, symmetrical or asymmetrical, occasionally slightly pubescent in axils, the main lobe 1.5–4.1 cm long and (0.7–)1.5–2.5cm broad, lower lobes c. 5(–14)mm, deltoid. **Leaves** unijugate nearly sessile, petioles 0–4(–7)mm, terminating in a branched tendril, the tendril fine or very robust; leaflets on a short (1mm), usually glabrous pulvinus, thick-membranous and hard when dry, both surfaces glabrous, often glaucous-grey, with thick wax, greasy to the touch on dry specimens; veins evident on both surfaces, primary veins sub-parallel, with very reticulate secondary veins and a reinforcing vein running around the margin of the leaf, 2.3–4(–6.8)cm long and 1.2–2.2(–2.5)cm broad, suborbiculate to wide-elliptic, apex usually acute, with a mucro (1–2mm) (length:width ratio c. 1.2–4). **Inflorescence** a raceme, at least as long as the leaflets of the subtending leaf, with a raceme of 3–7(–9) flowers borne on a robust, erect peduncle. Floral bracts absent, although a c.1mm bract-like process is sometimes present at the pedicel base of the apical flower. **Flowers** 15–20mm long, borne on 2–5mm, slender or thickened pedicels, pedicels becoming thicker when fruiting; borne in compact whorls, with inflorescence rachis elongating from anthesis. Calyx campanulate, tube 3 – 4mm long, pubescent; lower calyx teeth linear-acute, 5–7(–10)mm long, second and upper teeth successively shorter and curving upwards, the lower teeth longer than the tube. Corolla sky blue to lilac or purple, sometimes with white wing and/or keel petals; banner held erect, blade 11–19mm long and 12–22mm wide, notched (to 1mm) at the apex, claw c. 6mm long; wing blade 11–16mm long, 5.5–11mm wide with a basal pleated process, claw 6–8mm long, strongly curved; keel blade 9mm long, 4–6mm wide, claw 7–9mm long, fused along the entire length (including the claw); larger flowers typically have larger blades and shorter claws on each petal. Androecium diadelphous (9+1 stamens); staminal tube oblique. Ovary glabrous; style linear to slightly spathulate 5–8mm, with simple stigma. **Fruits** glabrous, red-brown to dull or very dark brown with prominent reticulate nerves, often with woolly false septa, linear, 6.5–8cm long and 5–6mm broad, 11–15-seeded. Seeds smooth, olive to dark red-brown to black 2–4mm across, with hilum c. one sixth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Battistin & Fernández, 1994; Schifino-Wittmann, 2001; Seijo & Fernández, 2003)

PHENOLOGY:
Flowering: (September) November to February (April).
Fruiting: December to February (May).
Flowering times are considerably later in southern populations (January to April), with fruiting January to May.

DISTRIBUTION (FIG. 5.16):
Argentina – Buenos Aires; Chubut, Neuquén, Río Negro, Santa Cruz. **Brazil** – Paraná, Santa Catarina; **Chile** – Región XI (Aysén); Región XII (Magellanes y la Antártica Chilena). **Uruguay**. Among low vegetation and in coastal areas (including dune slacks), open scrubland; in stony, gravelly and sandy soils, and in crevices on cliff-faces.

VERNACULAR NAMES:
Cape Horn pea (English), Lord Anson's pea (English), the Anson pea (English), South Sea pea (English) *Lathyrus magellanicus* of gardens (English – occasional horticultural use), Alberjilla silvestre (Spanish)

DIAGNOSTIC NOTES:
Lathyrus nervosus shows strong morphological affinities to *Lathyrus elegans* and *L. paraguariensis*. Differences are summarised in the table under *L. elegans*.

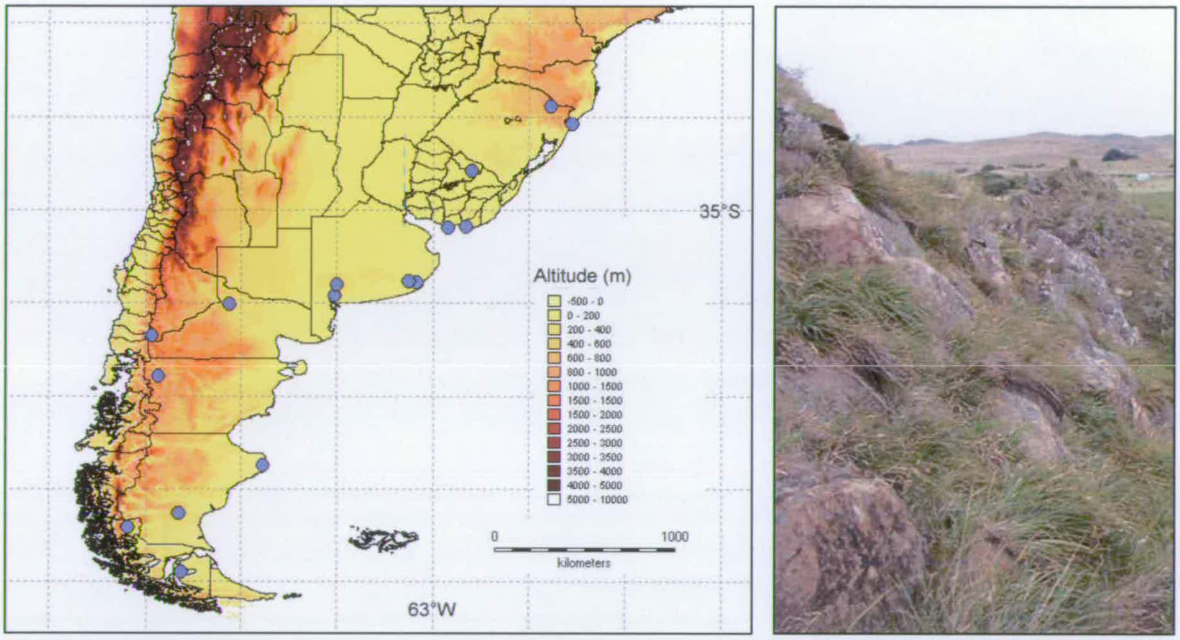
Lathyrus nervosus is an extremely widespread and quite variable species.

Plants from the south of the species' range (e.g. Buenos Aires Province and southwards through coastal Patagonia and into Chilean Tierra del Fuego) generally differ from those in the north (Brazil, Uruguay, NE. Argentina) in several ways:

- The overall size of southern specimens is typically smaller, including smaller, more rotund leaflets and stipules with acute apices. In the north of the range, leaflets are more elliptic or elliptic-ovate and leaflet and stipule apices tend to be somewhat more rounded.
- The habit is generally more prostrate and creeping. This may be a response to differing habitats. Plants in Patagonia and Tierra del Fuego live in exposed coastal gravel and sand, whilst those from northern Argentina, Uruguay and Brazil often grow amongst somewhat taller vegetation. The progeny of specimens from Tierra del Fuego cultivated under glass in Edinburgh, UK retain all the above features of the parent plants.
- Fewer flowers per raceme [2–4(–5)] in southern plants than in northern plants (5 – 9 flowers). There is no obvious geographical correlation with flower size, but those in the south tend to be more consistently large.

The seeds (or more probably the entire plants) were alleged to have been used as an emergency food for the members of Commodore Lord Anson's circumnavigation of the globe (1740 – 1744) during the war between Britain and Spain. Gorer et al. (1991) have identified this expedition as the most probable origin of the plants that appeared in Britain, gaining popularity as a garden plant during the late 18th century. *Lathyrus nervosus* remains the most popular member of sect. Notolathyrus in cultivation - certainly in the northern Hemisphere. Historical misidentifications have perpetuated themselves in the UK at least and this species is sometimes sold as *Lathyrus magellanicus*.

Figure 5.16 ***L. nervosus***
This species is found throughout temperate eastern and southern South America in open, rocky habitats



SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Balcarce Co. La Bachica *CBU, Cazzamiga & Montes 3595* (NY); Sierra de Ventana Sauce Grande, *Hauthal s.n.* (NY); km 25 on road Mar del Plata-Balcarce. Rocky outcrop, *Klitgaard 101* (K); Pdo. Tornquist Sierra de la Ventana, Abra de la Ventana, *Proyecto Ventania 319* (NY); Pdo. Tornquist Sierra de la Ventana: vertiente, *Proyecto Vantania 801* (NY); Pdo. Tornquist. Parque Prov. Tornquist, *Seijo 1206* (NY); Balcarce Sierra Bachicha, 6km N of the town, *Wall & Sparre 155* (K).

CHUBUT: Zona basale delle pendici settentrionali del monte Nahuel Pan, ad est di Esquel, *Pichi Sermolli & Bizzarri 7361* (K).

NEUQUEN: Dep. Los Lagos Camino a Villa La Angostura, Km25, Camino de tierra que sube al cerro y lleva a entrada de estancia, *Seijo 1188* (NY)

RÍO NEGRO: Río Negro Roca, *Roth s.n.* (NY); Dep. Bariloche Ruta 237 y vias del tren. En terreno pedregosos y soleado, *Seijo 1186* (K)

SANTA CRUZ: Growing among rocks at Deseado, *Andrews s.n.* (E); Lago Arg.[entino?], *Burmeister* (NY); Pr. Deseado, *Donat 26* (F, NY); Lago Argentino, declive herboso, *Dusén 5786* (K); Argentina Port Desire *King 37* (BM); In the vicinity of the south shores of Lake Argentine, from 30 to 50km westward of the Santa Cruz river., *Furlong 83a* (NY).

Brazil

RÍO GRANDE DO SUL: Brazil Río Grande do Sul Torres, *Hatschbach & Koczicki 27224* (NY); Passo do Socorro p. Vacaria, *Rambo 51535* (US); Torres Furnas, *Stehmann 750* (F); Torres Próximo ao mar, *Vianna ICN 28857* (F).

Chile

REGIÓN XI (AYSÉN): Puerto Ibáñez, Lago Buenos Aires, *Fuenzalida s.n.* (SGO)

REGIÓN XII (MAGELLANES Y LA ANTÁRTICA CHILENA): Prov. Ultima Esperanza: Torres del Paine: Salta Grande, *Gardner & Knees 6062* (E); Tierra del Fuego c. 32km S. of Porvenir on road to Caleta Joséfina (Onaisín) (53°26'S, 70°04'W),Wahía Inutil, E. slopes of valley, *Moore & Goodall 2* (K).

Uruguay

MALDONADO: *King 62* (BM); Piriápolis Cerro San Antonio (Ladera opuesta al mar), *Neffa 1997* (NY)

MONTEVIDEO: presented by, *M. Ernest Gibert no. 151* (K); Malvin, *Herter 463* (F, NY); Pajas Blancas entre rocas maritimas, *Rosengurtt B-2132* (NY)

SAN JOSÉ: Balneario Kiyú, *Del Puerto 3073* (US).

Cultivated specimens

UK, London, Chelsea Physick Garden, *No collector 2029 (*BM); UK, London, Hyde Park *May T.* (BM).

15. Lathyrus nigrivalvis Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p. 68. TYPE: ARGENTINA – Chaco, Fontana. 7 X 1933 *Burkart 598* (holotype SI!, isotype: K!).

Lathyrus nigrivalvis Burkart forma *puberulus* Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p. 71. TYPE: ARGENTINA – Formosa, Monte Iponá *Spegazzini 726* (Type not seen).

Annual or biennial herb, glabrous or nearly so, glaucous throughout, stems greying on drying, ovaries, fruits, buds and calyces blackening when dry, vegetative organs (e.g. leaflets and stipules) sometimes darkening at the bases. Rhizomes somewhat woody, slender, not running, giving rise to several stems, branching at the base. Stems clambering, to 70cm (–2m), with 1-2mm wings on the stems.

Stipules large, sagittate, the upper (primary) lobe orbiculate to lanceolate 12–17(–21)mm long and 7–12(–17)mm broad, typically broader and with a more rounded apex in the upper portions of the plant. Lower lobes equal or unequal, deltoid to 6mm. **Leaves** unijugate, terminating in a simple or branched tendril. Leaflets borne on a short (1mm), glabrous petiolule; upper and lower surfaces glabrous, glaucous grey-green, with the upper surfaces somewhat brighter; 2–3 primary veins apparent on the undersides of the leaflets and sub-reticulate venation apparent on the upper surface, narrow elliptic, narrow ovate to lanceolate, with distinctly rounded, mucronate apex 4.3–7.3cm long and 0.9–3.1cm wide. **Inflorescence** usually about the same length as the leaflets of the subtending leaf, but often considerably longer, with (1–)2–4 flowers borne on a robust, erect peduncle. Floral bracts minute(<0.5mm), blunt deltoid. **Flowers** small, 10–13(–15)mm long, borne on 3–5mm glabrous pedicels, held horizontally (at 90° to the main inflorescence axis). Calyx campanulate, tube c.4mm long, glabrous; lower calyx teeth linear, 4–7(–10)mm long, middle teeth subequal, linear or deltoid (3–6mm) and upper teeth shorter, deltoid 2–4(–6)mm, the middle and upper teeth curving upwards. Corolla sky blue to pale mauve-pink with banner pale pink, pale fuchsia to lilac, wings and keel often lighter (pale pink to white); banner obovate, blade held erect, 9mm long and 9mm wide, with no apical notch, claw 3mm long; wing blade 6mm long, 3mm wide with a basal pleated process, claw 3mm long; keel blade 7mm long, 3.5mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1); staminal tube somewhat oblique. Ovary glabrous; style c. 3 – 5mm, spathulate, often folding longitudinally when dried, with simple stigma. **Fruits** glabrous, mid-to dark brown, usually blackening on drying, linear, 5.5 – 6 cm long and 4 – 5mm broad, contracting around the seeds to give a distinctive nodose appearance (moniliforma from above), c. 10-seeded, often with woolly false septa separating the seeds. Seeds smooth, dark brown-black, somewhat purple tinged subspherical c. 3mm across, with hilum c. one sixth of the circumference.

CHROMOSOME NUMBER: 2n=14 (Senn 1938)

PHENOLOGY:
Flowering: August - early December (January)
Fruiting: October - January

DISTRIBUTION (FIG. 5.17):
Argentina – Chaco, Corrientes, Entre Ríos, Formosa, Santa Fé.
By creek banks and in seasonally flooded areas - from wet chaco through to forests surrounding Ríos Uruguay and Paraná

VERNACULAR NAMES:

Alberjilla (S. American Spanish)

DIAGNOSTIC NOTES (FIG. 5.18):

Lathyrus nigrivalvis is most likely to be confused with the other wetland species with glabrous ovaries. For differences, see *L. macrostachys*.

Confusion with *L. magellanicus* is also possible in the herbarium, although the two can be distinguished as *L. magellanicus* is a perennial plant of drier habitats (with a linear or only slightly spathulate style and usually has more than 4 flowers per raceme).

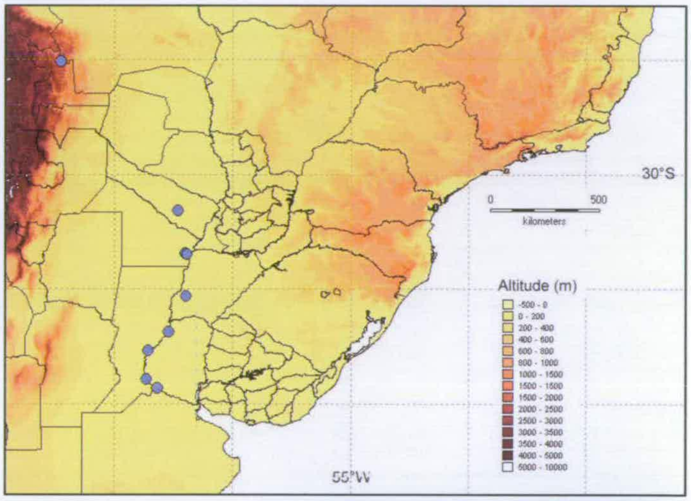


Figure 5.17 *L. nigrivalvis*
This species is found in wet Chaco swamps in the watershed of the Paraná river.

Figure 5.18 ***L. nigrivalvis***
(Below) Small, often paired flowers.
(Right) Habit - note glaucescence

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

CHACO: Las Palmas, *Jørgensen 2689* (US); Fontana (27.4160°S, 59.035°W), *Meyer 598* (K); Barranqueras Bajo anegadizo, cerca riacho Barranqueras (27.4780°S, 58.939°W), *Schulz 1.189* (F).

CORRIENTES: Empedrado Estancia Las Tres Marias, *Pedersen 6391* (K)

ENTRE RÍOS: Delta del Paraná islas frente a San Nicolas (33.2970°S, 60.188°W), *Burkart 15595* (F); La Paz isla Curuzú, Chalí Norte (30.837°S, 59.726°W), *Burkart et al. 29928* (F).

FORMOSA: Dpto Pirané NE de Palp Santo, entre Palo Santo et le Riacho Pilagá (25.5630°S, 59.352°W) *Charpin & Eskuche AC202333* (US); El Colorado Ribera baja del Río Bermejo carrizal (29.304°S -59.377°W) *Schulz 17.533* (F).

SANTA FÉ: Isla del Francés Frente a Rosario (32.9260°S, 60.644°W), *Burkart 8809* (F, NY); Timbó entre Colastine y Paraná (31.6640°S, 60.579°W), *Burkart et al. 23648* (F).

16. Lathyrus nitens Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 25.
TYPE: URUGUAY? Sello s.n. (lectotype, here designated: K!; isolectotypes E-GL! F! K!).

Perennial herb not blackening on drying. Rhizomes creeping; caudex decumbent, partially subterranean, giving rise to many erect, branching stems. Stems to 40cm, quadrangular, with slight ridges on two angles, but without wings, even in the upper portion of the plant. Lanulose-pubescent throughout, with simple golden hairs and scattered glandular hairs.

Stipules simple, without lower basal spur (i.e. not semisagittate or sagittate) 6–16mm long and 1–3mm broad at the base, smaller in the upper portions of the plant. **Leaves** unijugate, rarely with 3 leaflets (two on one side of the rachis, one on the other), terminating in a short (less than 2.5cm), usually simple, or branching tendril in 3-leafleted leaves; petioles dorsally compressed, 4–9mm long; leaflets with pubescent pulvini, both surfaces pubescent; primary veins parallel, with many connecting secondary veins, narrow elliptic, rounded at the apex and shortly mucronate, 35–45(–53)mm long and 5–6(–9)mm broad. **Inflorescence** a raceme, twice as long as the leaflets of the subtending leaf, with an erect peduncle bearing a raceme of c. 12 flowers arranged in pseudo-verticels. Floral bracts absent. Flowers 12–15mm long, borne on 2–3mm, pubescent pedicels, suberect. Calyx tube campanulate, 4–5mm long, densely pubescent; lower calyx teeth linear, acute, c. 5mm long, middle and upper teeth equal, deltoid, ca. 2mm; dissected flower not seen; ovary, densely pubescent, style not seen. **Fruits** sericeous-hairy, with simple and glandular hairs, chestnut to dark-brown, linear, c. 5.5cm long and 5mm broad, without woolly false septa.

PHENOLOGY:
Unknown

DISTRIBUTION: **Uruguay**? – Known only from Sello's collections, the protologue reads: *Sellow leg. In Montevideo?*

DIAGNOSTIC NOTES:
Lathyrus nitens is not known from collections other than Sello's. Specimens of *L. acutifolius* are often found under the name *L. nitens* in herbaria, although the two are distinct species. *Lathyrus linearifolius* is morphologically similar to *L. nitens* and *L. acutilfolius*. A table summarising the differences among these three species is

given under *L. acutifolius*. The only other species with which *L. nitens* might be confused are:

- *Lathyrus tomentosus* has far larger flowers (22–28mm versus 12–15mm long in *L. nitens*) and is tomentose hairy throughout (rather than pilose or lanulose-pubescent).
- *Lathyrus subulatus* never has more than 4 flowers per raceme (c. 12 in *L. nitens*), and leaflets only up to 3.5mm broad (5–9mm broad in *L. nitens*).

TYPES:

Lathyrus nitens appears to be only known from Sello's collections. The only extant Sello specimen I have seen with mature, open fruits is the Kew specimen. Although this specimen has no flowers, all of the diagnostic characters are present on the otherwise well preserved stems. Consequently, I have selected this specimen as the lectotype.

Photographs of a Berlin specimen are held in the Field Museum, Chicago and in New York, but these photographs do not show mature fruits. The Chicago specimen is accompanied by a fragment of stem and leaf, and a single flower (the only specimen I have seen with a flower). It is likely that these specimens all represent a single collection that was later dispersed to herbaria in the UK and USA.

Orobus nitens Alefeld is marked on the photograph from Berlin held in F and NY. However, this name appears never to have been published.

17. Lathyrus paraguariensis (Hassler) Kenicer comb. & stat. nov.

Lathyrus nervosus subsp. *paraguariensis* Hassler "nov. sspec. An spec. nova!" (1919), ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum*: **16**: 226. TYPE: PARAGUAY: ad flumen alto Paraná, *Fiebrig 6252* (holotype SI!).

Perennial herb, not blackening on drying. Rhizomes not seen, giving rise to several robust stems. Stems clambering to 1m, terete, with vertical ridges. Plant glabrous throughout.

Stipules large, hastate, asymmetrical; upper lobe 1.9–3.2cm long and 0.8–1.5cm broad, primary lower lobe deltoid, 5–8mm long, secondary lower lobe smaller.

Leaves unijugate, sessile, terminating in a branched tendril; tendrils unbranched for 10–15cm beyond the leaflets, then branching at the apex; leaflets sessile, erect, appearing to clasp stem at the base; upper surface grass green when fresh, lower surface somewhat glaucous grey-green when fresh, both surfaces glabrous; primary veins parallel, but masked by prominent reticulate secondary veins; very narrow elliptic-lanceolate, 9–15cm long and 0.7–1.5cm wide (L:W ratio 10+).

Inflorescence a loose raceme, usually longer than leaflets of the subtending leaf, with 16–30 flowers borne on a robust, erect peduncle to c.15cm. Floral bracts absent.

Flowers small, to 12mm long, borne on very slender 2mm, pubescent pedicels, somewhat pendulous. Calyx campanulate, tube c. 3mm long, glabrous; lower calyx teeth linear, c. 2mm long, the upper deltoid. Corolla pale purple-blue; banner oblong-panduriform, blade held erect, small, 7mm long and 10mm wide, with slight apical notch, claw 7mm long; wing blade 8mm long, 4mm wide with a basal pleated process, claw c. 7mm long; keel blade 8mm long, 4mm wide, claw 7mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9 + 1 stamens), staminal tube rounded-oblique. Ovary glabrous, brown, style c. 5mm long, with a simple stigma. **Fruits** glabrous, dull brown, linear, 6 – 7 cm long and c. 4mm broad, c. 17-seeded. Seeds not seen.

PHENOLOGY:
Flowering: November
Fruiting: December

DISTRIBUTION: **Brazil** – Paraná, Santa Catarina; **Paraguay**

ADDITIONAL SPECIMENS EXAMINED:

Brazil

RÍO GRANDE DO SUL: Bom Jesus, Ca. 50km N of Bom Jesus, rd to São Jaoquim (28°31'56"S, 50°05'19"W), *Miotto et al. 2220* (E!, FHO, ICN)

Neubert and Miotto (2001) record this species from Santa Catarina as well.

DIAGNOSTIC NOTES:

This species is undoubtedly closely allied to *L. nervosus* Lamarck and *L. elegans* Vogel, although they can be distinguished on the basis of calyx tooth length, flower number and leaflet shape, as well as distribution and habitat preferences (see description for *L. nervosus*).

TYPES:

Hassler (1919) was uncertain if this entity constituted a new species or an infraspecific taxon within *L. nervosus*. He does not appear to accept either unequivocally, presenting the taxon as follows:

> *443* Lathyrus nervosus *Lam. Dict. II 708. . .*
> *. . . ssp. Lathyrus paraguariensis Hassler nov. sspec. an spec. nova!*

This creates a difficult nomenclatural problem, that none of articles 24.4, 34 or 35 of the St Louis Code (Greuter et al. 2000) addresses appropriately. Although the taxon was accepted at species level by Burkart (1935) and by Neubert and Miotto (2001), neither author published it as a new combination. Consequently, I publish it here as a new combination, at species level.

18. Lathyrus paranensis Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p. 71. TYPE: ARGENTINA Buenos Aires. Delta, Miní. 4 XII 1931 *Burkart 4090* (lectotype here designated: SI!, isolectotype SI!).

Lathyrus magellanicus Lamarck forma *albiflorus* O. Kuntze (1898) Revisio Generum Plantarum III. London, Dulaud & Co.p.65 TYPE: ARGENTINA: Buenos Aires, Tandil XI 92 *Kuntze s.n.* (holotype NY!).

Lathyrus paranensis Burkart forma *albiflorus* Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p.74. Type: Uruguay Canelones entre Mosquitos y Piedras de Afilar. *Osten 20069* (not seen).

Annual herb to 100cm, darkening to brown or black on drying, particularly the calyces and at bases of the stipules. Rhizomes not creeping, giving rise to several stems. Stems scandent, to 1m, winged (to 2mm). Typically glabrous throughout, except for a fringe of hairs in the axils of the calyx teeth.

Stipules large, unequally sagittate to semisagittate, upper lobe lanceolate to linear-lanceolate, occasionally slightly falcate 15–35(–50)mm long and 6–15(–17)mm wide, larger lower lobe acute-triangular, 6–7(–12)mm long, the other lower lobe shorter.

Leaves unijugate, terminating in a branched tendril; leaflets sessile, with a few pilose hairs, somewhat glaucous, both surfaces glabrous or lower surface with very sparse pilose hairs; c. 5 parallel primary nerves conspicuous on the undersides of the leaflets, linear (54–)70–120(–135)mm long and 3–12(–15)mm wide.

Inflorescence much longer than the leaflets of the subtending leaf, 14–25(–45)cm total, with a loose raceme of 3–12 flowers borne on a robust, erect peduncle. Floral bracts present, minute (0.5–1mm), blunt. **Flowers** large, 17–21(–24)mm long, borne on slender 3–4mm, glabrous pedicels, held horizontally (at 90° to the main inflorescence axis) or somewhat erect. Calyx campanulate, tube c. 3–4mm long, glabrous, or with a fringe of hairs at the base of the teeth, darkening on drying, lower calyx teeth linear, far exceeding the calyx tube in length (6–9mm long), the middle and upper teeth deltoid to linear, 3–7mm long.

Corolla blue-violet to lilac, or white (recognised by Burkart 1935 as forma *albiflorus*), often with keel pale violet to white; banner blade held erect, orbicular, 18mm long and 18mm wide, with slight apical notch, claw 5mm long; wing blade 12mm long, 8mm wide with a basal pleated process, claw c. 7mm long; keel blade 17mm long, 9mm wide, claw 7mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1); staminal tube slightly oblique or truncate. Ovary glabrous, style linear, 9–12mm long, pubescent for <⅓ length, with a simple stigma.

Fruits held suberect, glabrous, black, linear, 6.5–9cm long and 5mm broad, c. 20-seeded, with woolly false partitions between the seeds. Seeds smooth, spherical, very dark red-brown, 2 – 3mm across, with hilum c. one sixth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Senn 1938; Schifino-Wittmann, 2001)

PHENOLOGY:

Flowering: October to November (February)

Fruiting: November to December (February).

DISTRIBUTION (FIG. 5.19):

Argentina – Buenos Aires, Corrientes, Entre Ríos; **Brazil** - Paraná, Río Grande do Sul; **Uruguay** – Banda Orientale, Rocha, San José, Soriano.

At the margins of water-filled channels and by standing water in wet forests, and among oter marginal vegetation near the Uruguay and Paraná rivers.

DIAGNOSTIC NOTES:

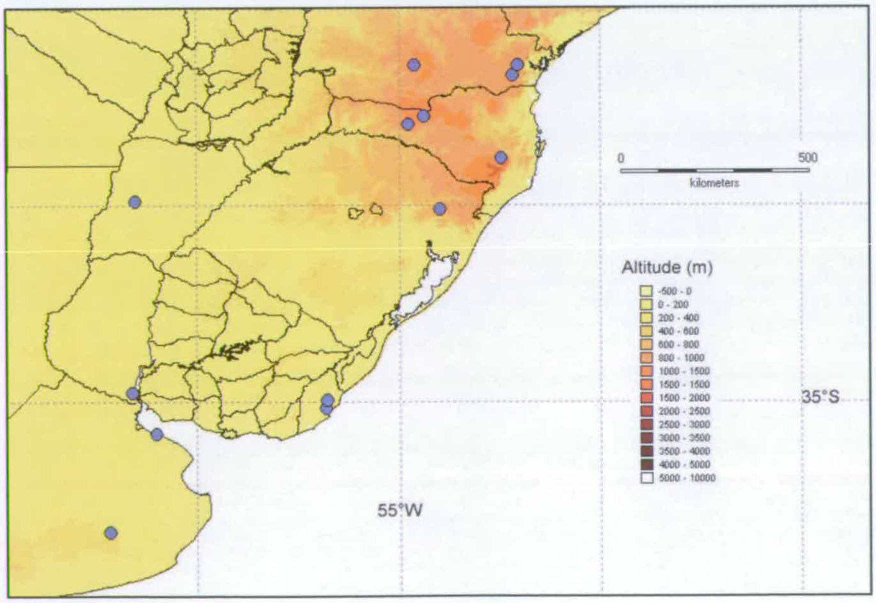
Lathyrus paranensis has morphological similarities to *L. parodii*, *L.nigrivalvis* and *L. macrostachys*. All are found in similar moist or waterlogged habitats (refer to the description of *L. macrostachys* for a summary of distinguishing characters).

EQUIVOCAL SPECIMENS AND OTHER NAMES:

Hatschbach 20378 (F, K, NY - from Piraquaren, Paraná, Brazil) is exceptionally pubescent throughout, with dense pilose hairs and has the smallest leaflets of any specimens seen. The leaflets tend to be very narrow elliptic, and with distinctly rounded apices. This degree of pubescence is unlike anything in *L. paranensis* or the other glabrous-ovaried wetland species (*L. nigrivalvis* and *L. parodii*), but the large flowers, with erect banners, and the long (1cm) style borne on a glabrous ovary identifies this as *L. paranensis*. Comparison with other, more recent collections from the area would be of great value to determine if this warrants a separate taxonomic identity.

The Kew specimens of the same collection are all unijugate. Plants from this collection have dried very black in colour and are small in all organs except for the flowers, which are large, and with long, linear styles. The specimens *Bartlett 21353* (from Uruguay - NY); *Hatschbach 2564* (Paraná, Brazil – SI); *Smith & Klein 13450* (Santa Catarina, Brazil – F) and *Smith & Klein 13965* (Santa Catarina, Brazil – NY), and *Smith & Reitz 10419* (Santa Catarina, Brazil – NY) show similar characteristics. Burkart annotated the specimen *Hatschbach 2564* with the name *L. magellanicus* var. *brasiliensis*, but never published it. Further collections from Southwestern Brazil are very desirable.

Figure 5.19 *L. paranensis*
This species is distributed in the watersheds of the Paraná and Uruguay rivers.



SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Delta del Paraná P. Miní, *Burkart 3937* (K); Río de La Plata Punta Lara (34.82°S, 58°W) *Cabrera 2427* (NY); Río de la Plata Isla Martin Garcia, *Cabrera 2855* (NY); Reveo El Progreso, *Dawson 356* (NY); Punta Lara (34.82°S, 58°W), *Dawson 1016* (NY); Sec. 1 Río Parana de Las Palmas. Recreo Naon 10m, *Eyerdam & Beetle 23103* (K). Zarate Las Palmas (34.08°S, 59.168°W) *Hunziker 1683* (K); Tandil (37.32°S, 59.14°W), *Kuntze s.n.* (NY); Delta Arroyo Mendez Grande, *Scala s.n.* (NY); Paraná Guaju, Buenos Aires, *Scala s.n.* (NY); Tandil La Cascada –(37.325°S, 59.145°W) *Troncoso 1275* (F, NY).
CORRIENTES: Dep. San Roque Estancia Caaguazú, 11Km NE de Chavarría, camino a Tacuaritas. Arroyo aprox. 2km al SW del casco. (28.9°S, 58.519°W) *Arbo, Cáceres., Ferrucci & Maruñak 6824* (NY).
ENTRE RIOS: Delta del Paraná Arroyo Martínez *Burkart 15081* (F); Dep. Gualguaychú Brazo Largo, ruta 14 (33.78°S, 58.6°W) *Troncoso et al. 2370* (F).

Brazil

PARANÁ: Ponta Grossa (Lagoa Dourada), *Dombrowski 9111* (US); Serrinha, in paludosis (25.697°S, 49.1857°W), *Dusén 8554* (BM, K); Piraquaren Pinhaes –(25.45°S, 49.06°W) *Hatschbach 20378* (F, K, NY); Mun. Palmas Santo Agostinho, *Hatschbach 53659 & V. Nicolack* (US, K); Guarapuava 10 km ao oeste de Guarapuava (25.44°S, 51.64°W) 1100m *Reitz & Klein 17.638* (F, NY).
RÍO GRANDE DO SUL: Porto Alegre Bei Saô Joaô, *Reineck & Czermack 600* (E); Caxias do Sul Fazenda Souza (29.12°S, 51.02°W) 780m *Scur 203* (NY, US).
SANTA CATARINA: Mun. Agua Doce Campos de Palmas 28.5 km southeast of Horizonte (Paraná) (26.75°S, 51.4°W) 1000 - 1200 m, *Smith & Klein 13450* (F);
Mun. Irani Campo de Irani (26.95°, 51.81°W) 700 - 900 m, *Smith & Klein 13965* (NY); Mun. Bom Retiro Fazenda Campo dos Padres, Campo dos Padres (27.8°S, 49.49°W) 1650m, *Smith & Reitz 10419* (NY).

Uruguay

BANDA ORIENTALE: *Gibert 804* (K).
ROCHA: hilly country 25km north of Castillos (33.96°S, 53.8°W), *Bartlett 21353* (NY); Castillos (34.164°S, 53.834°W) 50m, *Herter 426b* (NY).
SAN JOSÉ: Paso del Bote, *Herter 462c* (F).
SORIANO Juan Jackson Monzón-Heber, *Gallinal et al. PE 5359* (US, NY).

19. Lathyrus parodii Burkart (1935) Revisión de las especies de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**, Universidad de Buenos Aires, Buenos Aires. p.100 TYPE: ARGENTINA: Buenos Aires: Delta del Paraná: Canal la Serna. 4 XII 1931 *Burkart 4034* (holotype: SI!, isotype: K!)

Lathyrus parodii Burkart var. *brevipetiolata* Burkart ex Izaguerre & Beyhaut (1998) Las leguminosas en Uruguay y Regiones Vecinas **1**: Papilionoideae, Hemisferio Sur, Montevideo. p. 350 TYPE: BRAZIL: Río Grande do Sul: Bom Jesus *Dutra 1516* (holotype: SI!)

Perennial herb not blackening on drying. Rhizomes slender, creeping. Stems clambering to 1.5m, subquadrate, with wings c.1.5mm wide. Pilose-pubescent, near the nodes, with a line of hairs down the stem at 90° to the wings when viewed in cross section.

Stipules unequal sagittate to auriculate, large, the upper lobe lanceolate to broad-lanceolate with acute apex, 20–33mm long and 9–12mm broad, the lower lobes blunt deltoid to linear acute, 2–5mm long, pubescent in axils. **Leaves** unijugate, terminating in a branched tendril, petioles (1–)17–21mm long. Leaflets glabrous, glaucous; primary veins parallel, apparent on the undersides of the leaflets, lanceolate, 7.5–11cm long and 0.5–1.6cm wide.

Inflorescence a raceme, much longer than the leaflets of the subtending leaf, with 8–12 flowers borne on a robust, erect peduncle. Peduncle canaliculate. Floral bracts absent. **Flowers** small, 10–13mm long, borne on 1–3mm, glabrous pedicels, held somewhat erect (at 90˚ to the main inflorescence axis). Calyx campanulate, tube c. 3mm long, glabrous; lower calyx tooth lanceolate, to 8mm long, middle teeth slightly shorter and upper teeth much shorter (to 3mm), deltoid and curving upwards, all teeth ciliate or fringed with simple hairs. Corolla violet; banner blade held erect, orbicular, 8mm long and 11mm wide, with slight apical notch, claw 6mm long; wing blade 9mm long, 4mm wide with a basal pleated process, claw c. 5mm long; keel blade 6mm long, 3mm wide, claw 6mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1). Staminal tube slightly oblique. Ovary glabrous; style linear, c. 4mm long, with simple stigma.

Fruits glabrous, red-brown, linear, short 3.5–4cm long and c.5mm broad. Seeds smooth, dark brown-black, somewhat cuboidal, 2–3mm across, with hilum c. an eighth of the circumference.

CHROMOSOME NUMBER: 2n=14 (Senn 1938)

PHENOLOGY:

Flowering: December (March).

Fruiting: December - March

DISTRIBUTION:

Argentina – Buenos Aires. **Brazil** – Paraná

In inundated areas and other very moist soils, near forest margins.

DIAGNOSTIC NOTES:

This is a seldom recorded species, known from only a few collections. Although it is superficially similar to some of the more common glabrous-ovaried species from near the Uruguay and Paraná rivers (*L. macrostachys*, *L. nigrivalvis* and *L. paranensis*), *L. parodii* shows no trace of darkening on drying (refer to the description of *L. macrostachys* for further differences).

Hatschbach 15408 (US) has near-sessile leaves, so it is very similar to *Dutra 1516* (SI), the type of *Lathyrus parodii* Burkart var. *brevipetiolata* Burkart ex Izaguerre & Beyhaut. However, both of these specimens conform in all other ways to typical *L. parodii* and I see no merit in distinguishing them as varieties.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES:

Delta del Paraná *Burkart 4541* (K); Delta del Paraná Canal la Serna, *Burkart 4034* (K); Delta del Paraná Arroyo Brazo Largo. Pajonal Orero, *Burkart 8281* (F).

Brazil

PARANÁ:

S. Agostinho (mun. Palmas), *Hatschbach 15408* (US).

20. Lathyrus pubescens Hooker & Arnott (1831) Botany of *Captain Beechey's Voyage*. London, Henry G. Bohn. p.21; *Orobus pubescens* (Hooker et Arnott) Alefeld (1861) Ueber Vicieen. *Bonplandia* **9**: 143. TYPE: CHILE: Valparaiso *Cuming 484* (lectotype, here designated: E-GL!, isolectotypes E-GL! – 2 sheets, BM!)

Variable perennial herb, not blackening on drying. Rhizomes thickened, giving rise to many stems. Stems robust, clambering to 200(–300)cm, typically shorter (c. 50 cm), much branched above the base of the plant, unwinged, pubescent, with simple and glandular hairs, rarely near-glabrous.

Stipules semisagittate, the main lobe ovate to lanceolate, (5–)9–23mm long and (2–)5–14(–18)mm broad, with acute lower lobe, 4–12mm long. **Leaves** unijugate, occasionally bijugate on the upper leaves, petioles 9–24(–50)mm long, pubescent, dorsally compressed, terminating in a branched or simple tendril, sometimes with a long (to 12cm), very robust rachis between the leaflets and point of branching of the tendril, in which case, often with 3 or 4 alternate leaflets; leaflets borne on a 1-3mm, pubescent petiolule; upper surface dark green when fresh, lower surface slightly glaucous, both surfaces pubescent, with simple and glandular hairs, the upper surfaces typically less densely hairy than the lower and occasionally glabrous; parallel primary veins apparent on the undersides of the leaflets, elliptic to linear-lanceolate, (2–)2.6–6.5cm long and (0.5–)1–1.8(–2)cm wide.

Inflorescence a raceme of 7–13(–16) flowers borne on a robust, erect peduncle (3–)6–15(–25)cm, racemes often compact at the apex, becoming more spaced out as the inflorescence matures. Floral bracts absent. **Flowers** medium to large, 14–19(–23)mm long, borne on 2–3mm, pubescent pedicels, held horizontally (at 90° to the main inflorescence axis). Calyx truncate-campanulate, tube 2–7mm long with an abrupt base, giving a boxy appearance, densely pubescent with unequal teeth, the lower teeth acute 3–5mm long, the upper teeth shorter (topmost 1–2mm – half the length of the lowest tooth). Corolla sky blue to royal blue, sometimes with darker veins visible on the banner petal, the wing and keels often lighter or white; banner blade held erect, orbicular 15mm long and 15mm wide, with a slight apical notch, claw 4mm long; wing blade 13mm long, 5.5mm wide with a basal pleated process, claw 6mm long; keel blade 11mm long, 6mm wide, claw 6mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens). Staminal tube truncate or very slightly oblique at apex; style broadly spathulate with bipartite stigma 5–7mm long, the two fertile portions discoid flaps. In dried specimens the wings of the style or the apical sterile portion curl inwards, giving a linear, simple appearance from some angles in herbarium specimens. In addition, styles tend to twist during pressing, but living specimens do not have twisted styles. Ovary densely pubescent, with interspersed glands among the hairs.

Fruits pubescent, orange- to chestnut-brown, sometimes darker, pubescent, linear, 5–7cm long and 5–8mm broad, often with 'woolly' false septa between the seeds. Seeds 6–10 per pod, smooth, dark brown (purple-tinged) oblong-spherical 3–5mm across longest axis, with hilum c. one sixth to one eighth of the circumference.

DIAGNOSTIC NOTES (FIG. 5.20):

This is a very widespread and variable species, found on both sides of the Andes from sea level to 3800m (var. *monticola*). Its pubescence throughout (including a densely pubescent ovary), semisaggitate stipules and stigma with two separate terminal flaps distinguish it from *L. nervosus*, *L. magellanicus* and allied taxa. It can be distinguished from other similar species as follows:

- *L. tropicalandinus* has a simple stigma, and young flowers are somewhat pendent.
- *L. subulatus, L. acutifolius* and *L. nitens* are smaller plants, with slender or very slender leaflets.

Some Brazilian specimens of *L. pubescens* have relatively short, linear-lanceolate leaflets and long tendrils (see e.g. Henz 35529, Smith & Kline 13037, Wasum 4550, Sobral & Jarenkow 7988). However, this character suite is not constant or significant enough to warrant separation into another taxon, even at varietal level.

Williams Andrews s.n. (E, K) from Río Negro is a particularly interesting specimen, with somewhat fleshy leaflets and stout stems. The flowers are recorded as being white. The specimen de Marco de Kriebohn 238 (US) from Chubut province is very similar in overall appearance.

Figure 5.20 ***L. pubescens* var. *pubescens***

(Right) Inflorescence

(Below) Fruits showing nodose constrictions around the seeds.

Key to varieties of *Lathyrus pubescens*:

1a). Mature fruits held at 90° to inflorescence axis, with woolly false septa inside the valves. Tendrils usually branching. Lowland Argentina (<2000m) Brazil, Chile and Uruguay, rarely Bolivia. 20a) **var. *pubescens***

1b) Mature fruits held suberect, woolly internal tissue sparse. Tendrils usually simple. Andean NW Argentina and Bolivia. 20b) **var. *monticola***

20a) var. pubescens

Lathyrus purpureo-caeruleus Knowles et Westcott (1838) The Floral Cabinet and Magazine of Exotic Botany **2**: 126. TYPE: picture tab. 88 in protologue (lectotype, here designated: picture, tab. 88 in Knowles & Westcott, 1838)

Lathyrus petiolaris Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 29. TYPE: URUGUAY: Montevideo? *Sello s.n.* (lectotype designated here: K!, isotype E!)

Lathyrus dumetorum Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 626. TYPE: CHILE Quillota *Germain s.n.* (holotype SGO!, isotype SI!)

Lathyrus andicolus Gandoger (1913) Bulletin de la Société Botanique de France **60**: 459. (Type not seen P)

Lathyrus pubescens Hooker et Arnott forma *hirsutulus* Hassler (1919) ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum*: **16**: 226. TYPE: PARAGUAY Campo de San Ignacio. September. *Hassler 461* (holotype: SI!)

Tendrils usually branching. Mature fruits held at 90° to inflorescence axis, with woolly false septa inside the valves.

CHROMOSOME NUMBER: 2n=14 (Battistin & Fernández, 1994, Schifino-Wittmann, 2001; Seijo & Fernández, 2003)

PHENOLOGY:
Flowering: August to February (mainly October - December).
Fruiting: usually November to January.

DISTRIBUTION (FIG.5.21):
Argentina – Buenos Aires, Chubut, Córdoba, Entre Ríos, Jujuy, Río Negro, Salta, San Luis, Tucumán; **Bolivia** – Cochabamba; La Paz; **Brazil** – Río Grande do Sul, Santa Catarina; **Chile** – Región IV (Coquimbo), Región V (Valparaíso).
In open, dry areas - among rocks and at the base of cliffs on a wide range of soils, or in moister forest margins, clambering over surrounding vegetation.

VERNACULAR NAMES:
Alberjilla, alberjilla peluda (Spanish)

TYPES:

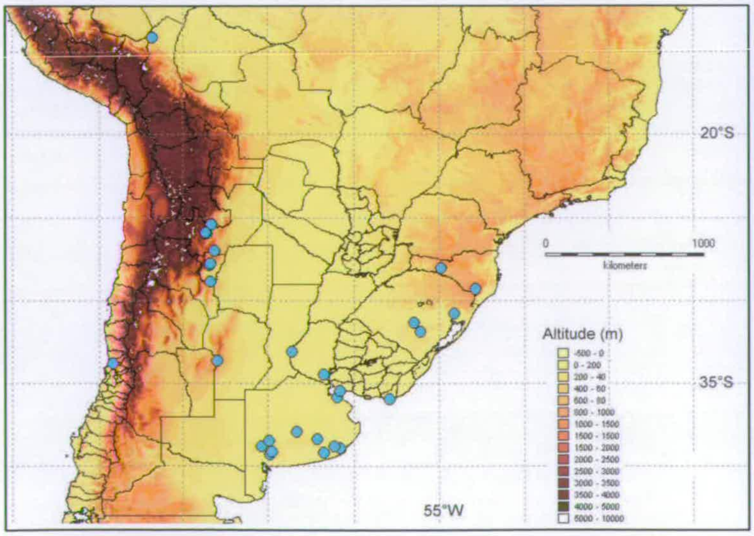
Hooker and Arnott's protologue (1831) mentions collections from 'Conception' (no collector mentioned), 'Valparaiso' (collected by Bridges) and 'the Islands of the

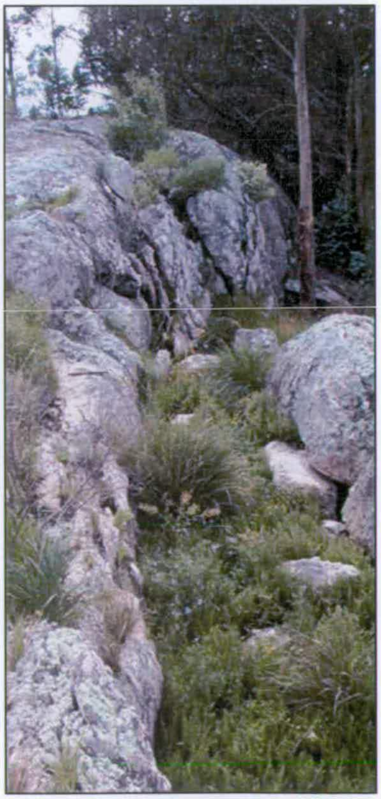
Parana River' (collected by Baird). Of these, oddly, none were found in the collections from Kew, the Natural History Museum, London or Edinburgh, where Hooker and Arnott's specimens are held. Hooker, in Botanical Miscellany III (1833) cited some of these same specimens again and included some further specimens. I was able to locate some of these specimens, and selected *Cuming 484* as the lectotype.

Lathyrus petiolaris Vogel was described based on Uruguayan specimens of *L. pubescens* with particularly long, (c. 5 cm) robust petioles, rachises and tendrils and large leaflets often subopposite on the rachis, as well as very stout, long peduncles. Knowles & Westcott's *L. purpureo-caeruleus* from southern Brazil appears to be similar, and the type specimen is recorded as having grown to a height of over 10 feet (3m) in cultivation. These two species are particularly similar to the very large, sometimes bijugate-leaved specimens from the opposite end of the variety's distribution (Coquimbo and Valparaíso regións, Chile e.g. *Cuming 484*, the new lectotype of the species).

These two groups from the eastern and western extremes conform in all other respects to the more commonly seen, smaller specimens of *L. pubescens*, so do not warrant taxonomic recognition. The differences seem to be related to habitat differences, with the larger species being found at woodland margins, and the smaller specimens in open sites.

Figure 5.21 *L. pubescens* var. *pubescens*
This variety is widely distributed in central South America, from coastal lowlands to c. 2000m in the southern and central Andes.
(Right) Typical habitats include rocky, open areas such as at Balcarce, Buenos Aires Province, Argentina





SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Partido de Tandil, Sierras del Tandil, Cerro Leones, *Abbiatti 4246* (NY); Lobería (38.165°S, 58.769°W) *Alboff s.n.* (NY)' Loma negra Olavarria (36.895°S, 60.331°W), *Boffa 22* (F, NY); Sierras de Balcarce, *Burkart 22310* (K); Piqüe en la Sierra de Curumalán, *Burkart 4690* (K); Punta Lara (34.822°S, 57.988°W), *Cabrera 1240* (NY); La Plata, Punta Lara, *Cabrera 1814* (NY); Ribera del Río de La Plata, Punta Lara, *Cabrera 2416* (NY); Sierra de la Ventana Partido de Tornquist, Arroyo de los Remauros, *Cabrera 4699* (NY); Partido de Tornquist Sierra de la Ventana, Parque Provincial, *Cabrera 5294* (NY); La Plata, Punta Lara. (34.822°S, 57.988°W), *Cabrera 5377* (F, NY); Sierra de la Ventana Partido de Saavedra (37.768°S, 62.36°W),*Cabrera 8082* (F); Cerro La Peregrina, 20km north of Mar del Plata, Road to Balcarce; among sedimentary rock on slope of the Cerro (37.884°S, 57.859°W) 50m, *Eyerdam et al. 23651* (F); Tandil cerro de Las Animas 400 m, *Fabris & Schwabe 4727* (NY); *Fox s.n.* (NY); Pampas, *Gillies s.n.* (E-GL); Trepadora 150 m, *Hudson 3942* (K); Campo La Susana 10km de la Este de Peralta (38.086°S, 61.788°W) 350 m, *Huidobro 1180* (NY); Part. Ole Olavarria Loma Negra, *Huidobro 1607* (NY); Km 25 on road Mar del Plata-Balcarce. Rocky outcrop (37.884°S, 57.859°W) 0m, *Klitgaard et al. 102* (K); Tandil (37.323°S, 59.142°W), *Kuntze s.n.* (NY); Sierra de Leuamalau *Kyle 1892* (BM); Tandil Cerro Los Nogales, *Pastore 1165* (F, K); Delta del Párana Barca Grande, *Rentzell SI 767* (F); Sierra de la Ventana, Río Napostá, *Reutzell 1096* (F); Delta Paraná Guajú, *Scala 173* (NY); Cerro Curra-malal grande, 700 m, *Scala s.n.* (NY); Pdo. Tornquist Parque Prov. Tornquist. En arroyo sin nombre pasando el arroyo Ventana, *Seijo 1205* (F, NY); Pdo. Cnel. Suáres, Abra El Pantanosos Viejo. En Sierra (37.463°S, 61.938°W), *Seijo 1215* (NY); Pdo. Cnel. Suárez, Abra El Pantanosos Viejo. *Seijo 1218* (F); Part. Tornquist 10km SE de Saldungaray por Ruta Prov. 72 hacia Dique Paso de Piedras. Arroyo Sauce Corto. En Barrancas del Arroyo e islas (38.293°S, 61.878°W), *Seijo 1345* (NY); Balcarce Cerro Bachicha 6km N of the town (37.788°S, 58.184°W) 130m *Sparre 236* (K); Saavedera (37.768°S, 62.36°W), *Villamil 3993* (NY).

CHUBUT:Pico Salamanca 21 XI 65 *de Marco de Kriebohn 238* (US).

CÓRDOBA: Talamanchita Sierra Chica, Potrem Arroyo Calinaga *Anbuleuder 8779* (NY).

ENTRE RÍOS: Delta del Paraná Río Ceibo (33.461°S 58.787°W), *Cabrera 2525* (NY); Diamante, sobre las barranas (32.073°S, 60.643°W), *Gamerro 1330* (F).

JUJUY: Perico del Cármen El-Ceibal - El Cármen (24.383°S, 65.267°W) *Pereira s.n.* (K, US).

RÍO NEGRO: Patagonia Conesa (on Río Negro) Found along the banks of streams, abundant in the vicinity of Conesa Williams Andrews *s.n.* (E, K).

SALTA: Rosario de Lerma Campo Quijano 1200 m, *Meyer 3537* (F, NY); Rosario de Lerma Campo Quijano (24.974°, 65.579°) 1500 m, *Venturi 8066* (F); Guachipas Alemanias (25°60'S, 65.63'W) 1500 m, *Venturi 9826* (K, NY).

SAN LUIS: Chacabuco Chorro de San Francisco En cascada, *Seijo 1866* (NY); Chacabuco Villa Larca, Chorro de San Ignacio (32.623°S, 64.984°W), *Seijo 2059* (NY).

TUCUMÁN: Tafi. La Zanja (27.849°S, 65.351°W), *Schreiter 56.005* (NY, US); Dep. Capital Camino de Anta Muerta a Villa Nogués. A 4Km de ante Muerta. En cerro (26.848°S, 65.385°W), *Seijo & Dematteis 1086* (NY).

Bolivia

COCHABAMBA: Cochabamba - Santa Cruz km. 175, *Badcock 370* (K)

LA PAZ Saavedra c. 23 km de Charazanien el Camino a Apolo (15°12'79"S, 68°49'40"W) (13.107°S, 68.733°W) 1894m *Wood, Ortuño, & Atahuachi 19024* (K).

Brazil

RIO GRANDE DO SUL: S. Leopoldo, In dumetis scandens (29.779°S, 51.156°W), *Henz 35529* (NY); Vicinity of Sao Leopoldo *Leite, 546* (NY); Caçapava do Sul em orla do caminho (30°21'51"S, 53°29'54"W) 350m, *Rossato 154* (US); Santana da Boa Vista Erva apoiante em campo arbustivo a beira da BR 392 (30.867°S, 53.123°W), *Sobral & Jarenkow 7988* (F); São Sepé próximo a Mina Chiappeta - beira do caminho, *Wasum 4550* (NY).

SANTA CATARINA: 5km de Sao Jaoquim, camino a Lajes (28.304°S, 49.884°W), *Krapovickas & Schinini 38350* (F); Mun. Irani Dry field, bog, gallery forest and ruderal, Campo de Irani (26°57'S, 51°50'W) 700–900 m, *Smith & Kline 13037* (NY).

Chile

REGIÓN IV (COQUIMBO): Illapel Caren, Quebrada Luncuman ca. 40km from Illapel, tributary of Illapel river; gravelly streambed 1000 m, *Worth & Morrison 16495* (K); La Higuera, *Philippi s.n.* (K).

REGION V (VALPARAISO): Quillota La Palma (32.799°S, 71.235°W) *Bertero 1077* (NY).

Uruguay

COLONIA: Parque Fomento (34.45°S, 57.832°W) *Del Puerto 3087* (US).

MALDONADO: Cerro Pan de Azucar, *Bartlett 20986* (F, US); Cerro Pan de Azúcar, *Pedersen 13621* (NY); *Capt. King 61* (BM).

MONTEVIDEO: *Christie 7* (K).

PARANÁ: *Tweedie s.n.* (K, NY).

RÍO NEGRO: Orillas del Río Uruguay Rincón de las Gallinas, arroyo de los Patos, Estancia de Goenaga, *Rosengurtt B-4074* (US).

TACUAREMBÓ: Valle Eden *Herter 3697* (NY).

20b) var. monticola Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6**: 17. TYPE: ARGENTINA. Tucumán dep. Tafí. La Cienga a 2800m. 4 Feb. 1933 *Burkart 5441* (holotype: SI!, isotypes: SI!, K!).

Lathyrus pubescens Hooker et Arnott var. *acutifolius* (Vogel) Grisebach (1879) Symbolae ad Floram Argentinam. *Abhandlungen der Königl. Ges. Der Wissenschaften zu Göttingen*. **24**: 107. TYPE: URUGUAY *Sello s.n.* (lectotype, here designated: K!; isolectotypes K! – two specimens, one attached to lectotype; E!).

Stems few-branched above ground. Tendrils simple. Leaflets lanceolate (6–7.7cm long by 0.9–1.8(2)cm wide). Mature fruits held sub-erect, with sparse woolly tissues (not constituting false septa) in the valves.

PHENOLOGY:

Flowering: (September) December to February (April)

Fruiting: December to May

DISTRIBUTION:

Argentina – La Pampa, Salta, Tucumán; **Bolivia** – Carviasco, Chuquisaca, Cochabamba, Incallajta-Carrasco, Potosí.

At forest margins in high altitude forest on the eastern slopes of the Andes and upper slopes of inter-Andean valleys, including cloud forest (2500–3800m)

DIAGNOSTIC NOTES:

Burkart proposed the variety *L. pubescens* Hooker & Arnott var. *monticola* Burkart to account for some high altitude specimens that he described as a seldom-branching plant with a relatively erect habit, simple tendrils, relatively few flowers (2–6) per raceme and legumes held somewhat erect on the inflorescence rachis. In addition to Burkart's characters, the woolly false septa between the seeds are sparser in each pod when compared to plants of *L. pubescens* from lower altitudes. However, the reduced number of flowers noted in Burkart's description is not consistent in many specimens that otherwise fit the description - individuals may have up to 10 flowers per raceme.

TYPES:

Grisebach (1879) recorded specimens of the never published '*L. pubescens* var. *acutifolius* Vogel' from Corrientes and Tucuman provinces in montane north-west Argentina. Grisebach did not cite any specimens and appears to have confused *L. pubescens* H. & A. and *L. acutifolius*.

Burkart originally (1939) treated this name as validly published, citing Grisebach (1879). In his later revision (1942) he realised his error and designated *Burkart 5441* (SI) from La Ciénga, Tucuman province, Argentina the type of the new name *L. pubescens* var. *monticola*. He also cited E.K. Balls 6211, from Cochabamba, Bolivia (US!, duplicates in E!, K! and BM!). These and many other plants displaying this character suite possess relatively long, lanceolate leaflets (6-7.7cm long by 0.9-1.8(2)cm wide) and stipules.

Neubert & Miotto (2001) followed Burkart (1942), treating *L. acutifolius* as separate from *L. pubescens*. However, they cited one specimen from Salta, western Argentina

(Santa Vitória, Lizoite, 4 April.1940, S. Col. BA 31457) as *L. acutifolius* Vogel. A duplicate of this specimen in SI! is evidently *L. pubescens* var. *monticola* Burkart and was determined as such by Burkart.

Some specimens such as *Badcock 370* (K!), which is from 10,000ft (3000m) in Cochabamba, Bolivia, are not completely consistent with the facies described above, appearing similar to typical lowland specimens of *L. pubescens*. Conversely, the specimens *Fortuna 84350* and *Troncoso 20.48* appear similar to more upland specimens (var. *monticola*), but are from lowland Argentina (La Pampa, at less than 200msm). Growth trials of upland seeds in lowland areas and vice versa would be able to determine if the var. *monticola* character suite has a genetic basis.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

LA PAMPA Catrilo Lonquimay, *Fortuna 84350* (NY); Sta. Rosa, camino a Gral. Acha., *Troncoso 20.48* (US).

SALTA: Santa Victoria Lazoite 3340 m, *Meyer 31457* (F).

TUCUMÁN: Tafí La Ciénga 2800m, *Burkart 5441* (K).

Bolivia

CARVIASCO: Incallajta 2800m , *Cáredenas 6274* (NY, US).

CHUQUISACA: Yamparaez In the canyon, Lombaya, between Tarabuco and Zudañez 2800 m, *Wood & Serrano 14434* (K); Zudañez c. 3km from first summit on ascent from Icla SE to Cordillera de los Sombreros, on road towards Azurduy 3200m, *Wood & Serrano 14695* (K); Oropeza. Río Mama Wasi c. 3km below Punilla below river crossing on side track down valley 2800m, *Wood 14584* (K); Chuanaca in Río Ravelo Valley 3000m, *Wood 9578* (K).

COCHABAMBA: Cerveceria Colón 9000ft., *Balls 6211* (BM, E, K, US); *Bang 1023* (E, K, NY); Prov. Arque Cochabamba 67 km hacia Oruro, unos 3Km antes de llegar al abra, 3400m, *Beck, St. G. 16821* (K, NY) ; Vila Vila (18°S, 65°30'W) 7000ft., *Brooke 6213* NHM; Ayopaya Sailapata, *Cáredenas 3187* (F); Tunari 3000m , *Cárdenas 6086* (K); Cerveceria Colon, Quebrada Colon, 20 Km east of Cochabamba in thicket along banks of Río Colón 2800m, *Eyerdam 24755* (F); Carrasco a 32km de Epizana por la carrettera que conduce a Santa Cruz 2860m, *Fernández Casas 7777* (NY); Prov. Quillacollo 70km westlich Cochabamba an der Strasse nach La Paz 3500m , *Feuerer 6431* (NY); Prov. Quillacollo Palca pampa 3600m, *Hensen 2169* (NY); Arque, Bombeo. 4km E. of Bombeo, main rd from Oruro to Cochabamba. (17°40'14"S, 66°28'08"W) 3595m, *Hughes 2271* (K); Quillacollo San Miguelito, Rd. NNW from Quillacollo towards Morochata, about 1km below bridge at San Miguelito on the flanks of the Cordillera Tunari (17°16'40", 66°19'25") 3570m, *Hughes 2416* (E); Tunari 3100m, *Kuntze 4/51892* (NY); Prov. Ayopaya Puente San Miguel, Above Liriuni on the Cochabamba-Vizcachas road, about 25 km NNW of Cochabamba 3800 m, *Ugent 4745* (NY); Prov. Ayopaya Puente San Miguel, Above Liriuni on the Cochabamba-Vizcachas road, about 25 km NNW of Cochabamba 3800m, *Ugent 4761* (NY); Quillacollo On road from Quillacollo to Misicuni/Cocapata in valley on S side of Cerro Tunari. Alt. 3200m, *Wood 17660* (K); On the ascent from the Cochabamba plain towards Oruro 3200m, *Wood 8946* (K).

INCALLAJTA-CARRASCO: Ollada, *Bruch s.n.* (NY).
POTOSÍ: Chayanta On road from Sucre to Ravelo c. 1-2km W. of departmental boundary between Punilla and Safiri, *Wood 18888* (K).
UNKNOWN: Toldos bei Bermejo, *Fieberg 3435* (K), Zaquiña 2700m, *Steinbach 8749* (E, F, NY).

21. Lathyrus pusillus Elliot (1824) A sketch of the Botany of South Carolina and Georgia 2. J.R. Schenk, Charleston. p.223. TYPE: USA South Carolina: St. John's Parish, Cooper River *Trescott s.n.* (holotype: CHARL)

Annual herb, not blackening on drying. Rhizomes slightly thickened and woody, but not persisting. Giving rise to many slender stems. Stems branching, clambering to 40(–60)cm, usually glabrous, with wings (to 1.5mm) in the upper portions of larger plants (particularly those from North America).

Stipules slightly unequal hastate to semisagittate-falcate, the upper (primary lobe), elliptic or wide elliptic, often acuminate, 6–20mm long and (1–)4–8.5(–12)mm wide, lower lobe(s) 5–8(–12)mm long. Stipules in North American specimens tend towards being falcate. Occasionally pubescent in the axils. **Leaves** unijugate, terminating in a weak, branched or simple tendril; petioles 5 – 15mm long; leaflets linear-lorate to narrow elliptic, 20–58mm long (–65mm long in exceptional N. American specimens) and 1.5–6(–10)mm wide (13mm in N. American specimens), both surfaces grass green when fresh, slightly glaucous below, both surfaces glabrous or occasionally sparsely pubescent; parallel venation apparent on the underside.

Inflorescence shorter to slightly longer than the leaflets of the subtending leaf, with (1–)2 (extremely rarely 3) flowers borne on a slender or thickened, erect peduncle. Peduncle often very short (2mm), but up to 80mm; appearing fasciated (as if formed from two fused peduncles) in S. American specimens. Floral bracts absent. **Flowers** small to medium, 5–14mm long, borne on 2–5mm long, glabrous pedicels. Calyx campanulate, 2–4mm long (half to one third the length of the calyx teeth), glabrous; teeth lorate, equal, ca. 4–9mm long. Corolla pale lilac to purple; banner with darker purple veins, blade held erect, orbicular, 11mm long and 11mm wide, with slight apical notch, claw 5mm long; wing often lighter than the banner, or white, blade oblong, 10mm long, 5mm wide with a deep basal pleated process, claw slender, c. 4mm long; keel same colour or lighter than the wings, blade 8mm long, 4.5mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous, (9+1). Staminal tube oblique. Ovary glabrous; style 2–5mm long, with simple stigma. **Fruits** glabrous, red-brown, linear, (20–)35–45mm long and 5–6mm broad, containing 10–14 seeds, and woolly 'false septa' between the seeds in some plants, chestnut brown to dark brown or olive-brown with dark spots 1.5–2.5mm across, with hilum c. one eighth of the circumference. Seeds smooth, very finely tuberculate, rugose or slightly echinate chestnut brown to dark brown or olive-brown with dark spots, 1.5–2.5mm across, with hilum c. one eighth of the circumference.

The species exhibits a disjunct distribution between the southwestern USA and temperate South America.

Key to subspecies of *Lathyrus pusillus*:

1a) Peduncles slender, seeds rugose to finely echinate. SW USA
21a) **subsp. pusillus**

1b) Peduncles thickened, Seeds smooth or very finely tuberculate. S. America.
21b) **subsp. crassipes**

21a) subsp. pusillus

Peduncles slender, 15 – 45mm long; flowers small, 5 – 8mm long; calyx c.2mm long, with teeth to 5mm; styles 2-3mm long seeds rugose to finely echinate.

PHENOLOGY:

Flowering: March to May

Fruiting: April to June.

DISTRIBUTION (FIG. 5.22):

United States of America - the Mississippi watershed and surrounding states – Alabama, Arkansas, Florida, Kansas, Louisiana, Mississippi, Missouri, Oklaoma, S. Carolina, Texas.

Pasture, forest margins and disturbed ground, on a wide range of moist soils, including sand, chalk and clay.

VERNACULAR NAMES:

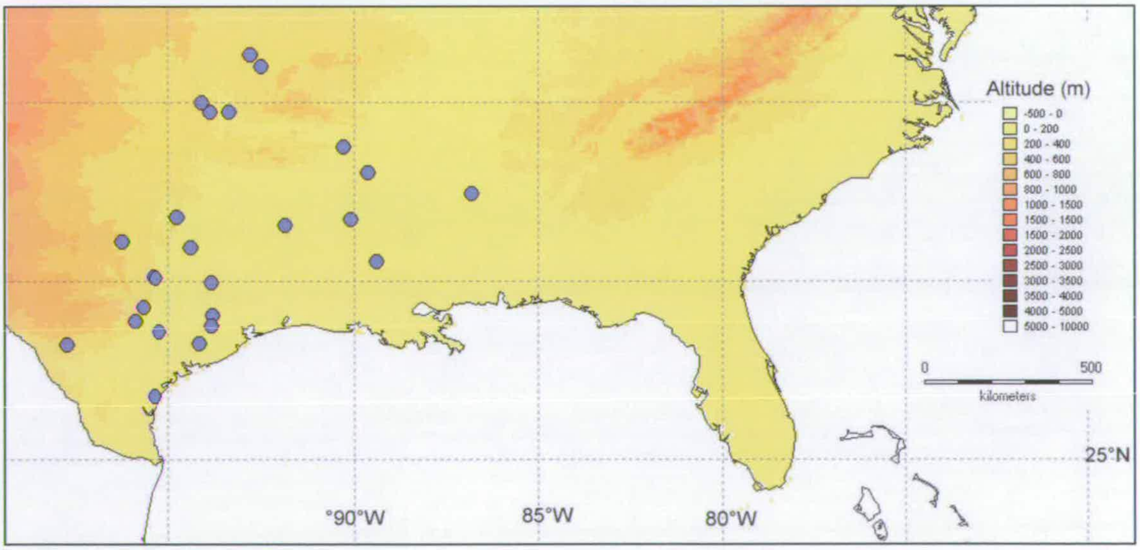
Singletary pea, Singletary vetch.

DIAGNOSTIC NOTES:

Lathyrus pusillus is the only species of *Lathyrus* in N. America that is a bijugate annual, with <3 flowers per raceme and could not be confused with any other species in this part of its range. See the description of subsp. *crassipes* below for features that distinguish it from similar S. American species.

Bush 29 (NY!) is an exceptionally leggy specimen with large, lorate leaflets to 70mm long and 6mm wide and with stems broadly winged (to 2mm). Wolff 1461 (F!) is also a particularly robust specimen with narrow-elliptic leaflets 54mm long and 14mm wide.

Figure 5.22 ***L. pusillus*** **subsp.** ***pusillus***
This variety is disjunct from the remainder of sect. Notlathyrus, and is the only taxon in the section found outside South America.



SELECTED ADDITIONAL SPECIMENS EXAMINED:

USA

ALABAMA Sumter County Between Emille + Ramsay, *Nauper 3191* (F, NY).
ARKANSAS: Lincoln Co. Varner (34.042°N, 91.62°W), *Bush 29* (NY); *Durand s.n.* (NY); Little Rock (34.753°N, 92.298°W), *Hasse s.n.* (NY); *Nuttall s.n.* (NY).
FLORIDA: Polk Co., *Milligan s.n.* (US).
KANSAS: Cherokee Co. (37.35°N, 94.823°W), *Hitchcock 1075* (NY).
LOUISIANA: *Hale 48* (NY); Ouachita Parish E. side Chennault Co Park, w side Russel Sage Area, W of Millhaven Rd, Monroe (32.72°N, 92.073°W), *Hill 29982* (NY) ; *Neal s.n.* (F); Caddo Parish North Lakeshore Drive, west of Logan Branch south of Blanchard (32.554°N, 93.857°W), *Thomas & Taylor 83091* (US).
MISSISSIPPI: Maddison Co. Natchez Trace Parkway (31.56°N, 91.4°W), *McDougall 1588* (US). Oktibbiha county Starkville, *Tracy 1353* (F, NY); Starkville (33.466°N, 88.816°W), *Tracy 574* (NY).
MISSOURI: Reding's Mills (37.027°N, 94.523°W), *Palmer 1939* (NY).
OKLAHOMA: I. Terr. Sapulpa (36.01°N 96.113°W, *Bush 924* (NY); Indian territory Ten miles north of Limestone Gap (35.761°N -95.91°W), *Butler s.n.* (F, NY); Ionkawa, *Johnson 77* (F); Ind. Ter. Muscogee (35.761°N -95.379°W), *Schmeck s.n.* (F).
SOUTH CAROLINA: juxta Cooper R., *Trescott s.n.* (NY).
TEXAS Houston, *Benke 4579* (F); Corpus Christi (27.773°N 97.411°W), *Benke 5373* (F); *Berlandier 487* (NY); Columbia, *Bush 1312* (NY); Columbia, *Bush 41* (NY); Navarro Co. 6 miles south of Richland (31.93°N 96.43°W), *Cory 51539* (NY); Houston 50 m, *Fisher 33171* (F); Brazos Cunty College Station, near the high school, *Fryxell 2617* (NY); Houston (29.756°N, 95.878°W), *Hall 105* (F, NY); Near Corpus Christi, *Heller s.n.* (NY); Johnston County Near Tishomiugo, *Houghton 3605* (NY); New Braunfels Comanche Spring (29.58°N, 97.275°W), *Lindheimer 770a* (F, NY); Dallas co. Below Dachmans Dam, *Lundell 8576* (US); Dublin (32.095°N, 98.34°N), *Mawell 40* (F); Harris County Houston, *Palmer 11449* (NY); Uvalde (29.215°N, 99.8°W), *Plank s.n.* (NY); Dallas (32.78°N, 96.8°W), *Reverchon 116* (NY); Austin (30.276°N, 97.74°W), *Rugel s.n.* (F); Tenant Co., *Ruth 380a* (F); Tenant Co. On railroad embankment near Polytechnic, *Ruth 380b* (F); Tenant Co. In sandy woods, *Ruth 380c* (NY); McLennan County south of Trading House Creek, *Smith 434* (NY); San Marcos (29.882°N, 97.96°W), *Stanfield s.n.* (NY); Hockley (30.03°N, 95.847°W), *Thaeroux s.n.* (F); Polk Co., *Tharp s.n.* (NY); Pierce (29.244°N, 96.205°W), *Tracy 9102a* (F, NY); Bell Co. 4mi. S. of Temple 31.0900 -97.3600 , *Wolff 1461* (F); Bell County 2 mi N. of Belton (31.115°N, 97.445°W), *Wolff 574* (NY); Houston County 15 miles SW of Crockett (30.964°N, 95.878°W), *Wolff s.n.* (NY); *Chapman s.n.* (NY); *Hale s.n.* (NY); *Palmer 5094* (F).

21b) Lathyrus pusillus subsp. crassipes (Gillies) Kenicer comb. & stat. nov.
Lathyrus crassipes Gillies in Hooker W.J. & Arnott G.A.W (1833) Contributions towards a flora of South America and the islands of the Pacific. Botanical Miscellany III John Murray, London. p.198 TYPE: ARGENTINA: Pampas of Buenos Aires *Gillies s.n.* (lectotype, here designated: E-GL!; isolectotypes: E!, K!)

Lathyrus montevidensis Vogel (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 22. *Lathyrus crassipes* Gillies var. *montevidesis* (Vog.) Grisebach (1879) Symbolae ad Floram Argentinam. *Abhandlungen der Königl. Ges. Der Wissenschaften zu Göttingen*. **24:** 107 (TYPE: not seen)

Lathyrus dicirrhus Clos (1847) in Gay C. (ed.) Historia Fiscia y Politica de Chile (Flora Chilena II). Claudio Gay, Paris. p.143. TYPE: CHILE: Valdivia enero 1835 Gay 64 (holotype: P!)

Lathyrus arvensis Philippi (1856) Plantarum Novarum Chilensium (Centuria Prima). *Linnaea* **28**: 624. *Lathyrus debilis* Clos var. *arvensis* (Phil.) Reiche. (1898) Estudios Críticos Sobre la Flore de Chile. Vol.2. Imprente Cervantes, Santiago de Chile. p.201 TYPUS: CHILE: In Campis prov Valdiviae, *Philippi s.n.* (holotype, SGO!; isotypes: SI!, K! Photograph: F!)

Lathyrus crassipes Philippi (1864) Plantarum novarum Chilensium *Linnaea* **33**: 54. Type: Chile: in prov. Valdivia Oct. 1862 *F. Philipii s.n.* (lectotype, here designated SGO!)

Lathyrus crassipes Gillies var. *brevipes* Grisebach (1879) Symbolae ad Floram Argentinam. *Abhandlungen der Königl. Ges. Der Wissenschaften zu Göttingen.* **24**: 107. *No specimens cited in protologue* TYPE: not seen

Lathyrus cicera L. var. *patagonica* Speg. (1897) Primitiae Florae Chubutensis. Revista de la Facultad de Agronomía y Veterinaria de la Plata **3** (32 & 33): 602. In pratis editoribus secus prope Cabo Roso *Spegazinni s.n.* TYPE: not seen

Lathyrus guaraniticus Hassler (1919) ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum*: **16**: 225. TYPE: PARAGUAY: Encarnacion Sept. 1915 *Rojas 1978* (holotype SI!)

Peduncles thickened, often very short (3mm), but up to 80mm, appearing fasciated – as if formed from two fused peduncles. Seeds smooth or very finely tuberculate. S. America.

CHROMOSOME NUMBER: 2n=14. (Senn 1938; Battistin & Fernández, 1994; Schifino-Wittmann, 2001; Seijo & Fernández, 2003)

PHENOLOGY:

Flowering:

- Tropical Andes - year round (mainly June - August)
- S. Brazil, Uruguay & NW. Argentina - September to November
- Temperate Valdivian zone - November to February

Fruiting: to one month after flowering periods.

DISTRIBUTION (FIG. 5.23):

Argentina – Buenos Aires, chaco, Córdoba, Corrientes, Entre Ríos, Misiones, Río Negro; Brazil – Río Grande do Sul, Santa Catarina; **Chile** – REGIÓN X (Los Lagos), as a possible seed alien. **Ecuador** – Galapagos, Loja; **Paraguay** – Misiones; **Peru** – Departments of Cajamarca, La Libertad Lambayeque, Lima, San Pablo; **Uruguay** – Banda Oriental, Canelones, Montevideo Soriano.

Pastures, roadsides and other disturbed grasslands – a ruderal on a wide range of moist soils, including seasonally flooded areas near the Paraná, Uruguay and other large rivers.

VERNACULAR NAMES:

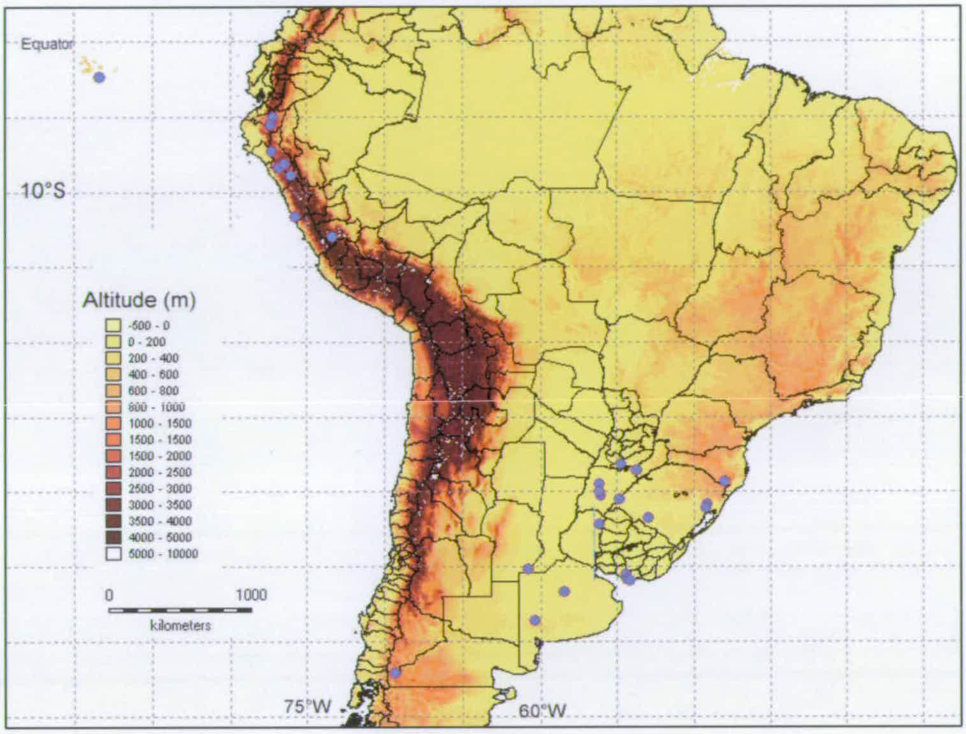
Alberjilla, Alberjilla enana (Spanish)

DIAGNOSTIC NOTES:

This is a widespread taxon. In Chile, it is generally replaced by *L. berterianus* and *L. campestris*, both of which can be morphologically similar. However, *L. berterianus* has semisagittate stipules, typically only a single flower per raceme, borne on a slender peduncle, and is more consistently pubescent. *L. campestris* has a pubescent ovary and is usually much smaller (<20cm) than *L. pusillus* subsp. *crassipes*.

Depauperate specimens of *L. magellanicus* may also be mistaken for *L. pusillus* subsp. *crassipes*, but *L. magellanicus* is a perennial plant, with more than 4 flowers per raceme.

Figure 5.23 ***L. pusillus*** **subsp.** ***crassipes***
This variety is widespread throughout temperate South America, where it is predominantly a weedy opportunist.



SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Pigüe, F.C.S. (37.6°S, 62.413°W) *Burkart 4776a* (K);Bahia Blanca, *Darwin 103* (E, K); Pampas of Buenos Ayres, *Gillies s.n.* (E, K).

CHACO: Campo Vélaz, ruta 11, *Schulz 12.411* (F).

CORDOBA: Depart Presid. Roque Saenz Peña un Poco antes de Laguna del Mont, entre Rufino y La Cesira (34.187°S, 62.805°W), *Hunziker 12863* (F, NY).

CORRIENTES: Dep. Mburucuyá Estancia Santa Maria (28.45°S, 58.226°W), *Pedersen 3991* (NY); Dep. Mercedes Estancia Itá Caabó (28.93°S, 58.154°W), *Pedersen 6183* (US); Mercedes Río Miriñay y Ruta 23, margen derecha del Río (29.181°W, 58.081°W), *Quarín 1674* (NY); Dep. San Martín Yapeyú, Costa del Río Uruguay (29.463°S, 56.817°W), *Schinini et al. 18425* (NY); Dep. San Martín 3 Cerros, Co. Capará, *Schinini et al. 18477* (NY); El Sombrerito, Est. Exp. INTA, *Schulz 11.806* (F).

ENTRE RÍOS: Ruta 14, Chajarí (30.749°S -54.981°W), *Nicora 6383* (F); dpto. Concordia Los Charrúas (31.167°S, 58.186°W), *Troncoso et. al. 2001* (F); Dep. Concordia arroyo Ayuí, *Troncoso et. al. 2086* (F).

MISIONES Dep. Candelaria Profundidad (27.565°S, 55.718°W), *Krapovickas et al. 25702* (F); Dep. Oberá Colonia Guaraní. Paraje Samambaya, Chacra de R. Schegg a 6km de Ruta 14, *Kurtz & Kurtz 14* (NY).

RÍO NEGRO: Nahuelhuapi San Carlos de Bariloche (41.138°S, 71.312°W) 800m, *Buchtien s.n.* (US).

Brazil

Río Grande do Sul: Lagôa dos quadros, *Kleerekoper 14* (NY); Vicinity of Sao Leopoldo (29.78°S, 51.15°W), *Leite 549* (NY); P. Alegre Morro da Policia , *Rambo 43626* (E); Porto Alegre (30.031°S, 51.217°W) , *Reineck & Czermak 98* (E) ;
Santa Catarina: A 10km de S. Joaquim (28.293°S, 50°W) 1400m , *Pabst 6211* (NY).

Chile

Región V (Valdivia): *Buchtien s.n.* (E, US, K); Prope urbum Valdivia, *Philippi 70* (E, K).

Ecuador

Galapagos: So. Pacific Ocean Isle of St. Marys (1.29°S, 90.447°W), *Eights s.n.* (US)
Loja: 55km S. Loja Hac. Huiaco-Pamba (4.53°S 79.42°W), *Espinosa 2326* (F); Loxa (Loja) (4°S, 79.285°W), *Hartweg 728* (E, K, NY).

Paraguay

Misiones Santiago Estancia "La Soledad" (27.143°S, 56.761°W), *Pedersen 6557* (K, US).

Peru

Cajamarca Prov. Contumazá Dto. Contumazá surounding of Contumazá (7.367°S, 78.805°W) 2870m, *Binder et al. 1999/81* (F); Prov. Contumazá Chiñac (Cerca a Guzmango) (7.382°S, 78.898°W) 2200m, *Sagástegui & Leiva 12540* (F); Prov. Contumazá Alrededores de Guzmango 2500m, *Sagástegui & López 10565* (F); Prov. Cajamarca caserio de Otusco 2700m, *Sánchez-Vega 1572* (F, NY); Prov. San Pablo. Distrito San Pablo; El Molino 2200m, *Sánchez-Vega 664* (F); Prov. Cajamarca Distrito San Juan, Carretera San Juan - Huacraruco 2350m , *Sánchez-Vega 709* (F).
La Libertad Sanchez Carion Huamachuco, Rd Huamachuco to Marca Huamachuco ruins (7.812°S, 78.052°W) 3230m , *Eastwood 64* (E).
Lambayeque Ferreñafe Inkawase (Incahuasi) (6.23°S, 79.317°W) 2855m, *Quiroz 3166* (NY).
Lima Prov Chancay 5km north of Barranca –(10.65°S, 77.777°W), *Stork et al. 9097* (K).
San Pablo Distrito San Pablo Encima de El Molino 2300m , *Sánchez Vega 683* (F); Mito (11.947°S, 75.335°W) 9000 ft., *MacBride 3424* (F).

Uruguay

Banda Oriental: Bois de Sta. Lucia (34.47°S, 56.395°S), *Gibert 793* (K).
Canelones: Río Santa Lucía Puerto Jackson, *Rosengurtt B5212* (US).
Montevideo: (34.84°S, 56.34°W) 50m, *Herter et al. 245* (F, NY);34 °54', *Isabelle s.n.* (F, K); Punta Gorda 0m, *Rosengurtt B433* (NY).
Soriano: Juan Jackson Monzón-Heber, *Gallinal et al. PE-5352* (NY); Juan Jackson Monzón-Heber, *Gallinal et al. PE-626½* (NY).

22. Lathyrus subandinus Philippi (1862). *Anales Universidad de Santiago* **2**: 443 – 444. Type: Chile. Cordillera de la Dehesa, Pilobi *Philippi s.n.* (lectotype, here designated: SGO!)

Perennial herb, not blackening on drying. Rhizomes woody, slender or somewhat thickened, creeping, with branching caudex – giving rise to many stems. Stems decumbent to suberect, branching both at the base and higher up, to 40(–70)cm tall, terete, unwinged, sometimes slightly angled. Grey-glaucous and pubescent throughout, with long, silvery, sometimes gland-tipped hairs.

Stipules semisagittate, rarely sagittate, the upper lobe (9–)12–17(–20)mm long and 3–8mm broad, lanceolate, in which case often somewhat curved (falcate) to ovate, the lower lobe deltoid to linear, acute 3–7(–13)mm long, in sagittate stipules, the upper lobe ovate, with an attenuate apex and very small (c. 2mm), acute secondary lower lobe. **Leaves** unijugate, terminating in a simple, or rarely a branched, tendril (very rarely aristate), petioles c.0.8–1.8cm long, somewhat dorsally compressed, semi-circular in cross section; leaflets borne on a short (1mm), densely pubescent pulvinus; upper and lower surfaces both grey glaucous, and with white hairs; primary nerves parallel, conspicuous on the undersides of the leaflets, lanceolate to elliptic, apex acute or rounded, with a short mucro (2–)2.8–4.3(–6.7)cm long and (0.6–)0.8–1.2(–2)mm broad, basal lobe acute, 3–6mm long.

Inflorescence a pseudo-verticillate raceme, at least as long as the leaflets of the subtending leaf, with (4–)5–10 flowers borne on an often very robust, erect peduncle c. 8–25cm long. Floral bracts minute to c. 1mm. **Flowers** pleasantly scented, relatively small, 12–14mm long, borne on stout, 2 – 5mm densely pubescent pedicels, held somewhat erect. Corolla violet, often with lighter / white keel. Calyx campanulate, tube c.4mm, densely lanulose-pubescent; long; teeth equilateral-deltoid 3 – 4mm long, the upper equal or very slightly shorter than the second and lower teeth. Corolla bicoloured; banner violet, blending to white at the claw, blade held erect, orbicular, 12mm long and 14mm wide, with a shallow apical notch, claw 5mm long; wings white, often with purple veins, blade 10mm long, 7mm wide with a basal pleated process, claw c. 5mm long; keel usually white, blade 9mm long, 5mm wide, claw 5.5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1). Staminal tube truncate at apex. Ovary densely sericeous-hairy; style broadening slightly towards the tip, 5-6mm long with a simple stigma. **Fruits** densely pubescent with sericeous hairs, red-brown, linear-trapezoid (broadening at the apex), 4.5–6cm long and 6–7mm broad, 8–12-seeded, without woolly false septa. Seeds smooth, dark brown, subspherical, c.5mm across, with hilum c. one tenth of the circumference.

PHENOLOGY:

Flowering: October to January.

Fruiting: December to January

DISTRIBUTION (FIG. 5.24):

Chile – Región IV (Coquimbo), Metropolitana de Santiago, Región V (Valparaíso) and possibly also in Región VI (O'Higgins? **Argentina** – Mendoza?

Andean sclerophyllous matorral areas (Matorral Andino Esclerófilo), on sunny screes and dry gravel at (1200–) 1600 – 3000m, above Santiago de Chile and surrounding areas.

VERNACULAR NAMES: Arvejilla de cordillera, Clarincillo de cordillera (Chilean Spanish)

DIAGNOSTIC NOTES (FIG. 5.25):

Lathyrus subandinus Philippi is quite variable in size, depending on exposure of the site in which it is growing. Morphologically it appears closely allied to *L. multiceps* Clos. However, *L. subandinus* can be distinguished by its larger, lanceolate to elliptic (rather than lorate to narrow-elliptic) leaflets and broader stipules, combined with inflorescences with more (5+), relatively small (<15mm) horizontal to erect flowers in pseudo –verticils, and consistently stubby, deltoid calyx teeth. Plants of *L. subandinus* also have a more silvery hue, even when dry. Distribution and habitats also differ considerably, with *L. subandinus* found mainly in the areas around Santiago de Chile, in relatively dry, treeless areas at altitudes of over 1600m. *Lathyrus multiceps* is found in more mesophytic forested areas further to the south (Región VII – Maule, and southwards in Chile and neighbouting areas of Argentina). The distribution of *L. subandinus* on the Chilean central Cordillera appears to mirror the distribution of *L. macropus*, on the Argentine side of the Andes. There are also morphological similarities between the two species, particularly in the overall pubescence and the very robust peduncles. There should be no confusing the two species, as *L. subandinus* has unijugate leaves and simple stigmas, while *L. macropus* has multijugate leaves and bipartite stigmas.

TYPES:

The lectotype chosen here is one of two specimens in SGO of an appropriate age for Philippi to have seen them before publishing the name in 1862.

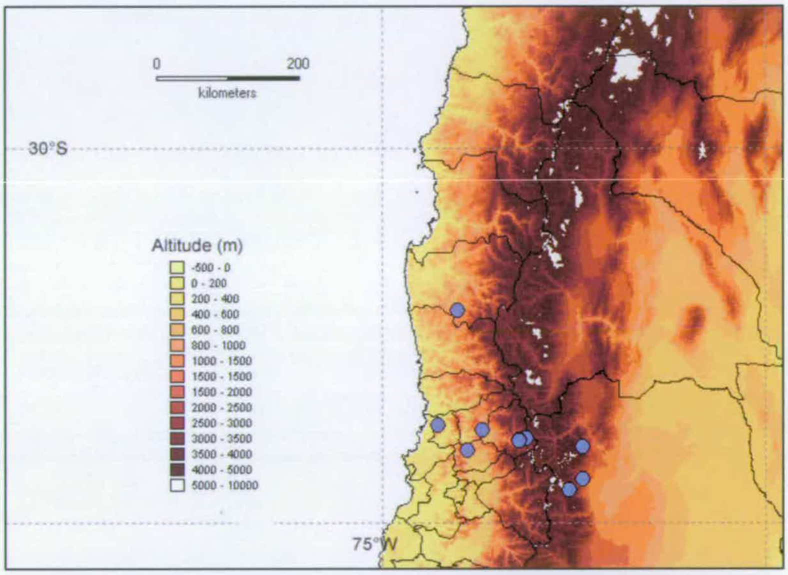


Figure 5.24 *L. subandinus*
This species is distributed in high montane, summer arid / winter snow areas around Santiago de Chile.

Figure 5.25 *L. subandinus*
Flowers and habit.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina*

MENDOZA: Uspallata-Pass der Chilenischen Hochcordillere (33°S. Breite): Juncal auf den Bergen 2300m *Buchtien s.n.* (E)

* Note that the exact locality of this specimen relative to the Argentina/Chile border is somewhat uncertain.

Chile

Region IV Coquimbo: Cordillera de Combarbalá Río Torca 2400m *Jiles 4085* (NY)
Región Metropolitana de Santiago: Rungue 1200m *Caleu, Kerr & Rable s.n.* (K); Cordillera de los Andes Road to Farellones. Steep roadside rocky banks. 1900m *Gardner & Knees 6116* (E); Cordillera de Santiago de Chile *Collector unknown* (F);
Region V: Valparaiso: Al pié de la Cuesta de Juncal, camino internacional a la Argentina. *Bailey s.n.* (SGO); Río Blanco 4000 - 5000ft. *Elliot 227* (E, K); Zwischen Río Blanco und Juncal (Uspallata pass) 1600m *Günther & Buchtien s.n.* (BM); Aconcagua, km. 55 east of Los Andes, just below Portillos. 2400m *Hutchison 164* (F, K, NY, US); Aconcagua, Valley nr. San Felipe 6000ft. *Laudemay 260* (K); Aconcagua , Quillota Cerro Caquis, ca. 15km east of Melon; steep, dry west-facing prophyry [sic] talus below Caquis. 1700m *Morrison 16885* (K); Aconcagua, Portillo 3000m *Sparre 1729* (K); Aconcagua, 1.8km above Juncal on Camino Internacional 60; elev. 2400m 32°50'S, 70°10'W. *Solomon & Solomon 4245* (SGO).
Región unknown: *Bridges 245* (E); Baths of Collia, *Cuming 268* (E), K - specimen on same sheet as *Cuming 136 – L. cabrerianus*).

23. Lathyrus subulatus Lamarck (1788) Encyclopédie méthodique ou par ordre de materieres. II (Cic. – Gor.) Panckouke, Paris. p. 707. Type: Uruguay des environs de Monte Video *Commerson s.n.* (holotype P!)

Lathyrus debilis Vogel(1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 26. Type: Brazil *Sellow s.n.* (lectotype here designated: K!, isolectotypes K!, E!)

Lathyrus subulatus Lamarck var. *longifolius* Hassler - (1919) ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum*: **16** 225. Type: Paraguay Campo de san Ignacio sept. 1914 Hassler 420 (holotype: SI!)

Lathyrus missionum Hassler (1919) Ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum*: **16**: 224. Type: Paraguay Campo di San Ignacio 1914 *Hassler 463* (holotype: SI!)

Delicate perennial herb, not blackening on drying. Rhizomes fine, or slightly thickened and woody, running. Stems prostrate to suberect, with short internodes, creating a very compact plant to 20(–30)cm tall, quadrate, sometimes strongly angled with ridges, but without wings, branching at or above ground level. Sericeous-hairy throughout.

Stipules small, semisagittate, the main (upper lobe) linear-subulate (4–)8–18(–20)mm long and (0.2–)0.4–1.5mm broad, lower lobe a reflexed basal spur. Lower lobe minute in some rare individuals. **Leaves** unijugate, terminating in an arista or very fine, simple (rarely, branched) tendril. Branched tendrils more common on individuals with leaflets >40mm long; leaflets subsessile, linear-subulate, both surfaces pubescent, with parallel veins prominent on the undersides (10–)15–65mm long and 0.7–3.5mm broad.

Inflorescence at least twice as long as the leaflets of the subtending leaf, with terminal cluster of 2–4 flowers borne on a robust, erect peduncle. Floral bracts absent. **Flowers** 12–16mm long, borne on c.2mm, pubescent pedicels, held erect. Calyx campanulate, tube 4–6mm long, sericeous-pubescent with white simple hairs; calyx teeth with marginal glandular hairs, deltoid to linear, acute, the upper c. 3–5mm long, the upper very slightly shorter. Corolla sky blue or lilac to pale violet with darker veins on the banner; banner blade held erect, slightly folded longitudinally, 12mm long and 11mm wide, with no apical notch, claw 4mm long; wing blade 9mm long, 4.5mm wide with a basal pleated process, claw c. 6mm long; keel blade 5.5mm long, 3.5mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1). Staminal tube truncate at apex. Ovary densely sericeous-hairy; style 3–4mm long, spathulate (obdeltoid), with two stigmatic flaps folding adaxially when dry. **Fruits** pubescent, with c. 10-12 seeds, red-brown, linear, to 5.5cm long and 4mm broad. Mature seeds not seen.

PHENOLOGY:

Flowering: September to January

Fruiting: December to February

DISTRIBUTION (FIG. 5.26):

Argentina – Buenos Aires, Córdoba, Corrientes, Entre Ríos. **Brazil?**; **Uruguay** – Montevideo.

In meadows and dry grasslands on hills, on a wide range of soils – gravel, sand, clay and loam.

DIAGNOSTIC NOTES (FIG. 5.27):

This species shares similarities with *L. tomentosus*, *L. acutifolius* and, to a lesser degree, their allies (*L. linearifolius* and *L. nitens*). However, the combination of a prostrate habit, slender (<4mm broad) leaflets and relatively few (<5), erect, lilac flowers prevent its confusion with any other species.

Meyer & Sleumer 15528 (US) is the type of the unpublished *L. multiceps* Clos var. *achalensis* Burkart. This specimen is from relatively far outside the typical range of the species - La Punilla, Córdoba Province at 2200m altitude.

OTHER NAMES:

The following specimens have determinations with names that cannot be traced to a place of publication:

Lathyrus hookeriana Gillies, appears as an 'n.sp.' determination on two specimens (*Gillies s.n.*, Pampas of Buenos Aires E-GL, K). This name was never published, although the orthographic variant *L. hookerianus* Gillies is recorded as a synonym of in *L. subulatus* Lam. in Hooker & Arnott (1833).

Lathyrus prostratus Lamarck is a determination on *Herter & Strahl 458* (NY).

Lathyrus multiceps Clos. var *achalensis* Burkart is a Burkart determination on *Meyer & Sleumer 15528*.

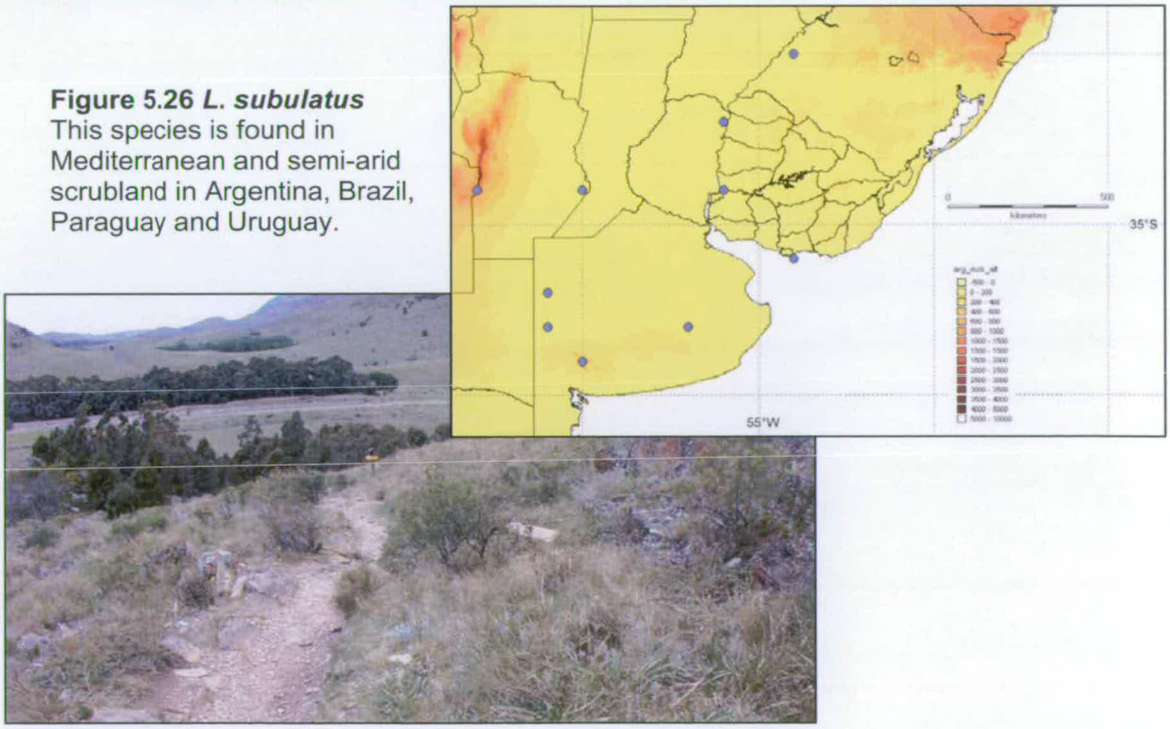


Figure 5.26 *L. subulatus*
This species is found in Mediterranean and semi-arid scrubland in Argentina, Brazil, Paraguay and Uruguay.

Figure 5.27 *L. subulatus*

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

BUENOS AIRES: Partido de Pellegrini Entepa primitive, *Cabrera 6913* (NY); Sierra la Ventana *Dusén 6315* (K); Pampas of Buenos Aires, *Gillies s.n.* (E - 3 sheets, K); Sierra de Ventana *Hauthal 68* (NY); Sierra de la Ventana 300m, *Huidobro 1334* (NY); El Via(?) F.C.P. *King 259* (BM); Tandil, *Kuntze s.n.* (NY); Carhue *Parodi 10465* (K); Cerros al sur de Pigüe, *Scala s.n.* (NY); Tandil *Troncoso 1245* (F)

CORDOBA: Dep. Punilla Pampa de Achala: El Condor 2200m *Mey 15528* (US); B. Ville S. Marco, *Parodi 3111* (K).

CORRIENTES: Santo Tomé Estancia "Garruchos" *Pedersen 9239* (K, NY, US)

ENTRE RÍOS: Federación Estancia "Buena Esperanza" Rather dry grasslands soil heavy loam, *Pedersen 4710* (NY).

Brazil?

(Locality unreliable?) *Sello s.n.* (E, K).

Uruguay

Montevideo: *Christie 45* (K); *Commerson s.n.* (F); *Cuming 76* (BM); Atahualpa 25 - 50m *Herter & Strahl 458* (F, NY); 34° 54' 8" S, *Isabelle* (F); *Nilsen s.n.* (BM); Cerro *Collector unknown No. 465* (K); Soriano: Juan Jackson. Sta. Elena *Gallinal* et al. *B-93* (NY, US). Locality unknown: *Fair 1671* (K); *Herb. Dr. Florentino Felippone 5228* (K); Sierra de Toli *Kuntze s.n.* (NY); Río Grande *Tweedie s.n.* (E).

24. Lathyrus tomentosus Lamarck (1788) Encyclopédie méthodique ou par ordre de materieres. **II (Cic. – Gor.)** Panckouke, Paris. p. 709. Type: Argentina Buenos Aires *Commerson s.n.* (holotype: P!)

Lathyrus sericeus Lamarck (1788) Encyclopédie méthodique ou par ordre de materieres. **II (Cic. – Gor.)** Panckouke, Paris. 708. Type: Uruguay Monte Video in locis sterilibus *Commerson s.n.* (holotype: P!, isotype: F!)

Perennial herb, not blackening on drying. Rhizomes woody, thickened, running, or forming deep tap roots, Stems decumbent, to suberect, to 80cm tall (stems to 150cm long), much branched underground and above, quadrate, without wings, sericeous-hairy throughout, especially on all parts of the infloresence. Hairs long, silvery, appressed, giving a silver-grey sheen to the entire plant when fresh, turning slowly golden after drying, interspersed with glandular hairs.

Stipules large, semisaggitate, the main (upper) lobe lanceolate (1.1–)1.5–2.7cm long and (4)5–8(–11)mm broad; the lower lobe lanceolate, 4–7(–9)mm long. **Leaves** unijugate, terminating in a short (<5cm) simple or branching tendril. Leaflets borne on a short (1mm), pubescent petiolule; both surfaces densely tomentose-hairy with appressed, silky white hairs, becoming golden as dried specimens age, with parallel veins, but these often masked by hairs, elliptic to lanceolate (rarely linear-elliptic) (25–)30–55mm long and 0.2–5.5(–9)mm broad, apex acute.

Inflorescence at least twice as long as the leaflets of the subtending leaf, 6–14cm long with dense apical cluster of (2–)4–6(–8) flowers borne on a robust, erect peduncle. Floral bracts absent. **Flowers** very large, 2.2–2.8cm long, borne on c.4mm, pubescent pedicels, held slightly erect. Calyx campanulate, tube 5–7mm long, sericeous-pubescent;. calyx teeth acute triangular 5–8mm long, the upper subequal (approximately 1mm shorter). Corolla creamy or pure white, with lilac to violet lines at the base of the banner blade, drying dirty orange; banner blade held erect to reflexed, rhombic, 18mm long and 16mm wide, with a deep apical notch (c. 2mm), claw 7mm long; wing blade rhombic 15mm long, 8mm wide with a basal pleated process, claw very fine, c. 5mm long; keel blade 14mm long, 6mm wide, claw 6mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1); staminal tube truncate at apex. Ovary densely sericeous-hairy, with appressed silvery hairs (turning golden in the herbarium) and red glandular hairs scattered underneath these; style 7–10mm, curving backwards towards the dorsal suture of the pod when dry - sometimes describing a complete revolution (i.e. beginning to coil), broadly spathulate; stigma bifid, veins in the style diverging below half way, to serve the two stigmatic 'flaps'. **Fruits** 10–14 seeded densely tomentose-hairy, with appressed golden or silvery hairs hairs, red-brown beneath these, linear, (3–)4–6 cm long and 5–6mm broad with woolly false septa between the seeds. Seeds smooth, rounded to cuboidal, dark brown, 2–3mm across, with hilum less than one twelfth of the circumference.

CHROMOSOME NUMBER: 2n=14. (Seijo & Fernández, 2003)

PHENOLOGY: Flowering: October to December
Fruiting: December to February.

DISTRIBUTION (FIG. 5.28):
Argentina – Buenos Aires, Córdoba. **Brazil?**, **Uruguay** – Montevideo.
In open sites on sandy and gravely soils among scrubby, at least partially xerophytic vegetation and dry open ground in pampa. Usually in ungrazed areas, including coastal dunes.

DIAGNOSTIC NOTES (FIG. 5.29):
Lathyrus tomentosus is an unmistakable species, distinguished by the combination of a decumbent habit, few (<4 per raceme), large (>20mm long) predominantly whitish flowers, and the luxuriant silvery tomentose hair on the entire plant. The pubescence, low habit and, thickened rhizome are adaptations to the seasonally arid areas in which it is found.

TYPES:
Lamarck's *L. sericeus* refers to plants with scandent stems, relatively short petioles and very short, simple, recurved tendrils. However, there are many intermediates between Lamarck's two type specimens and both specimens are clearly the same in all other characters. Both types are extant, and both names were published on the same date. The modern literature accepts *L. tomentosus* and there is no justification for changing this as the accepted name for the species.

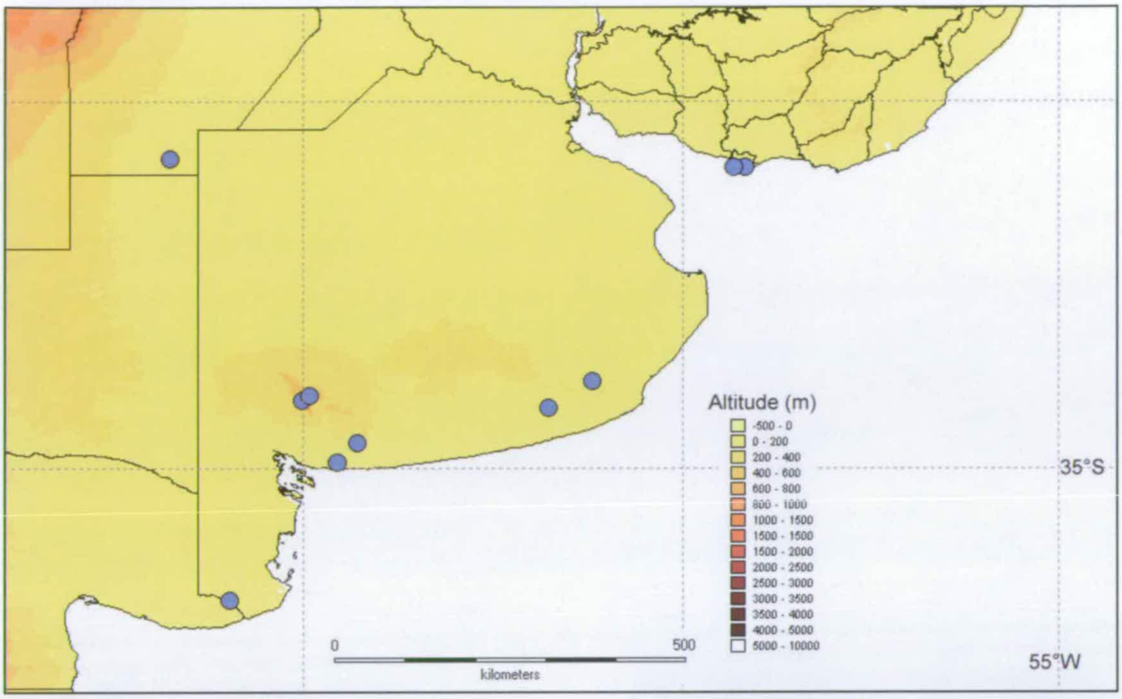


Figure 5.28 (Above) ***L. tomentosus***
This species is found in Mediterranean and semi-arid areas of Argentina and Uruguay

Figure 5.29 ***L. tomentosus***
(Right) Inflorescence
(Bottom right) Habit and deep tap root.
(Below) Semi-erect fruits showing recurved styles.

Additional Specimens Examined:

Argentina

Buenos Aires: Sierras de Tandil Cerras prente al Cahorio *Abbiatti 4325* (NY); Sierra de la Ventana Estancia Leines *Alboff 42* (NY); Lobería *Alboff s.n.* (NY) Monte Hermoso *Carette s.n.* (NY); Monte Hermoza, outside of Bahia Blanca, Coast of Patagonia *Darwin 1001* (E, K,); Pampas of Buenos Aires *Gillies s.n.* (E - 2 sheets, K); Balcarce Sierra Buenavista, Balcarce *Hunziker 4538* (NY); Partido Patagones Isla del Jabalí, *Myndel Pedersen 13231* (NY); Tandil Los Nogales *Pastore 1167* (F); Pdo. Tornquist Sierra de la Ventana Casa de Piedra *Seijo 1204* (NY); Pdo. Tornquist Parque Prov. Tornquist *Seijo 1207* (NY); Part. Tornquist Camino entre Sierra Ventana y Villa Ventana Ruta Prov. 76 *Seijo 1355* (K, NY); *Tweedie s.n.* (K); Balcarce Co. La Bachicha *Villamil 3.594* (NY).

Córdoba: Italó F.C.P. 140m *King 465* (BM).

Locality unknown: In the collection found chiefly at Port Desire *Collector unknown s.n.* (BM).

Brazil?

Sello s.n. (E-GL).

Uruguay

Montevideo: *Collector unknown no. 823* (K); Punta Gorda in collibus arenosus *Osten 5287* (US).

Locality unknown:

Republique Oriental Del Uruguay, 34°54'8"S *Isabelle s.n.* (K); Banda Oriental *Tweedie s.n.* (BM).

Locality unknown

Tweedie s.n. (K), *Williams Andrews s.n.* (E-GL)

25. Lathyrus tropicalandinus Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6:** 16. Type: Argentina Catamarca, Tinogasta, La Tranca, 3300m, *Schreiter 6206.* (lectotype, here designated: SI!)

Lathyrus longipes var. *peruvianus* J.F. MacBride (1943) Lathyrus in *Flora of Peru*; *Field Museum of Natural History - Botany* **13** (3): 3354 Type: Peru: Cani Pueblo 7 miles N.E. of Mito about 8500 feet. April 16–26 1923. *MacBride 3445* (holotype: F!)

Lathyrus multiceps Clos var. *peruviana* Burkart (1942) Nuevas contribuciónes a la sistemática de las especies Sudamericanas de *Lathyrus*. *Darwiniana* **6:** 20. Type: Peru: Ollantaytambo, in a canyon about 3000m. April 24 1915 *Cook & Gilbert 286* (holotype: US!)

Variable perennial herb, not blackening on drying, except rarely at the bases of the leaflets. Rhizomes woody, thickened, giving rise to many stems. Stems clambering, much branched, to 2m, quadrate to terete, striated, with angled corners, the angles occasionally becoming slight (c. 1mm) wings in upper stems of large plants, glabrous to pubescent - if pubescent, then with simple, white hairs and sparse, red, glandular hairs. Degree of pubescence typically consistent throughout the plant.

Stipules semisagittate or semihastate, rarely sagittate or hastate on main stems in the upper parts of the plant, the upper lobe lanceolate to deltoid 10–20(–36)mm long, 3–9mm wide, lower lobe deltoid to linear 3-6(– 15)mm long, sometimes with an undulate or dentate margin or a secondary spur, (typically larger in the upper portions of the plant, but smaller on secondary branches). **Leaves** unijugate, with petioles 1.5–3(–3.5)cm, terminating in a fine, simple or branching tendril. Leaflets typically drying green, but occasionally blackening somewhat at bases and apices, borne on a short (1mm), petiolule, lanceolate or narrow ovate to elliptic, (3.5–) 4.1–6.4(–7.3)cm long and (1–)1.4–2.1(–2.9)cm broad, apex rounded or obtuse, with a short (1mm mucro) 3–5 parallel or subparallel primary veins conspicuous on the undersides of the leaflets, these sometimes bearing simple, white hairs in otherwise glabrous specimens.

Inflorescence at least as long as the leaflets of the subtending leaf, a lax raceme of 6 – 15 flowers borne on an erect, 6.5–14cm long peduncle. Floral bracts absent.

Flowers medium to large, 14–20(–23)mm long, pendulous, borne on slender 6–10mm pedicels. Calyx campanulate, tube 4–6mm long, glabrous or pubescent, often tinged dark blue-black, but typically drying green, lower calyx teeth very narrow elliptic to deltoid, 5–6(–8)mm, upper teeth typically shorter, 3–5mm. Corolla dark, rich purple to blue, often with white keel and wings and darker veins; banner very broadly ovate, blade held erect, orbicular 13mm long and 14mm wide, with no apical notch, claw 5mm long; wing blade 12mm long, 6.5mm wide with two pleated processes either side of a raised boss, claw c. 5mm long; keel blade 11mm long, 5mm wide, claw 5mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1). Staminal tube truncate at apex. Ovary pubescent except at apex, style linear, 4–7mm long, with simple stigma.

Fruits green when immature, often with faint purple tinge, maturing to rich brown, puberulent to lanulose-pubescent, c. 12-seeded, linear- trapezoid (broadening at the apex) 5–6.2cm long and c. 6–9mm broad. Without woolly false septa. Seeds smooth, light brown, 2–3mm across, with hilum c. a quarter of the circumference.

PHENOLOGY:

Flowering October to May (year-round)

Fruiting: November to May (year round)

DISTRIBUTION (FIG. 5.30):

Argentina - Catamarca, Jujuy, Tucumán, Salta; **Bolivia** – Department of La Paz; **Peru** - Departments of Ancash, Apurimac, Ayacucao, Cajamarca Cale, cuzco, Huancavélica Huancayo, La Libertad, Lima, Junin, Otuzco, Puno.

At forest margins, scrambling over neighbouring plants, and on stony ground, rocky slopes/cliffs amongst scrub and semi-scrub vegetation, with e.g. *Berberis* spp. 2800 - 3900m.

VERNACULAR NAMES:

Purun poroto (Quechua), Purun silvestre (mixed Quechua – Spanish), Pabitos/Pabitos (mixed Quechua –Spanish), Pajarillo del Cerro (Spanish), Pajarillo a Cuenruello.

DIAGNOSTIC NOTES:

Lathyrus tropicalandinus Burkart is a variable species, covering a wide geographical range and showing a wide variation of morphological characteristics. In particular, the degree and distribution of pubescence and the shape and size of stipules and leaflets varies greatly amongst individuals.

Perhaps the best diagnostic character is the lax infloresence with pendulous blue-bannered flowers. In the herbarium, leaflets are often crisply coriaceous and may be somewhat translucent. Leaflets are thicker and usually waxy in sympatric taxa such as *L. elegans* and *L. magellanicus* var. *gladiatus*.

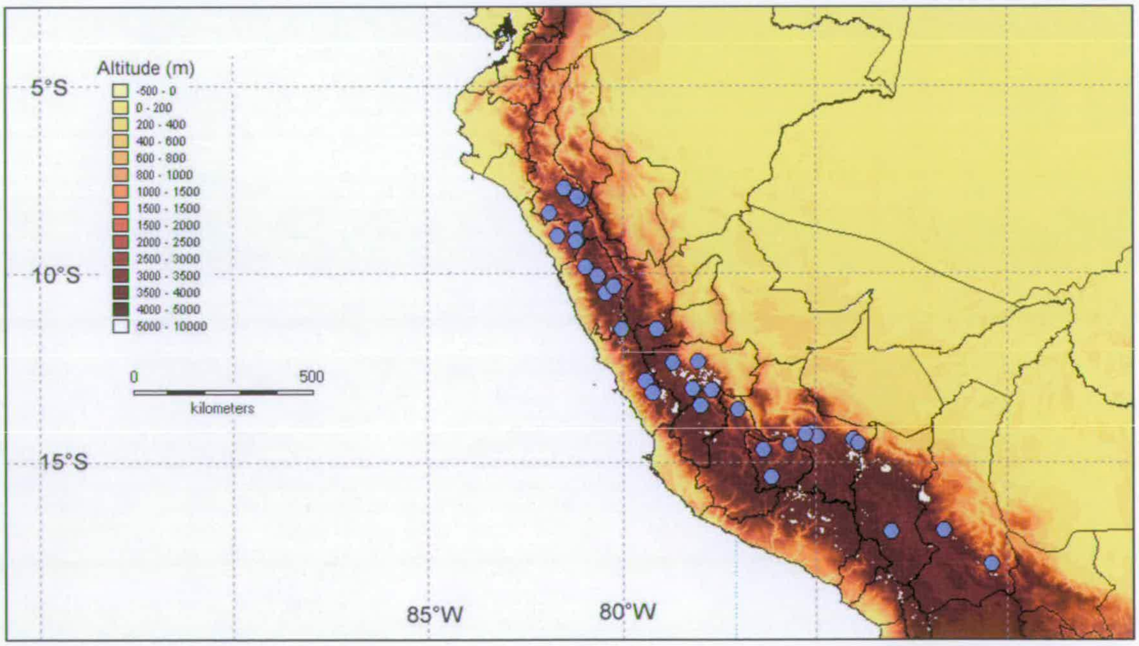
Pubescent individuals have been referred to *Lathyrus tropicalandinus* var. *peruviana* (MacBride) Burkart or MacBride's original *Lathyrus longipes* var. *peruvianus*. although Burkart's comb. nov. was not actually published and a holotype was not designated. However, the degree of pubescence is highly variable and does not appear to correlate with any other characters, habitat or distribution. Consequently, I do not accept this variety.

The species is used as a Maté herb. (i.e. as a leaf infusion beverage)

TYPES:

Many herbarium sheets of *L. tropicalandinus* Burkart are determined as *Lathyrus longipes* Philippi. However, the original holotype specimen of this species [Philippi Cordillera de San Fernando 1843 (SI!)] is a specimen of *L. magellanicus* (Burkart 1942). Consequently, Burkart's 1935 description of *Lathyrus longipes* was published in error. Burkart realised this, and later (1942) renamed the species *L. tropicalandinus*, without designating a new type for the species. I have selected *Schreiter 6206* as the lectotype. This is one of the specimens from Darwinion cited in Burkart's 1937 account, and is in good condition.

Figure 5.30 (Below) *L. tropicalandinus*
This species is found in high altitude temperate forest on the eastern and central parts of the tropical Andes, from Catamarca Argentina, through Bolivia to Peru, where it is fairly common. None of the Argentine accessions held in SI are shown on this map.



SELECTED ADDITIONAL SPECIMENS EXAMINED:

Argentina

CATAMARCA: Andalgalá, El Candado, *Jörgensen 964* (SI)

Bolivia

LA PAZ Between La Granja and Illimani 3800m, *Julio, Bro. 108* (US); Larecaja Viciniis Sorata ad rivulum de Mausanani, in dumosis 2650m, *Mandon G.* (NY); Sorata Ad rivulum de Mansanani in dumosis 2650m, *Mandon 726* (K, NY); 10000ft., *Rusby 1011* (E, F, NY).

Peru

ANCASH Huaraz, Cordillera Blanca Parque Nacional Huascaràn, *Bernardi Charpin & Jacquemoud 16468* (NY); Yungay Quebrada de Llanganuco, ca. 25km above Yungay (9°05'S, 77°35'W) 3750m, *Dillon* et al. *4462* (F, NY); Yungay Huascarán National Park, Llanganuco Sector (9°03'S, 77°35'W) 3700–3900m, *Smith & Escalona 10227* (F); Yungay Huascaràn National Park, Llanganuco Sector, Orconcocha (9°04'S, 77°37'W) 3900m, *Smith, Stein & Todzia 9427* (F); Huaylas Huascarán National Park, trail between Auquispuquio and Cerro Cunka (8°50'S, 77°59'W) 3400–3240m , *Smith, Valencia & Buddensiek 12129* (F).

APURIMAC Valley of Río Colcachaca at Cotarusi-Colca ca. 1km above junction w. Río Chalhuanca ca. 15km (air) S of Chalhuanca. 3000–3100m , *Iltis* et al. *564* (NY); Andahuaylas Pincos; in shrubland 2700m , *Stork & Horton 10681* (F).

AYACUCAO: Below Yanamonte 2700 m, *Weberbauer 5595* (F).

CAJAMARCA: Celendin La Quintanilla, Sucre 3000m, *Chaman s.n* (NY); Contumazá Bosque Cachil, fragment of montane forest [ca. 100 ha.] (7°24'03"S, 78°46'44"W) 2400m, *Dillon* et al. *6512* (F, NY); Celendin In rolling hills 17km SW of Celendin rd to Cajamarca (6°55'29"S, 78°11'32"W) 3050m, *Hughes 2219* (E, K); Contumazá Cerro Chungarrán (Guzmango) 2700m , *Mostacero & Diestra 9183* (NY); Celendin Cerca a Oxamarca, al S. de Celendin 2900m , *Sánchez Vega & Ruiz Vigo 1789* (F, NY); Hualgayoc Centro Minero CESMA ruta a Bambamarca. 3200m, *Sánchez Vega & Ruiz Vigo 2085* (F).

CALEA: Quebrada de S. Salvador 3050m, *Vargas 123* (F).

CUZCO: Ollantaytambo In a canyon 3000m, *Cook & Gilbert 286* (US); Urubamba Cincheros Antakillqa hillside (13°23'S, 72°2'W) 3600–3900m, *Davis* et al. *1695* (F, NY); Valle del Urubamba Allantaibambo (Ollantaitambo) 2800m, *Herrera 3420* (F); Urubamba Lower end of Quebrada Pumahuaca, a deep side-valley of R. Urubamba ca.2-4km NW of Urubamba. SW-facing slopes with xerophytic scrub forest. (13°12'S, 72°3'W) 3200–3600m, *Iltis* et al. *1009* (NY); Calca Laderas rocosas, *Marin 1325* (F); Jucay, *Soukup 731* (F); Canas Asuncion bridge, Apurimac river; among herbaceous plants 3730m, *Vargas 11030* (F, K); Quispicanchis Cloud forest, rocky outcrop, edge of roadside between Marcapata and Abra Hualla Hualla 3340m , *Wasshausen & Encarnación 827* (K, NY, US); Quispicanchi Marcapata valley near Chilechile 2200–2300 m, *Weberbauer 7873* (F, US).

HUANCAVÉLICA: Tayacaja Quebrada, 0.5km east of Surcubamba; trailing on moist, shrub-shaded bank 2500m, *Stork & Horton 10342* (F, K); Yauli; twining over Berberis and other shrubbery 3600m, *Stork & Horton 10857* (K); I Ayán, abajo de Conaica 3300–3350m, *Tovar 143* (US).

HUANCAYO: Quebrada de Occopilla, *Soukup 3648* (US).
JUNIN: Tarma surrounding of Alcobamba (11°21'114"S, 75°38'682"W), *Binder & Daxberger 1999/412* (F); Huancayo 3700m, *Ledig 26* (F); Cani, Pueblo, 7 miles N.E. of Mito 8500 ft., *Macbride 3445* (F); Tarma Cultivated lands and steep slopes between Acobamba and Tarma 3000–3100m, *Weigend 97/25* (F).
LA LIBERTAD: Santiago de Chuce Huacás (Cachicadán) 2800m , *Mostacere & Diestra 11925* (F, NY).
LIMA: Huarochiri Between Infiernillo and Río Blanco 3400m, *Asplund 10836* (US); Huarochirí Infiernillo; in sandy soil, hillsides 3200m , *Goodspeed, Stork & Horton 11612* (F, K); Rió Blanco 3000–3500 m, *Killip & Smith 21570* (F, NY); Matucana, *MacBride & Featherstone 327* (F); Matucana 8000ft., *MacBride 2941* (NY); Huariaca, *Macbride 3112* (F); Cajatambo, *Sandeman 5368* (K); Km. 94 Caretera Central, Dist. of Matucana Huarochirí, *Saunders 260* (BM).
OTUZCO: La Libertad Alrededores de El Hórcon (ruta a Samne) 2850m , *Leiva, Miñano & Palacios 750* (F, NY).
PUNO: Near Puno 4000 m, *Soukup 417* (F).

26. Lathyrus woodii Kenicer sp. nov.
holotype: Bolivia, La Paz, Saavedra, Immediamente ariba del segundo puento bajando de Charazani a Camata borde del Río. Alt. 2530m. (15°11'46"S, 68°53'03"W). 2nd February 2003, *Wood, Ortuño & Atahuachi 18975* (K).

Herba perennis scandens usque ad 4m alta, caule in partibus superioribus levissime alata. Folia unijugata, cirrhosa, foliola lanceolata usque anguste elliptica, pubescentia. Ovario glabro. L. hasslerianae *similis sed floribus coeruleisdiffert.*

Perennial herb, not blackening on drying. Rhizome not seen. Stems slender, climbing over other vegetation to 4m, quadrate, with very slight (1mm broad) wings in the upper parts of the stem. Pilose-pubescent on stems and leaves, with simple, curly hairs.

Stipules semisagittate to hastate, the upper lobe 8–17mm long, 8–10mm wide, lower lobe 2 – 3(–6)mm long. **Leaves** unijugate, petiole 12-30mm long terminating in a branched tendril. Leaflets lanceolate to very narrowly elliptic, 50 – 63(–110)mm long and 16–25(–35)mm wide. Bright green when fresh and when dry, pubescent on undersides, with simple curly and glandular hairs.

Inflorescence a loose raceme, subequal to twice as long as the leaflet of the subtending leaf, with 6–14 pendulous flowers borne on a curved, erect peduncle, densely pubescent with curled simple hairs and many glandular hairs. Floral bracts absent, or occasionally present (to 2mm, linear). **Flowers** c. 13–18mm long, borne on slender, c. 5mm long pedicels, pedicels thickening in fruit. Calyx campanulate, tube 2– 4mm long, sparsely pubescent, with simple, curly hairs, these interspersed with glandular hairs; calyx teeth much shorter than the tube, deltoid, slightly upcurved, the lower teeth, c. 4mm long, the upper very slightly shorter. Corolla blue to lilac, banner panduriform, blade held erect, 6mm long and 7mm wide, with no apical notch, claw 8mm long; wing blade 6mm long, 4mm wide with a basal pleated process, claw c. 10mm long; keel blade 8mm long, 5mm wide, claw 8mm long, keel fused along the entire length of the lower margin (including the claw). Androecium diadelphous (9+1 stamens); staminal tube truncate at apex. Ovary, glabrous; style linear, c. 5mm long, with simple stigma. **Fruits** c. 10-seeded, valves glabrous, with reticulate venation, rich red-brown, elongate-trapezoid, 4.5–5cm long and 7–8mm wide. Seeds smooth, light brown, 2–3mm across, with hilum c. a quarter of the circumference.

PHENOLOGY:

Flowering: August to May (year-round)
Fruiting: August to June (year-round)

DISTRIBUTION:

Bolivia – Departments of Cochabamba and La Paz; Southern **Peru** – Department of Puno.

At margins of warm temperate forests, above 2500m.

DIAGNOSTIC NOTES:

This species might be confused with several others, but differs in the following ways:

- *Lathyrus tropicalandinus* has pubescent ovaries, and the flowers only rarely reach 18mm in length.

- *Lathyrus elegans* is glabrous throughout. *Lathyrus woodii* has pilose-pubescence on the calyces, much of the stems, the undersides, axils, petioles and pulvini of the leaflets, with glandular hairs scattered throughout. Plants of *L. woodii* are generally more slender than *L. elegans*, with relatively feeble peduncles and lax inflorescences.
- *Lathyrus hasslerianus* is not known from Bolivia or Peru, has very glaucous leaves and yellow flowers.

NAME:
The species is named for John Wood, of the University of Oxford, whose many superb collections from Bolivia and surrounding areas include this species.

SELECTED ADDITIONAL SPECIMENS EXAMINED:

Bolivia

COCHABAMBA: Carrasco Sector Siberia *Fernandez Casas 7905* (NY); Tunari *Kuntze s.n.* (NY)

LA PAZ: Bautista Saavedra, Amarete-Tal, link Talseite bei der Mine Sica *Feuerer 8300b* (NY); La Paz Bautista Saavedra, camino Charazani-Cumata, antes del segundo Puente, *Schmit at al. 225* (NY).

Peru

PUNO: Carabaya across Río San Goban from Ollachea, 13.8110°S, 70.4580°W, *Boeke & Boeke 3058* (NY).

UNKNOWN: Lechlen, *Unic. 118* (K).

Appendix 1

Visual glossary for tribe Fabeae

Note: Leaf architecture terminology throughout this work follows Hickey (1974)

Figure G1: Whole plant

Lathyrus quinquenervius as a 'typical' member of tribe Fabeae.

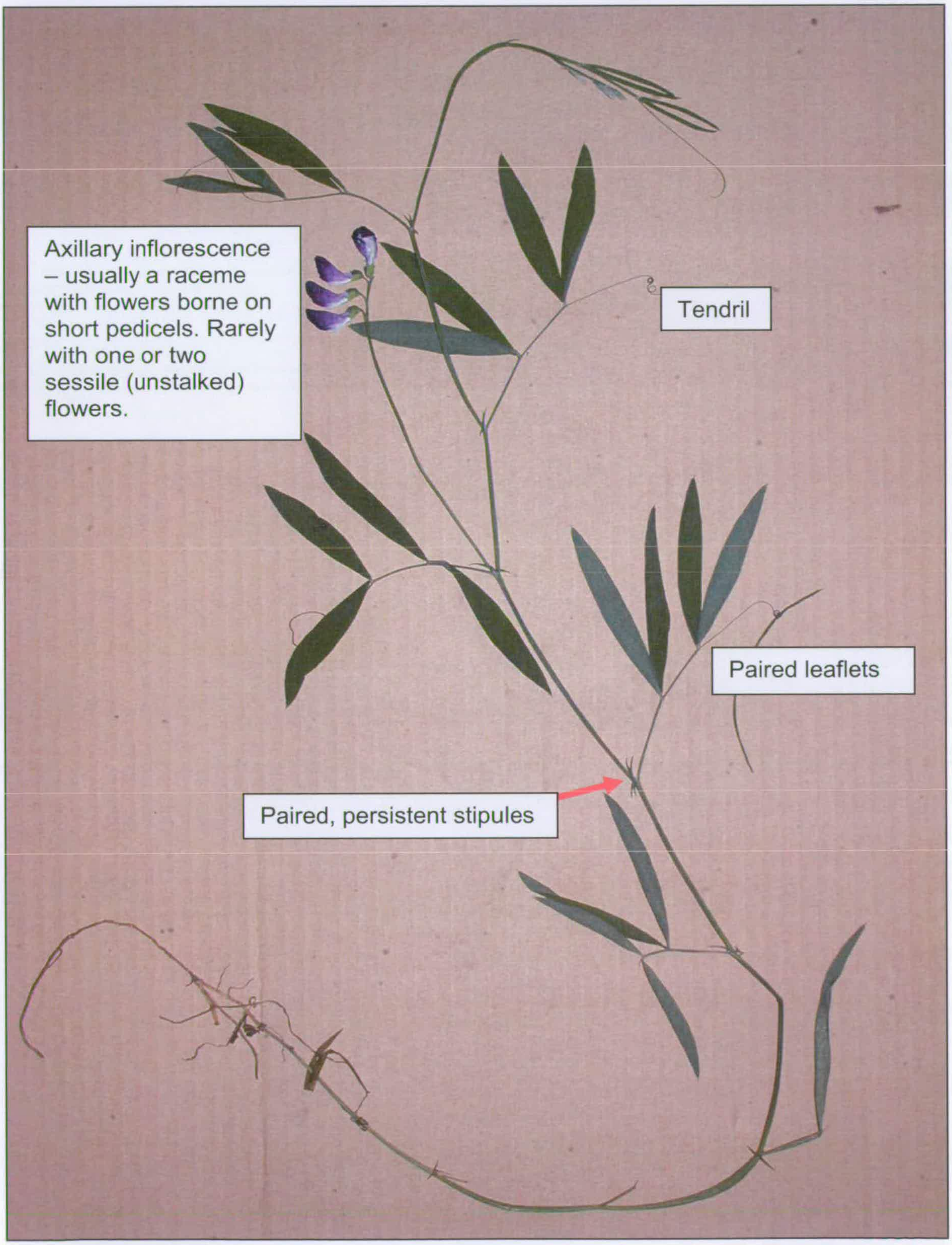


Figure G2: Stipules
Above: Selected stipules of *Lathyrus* species, not to scale.
1) Hastate; 2) sagittate; 3) subulate-semisagittate; 4, 5) semisagittate

Figure G3: Leaf forms
Left: Leaves of *Lathyrus macropus*, are **tendrillous** (possessing a tendril), and **multijugate**, in this case with four pairs of leaflets. The leaflets have strong parallel venation.

Leaves of *L. linifolius* (below) are **multijugate**, in this case **bijugate**, with two pairs of leaflets. The terminal tendril is reduced to a bristle (**arista**), so the leaf is said to be **etendrillous** (i.e. 'without' a tendril).

Arista – a terminal bristle on the rachis of the leaf

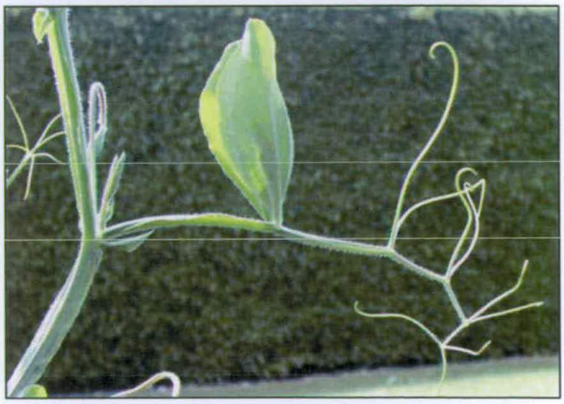


Figure G3b: Leaf forms
Above: leaf of *Lathyrus odoratus*, showing only one pair of leaflets (**unijugate**)

Figure G4: Leaflet ptyxis
Cross-sectional diagrams of leaflet ptyxis types. Basal circles represent rachises. Left, **supervolute** (unfurling) vernation, as seen in *Lathyrus* and *Vavilovia*. Right, conduplicate (unfolding) vernation found in *Lens*, *Pisum* and *Vicia*.

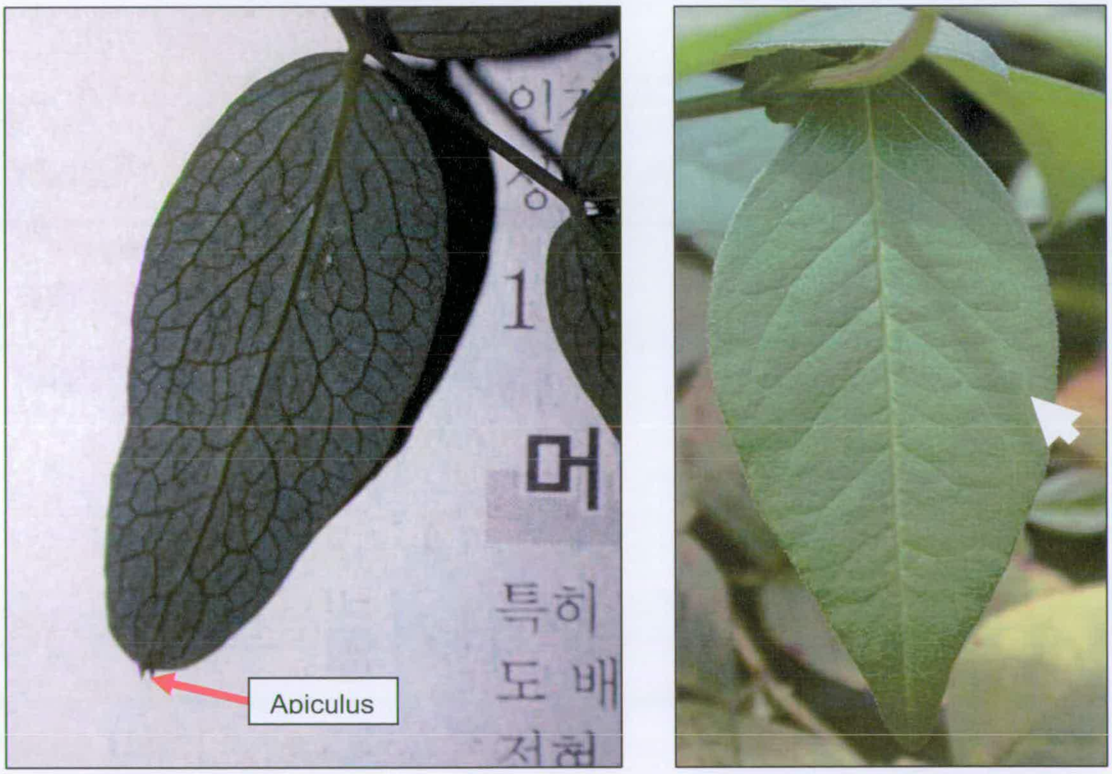


Figure G5: Leaflets
Above: Leaflet venation in *Lathyrus vaniotii* (left), and *Vicia unijuga* (right). Most *Lathyrus* species are **camptodromous**, with veins reaching the margins of the leaflet. In the *Vicia*, leaflet venation is strongly **brochidodromous**, with the secondary veins looping backward from the margins (white arrow). Leaflets of *L. vaniotii* are **apiculate**, with a discrete point (apiculus) at the tip.

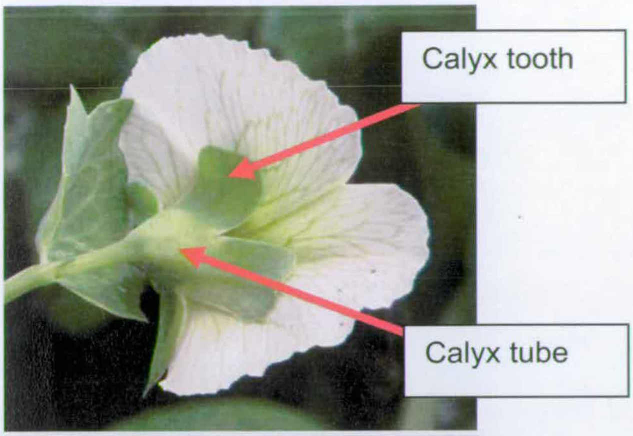


Figure G6: Calyx
Left: Adaxial (rear) view of flower in *Pisum* cv., showing calyx tube and teeth.

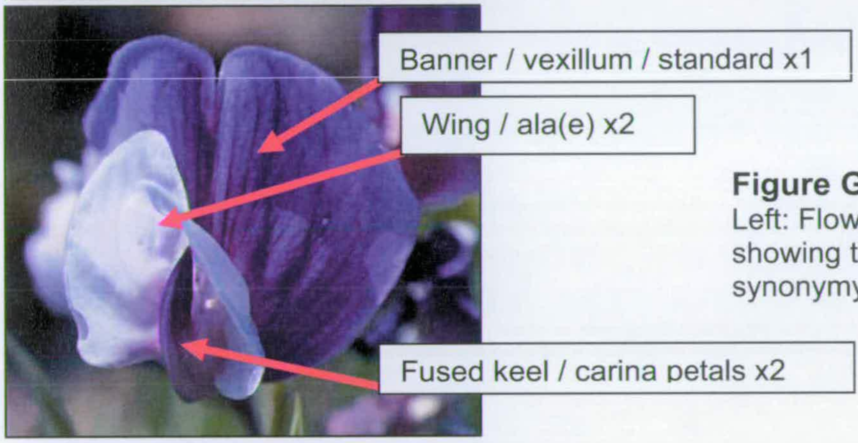


Figure G7: Corolla
Left: Flower of *Lathyrus multiceps*., showing three petal types, with synonymy for petal terminology

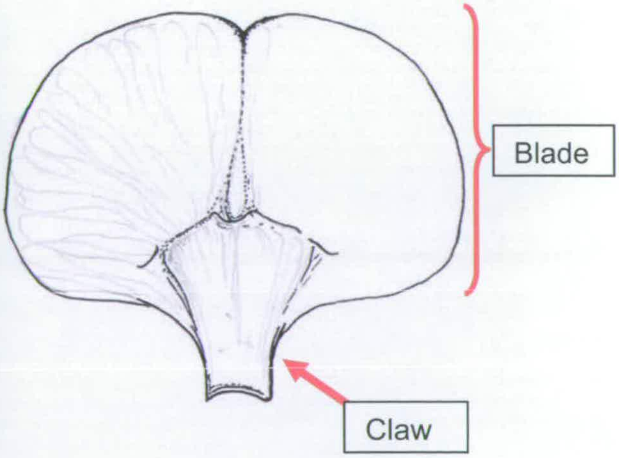


Figure G8a: Banner petal
Left and above: Flower of *Lathyrus sylvestris*, showing stenonychoid banner petal (i.e. with the claw broadening to a very broad blade)

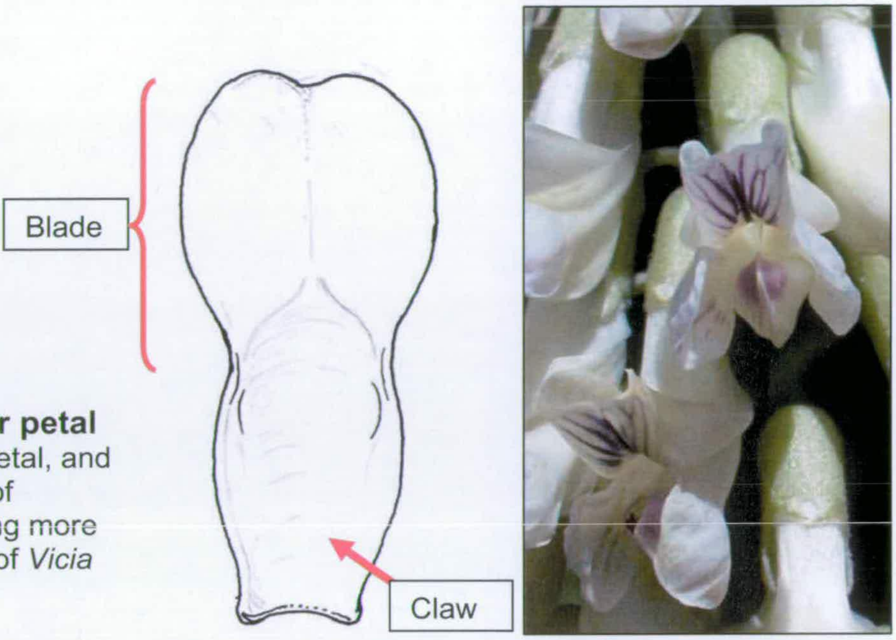


Figure G8b: Banner petal
Left: Oblong banner petal, and (far left) entire flower of *Vicia sylvatica*, showing more slender flower typical of *Vicia* species.

Figure G9: Wing petal
Right: Wing petal of *Lathyrus tropicalandinus*, showing claw and blade

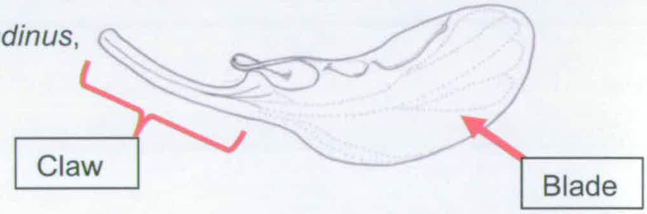
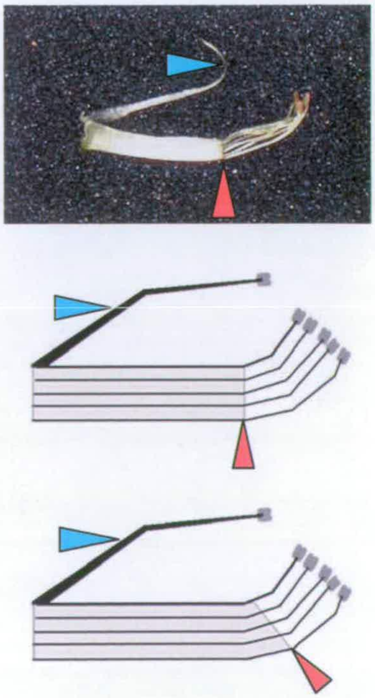


Figure G10: Androecium
Stamens in Fabeae (*Lathyrus cabrerianus* is shown top right) are **diadelphous**, with 9 stamens fused together by membranous tissue into a tube, and the one remaining stamen separate (blue triangle). The tube is open on the adaxial surface, allowing the developing fruit to grow unconstrained by the staminal tube as it pushes the adaxial stamen out the way as it grows.

The end of the staminal tube, at the point where the filaments become free from the membrane, is **truncate** in most species of *Lathyrus*, (right, centre) and **oblique** in most species of *Vicia* (right, bottom). Red arrows indicate the end of the staminal tube



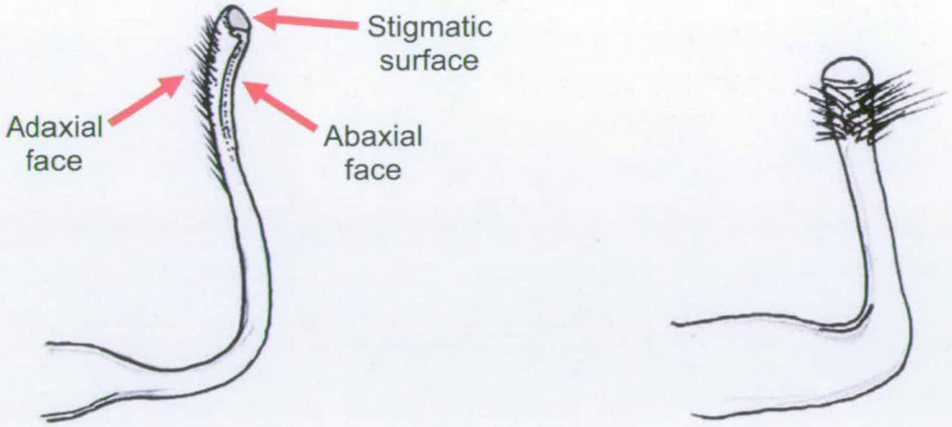


Figure G11: Styles
Above: styles of *Lathyrus* (left), and *Vicia* (right), showing patterns of pubescence. Pubescence is always in the apical half of the style. In *Lathyrus*, *Lens*, *Pisum* and *Vavilovia*, styles are adaxially pubescent. In *Vicia*, styles may be pubescent on the abaxial face, rarely on the adaxial face, and most commonly around the entire style. In some species of Vicia, the styles are abaxially tufted (as shown above, right).

Appendix 2

Lathyrus in the *Flora of China*

The original standard Chinese language account of *Lathyrus* for the *Flora of China* was written by late H.P. Tsui (1998). This account formed the basis for the English language account written by myself for the *Flora of China* English language edition. The English language account is presented as submitted, below and is due for publication in 2007-8. My revision of Tsui's work resulted in a new variety and a new state in *Lathyrus palustris*:

- *Lathyrus palustris* var. *sinomontanus* Kenicer
- *Lathyrus palustris* var. *exalatus* (H.P. Tsui) Kenicer

More than 1500 herbarium specimens from the following herbaria were examined for this account:

Natural History Museum, London (BM); Natural History Museum and Institute , Chiba, Japan (CBM); Royal Botanic Garden Edinburgh (E); Royal Botanic Gardens, Kew (K); The Makino Herbarium, Tokyo Metropolitan University (MAK); Institute of Botany, Chinese Academy of Sciences (PE); Tokyo University (TI).

Determinations were added to all undetermined and wrongly determined specimens seen at these herbaria.

The herbarium research was supplemented by field observations and collections of living specimens in northern China, South Korea and Japan.

Appendix 2

Lathyrus Linnaeus, Sp. Pl. 2: 729. 1753.

Shan li dou shu (Mountain peas)

Annual or perennial herbs; stem erect or climbing, winged or wingless. Leaves paripinnate, with 1-many pairs of leaflets, rarely phyllodic or reduced to modified stipules, terminating in branched or simple tendril or aristate; stipules semisagittate or sagittate, sometimes large and leaf-like; leaflets elliptic, ovate, ovate-oblong, lanceolate or linear; veins parallel, pinnate or reticulate. Racemes axillary, pedunculate with 1 to many flowers; flowers purple, pink, yellow or white, sometimes crimson, brick red or orange; calyx campanulate, unequally or equally toothed. Style dorsally compressed, linear or spathulate, pubescent on adaxial (inner) surface. Legume laterally compressed, dehiscent. Seeds 2 to many.

About 160 species: mainly in Asia, Europe, and North America with some South American endemics; 18 species (three endemic) in China. The yellow-flowered species of south-east China are a particularly difficult and poorly understood group, represented by only limited collections.

1a. Leaves without tendril at apex (aristate).
 2a. Stem slightly winged; leaflets with 3 (sometimes 4 or 5) parallel veins . 13. *L. komarovii*
 2b. Stem wingless; leaflets with reticulate veins.
  3a. Flowers purple-red; stipules linear or spur-like (subulate) .... 8. *L. vaniotii*
  3b. Flowers orange-yellow or yellow; stipules foliaceous (>3mm wide)
   4a. Leaflets ovate or elliptic ovate .... 6. *L. gmelinii*
   4b. Leaflets linear to linear-lanceolate .... 7. *L. krylovii*
1b. Leaves with simple or branched tendril at apex.
 5a. Stem winged (>1mm).
  6a. Leaves with 1 pair of leaflets; style twisted.
   7a. Racemes with 5–15 flowers .... 17. *L. latifolius*
   7b. Racemes with 1–3 (4) flowers.
    8a. Leaflets elliptic, ovate-oblong to elliptic; flowers 20–30 mm; legume wingless .... 16. *L. odoratus*
    8b. Leaflets lanceolate to linear; flowers 12–15 (–24) mm; legume winged at suture .... 15. *L. sativus*
  6b. Leaves with more than 1 pair of leaflets; style not twisted.
   9a. Stipules similar to leaflets, 3.5 cm or longer; leaflets oval to oblong... 2. *L. pisiformis*
   9b. Stipules less than 3.5 cm; leaflets linear, linear-lanceolate or elliptic-lanceolate.
    10a. Leaflets with pinnate or sub-parallel veins, stipules without reflexed basal spur .... 11. *L. palustris*
    10b. Leaflets with 5 prominent parallel veins, stipules with reflexed basal spur .... 12. *L. quinquenervius*

5b. Stem wingless.
11a. Leaves with 1 pair of leaflets.
12a. Flowers yellow, stipules sagittate .... 18. *L. pratensis*
12b. Flowers purple-red, stipules semi-sagittate.. 14. *L. tuberosus*
11b. Leaves with more than 1 pair of leaflets.
13a. Stipules large, subequal or equal to leaflets; leaflets ovate to broadly ovate .... 1. *L. davidii*
13b. Stipules obviously smaller than leaflets.
14a. Leaflets large, 9–12 cm long, ovate-lanceolate, strongly caudate at apex .... 9. *L. caudatus*
14b. Leaflets < 9cm long, not strongly caudate at apex.
15a. Stem procumbent; stipules sagittate .... 5. *L. japonicus*
15b. Stem erect; stipules semisagittate.
16a. Lowest calyx tooth equal to tube, leaflets with sub-parallel veins, oblong-lanceolate.. 11. *L. palustris*
16b. Lowest calyx tooth shorter than tube, Leaflets with reticulate veins, not oblong-lanceolate.
17a. Leaflets narrowly elliptic or narrowly ovate; corolla yellow .. 10. *L. anhuiensis*
17b. Leaflets elliptic, ovate or oblong; corolla pink or purple.
18a. Plant 20–30 cm high; racemes with 2–5 flowers .... 3. *L. humilis*
18b. Plant 80–100 cm high; racemes with 9–11 (–13) flowers .... 4. *L. dielsianus*

1. Lathyrus davidii Hance, J. Bot. 9: 130. 1871.

Da shan li dou

Perennial herbs with tuberous roots, 1–1.8 m; stems, strong, erect or decumbent, glabrous, wingless, hollow in lower parts. Leaves with strong, branched tendrils; stipules large, often similar to leaflets 4–6 cm long, semisagittate, ovate, entire or sometimes dentate at base; leaflets (2) 3–4 (–5) paired, usually ovate, mucronate, entire, 4–7 × 5–11 cm, glabrous, with reticulate veins. Racemes axillary, subequal to the leaf, with 10-40 flowers; calyx campanulate, ca. 5 mm, glabrous, shortly toothed. Flowers yellow, maturing to orange 1.5–2 cm; banner elliptic, with claw; wings subequal to banner, auriculate at base. Ovary linear, glabrous. Legume linear, orange-brown 8–15 cm. Seeds broadly oblong, purple-brown, smooth. Fl. May–Jul, fr. Aug–Oct.

Forest margins, scrub forests, slopes; below 1800 m. Anhui, Gansu, Hebei, Henan, Heilongjiang, Hubei, Hunan, Jilin, Nei Mongol, Shanxi, Shaanxi, Shandong [Japan, Korea, Russia].

2. Lathyrus pisiformis Linnaeus, Sp. Pl. 2: 734. 1753.

Da tuo ye shan li dou

Perennial herbs, to 2 m; stem erect, glabrous, winged. Leaves with branched tendril at apex; stipules large, 3.5–6.5 cm, ovate or elliptic, glabrous, often with dentate basal lobe; leaflets 3–5 paired, narrowly ovate, ovate-lanceolate or elliptic-lanceolate, 5.5–9 × 2–3 cm, glabrous, with sub-parallel veins. Racemes axillary, with 8–14 flowers; calyx campanulate, ca. 12 mm, glabrous, unequally toothed. Flowers red-purple; banner 13 mm, retuse at apex, often with darker veining; wings auriculate at base; keels ca. 12 mm. Ovary linear, glabrous. Legume ca. 45 × 5.5 mm, dark brown. Seeds oblate spherical, light yellow, smooth. Fl. May–Jun, fr. Jul–Aug.

Forests, valleys, river banks; 1100–1500 m. Xinjiang [Russia; N. Europe].

3. Lathyrus humilis (Seringe) Sprengel, Syst. Veg. 3: 363. 1826.

Ai shan li dou

Orobus humilis Seringe in Candolle, Prodr. 2: 371. 1825; *Lathyrus altaicus* Ledebour.

Perennial herbs, 20–30 cm high; stem slender, erect, sometimes branching, puberulent, wingless. Leaves paripinnate; tendril weakly branched or simple; stipules 1–1.6 cm, foliose, semisagittate, dentate; leaflets (2)3–4 paired, ovate or elliptic, 1.5–3 (–5) × 1–2 cm, glabrous or abaxially puberulent, with reticulate veins. Racemes axillary, shorter than leaf, with 2–5 flowers; calyx campanulate, lowest tooth ca. half length of tube. Flowers purple-red, 1.5–2 cm; banner rotund, with claw; wings and keels auriculate at base. Ovary linear, glabrous. Legume linear, 4.3–5 cm. Seeds elliptic, red-brown, smooth. Fl. May–Jul, fr. Aug–Sep.

Forest margins, scrub forests, hill grasslands; below 2500 m. Gansu, Heilongjiang, Hebei, Jilin, Liaoning, Nei Mongol, Shanxi, Xinjiang [Korea, Mongolia, Russia].

4. Lathyrus dielsianus Harms, Bot. Jahrb. Syst. 29: 417. 1901.

Zhong hua shan li dou

Lathyrus wilsonii Craib.

Lathyrus davidii Hance var *roseus* C.W. Chang Fl. Tsinglingensis 1(3): 450. 1981.

Perennial herbs, 80–100 cm high; stem erect, glabrous, wingless. Leaves with simple or branched tendril; stipules oblique-ovate, toothed; on upper leaves often lanceolate, entire; leaflets (2) 3–4 (–5) paired, ovate to ovate-lanceolate, 3.5–5.5 (–6.5) × 1.3–2 (–3.5) cm, glabrous, with reticulate veins. Racemes axillary, shorter than or subequal leaf, with 9–11 (–13) flowers; calyx campanulate, 7–8 mm, glabrous, short-toothed, lowest tooth shorter than tube 1.5–2 mm. Flowers pink or purple, 1.8–1.9 cm; banner rotund, with claw; wings obovate, auriculate at base. Ovary linear, glabrous. Legume linear, 5.5–8 cm, brown. Seeds elliptic, ca. 5 mm, smooth. Fl. May–Jun, fr. Jul–Aug.

Forests, slopes, river banks. Hubei, Shaanxi, Shanxi, Sichuan. Endemic to China.

5. Lathyrus japonicus Willdenow, Sp. Pl. 3: 1092. 1802.

Hai bin shan li dou

Perennial herbs, 15–50 cm high; stem stoloniferous, creeping, wingless. Leaves with branched or simple tendril; stipules 1–3 cm, sagittate, glabrous; leaflets 3–5 paired, long elliptic or obovate, 25–33 × 11–18 mm, glabrous, with reticulate veins visible on both surfaces. Racemes axillary, shorter than leaf, with 2–5 flowers; calyx campanulate, 9–10 (–12) mm, glabrous, calyx teeth unequal, lowest tooth 5–6 mm. Flowers purple, ca. 21 mm; banner rotund, with claw; wings narrowly obovate, occasionally white. Ovary linear, glabrous or rarely hairy. Legume compressed, ca. 5 cm, brown or purple-brown, glabrous or puberulent. Seeds subglobose. Fl. May–Jul, fr. Jul–Aug.

Seashores. Hebei, Liaoning, Shandong, Zhejiang [widely distributed on coasts of Asia, Europe, North America and Chile]. Although widely recognized, the two forms appear to be sympatric and intrograde. Plants with white wings and keels have been described as forma *albiflorus* Miyabe et. Tatew. in Transactions of the Sapporo Natural History Society 14: 185 (1936).

1a. Plant glabrous or slightly hairy .... 5a. forma *japonicus*
1b. Plant obviously hairy .... 5b. forma *pubescens*

5a. Lathyrus japonicus forma. **japonicus**

Hai bin shan li dou (yuan bian zhong)

Pisum maritimum Linnaeus. Species Plantarum 2: 727. 1753.

Lathyrus japonicus subsp. *maritimus* (Linnaeus) P. W. Ball; *L. maritimus* (Linnaeus) Bigelow;

Plants glabrous or puberulent.

Seashores. Hebei, Jiangsu, Liaoning, Shandong, Zhejiang [widely distributed on coasts of Asia, Europe, and North America].

5b. Lathyrus japonicus forma **pubescens** (Hartman) H. Ohashi & Tateishi, J. Jap. Bot. 52: 234. 1977.

Mao hai bin shan li dou

Pisum pubescens Hartman, Handb. Scand. Fl., ed. 2, 198. 1832; *Lathyrus aleuticus* (Greene ex T. G. White) Pobedimov; *L. japonicus* var. *aleuticus* (Greene ex T. G. White) Fernald; *L. maritimus* var. *aleuticus* Greene ex T. G. White; *L. maritimus* f. *pubescens* Saelan; *L. maritimus* var. *velutinus* Fries.

Plants obviously pubescent.

Seashores. Hebei, Jiangsu, Liaoning, Shandong, Zhejiang [widely distributed on coasts of Asia, Europe, and North America].

6. Lathyrus gmelinii (Fischer ex Candolle) Fritsch, Sitzungsber. Kaiserl. Akad. Wiss., Math.-Naturwiss. Cl., Abt. 1, 104: 516. 1895.

Xin jiang shan li dou

Lathyrus laevigatus Fritsch subsp. *gmelinii* (Fischer ex Candolle) Hendrych; *L. luteus* (Linnaeus) Moench var. *gmelinii* (Fischer ex Candolle) Reichenbach.

Perennial herbs, 60–150 cm high; stem erect, glabrous, wingless. Leaves aristate at apex; stipules foliose, semisagittate, 15–30 × 4–10 mm, glabrous, toothed; leaflets 3–4 paired, ovate, elliptic or long elliptic, rarely lanceolate, 3–6 (–9) × 1–5 cm, glabrous, with pinnate veins. Racemes axillary, longer than leaf, with 7–12 flowers, glabrous; calyx campanulate, ca. 1 cm, glabrous, lowest tooth 2 mm. Flowers orange-yellow, 2.5–3 cm; banner ovate, with claw; wings obovate, auriculate at base. Ovary linear, ca. 1.8 cm, glabrous. Legume linear, 6–8 cm, brown. Seeds light brown, smooth. Fl. May–Jul, fr. Jul–Aug.

Forests, river banks; 1400–2400 m. Xinjiang [Russia]. This and a number of other Eurasian taxa may represent entities in *Lathyrus laevigatus* (Waldst. et Kit) Grenier, from which they are poorly distinguished.

7. Lathyrus krylovii Sergievskaja, Sist. Zametki Mater. Gerb. Krylova Tomsk. Gosud. Univ. Kuybysheva 3–4: 3. 1933.

Xia ye shan li dou

Lathyrus laevigatus Fritsch subsp. *krylovii* (Sergievskaja) Hendrych.

Perennial herbs, 60–80 cm high; stem erect, glabrous, wingless. Leaves aristate at apex; stipules semisagittate, lanceolate or linear, 10–25 × 3–7 mm; leaflets 2–4 paired, linear, to linear-lanceolate, 5–13 × 0.3–1.6 cm, glabrous, with pinnate veins. Racemes longer than leaf, with 2–4 flowers; calyx campanulate, ca. 8 mm, glabrous, lowest tooth ca. 1.5 mm. Flowers yellow, 2–5 cm; banner rotund, ca. 2.7 cm, with claw; wings narrowly obovate, auriculate at base. Ovary linear, glabrous. Legume linear, 8–9 cm, brown. Seeds elliptic, 3–4 mm. Fl. Jun–Jul, fr. Aug–Sep.

Hill forests; ca. 1800 m. Xinjiang [Russia].

8. Lathyrus vaniotii H. Léveillé, Repert. Spec. Nov. Regni Veg. 7: 230. 1909;

Dong bei shan li dou

Perennial herbs, 40–70 cm high; stem erect, glabrous, wingless. Leaves aristate at apex; stipules semisagittate, subulate, occasionally linear, falcate with a short (2mm) basal spur, 5–15 × 1–3 mm; leaflets (2) 3–4 (–6) paired, lanceolate or narrowly lanceolate on lower stem leaves, narrowly ovate, rarely oblong on upper stem leaves, 4–6 × 1.5–2.5 cm, glabrous, with reticulate veins, dark green above, glaucous-grey below, apex shortly mucronate. Racemes axillary, with 4–8 flowers; calyx campanulate, ca. 11

mm, glabrous, lowest tooth 4 mm. Flowers purple-red, 1.8–2.5 cm; banner ca. 21 mm, with claw; wings equal banner, ovate. Ovary linear, glabrous. Fl. May–Jun.

Forested slopes. Heilongjiang, Jilin [Korea].

9. Lathyrus caudatus Z. Wei & H. P. Tsui, Bull. Bot. Res., Harbin 4(1): 49. 1984.

Wei ye shan li dou

Perennial herbs, to 120 cm high; stem strong, erect, branched, sparsely glandular, wingless. Leaves with simple or weakly branching tendril; stipules semisagittate, linear-lanceolate, 12–18 × 1.5–2 mm; leaflets 4–5 paired, ovate-lanceolate, 9–12 × 2.5–4 cm, glabrous, with 5 prominent veins. Racemes axillary, ca.10 cm, with many flowers; calyx campanulate, unequal toothed, lowest tooth ca.7 mm. Flowers light yellow, 1.8–2 cm; banner rotund, with claw; wings slightly shorter than keels. Ovary linear, glabrous, brown glandular. Legume linear, 6–8 cm, brown glandular. Seeds 8–12.

Scrub forests; ca. 150 m. Zhejiang (Jiande Xian). Endemic to China, known only from the type collection.

10. Lathyrus anhuiensis Y. J. Zhu et R. X. Meng, Acta. Phytotax. Sin. 24: 402. 1986.

An hui shan li dou

Perennial herbs, 80–120 cm high; stem erect, much branched, glabrous, wingless. Leaves 10–30 cm, mucronate or with a simple tendril at apex; stipules semisagittate, 8–15 × 2–5 mm; leaflets 3–8 paired, narrowly elliptic or narrowly ovate, 3–7 × 1–3 cm, entire, glabrous, with pinnate veins. Racemes axillary, subequal or shorter than leaf, with ca. 10 flowers; calyx campanulate, unequal, longest tooth less than 1/5 of tube. Flowers yellow, 14–18 mm; banner broadly obovate, with claw; wings shorter than banner, obovate, subequal to keel. Ovary linear, ca. 11 mm, purple-brown glandular-hairy; style curved inward. Legume linear, 6–8 cm, light brown. Seeds oblong, brown. Fl. May–Jul, fr. Jun–Sep.

SE Anhui (Xuancheng Xian), Hupeh. Endemic to China, known only from the type collection (not available for this revision).

The plants described as *Lathyrus henanensis* S.Y.Wang (Fl. Henan, 2: 347. 1988.) may represent individuals of this species, but *L. henanensis* S.Y. Wang is described as having a glabrous ovary and branching tendrils.
Two incomplete Augustine Henry specimens may represent additional collections of this taxon; Aug. Henry 6595, held at BM and a specimen dated 1889, held at K.

11. Lathyrus palustris Linnaeus, Sp. Pl. 2: 753. 1753.

Ou shan li dou

Perennial herbs, 15–100 cm high; stem climbing, branched, pubescent or glabrous, winged or unwinged. Leaves with simple or branched tendril at apex; stipules semisagittate, 12–25 (–30) × 2–10 mm; leaflets 2–4 paired, linear to broadly lanceolate, without reflexed basal spur, 3–6 × 0.4–1(–1.5) cm, pubescent; veins pinnate or subparallel, prominent on abaxial leaf surface. Racemes axillary, longer than leaf, with (2) 3–4 (–10) flowers; calyx campanulate, unequal toothed. Flowers purple, 13–15 (–20) mm; banner obovate, with claw; wings shorter than banner, obovate and longer than keels. Ovary linear. Legume linear, 3–4 cm, beaked at apex. Fl., fr. Jul–Sep.

Marshes, wet meadows, a weed of rice fields; 0 –3500m. Gansu, Hebei, Heilongjiang, Hubei, Jiangsu, Jilin, Liaoning, Nei Mongol, Qinghai, Shanxi, Sichuan, Xinjiang, Xizang, Yunnan Zhejiang [Japan, Korea, Mongolia, Russia, Europe, North America].

Lathyrus palustris is widely distributed in the north temperate zone in Europe, Russia, East Asia and North America. It is a highly variable taxon with many entities described from it, although few of these stand up to scrutiny. East Asian specimens are often referred to subsp. pilosus, but this is based purely on pubescence, a character with no other correlates. Consequently we treat pubescent individuals at the varietal level. This species is often confused with *L. quinquenervius* (Miq.) Litvinov. See the entry on that species for distinguishing characters.

1a. Stem winged (subsp. *palustris* L.).
  2a. Leaves with branched tendril; leaflets 2–4-paired; racemes (2 or)3- or 4(or 5)-flowered, pubescent .... 11a. var. *pilosus*
  2b. Leaves with unbranched, short tendril; leaflets 1- or 2(or 3)-paired; racemes 1- or 2(–4)-flowered, puberulent or glabrous .... 11b. var. *sinomontanus*
1b. Stem wingless (subsp. *exalatus* H. P Tsui, Bull. Bot. Res., Harbin 4(1): 54. 1984.).
.... 11c. var. *exalatus*

11a. Lathyrus palustris var. **pilosus** (Chamisso) Ledebour, Fl. Ross. 1: 686. 1842.

Mao shan li dou (yuan bian zhong)

Lathyrus pilosus Chamisso, Linnaea 6: 548. 1831.

Plant pubescent. Stem winged. Leaves with branched tendril; leaflets 2–4 paired; stipules semisagittate; racemes with (2) 3–4 (–5) flowers.

• Gansu, Hebei, Heilongjiang, Hubei, Jiangsu, Jilin, Liaoning, Nei Mongol, Qinghai, Shanxi, Zhejiang [Japan, Korea, Mongolia, Russia]. Glabrous plants with the characteristics of var. pilosus can be referred to the autonym, var. palustris, but such individuals have not been observed from China.

11b. Lathyrus palustris var.**sinomontanus** Kenicer. var. nov. Plants of the Vicinity of Yun-Nan-Sen. Collected by E. E. Maire Pro Vicar Apostolic of Yunnan. Received November 1906. *E.E. Maire 2072*, (Type here designated: KUN, isotypes: BM and E)

Lathyrus palustris var. *linearifolius* Seringe in Candolle

Xian ye shan li dou

Plant puberulent or glabrous 10-40cm high. Stem usually narrowly winged; Leaves with short, simple tendril at apex; stipules linear; leaflets 1–2 (–3) paired, linear, rarely elliptic-lanceolate. Racemes with 1–2 flowers, rarely 3–4.

- Sichuan, Yunnan.

11c. Lathyrus palustris var. **exalatus** (H.P. Tsui) Kenicer stat. nov.

Wu chi shan li dou (yuan bian zhong)

Plant glabrous, occasionally puberulent. Stems wingless Stipules large, 12–25 (–30) × 2–8 mm; leaflets usually broadly lanceolate, veins sub-parallel, 3–6 × 0.5–1 (–1.5) cm. Racemes lax with (2) 3–8 (–10) flowers.

- Shanxi, Sichuan, Xinjiang, Xizang, Yunnan.

12. Lathyrus quinquenervius (Miquel) Litvinov in Komarov & Alissova-Klobukova, Opred. Rast. Dal'ne-Vost. Kraia 2: 683. 1932.

Shan li dou

Vicia quinquenervia Miquel, Ann. Mus. Bot. Lugduno-Batavi 3: 50. 1867.

Perennial herbs, 20–80 cm high; stem erect or clambering over surrounding vegetation, rarely branched, winged. Leaves with simple tendril; stipules linear, with reflexed basal spur, often sickle-shaped (falcate), 7–23 × 0.2–2 mm; leaflets 1–2 (–3) paired, elliptic-lanceolate or linear-lanceolate, 35–80 × 5–8 mm, pubescent, with 5 stiff, prominent parallel veins, rigid when dry. Racemes axillary with 5–8 flowers; calyx campanulate, pubescent, lowest tooth equal to tube. Flowers purple-blue or purple, sometimes with white wings and keel (12) 15–20 mm; banner rotund, with claw; wings narrowly obovate, auriculate at base. Ovary densely hairy. Legume linear, 3–5 cm. Fl. May–Jul, fr. Aug–Sep.

This species is often confused with *Lathyrus palustris* but can be distinguished by the five strong parallel nerves in long, slender leaflets. The linear, acute stipules with a reflexed basal spur, the strong wings on the stems and the simple tendrils also aid in identification.

Forests, hill slopes, roadsides; below 2500 m. Gansu, Heilongjiang, Hebei, Hubei, Henan, Jiangsu, Jilin, Nei Mongol, Qinghai, Shanxi, Shengdong, Sichuan [Japan, Korea, Russia]. Herbarium specimens are often mislabeled as L. palustris var. linearifolius.

13. Lathyrus komarovii Ohwi, J. Jap. Bot. 12: 329. 1936.

San mai shan li dou

Orobus alatus Maximowicz, Prim. Fl. Amur. 83. 1859; *Lathyrus alatus* (Maximowicz) Komarov (1904), not Tenore (1811), nor Smith (1813); *O. vernus* Linnaeus var. *alatus* (Maximowicz) Regel.

Perennial herbs, 40–70 cm high; stem erect, rarely branched, glabrous, narrowly winged. Leaves aristate at apex; leaf rachis narrowly winged; stipules semisagittate, 15–25 × 3–8 (–12) mm, rarely dentate; leaflets (2) 3–5 paired, narrowly ovate to oblanceolate, acuminate, glabrous, with 3(–5) parallel veins sunken on adaxial surface, raised on abaxial. Racemes axillary, shorter than leaf, with 3–8 flowers; bracts membranous, persistent; calyx campanulate, glabrous, lowest tooth ca. 5 mm, equal to the tube. Flowers purple, 13–18 mm; banner rotund, with claw; wings shorter than banner, auriculate at base. Ovary linear, glabrous. Legume linear, 3.7–4.5 cm, black-brown, glabrous. Seeds subglobose, brown, smooth. Fl. May–Jun, fr. Jun–Aug.

Forests, grasslands. Heilongjiang, Jilin, Nei Mongol [Korea, Russia].

14. Lathyrus tuberosus Linnaeus, Sp. Pl. 2: 732. 1753.

Mei hong shan li dou

Perennial herbs; rhizomes bearing small tubers. Stems 30–120 cm high, erect, glabrous, wingless. Leaves with simple or branched tendril at apex; stipules semisagittate, 5–20 × 1–4 mm; leaflets 1 paired, elliptic, oblong or obovate, glabrous, with parallel veins. Racemes axillary, 2–7 flowers; calyx campanulate, 6–7 mm, lowest tooth shorter than tube. Flowers purple-red, 1.5–2 cm; banner subovate, with claw; wings obovate, auriculate at base. Ovary linear; style twisted. Legume linear, 2–4 cm, brown, glabrous. Seeds elliptic, brown, tuberculate. Fl. Jun–Aug, fr. Aug–Sep.

Water meadows, river banks; 500–2400 m. Xinjiang [Kazakhstan, Russia; Europe].

15. Lathyrus sativus Linnaeus, Sp. Pl. 2: 730. 1753.

Jia shan li dou

Annual herbs, 30–50 (–70) cm high; stem suberect, glabrous, winged. Leaves with tendril at apex; leaf rachis winged; stipules semisagittate, 18–25 × 2–5 mm; leaflets 1 paired, lanceolate to linear, 18–25 × 2–4 mm, entire, with parallel veins. Racemes with 1 flower, rarely 2; rachis 3–6 cm; calyx campanulate, subequal toothed, 2–3 times longer than tube. Flowers white, blue or pink. Ovary linear; style twisted. Legume subelliptic, 2.5–3.5 (–4) cm, 2 winged along sutures. Seeds smooth. Fl. Jun–Jul, fr. Aug.

Cultivated as a fodder crop in N. China, casual elsewhere [native to N Africa, SW Asia, and Europe].

16. Lathyrus odoratus Linnaeus, Sp. Pl. 2: 732. 1753.

Xiang wan dou

Annual herbs, 50–200 cm high; stem climbing, much branched, somewhat hairy, winged. Leaves with branched tendril at apex; leaf rachis winged; stipules semisagittate; leaflets 1 paired, ovate-oblong or elliptic, 2–6 × 0.7–3 cm, entire, with pinnate veins, rarely subparallel veins. Racemes axillary, longer than leaf, with 1–3 (–4) flowers; calyx campanulate, equal toothed and longer than tube. Flowers usually purple, or other colors. Ovary linear; style twisted. Legume linear, 5–7 cm, brown-yellow, pubescent. Seeds smooth. Fl., fr. Jun–Sep.

Widely cultivated in China and Worldwide as an ornamental and cut flower [native to Sicily].

17. Lathyrus latifolius Linnaeus, Sp. Pl. 2: 733. 1753.

Kuan ye shan li dou

Perennial herbs, to 3 m high; stem erect, quadrangular, pubescent or glabrous, winged. Leaves with branched tendril at apex; stipules semisagittate, lanceolate to ovate; leaflets 1 paired, elliptic to elliptic-rotund, or ovate to linear, (3) 4–15 × 0.3–5 cm, with parallel veins. Racemes with 5–15 flowers; calyx campanulate, ca. 6 mm, equally 5 toothed. Flowers purple to pink, (15) 20–30 mm, style twisted. Legume 5–11 cm, brown, glabrous. Seeds 10–15.

Cultivated in Shaanxi [native to Europe]. Cultivated worldwide in temperate areas as an ornamental and fodder crop.

18. Lathyrus pratensis Linnaeus, Sp. Pl. 2: 733. 1753.

Mu di shan li dou

Perennial herbs, 30–120 cm high; stem decumbent or climbing, wingless. Leaves with simple or branched tendril at apex; stipules sagittate, (5) 10–45 × 3–10 (–15) mm; leaflets 1 paired, elliptic, lanceolate or linear-lanceolate, 10–30 (–50) × 2–9 (–13) mm, puberulent, with parallel veins. Racemes axillary, 3 to 6 times longer than leaf, with 5–12 flowers; calyx campanulate, pubescent, lowest tooth longer than tube. Flowers yellow, 12–18 mm; banner rotund, ca. 14 mm, with claw; wings slightly shorter than banner. Legume linear, 2.5–4.5 cm, black. Seeds rotund, yellow or brown, smooth. Fl. Jun–Aug, fr. Aug–Oct.

Forests, hill slopes, roadsides. Gansu, Hubei, Heilongjiang, Qinghai, Shaanxi, Sichuan, Xinjiang, Yunnan [Asia; Europe].

Appendix 3

Papers and international conference presentations

Publication

- Kenicer Gregory J.; Kajita, Tadashi, Pennington R. Toby & Murata, Jin. (2005) Systematics and biogeography of *Lathyrus* (Leguminosae) based on internal transcribed spacer and cpDNA sequence data. *American Journal of Botany* **92**: 1199-1209.

Lathyrus (Leguminosae; Papilionoideae) is the largest genus in tribe Fabeae and exhibits an intriguing extratropical distribution. We studied the systematics and biogeography of *Lathyrus* using sequence data, from accessions representing 53 species, for the internal transcribed spacer plus 5.8S-coding region of nuclear ribosomal DNA as well as the *trnL-F* and *trnS-G* regions of chloroplast DNA. Our results generally supported recent morphology-based classifications, resolving clades corresponding to sections Lathyrus and Lathyrostylis, but question the monophyly of the large, widespread section Orobus sensu Asmussen and Liston. Sections Orobus, Aphaca, and Pratensis form a predominantly northern Eurasian--New World clade. Within this clade, the North American and eastern Eurasian species, including both Holarctic species (*L. palustris* and *L. japonicus*), form a transberingian clade of relatively recent origin and diversification. The South American Notolathyrus group is distant from this transberingian lineage and should be reinstated as a distinct section within the northern Eurasian--New World clade. The Notolathyrus lineage reached the New World most probably through long-distance dispersal from Eurasia. The remaining sections in the genus are centered on the Mediterranean region.

Key words: Bering land bridge; biogeography; cpDNA; extratropical distribution; internal transcribed spacer; *Lathyrus*; Leguminosae; Notolathyrus.

Conference presentation

- **Phylogenetic analyses of genera in the tribes Trifolieae and Fabeae (Leguminosae) using nucleotide sequence data of the plastid gene *matK*.**

  Presented at Botany 2004, Snowbird, Utah.

Steele, Kelly P.[2], Kenicer, Gregory J.[3], Wojciechowski, Martin F.[1].

1 - Arizona State University, School of Life Sciences, PO Box 874501, Tempe, Arizona, 85287-4501, USA
2 - Arizona State University East, Department of Applied Biological Sciences, 7001 E. Williams Field Road, Mesa, Arizona, 85212, USA
3 - University of Edinburgh, and Royal Botanic Garden Edinburgh, Institute of Cell and Molecular Biology, Edinburgh, United Kingdom

Phylogenetic analyses using nucleotide sequences of the plastid gene matK from 84 species from most genera traditionally included in the tribes Trifolieae and Fabeae (syn. Vicieae) support the monophyly of most currently recognized genera except for the genus *Vicia*. Results also indicate that *Trifolium* is the sister group to a clade composed of genera in the Fabeae (*Vicia*, *Lens*, *Pisum*, and *Lathyrus*) rather than being in a clade with other genera in the Trifolieae, the tribe in which *Trifolium* is traditionally placed. To provide further information on relationships within some larger genera in these two tribes, to include genera not sampled previously (such as *Vavilovia*), and to test the conclusions of earlier studies, nucleotide sequences of both the adjacent 5' trnK intron and the matK gene were utilized and approximately 45 species were added to the data set. Results indicate that *Vavilovia* is sister to *Pisum*, forming a group that is sister to all species of *Lathyrus*. Results of these analyses generally support the hypotheses that *Vicia* is paraphyletic; that *Lathyrus*, *Medicago*, and *Trifolium* are each monophyletic; and that *Melilotus* is nested within a paraphyletic group of *Trigonella* species. Increased sampling provides support for the hypothesis that species in *Medicago* section Buceras form a clade that is sister to the remaining species in the genus. Relationships retrieved for the increased sample set of *Lathyrus* indicate two major clades within the genus, which reflect 'oroboid' and 'lathyroid' lineages. Results of phylogenetic analyses are used to consider plausible hypotheses of biogeographic origins and distribution patterns, particularly for species with a primarily north temperate distribution. Hypotheses on the independent origin of trifoliate leaves in *Trifolium*, Ononis, and the clade comprising *Medicago* and *Trigonella* are also considered.

Conference posters

- **Phylogeny and systematics of the genus *Lathyrus* (Fabaceae): evidence from nuclear ITS sequences**

  Presented at the 17th International Botanical Congress, Vienna 2005.

  Susana S. Neves[1], Gregory J. Kenicer[2], Pedro Fevereiro[1,3], Maria Carlota Vaz Patto[1]

  1 - Instituto de Tecnologia Química e Biológica (ITQB), Universidade Nova de Lisboa, Oeiras, Portugal.
  2 - Royal Botanic Garden Edinburgh (RBGE), Scotland, United Kingdom
  3 - Departamento de Biologia Vegetal, Faculdade de Ciências da Universidade de Lisboa, Portugal

  The genus *Lathyrus* (Fabaceae) comprises c. 160 species of annual and perennial herbs, morphologically and ecologically diverse, with a worldwide distribution. Due to their resistance to drought and flooding, some *Lathyrus* species (e.g. *L. sativus* - grass pea - and *L. cicera* - chickling vetch) have great agronomic potential as supplementary sources of calories and protein for human populations and as forage crops in the poorest regions in the World. The systematics and phylogeny of the genus have been investigated using both morphology and molecular data, mostly plastid DNA. We used the nrDNA ITS region to investigate the relationships in the genus, including a representative sampling of its sections and main clades, as well as species from other genera in the tribe Vicieae. *Lathyrus* and *Pisum* are shown as a strongly supported monophyletic group. Phylogenetic resolution within *Lathyrus* is still low, but it might be improved with the increasing sampling. Nevertheless, various groups are recognized, some confirming previously suggested associations, such as the affinity of Sect. *Aphaca* to Sect. *Pratensis*, and the close relationship of *L. clymenum* and *L. ochrus*.

- **Molecular phylogenetics of *Lathyrus* (Leguminosae) using nuclear and chloroplast sequence data: a preliminary assessment.**

  Presented at the Shokkubutsu Bunruigakkai, Kobe 2003.

  ク゛レコ゛リ ケニサー (Gregory Kenicer, Royal Botanic Garden Edinburgh)
  梶田忠(Tadashi Kajita, University of Tokyo Botanical Garden)
  邑田仁(Jin Murata, University of Tokyo Botanical Garden)

Lathyrus L. is a relatively large and widespread genus of temperate herbaceous legumes with centres of diversity in Western and Eastern Eurasia, and North and South America. Many disparate treatments of geographical or taxonomic groupings have been produced but the few overall syntheses that have been attempted have left a number of key areas unresolved. In particular, the relationships within the putatively basal section Orobus, the connections between the Old and New Worlds, and relationships with other members of the Vicieae. As a part of ongoing research into the nature of these relationships, preliminary findings from nuclear ITS and chloroplast *trn*L-*trn*F intergenic spacer/trnL intron sequence data are presented. The resolution provided by these two regions gives some confirmation of other molecular (restriction site map based) research as well as new insights into the relationships of the group above the generic level. However, for the purposes of infrageneric classification and clarification of geographical relationships, these datasets are less robust. This is particularly so within the morphologically variable but apparently homoplastic section Orobus, which is the key group in the wider study. The high level of morphological homoplasy seen in section Orobus is reflected in homoplasy in sequence data, making the relationships within Eurasian members of section Orobus hard to define from these two genome regions. These results agree with those of the earlier restriction site mapping work. Thus discussion focuses on possible reasons why the phylogeny of *Lathyrus* has so far proven difficult to resolve on a worldwide level. Despite low bootstrap support, Neighbor-Joining (NJ) trees based on these sequence data suggest that a recent major reclassification of the Vicieae needs to be reappraised and also indicate some interesting infrageneric patterns. The NJ trees will therefore be used to suggest key areas for further investigation.

Appendix 4

CD-ROM Contents list

The CD-ROM that accompanies this thesis contains the following files:

Sequence data

Aligned sequence data for all accessions analysed for:

- *matK* region (chapter 3).
- Combined analysis; ITS, *trnL–F* and *trnS–G* regions, with indel coding at the end of the matrix (chapter 4).

Each file is presented in nexus format, with an example datablock used in PAUP* for the analyses presented in chapters 3 and 4.

Images

- An image bank of wild-collected and cultivated members of tribe Fabeae is included. All are jpeg format. Files are labelled by species name, with a separate folder containing images of the South American species.

Thesis PDF version

- **A PDF of this complete thesis is also included. For the visually impaired, please view on Adobe Reader version 7.0 or later, and select:**
  >'View' menu
  >'Read out loud'

Bibliography

Abrams L. (1944) *Illustrated Flora of the Pacific States: Washington, Oregon and California*, vol. II. Stanford University Press, Palo Alto, pp. 618–628.

Acevedo R. (1928) Sobre el género *Lathyrus* L. en Chile. *Revista Chiulena de Historia Natural* **31**: 123–126.

Aïnouche A.-K. & Bayer R.J. (1999) Phylogenetic relationships in *Lupinus* (Fabaceae: Papilionoideae) based on internal transcribed spacer sequences (ITS) of nuclear ribosomal DNA. *American Journal of Botany* **86**: 590–607.

Alefeld F.G.C. (1861) Ueber Vicieen. *Bonplandia* **9**: 138–153.

Alfaro M.E., Zoller S. & Lutzoni F. (2003) Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markoff chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. *Molecular Biology and Evolution* **20**: 255–266.

Alice L. & Campbell C.S. (1999) Phylogeny of *Rubus* (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. *American Journal of Botany* **8**: 81–97.

Allan G.J. & Porter J.M. (2000) Tribal delimitation and phylogenetic relationships of Loteae and Coronilleae (Faboideae: Fabaceae) with special reference to *Lotus*: evidence from nuclear ribosomal ITS sequences. *American Journal of Botany* **87**: 1871–1881.

Allen O.N. & Allen E.K. (1981) *The Leguminosae, a Sourcebook of Characteristics, Uses and Nodulation.* University of Wisconsin Press, Madison.

Allkin R., MacFarlane T.D., White R.J., Bisby F.A. & Adey M.E. (1985) *The Geographical Distribution of* Lathyrus *L.* Southampton University, Southampton.

Ambrose M. & Maxted N. (2000) Peas (*Pisum* L.). In: Maxted N. & Bennett S. (eds) *Plant Genetic Resources of Legumes in the Mediterranean.* Kluwer, Dordrecht.

Angiosperm Phylogeny Group. (1998) An Ordinal Classification for the Families of Flowering Plants. *Annals of the Missouri Botanical Garden*. **85**: 531 – 553.

Angiosperm Phylogeny Group (2003) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Botanical Journal of the Linnean Society* **141**: 399–436.

Arechavaleta J. (1901) Flora Uruguaya I. *Anales del Museo Nacional de Montevideo*

3: 368–375.

Arora R.K., Mathur P.N., Riley K.W. & Adham Y. (eds) 1995 Lathyrus *Genetic Resources in Asia. Proceedings of a Regional Workshop.* International Plant Genetic Resources Institute (Office for South Asia), New Delhi.

Ascherson P. & Graebner P. (1909) Synopsis der Mitteleuropäischen Flora, vol. 6. Wilhelm Engelmann, Leipzig, pp. 1000–1063.

Asmussen C. & Liston A. (1998) Chloroplast DNA characters, phylogeny and classification of *Lathyrus* (Fabaceae). *American Journal of Botany* **85**: 387–401.

Atkins H., Preston J. & Cronk Q.C.B. (2001) A molecular test of Huxley's line: *Cyrtandra* (Gesneriaceae) in Borneo and the Philippines. *Biological Journal of the Linnaean Society* 72: 143–159.

Autran E. (1907) Les Parcs nationaux argentins. *Trabajos de la Museo de Farmacologia de Buenos Aires* **13**: 1–41.

Avise J.C. (1994) *Molecular Markers, Natural History and Evolution.* Chapman & Hall, New York.

Axelrod D.I. (1948) Climate and evolution in western North America. *Evolution* **2**: 127–144.

Axelrod D.I. (1952) A theory of Angiosperm evolution. *Evolution* **6**: 29–60.

Axelrod D.I. (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution* **20**: 1–15.

Azuma H., Garcia-Franco J., Rico-Gray V. & Thien L. (2001) Molecular phylogeny of the Magnoliaceae: the biogeography of tropical and temperate disjunctions. *American Journal of Botany* **88**: 2275–2285.

Badr A., El Shazly H., El Rabey H. & Watson L.E. (2002) Systematic relationships in *Lathyrus* sect. Lathyrus (Fabaceae) based on amplified fragment length polymorphism (AFLP) data. *Canadian Journal of Botany* **80**: 962–969.

Bal A.K. & Khetmalas M.B. (1996) Pre- and postwinter changes in the root nodules of *Lathyrus maritimus* (L.) Bigel. with special reference to storage organelles. *International Journal of Plant Sciences* **157**: 432–439.

Ball P.W. (1968) *Lathyrus.* In: Tutin T.G., Heywood V.H., Burges N.A., Moore D.M., Valentine D.H., Walters S.M. & Webb D.A. *Flora Europaea*, vol. II. Cambridge University Press, Cambridge, pp. 136–143.

Barneby R.C. & Reveal J.L. (1971) A new species of *Lathyrus* (Fabaceae) from the

Death Valley region of California and Nevada. *Aliso* **7**: 361–364.

Bässler M. (1966) Die Stellung des Subgenus *Orobus* (L.) Baker in der Gattung *Lathyrus* L. und seine systematische Gliederung. *Feddes Repertorium* **72**: 69–97.

Bässler M. (1971) Beitrage zur Nomenklatur der Gattung *Lathyrus* L. *Feddes Repertorium* **82**: 433–439.

Bässler M. (1973) Revision der eurasiatischen arten von *Lathyrus* L. sect. *Orobus* (L.) Gren. et. Godr. *Feddes Repertorium* **84**: 329–447.

Bässler M. (1981) Revision von *Lathyrus* L. sect. *Lathyrostylis* (Griseb.) Bässler (Fabaceae). *Feddes Repertorium* **92**: 179–254.

Bässler M. & Stohr G. (1977) Nomenklatorische Notizen zur Neuauflage des Kritischen Bandes der Exkursionsflora von W. Rothmaler. *Feddes Repertorium* **88**: 417–420.

Battistin A. & Fernández A. (1994) Karyotypes of four South America native species and one cultivated species of *Lathyrus* L. *Caryologia* **47**: 325–330.

Becerra J.X. (1997) Insects on plants: macroevolutionary trends in host use. *Science* **276**: 253–256.

Becerra J.X. (2003) Synchronous coadaptation in an ancient case of herbivory. *Proceedings of the National Academy of Sciences of the USA* **100**: 12804–12807.

Becerra J.X. & Venable D.L. (1999) Macroevolution of insect–plant associations: the relevance of host biogeography to host affiliation. *Proceedings of the National Academy of Sciences of the USA* **96**: 12626–12631.

Becerra J.X., Venable D.L., Evans P.H. & Bowers W.S. (2001) Interactions between chemical and mechanical defenses in the plant genus *Bursera* and their implications for herbivores. *American Zoologist* **41**: 865–876.

Bell C.D. & Patterson R.W. (2000) Molecular phylogeny and biogeography of *Linanthus* (Polemoniaceae). *American Journal of Botany* **87**: 1857–1870.

Bell E.A. (1971) Comparative biochemistry of non-protein amino acids. In: Harborne J.B., Boulter D. & Turner B.L. Chemotaxonomy of the Leguminosae. Academic Press, London, pp. 179–206.

Bell E.A., Lackey J.A. & Polhill R.M. (1978) Systematic significance of canavanine in the Papilionoideae. *Biochemical Systematics and Evolution* **6**: 201–212.

Ben Brahim N., Salhi A., Chtourou N., Combes D. & Marrakchi M. (2002) Isozymic polymorphism and phylogeny of 10 *Lathyrus* species. *Genetic Resources and Crop*

Evolution **49**: 427–436.

Bentham G. (1859) Leguminosae in Martius' *Flora Brasiliensis*, vol. 15. Leipzig, pp. 111–116

Ben-Ze'ev N. & Zohary D. (1973) Species relationships in the genus *Pisum* L. *Israel Journal of Botany* **22**: 73–91.

Bianco C.A., Cantero J.J., Nuñez O. & Petryna L. (2001) Flora de lo Centro de la Argentina – Iconografia. Universidad Nacional de Río Cuarto, Cordoba.

Bigelow J. (1824) *A Collection of Plants of Boston and its Vicinity*, 2nd edn. Charles C. Little & James Brown, Boston.

Birdsong B.A., Alston R. & Turner B.L. (1960) Distribution of canavanine in the family Leguminosae as related to phyletic groupings. *Canadian Journal of Botany* **38**: 499–505.

Bleeker W., Weber-Sparenberg C. & Hurka H. (2002) Chloroplast DNA variation and biogeography in the genus *Rorippa* Scop. (Brassicaceae). *Plant Biology* **4**: 104–111.

Bohs L. & Olmstead R.G. (1999) *Solanum* phylogeny inferred from chloroplast DNA sequence data. In: Nee M., Symon D.E., Lester R.N. & Jessop J.P. (eds) *Solanaceae IV: Advances in Biology and Utilization*. Royal Botanic Gardens, Kew, Richmond, pp. 97–110.

Boissier E. (1845) *Diagnoses Orientalium Novarum Plantarum*, series I, vol. 6. Geneva Ferd, Ramboz.

Boissier E. (1849) *Diagnoses Orientalium Novarum Plantarum*, series I, vol. 9. Geneva Ferd, Ramboz.

Boissier E. (1872) *Flora Orientalis*, vol. 2. H. George, Lyon.

Bollback J.P. (2002) Bayesian model adequacy and choice in phylogenetics. *Molecular Biology and Evolution* **19**: 1171–1180.

Bott M.H.P., Saxov S., Talwani M. & Thiede J. (eds) (1983) Structure and development of the Greenland–Scotland ridge: new concepts and methods. Plenum, New York.

Boufford D.E. & Spongberg S.A. (1983) Eastern Asian–Eastern North American phytogeographical relationships – a history from the time of Linnaeus to the twentieth century. *Annals of the Missouri Botanical Garden* **70**: 423–439.

Brako L. & Zarruchi J.L. (1993) *Catalogue of the Flowering Plants and*

Gymnosperms of Peru. Missouri Botanical Garden Press, St Louis.

Bremer K. (1994) Branch support and tree stability. *Cladistics* **10**: 295–304.

Brightmore D. & White P.H.F. (1963) *Lathyrus japonicus* Willd. *Journal of Ecology* **51**: 795–801.

Britten J. (1901) Notes on *Lathyrus*. *Journal of Botany* **39**: 96–101.

Broich S.L. (1986) A new species of *Lathyrus* (Fabaceae) from northwestern California. *Madroño* **33**: 136–143.

Broich S.L. (1987) Revision of the *Lathyrus vestitus–laetiflorus* complex (Fabaceae) *Systematic Botany* **12**: 139–153.

Broich S.L. (1989) Chromosome numbers of North American *Lathyrus* (Fabaceae) *Madroño* **36**: 41–48.

Brummitt R.K. (2002) How to chop up a tree. *Taxon* **51**: 31–41.

Brummitt R.K. (2003) Further dogged defence of paraphyletic taxa. *Taxon* **52**: 803–804.

Brummitt R.K. & Sosef M.S.M. (1998) Paraphyletic taxa are inherent in Linnaean classification – a reply to Freudenstein. *Taxon* **47**: 411–412.

Brunsberg K. (1977) Biosystematics of the *Lathyrus pratensis* complex. *Opera Botanica* **41**: 1–78.

Buckley T.R., Arensburger P., Simon C. & Chambers G.K. (2002) Combined data, Bayesian phylogetics, and the origin of the New Zealand cicada genera. *Systematic Biology* **51**: 4–18.

Bunge M. (1981) Biopopulations, not biospecies, are species and evolve. *Behavioral and Brain Sciences* **4**: 284–285.

Burkart A. (1937) Revision de las especias de *Lathyrus* de la Republica Argentina. *Revista de la Facultad de Agronomía y Veterinaria* **8**: 1–127.

Burkart A. (1942) Nuevas contribuciones a la sistematica de las especies sudamericanas de *Lathyrus*. *Darwiniana* **6**: 9–30.

Burkart A. (1966) Notas sobre las especies Argentinas de *Vicia* (Leguminosae) del area mesopotamico–pampaena. *Darwiniana* **14**: 161–193.

Burkart A. (1967) Leguminosae. In: Cabrera A.L. (ed.) *Flora de la Província de Buenos Aires*, vol. 4. Colleccion Cientifica Instituto Naçional de Tecnologia Agropecuaria, Buenos Aires, pp. 605–619.

Burnham R.J. & Graham A. (1999) The history of Neotropical vegetation: new developments and status. *Annals of the Missouri Botanical Garden* **86**: 546–589.

de Candolle A. (1825) *Prodromus Systema Naturalis Regnum Vegetabilis*, vol. 2. Treuttel & Wurtz, Paris.

Carpenter J. (1996) Uninformative bootstrapping. *Cladistics* **12**: 177–181.

Castoe T.A., Doan T.M. & Parkinson C.L. (2004) Data partitions and complex models in Bayesian analysis: the phylogeny of Gymnopthalmid lizards. *Systematic Biology* **53**: 448–469.

Caujapé-Castells J. & Jansen R.K. (2003) The influence of the Miocene Mediterranean desiccation on the geographical expansion and genetic variation of *Androcymbium gramineum* (Cav.) McBride (Colchiceae). *Molecular Ecology* **12**: 1515–1525.

Cavanilles J. (1791) Icones et descriptiones Plantarum, vol. I. Lazaro Gatguer, Madrid, p. 58.

Chandler G., Bayer R.J. & Crisp M.D. (2001) A molecular phylogeny of the endemic Australian genus *Gastrolobium* (Fabaceae: Mirbelieae) and allied genera using chloroplast and nuclear markers. *American Journal of Botany* **88**: 1675–1687.

Chaney R.W. (1940) Tertiary forests and continental history. *Geological Society of America Bulletin* **51**: 469–488.

Chaney R.W. (1947) Tertiary centers and migration routes. *Ecological Monographs* **17**: 139–148.

Chapman G.T.L. & Tweddle M. (1995) A new herbal by William Turner (1551), vol. 1. Cambridge University Press, Cambridge.

Chen Z.-D., Manchester S.R. & Sun H.-Y. (1999) Phylogeny and evolution of the Betulaceae as inferred from DNA sequences, morphology, and paleobotany. *American Journal of Botany* **86**: 1168–1181.

Chiang T.-Y., Schaal B.A. & Peng C.-I. (1998) Universal primers for amplification and sequencing a noncoding spacer between the atpB and rbcL genes of chloroplast DNA. *Botanical Bulletin of Academica Sinica* **39**: 245–250.

Chodat R. & Wilczek E. (1902) Enumeration critique des plantes récoltées par M.E. Wilczek á Saint-Raphaël et dans la vallée de l'Atuel. *Bulletin de la Herbier Boissier 2me série* **2**: 475–490.

Choi B.-H., Seok D.-I., Endo Y. & Ohashi H. (2006) Phylogenetic significance of stylar features in genus *Vicia* (Leguminosae): an analysis with molecular phylogeny.

Journal of Plant Research **119**: 513–523.

Chtourou-Ghorbel N., Lauga B., Combes D. & Marrakchi M. (2001) Comparative genetic diversity studies in the genus *Lathyrus* using RFLP and RAPD markers. *Lathyrus and Lathyrism Newsletter* **2**: 62–68.

Citerne H.L., Möller M. & Cronk Q.C.B. (2000) Diversity of *cycloidea*-like genes in Gesneriaceae in relation to floral symmetry. *Annals of Botany* **86**: 167–176.

Clarke G.C.S. & Kupicha F.K. (1976) The relationships of the genus *Cicer* L. (Leguminosae): the evidence from pollen morphology. *Botanical Journal of the Linnean Society* **72**: 35–44.

Cleef A.M. (1979) The phytogeographical position of the Neotropical vascular Paramo flora with special reference to the Colombian Cordillera Oriental. In: Larsen K. & Holm-Nielsen L.B. (eds) *Tropical Botany.* Academic Press, London, pp. 175–184.

Clos D. (1847) *Lathyrus*. In: Gay C. (ed.) *Historia Fiscia y Politica de Chile (Flora Chilena,* vol. II*).* Claudio Gay, Paris.

Colla L.A. (1832) *Plantae Rariores in Regionibus Chilensibus. A. Clarissimo M.D. Bertero, Nuper detectae et Ab. A. Colla in Lucem editae*, fascicle 2, pp. 59–61.

Correa M.N. (1984) *Flora Patagonica*, vol. IVb. Instituto Naçional de Tecnologia Agropecuaria, Buenos Aires.

Cox C.B. (2001) The biogeographic regions reconsidered. *Journal of Biogeography* **28**: 511–523.

Cracraft J. (1987) Species concepts and the ontology of evolution. *Biology and Philosophy* **2**: 329–346.

Cracraft J. (1989) Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Otte E. & Endler J.A. (eds) *Speciation and its Consequences*. Sinauer Associates, Sunderland, pp. 28–59.

Cracraft J. (1997) Species concepts in systematics and conservation biology – an ornithological viewpoint. In: Wilson M.R. (ed.) *Species: the Units of Biodiversity*, Systematics Association special vol. 54. Chapman and Hall, London.

Crawford D.J., Lee N.S. & Stuessy T.F. (1992) Plant species disjunctions: perspectives from molecular data. *Aliso* **13**: 395–409.

Croft A.M., Pang P.C.K., Taylor P.W.J. (1999) Molecular analysis of *Lathyrus sativus*

L. (grasspea) and related *Lathyrus* species. *Euphytica* **107**: 167–176.

Cronk Q.C.B. (1998) The ochlospecies concept. In: Huxley C.R., Locke J.M. & Cutler D.F. (eds) *Chorology, Taxonomy and Ecology of the Floras of Africa and Madagascar*. Royal Botanic Gardens, Kew, Richmond, pp. 155–170.

Cronn R.C., Small R.L., Haselkorn T. & Wendel J.F. (2002) Rapid diversification of the cotton genus (*Gossypium*: Malvaceae) revealed by analysis of sixteen nuclear and chloroplast genes. *American Journal of Botany* **89**: 707–725.

Czeczott H. (1939) A contribution to the knowledge of the flora and vegetation of Turkey. *Feddes Repertorium* **107**: 1–281.

Czefranova Z.V. (1971a) Review of the species of the genus *Lens* Mill. *Novitiates Systematicae Plantarum Vascularum* **8**: 197–204. [English translation by the US Department of Agriculture and National Science Foundation. Amerind Publishing, New Delhi.]

Czefranova Z.V. (1971b) Summary of the taxonomy of the genus *Lathyrus* L. *Novitiates Systematicae Plantarum Vascularum* **8**: 205–213. [English translation by the US Department of Agriculture and National Science Foundation. Amerind Publishing, New Delhi.]

Davis C.C., Bell C.D., Mathews S. & Donoghue M.J. (2002) Laurasian migration explains Gondwanan disjunctions: evidence from Malpighiaceae. *Proceedings of the National Academy of Sciences of the USA* **99**: 6833–6837.

Davis P.H. (1970) *Lathyrus*. In: Davis P.H. (ed.) *Flora of Turkey*, vol. 3. Edinburgh University Press, Edinburgh, pp. 328–369.

De Castro O., Cozzolino S., Jury S.L. & Caputo P. (2002) Molecular relationships in *Genista* L. sect. *Spartocarpus* Spach (Fabaceae). *Plant Systematics and Evolution* **231**: 91–108.

Demesure B., Sodzi N. & Petit R.J. (1995) A set of universal primers for amplification of polymorphic non-coding regions of mitochondrial and chloroplast DNA in plants. *Molecular Ecology* **4**: 129–131.

Denduangboripant J. & Cronk Q.C.B. (2000) High intraindividual variation in internal transcribed spacer sequences in *Aeschynanthus* (Gesneriaceae): implications for phylogenetics. *Proceedings of the Royal Society of London series B* **267**: 1047–1415.

Denduangboripant J., Mendum M. & Cronk Q.C.B. Evolution in *Aeschynanathus*

(Gesneriaceae) inferred from ITS sequences. *Plant Systematics and Evolution* **228**: 181–197.

Diels L. (1901) Die Flora von Central-China. *Botanische Jahrbuch* **29**: 169–659.

Dogan M., Kence A. & Tigin C. (1992) Numerical taxonomic study on Turkish *Lathyrus* (Leguminosae). *Edinburgh Journal of Botany* **49**: 333–341.

Don G. (1832) *A General System of Gardening and Botany*, vol. 2. Gilbert & Rivington, London.

Donoghue M.J. (1985) A critique of the biological species concept and recommendations for a phylogenetic alternative. *The Bryologist* **88**: 172–181.

Donoghue M.J. & Smith S.A. (2004) Patterns in the assembly of temperate forests around the Northern Hemisphere. *Philosophical Transactions of the Royal Society series B – Biological Sciences* **359**: 1633–1644.

Donovan Bailey C., Doyle J.J., Kajita T., Nemoto T. & Ohashi H. (1997) The chloroplast rpl2 intron and ORF184 as phylogenetic markers in the legume tribe Desmodieae. *Systematic Botany* **22**: 133–138.

Douady C.J., Delsuc F., Boucher Y., Doolittle W.F. & Douzery J.P. (2003) Comparison of Bayesian and maximum likelihood bootstrap measures of phylogenetic reliability. *Molecular Biology and Evolution* **20**: 248–254.

Doyle J.J. (1995) DNA data and legume phylogeny progress report. In: Crisp M.D. & Doyle J.J. (eds) *Advances in Legume Systematics*, part 7. *Phylogeny*. Royal Botanic Gardens, Kew, Richmond.

Doyle J. (1998) Phylogenetic perspectives on nodulation: evolving views of plants and symbiotic bacteria. *Trends in Plant Science* **3**: 473–478.

Doyle J.J. & Davis J.I. (1998) Homology in molecular phylogenetics: a parsimony perspective. In: Soltis D.E., Soltis P.S. & Doyle J.J. (eds) *Molecular Systematics of Plants*, vol. II. *DNA Sequencing*. Kluwer, Boston.

Doyle J.J. & Doyle J.L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* **19**: 11–15.

Doyle J.J., Doyle J.L., Ballenger J.A. & Palmer J.D. (1996) The distribution and phylogenetic significance of a 50kb chloroplast DNA inversion in the flowering plant family Leguminosae. *Molecular Phylogenetics and Evolution* **5**: 429–438.

Doyle J.J., Doyle J.L., Ballenger J.A., Dickson E.E., Kajita T. & Ohashi H. (1997) A phylogeny of the chloroplast gene rbcL in the Leguminosae: taxonomic correlations and insights into the evolution of nodulation. *American Journal of Botany* **84**: 541–554.

Doyle J.J., Doyle J.L., Brown A.H.D. & Palmer R.G. (2002) Genomes, multiple origins and lineage recombination in the glycine tomentella (Leguminosae) polyploid complex: histone H3-D gene sequences. *Evolution* **56**: 1388–1402.

Ehrlen J. (1992) Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* **73**: 1820–1830.

Ehrlen J. (1995a) Demography of the perennial herb *Lathyrus vernus* I. Herbivory and individual performance. *Journal of Ecology* **83**: 287–295.

Ehrlen J. (1995b) Demography of the perennial herb *Lathyrus vernus* II. Herbivory and population dynamics. *Journal of Ecology* **83**: 297–308.

Ehrlen J. & Eriksson O. (1995) Pollen limitation and population growth in a herbaceous perennial legume. *Ecology* **76**: 652–656.

Ekim T., Kouvacu M., Erik S. & Ilarslan R. (eds) (1989) Türkiye'nin tehlike altindaki nadir ve endemic bitki turleri (serie no. 18) [List of rare, threatened and endemic plants in Turkey prepared according to IUCN Red Data Book categories]. Türkiye Tabiatini Koruma Dernegi, Ankara.

Elliot S. (1824) A Sketch of the Botany of South Carolina and Georgia, vol. 2. J.R. Schenk, Charleston.

Endo Y. & Ohashi H. (1995) The morphology of styles and stigmas in *Vicia* (Leguminosae), and its systematic implications. *Journal of Plant Research* **108**: 17–24.

Endo Y. & Ohashi H. (1996a) The infrageneric positions of East Asian species of *Vicia* (Leguminosae). *Journal of Japanese Botany* **71**: 254–262.

Endo Y. & Ohashi H. (1996b) The pollen morphology of *Vicia* (Leguminosae). *American Journal of Botany* **83**: 955–960.

Endo Y. & Ohashi H. (1997a) Cladistic analysis of phylogenetic relationships among tribes Cicreae, Trifolieae, and Vicieae (Leguminosae). *American Journal of Botany* **84**: 523–529.

Endo Y. & Ohashi H. (1997b) The morphology and anatomy of styles in Vicieae (Leguminosae). *Journal of Japanese Botany* **72**: 9–18.

Endo Y. & Ohashi H. (1998) The features of cotyledon areoles in Leguminosae and their systematic utility. *American Journal of Botany* **85**: 753–759.

Endo Y., Choi B.-H. & Ohashi H. (2000) Distinction between *Vicia americana* and

V. bungei (Leguminosae). *Journal of Japanese Botany* **75**: 92–97.

Eriksson T., Donoghue M.J. & Hibbs M.S. (1998) Phylogenetic analysis of *Potentilla* using DNA sequences of nuclear internal transcribed spacers (ITS), and implications for the classificaion of the Rosoideae (Rosaceae). *Plant Systematics and Evolution* **211**: 155–179.

Eriksson T., Hibbs M.S., Yoder A.D., Delwiche C. & Donoghue M.J. (2003) The phylogeny of Rosideae (Rosaceae) based on sequences of the internal transcribed spacers (ITS) of nuclear ribosomal DNA and trnL/F region of chloroplast DNA. *International Journal of Plant Sciences* **164**: 197–211.

Farris J.S., Källersjö M., Kluge A.G. & Bult C. (1995) Testing significance of incongruence. *Cladistics* **10**: 315–319.

Farris J.S., Albert V.A., Källersjö M., Lipscomb D. & Kluge A. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics* **12**: 99–124.

Fauquette S., Suc J.-P., Guiot J., Diniz F., Feddi N., Zheng A., Bessais E. & Drivaliari A. (1999) Climate in the West Mediterranean area during the Pliocene. *Palaeogeography, Palaeoclimatology, Palaeoeclogy* **152**: 15–36.

Fedchenko B.A. (1948) *Lathyrus*. In: Komarov V.L., Shishkin B.K. & Bobrov E.G. *Flora of the USSR*, vol. XIII. Leguminosae: *Oxytropis*, *Hedysarum*. [1972 translation by the Israeli Program for Scientific Translation, Jerusalem.]

Fennell S.R., Powell W., Wright F., Ramsay G. & Waugh R. (1998) Phylogenetic relationships between *Vicia faba* (Fabaceae) and related species from trnL sequences. *Plant Systematics and Evolution* **212**: 247–259.

Ferguson M.E., Maxted N., van Slageren M. & Robertson L.D. (2000). A re-assessment of the taxonomy of *Lens* Mill. (Leguminosae, Papilionoideae, Vicieae). *Botanical Journal of the Linnean Society* **133**: 41–59.

Frakes L.A., Francis J.E. & Syktus J.I. (1992) Climate modes of the Phanerozoic: the history of the earth's climate over the past 600 million years. Cambridge University Press, Cambridge.

Franchet A. (1882) Catalogue des plantes. *Memoires de la Societe Nationale des Sciences Naturelles de Cherbourg* **24**: 212–213.

Francisco-Ortega J., Jansen R.K. & Santos-Guerra A. (1996) Chloroplast DNA evidence of colonization, adaptive radiation, and hybridization in the evolution of the Macaronesian flora. *Evolution* **93**: 4085–4090.

Fu Y.C. (1977) *Lathyrus*. In: Ma Y.C., Fu H.C. & Chen S. (eds) *Flora Intramongolica*, vol. 3. Inner Mongolia People's Press, Hohhot, pp. 274–276. [In standard Chinese]

Fujii N., Ueda K., Watano Y. & Shimizu T. (1997) Intraspecific variation of chloroplast DNA in *Pedicularis chamissonis* Steven (Scrophulariaceae) and geographic structuring of the Japanese 'alpine' plants. *Journal of Plant Research* **110**: 195–207.

Fukuda T., Yokoyama J. & Ohashi H. (2001) Phylogeny and biogeography of the genus *Lycium* (Solanaceae): inferences from chloroplast DNA sequences. *Molecular Phylogenetics and Evolution* **19**: 246–258.

Garcia-Jacas N., Susanna A., Mozaffarian V. & Ilarslan R. (2000) The natural delimitation of*Centaurea* (Asteraceae: Cardueae): ITS sequence analysis of the*Centaurea jacea* group. *Plant Systematics and Evolution*. 223: 185 – 199.

Gandoger M. (1913) Manipulos plantarum novarum praecipue Americae Australioris. *Bulletin de la Société Botanique de France* **60**: 454–462.

Gaut B.S., Muse S.V., Clarke W.D. & Clegg M.T. (1992) Relative rates of nucleotide substitution at the rbcL locus in monocotyledonous plants. *Journal of Molecular Evolution* **35**: 292–303.

Gielly L. & Taberlet P. (1994) The use of chloroplast DNA to resolve plant phylogenies: noncoding versus rbcL sequences. *Molecular Biology and Evolution* **11**: 769–777.

Gleason H.A. (1968) *New Britton & Brown Illustrated Flora*, vol. 2. Hafner–New York Botanical Garden, New York.

Goldblatt P. (1981) Cytology and phylogeny of Leguminosae. In: Polhill R.M. & Raven P.H. (eds) *Advances in Legume Systematics*, part 1. Ministry of Agriculture, Fisheries and Food, London.

Gorer R., Harvey J.H. & Vickery R. (1991) The mysteries of Lord Anson's pea. *The Plantsman* **13**: 129–140.

Gourlay C.W., Hofer J.M. & Ellis T.H. (2000) Pea compound leaf architecture is regulated by interactions among the genes *unifoliata*, *cochleata*, *AFILA* and *TENDRIL-LESS*. *The Plant Cell* **12**: 1279–1294.

Goyder D.J. (1986) The genus *Lathyrus*. In: Kaul A.K. & Combes D. (eds) *Lathyrus and Lathyrism*. Third World Medical Research Foundation, New York.

Graham A. (1993) History of the vegetation: Cretaceous (Maastrichtian) Tertiary. In: Flora of North America Editorial Committee (eds) *Flora of North America North of Mexico*, vol. 1. Oxford University Press, New York, pp. 57–70.

Graham A. (2001) History of North American Vegetation – Cretaceous (Maastrichtian) – Tertiary. In: Flora of North America Editorial Committee (eds) *Flora of North America*, vol. 1. Oxford University Press, New York.

Great Plains Flora Association (1986) Flora of the Great Plains. University Press of Kansas, Lawrence.

Grenier M. & Godron M. (1848) *Flore de France*, vol. 1. J.-B. Bailliere, Paris.

Greuter W., Wagenitz G., Agababian M. & Hellwig F.H. (2001) (1509) Proposal to Conserve the Name *Centaurea* (Compositae) with a Conserved Type. *Taxon* **50**: 1201-1205

Grintescu I. (1957) *Lathyrus*. In: Savulescu T. (ed.) *Flora Republicii Populare Romine.* Editio Academae Reipublicae Popularis Romaniae, Bucharest, pp. 405–445. [In Romanian]

Grisebach A. (1874) Plantae Lorentzianae (Bearbeitung der ersten und zweiten Sammlung argentenischer Pflanzen des Professor Lorentz zu Cordoba). *Abhandlungen der Königlichen Gesellschaft Der Wissenchaften zu Göttingen* **19**: 73–74.

Grisebach A. (1879) *Symbolae ad Floram argentinam*. Dietrichse Verlags-Buchhandlung, Göttingen.

Grivet D., Heinze B., Vendramin G.G. & Petit R.J. (2001) Genome walking with consensus primers: application to the large single copy region of chloroplast DNA. *Molecular Ecology Notes* **1**: 345–349.

Gunn C.R. (1969) Genera, types and lectotypes in the tribe Vicieae (Leguminosae). *Taxon* **18**: 725–733.

Gunn C.R. & Kluve J. (1976) Androecium and pistil characters for the tribe Vicieae (Fabaceae). *Taxon* **25**: 563–575.

Guo Q., Rickleffs R.E. & Cody M.L. (1998) Vascular plant diversity in eastern Asia and North America: historical and ecological explanations. *Botanical Journal of the Linnaean Society* **128**: 123–136.

Gutiérez J.F., Vaquero F. & Vences F.J. (1994) Allopolyploid vs. autopolyploid origins in the genus *Lathyrus* (Leguminosae). *Heredity* **73**: 29–40.

Hably L., Kvacek Z. & Manchester S.R. (2000) Shared taxa of land plants in the Oligocene of Europe and North America in the context of Holarctic phytogeography. *Acta Universitatis Carolinae – Geologica* **44**: 59–74.

Hamilton M.B. (1999) Four primer pairs for the amplification of chloroplast regions with intraspecific variation. *Molecular Ecology* **8**: 521–523.

van der Hammen T. & Cleef A.M. (1985) Development of the high Andean Paramo flora and vegetation. In: Vuilleumier F. & Monasterio M. *High Altitude Tropical Biogeography.* Oxford University Press, New York, pp. 153–201.

Hammett K.R.W., Murray B.G., Markham K.R. & Hallett I.C. (1994) Interspecific hybridization between *Lathyrus odoratus* and *L. belinensis*. *International Journal of Plant Sciences* **155**: 763–771.

Hammett K.R.W., Murray R.R., Markham I.C., Hallett I.C. and Osterloh I. (1996) New interspecific hybrids in *Lathyrus* (Leguminosae): *Lathyrus annuus* × *L. hierosolymitanus*. *Botanical Journal of the Linnean Society* **122**: 89101.

Hanelt P. & Mettin D. (1989) Biosystematics of the genus *Vicia* L. (Leguminosae). *Annual Review of Ecology and Systematics* **20**: 199–223.

Hara H. (1943) Nihon San Renrisou rui [Notes on Japanese *Lathryus*]. *Journal of Japanese Botany* **19**: 296–299. [In Japanese]

Harborne J.B., Boulter D. & Turner B.L. (1971) *Chemotaxonomy of the Leguminosae*. Academic Press, London.

Hasebe M., Ando T. & Iwatsuki K. (1998) Intrageneric relationships of maple trees based on the chloroplast DNA restriction fragment polymorphisms. *Journal of Plant Research* **111**: 441–451.

Hassler E. (1919) Ex Herbariano Hassleriano: Novitates Paraguariensis XXIII. *Feddes Repertorium Novarum Speciarum* **16**: 220–233.

Hauman-Merck L. (1913) Etude phytogéographique de la région du Rio Negro inférieur. *Anales de la Museo Nacional de Historia Naturale Buenos Aires* **24**: 289–443.

Hegi G. (1924) *Illustriete Flora von Mitteleuropa*, vol. IV (3). Carl Hanser, Munich.

Henze K., Horner D.S., Suguri S., Moore D.V., Sánchez L.B., Muller M. & Embley T.M. (2001) Unique phylogenetic relationships of glucokinase and glucopsephosphate isomerase of the amitochondriate eukaryotes *Giardia intestinalis*, *Spironucleus barkhanus* and *Trichomonas vaginalis*. *Gene* **281**:

123–131.

Hershkovitz M.A., Zimmer E.A. & Hahn W.J. (1999) Ribosomal DNA sequences and angiosperm systematics. In: Hollingsworth P.M., Bateman R.M. & Gornall R.J. (eds) *Molecular Systematics and Plant Evolution.* Taylor and Francis, London.

Herter G. (1930) *Estudios Botanicos en la Region Uruguaya.* Ministerio de Industrias, Montevideo.

Hewitt G. (2000) The genetic legacy of the Quaternary ice ages. *Nature* **405**: 907–913.

Hicken C.M. (1910) Chloris platensis Argentina. *Apuntes de Historia Natural* **2**: 1–292.

Hicken C.M. (1912) Conistellum Neuqueni. *Boletim de la Sociedad Physis* **1**: 116–133.

Hickey L.J. (1974) A revised classification of the architecture of dicotyledonous leaves. In: Metcalfe C.R. & Chalk L. (eds) Anatomy of the Dicotyledons, Volume I, Second Edition. Clarendon Press, Oxford.

Hijmans R., Guarino L., Jarvis A. & O'Brien R. (2005) *DIVA GIS Mapping and analysis of spatial data, version 5.2.0.2*. DIVA-GIS.org.

Hill P., Burford D. Martin D.M.A. & Flavell A.J. (2005) Retrotransposon populations of *Vicia* species with varying genome size. *Molecular Genetics and Genomics* **273**: 371 – 381.

Hillis D.M. & Bull J.J. (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology* **42**: 182–192.

Hilu K.W. & Liang H. (1997) The matK gene: sequence variation and application in plant systematics. *American Journal of Botany* **84**: 830–839.

Hitchcock C.L. (1952) A revision of the N. American species of *Lathyrus*. *University of Washington Publications in Biology* **5**: 1–104.

Hitchcock C.L., Cronquist A., Owenby M. & Thompson J.W. (1961) *Vascular Plants of the Pacific Northwest*, vol. 3. University of Washington Press, Seattle.

Hofer J., Turner L., Hellens R., Ambrose M., Matthews P., Michael A. & Ellis N. (1997) *UNIFOLIATA* regulates leaf and flower morphogenesis in pea. **7**: 581-587.

Hofer J.M.I. & Ellis T.H.N. (1998) The genetic control of patterning in pea leaves. *Trends in Plant Science – Perspectives* **3**: 439–444.

Holder M. & Lewis P.O. (2003) Phylogeny estimation: traditional and Bayesian approaches. *Nature Reviews Genetics* **4**: 275–284.

Holm L., Pancho J.V., Herberger J.P. & Plucknett D.L. (1979) *A Geographical Atlas of World Weeds.* Wiley Interscience, New York.

Hooker J.D. (1847) The botany of the Antarctic Voyage I. *Flora Antarctica* **2**: 259–261.

Hooker W.J. (1837) *Icones Plantarum*, vol. 1. Longman, Rees, Orne, Brown, Green & Longman, London.

Hooker W.J. & Arnott G.A.W. (1831) *Botany of Captain Beechey's Voyage.* Henry G. Bohn, London.

Hooker W.J. & Arnott G.A.W. (1833) Contributions towards a flora of South America and the islands of the Pacific. *Botanical Miscellany* **3**: 102–111.

Hopkins D.M. (ed) (1967) *The Bering Land Bridge.* Stanford University Press, Palo Alto.

Hu J.-M., Lavin M., Wojciechowski M.F. & Sanderson M.J. (2000) Phylogenetic systematics of the tribe Millettieae (Leguminosae) based on chloroplast trnK/matK sequences and its implications for evolutionary patterns in Papilionoideae. *American Journal of Botany* **87**: 418–430.

Hu J.-M., Lavin M., Wojciechowski M.F. & Sanderson M.J. (2002) Phylogenetic analysis of nuclear ribosomal ITS/5.8S sequences in the tribe Milletieae (Fabaceae): Poecilanthe–Cyclobium, the core Milletieae and the *Callerya* group. *Systematic Botany* **27**: 722–733.

Huelsenbeck J.P. & Ronquist F. (2001) MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755.

Huelsenbeck J.P., Ronquist F., Nielsen R. & Bollback J.F. (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* **294**: 2310–2314.

Hughes C. & Eastwood R. (2006) Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the USA* **103**: 10334–10339.

Hultèn E.O.G. (1937) *Flora of the Aleutian Islands and Westernmost Alaskan Peninsula.* Bokforlags Actiebolaget Thule, Stockholm.

Hultèn E.O.G. (1960) *Flora of the Aleutian Islands and Westernmost Alaskan Peninsula*, 2nd edn. K. Cramer, Codicote.

Hultèn E. (1968) *Flora of Alaska and Neighboring Territories – a Manual of the*

Vascular Plants. Stanford University Press, Palo Alto.

Humphries C.J. & Parenti L.R. (1999) *Cladistic Biogeography – Interpreting Patterns of Plant and Animal Distributions*, 2nd edn. Oxford University Press, Oxford.

International Legume Database and Information Service (2002) *World Database of Legumes*, version 6.05. International Legume Database and Information Systems, Southampton.

Iseley D. (1992) Innovations in Californian *Trifolium* and *Lathyrus*. *Madrono* **39**: 90–97.

Iwatsuki K. & Ohba H. (1994) The floristic relationship between East Asia and eastern North America. In: Miyawaki A., Iwatsuki K. & Gardtner M.M. (eds) Vegetation in eastern North America. University of Tokyo Press, Tokyo, pp. 61–74.

Izaguirre P. & Beyhaut R. (1998). *Las leguminosas en Uruguay y regiones vecinas, parte I*. Editorial Hemisferio Sur, Montevideo.

Jansen D.H. (1969) Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* **23**: 1–27.

Jermy T. & Szentesi Á. (2003) Evolutionary aspects of host plant specialisation – a study on bruchids (Coleoptera: Bruchidae). *Oikos* **101**: 296–204.

Johnson C.P. & Sowerby J.E. (1862) *The Useful Plants of Great Britain.* Hardwicke, London.

Johnson K.P., Drown D.M. & Clayton D.H. (2001) A databased parsimony method of cophylogenetic analysis. *Zoologica Scripta* **30**: 79–87.

Johnson L.A. & Soltis D.E. (1994) *mat*K DNA sequences and phylogenetic reconstruction in Saxifragaceae s. str. *Systematic Botany* **19**:143–157.

Johnson L.A. & Soltis D.E. (1995) Phylogenetic inference in Saxifragaceae sensu stricto and *Gilia* (Polemoniaceae) using *mat*K sequences. *Annals of the Missouri Botanical Garden* **82**:149–175.

Johnson T. (1975) *John Gerrard: The Herbal of General History of Plants. The Complete 1633 Edition as Revised and Enlarged by Thomas Johnson.* Dover, New York.

Johnston I.M. (1938) New or noteworthy plants from temperate South America. *Journal of the Arnold Arboretum* **19**: 248–263

Jones W.H.S. (1992) *Pliny: Natural History*, books XXIV–XXVII. Harvard University Press, Cambridge.

Jørgensen P.M. & Léon-Yámez S. (1999) *Catalogue of the Vascular Plants of Ecuador.* Missouri Botanical Garden Press, St Louis.

Kajita T., Kamiya K., Nakamura K., Tachida H., Wickneswari R., Tsumura Y., Yoshimaru H. & Yamazaki T. (1998) Molecular phylogeny of Dipterocarpaceae in Southeast Asia based on nucleotide sequences of *mat*K, *trn*L intron and *trn*L–*trn*F interegenic spacer region in chloroplast DNA. *Molecular Phylogenetics and Evolution* **10**:202–209.

Kajita T., Ohashi H., Tateishi Y., Donovan Bailey C. & Doyle J.J. (2001) *rbcL* and legume phylogeny, with particular reference to Phaseoleae, Millettieae, and allies. *Systematic Botany* **26**: 515–536.

Kass E. & Wink M. (1995) Molecular phylogeny of the Papilionoideae (Leguminosae) *Rbc*L gene sequences versus chemical taxonomy. *Botanica Acta* **108**: 149–162.

Käss E. & Wink M. (1996) Molecular evolution of the Leguminosae: phylogeny of the three subfamilies based on *rbcL*–sequences. *Biochemical Systematics and Ecology* **24:** 365–378.

Käss E. & Wink M. (1997a) Molecular phylogeny and phylogeography of *Lupinus* (*Leguminiosae*) inferred from nucleotide sequences ofg the *rbc*L gene and ITS 1 + 2 regions of rDNA. *Plant Systematics and Evolution* **208**: 139–167.

Käss E. & Wink M. (1997b) Phylogenetic relationships in the Papilionoideae (family Leguminosae) based on nucleotide sequences of cpDNA (*rbc*L) and ncDNA (ITS 1 and 2). *Molecular Phylogenetics and Evolution* **8**: 65–88.

Katinas L., Morrone J.J. & Crisci J.V. (1999) Track analysis reveals the composite nature of the Andean biota. *Australian Journal of Botany* **47**: 111–130.

Kato M. & Iwatsuki K. (1983) Phytogeographic relationships of pteridophytes between temperate north America and Japan. *Annals of the Missouri Botanical Garden* **70**: 724–733.

Keals N., Hardie D. & Emery R. (1998) Bruchids: secret seed eaters. In: *Proceedings of the Australian Postharvest Technical Conference*. Commonwealth Scientific and Industrial Research Organisation, Canberra, pp. 52–54.

Kenicer G.J., Kajita T., Pennington R.T. & Murata J. (2005) Systematics and biogeography of *Lathyrus* (Leguminosae) based on internal transcribed spacer and cpDNA sequence data. *American Journal of Botany* **92**: 1199–1209.

Kim Y.D., Kim S.H. & Landrum L.R. (2004) Taxonomic and phytogeographic implications from ITS phylogeny in *Berberis* (Berberidaceae) **117**: 175–182.

Kitagawa M. (1934) *Lathyrus vaniotii*. In: Nakai T (ed.) *Iconographia Plantarum Asiae Orientalis*. Shunyodo, Tokyo.

Kloz J. (1971) Serology of the Leguminosae. In: Harbourne J., Boulter D. & Turner B.L. (eds) *Chemotaxonomy of the Leguminosae*. Academic Press, London, pp. 309–365.

Knowles G.B. & Westcott F. (1838) *Lathyrus purpureo-coeruleus*. *The Floral Cabinet and Magazine of Exotic Botany* **2**: 126, 177–178.

Knowles G.B. & Westcott F. (1839) *Lathyrus armitageanus*. *The Floral Cabinet and Magazine of Exotic Botany* **3**: 81.

Koch M. & Al-Shebaz I. (2002) Molecular data indicate complec intra- and intercontinental differentiation of American *Draba* (Brassicaceae). *Annals of the Missouri Botanical Garden* **89**: 88–109.

Koch M., Haubold B. & Mitchell-Olds T. (2001) Molecular systematics of the Brassicaceae: evidence from coding plastid *matK* and nuclear CHS sequences. *American Journal of Botany* **88**: 534–544.

Krutzsch W. (1989) Paleogeography and historical paleogeography in the Neophyticum. *Plant Systematics and Evolution* **162**: 5–61.

Kunio I., Boufford D.E. & Ohba H. (eds) (1993) *Flora of Japan*, vol. 2b. Kodansha, Tokyo.

Kuntze O. (1898) *Revisio Generum Plantarum*, vol. III. Dulaud, London.

Kupicha F.K. (1974) *Taxonomic studies in the tribe Vicieae (Leguminosae)*. PhD thesis, University of Edinburgh, Edinburgh.

Kupicha F.K. (1975) Observations on the vascular anatomy of the tribe Vicieae (Leguminosae). *Botanical Journal of the Linnaean Society* **70**: 231–242.

Kupicha F.K. (1976) The infrageneric structure of *Vicia*. *Notes from the Royal Botanic Garden Edinburgh* **34**: 287–326.

Kupicha F.K. (1977) The delimitation of the tribe Vicieae (Leguminosae) and the relationships of *Cicer* L. *Botanica Journal of the Linnean Society* **74**: 131–162.

Kupicha F.K. (1981) *Vicieae*. In: Polhill R.M. & Raven P.H. (eds) *Advances in Legume Systematics*, part 1. Ministry of Agriculture, Fisheries and Food, London, pp. 377–381.

Kupicha F. (1983) The infrageneric structure of *Lathyrus*. *Notes from the Royal Botanic Garden Edinburgh* **41**: 209–244.

Ladzinsky G. & Abbo S. (1996) Genetic diversity in the genus *Lens*. In: Pickersgill B. & Lock J.M. (eds) *Advances in Legume Systematics*, part 8. *Legumes of Economic Importance.* Royal Botanic Gardens, Kew, Richmond, pp. 53–64.

Lamarck M. le Chevalier de (1788) *Encyclopédie méthodique ou par ordre de materieres*, vol. II. Panckouke, Paris.

Lambein F., Chaudhury B. & Kuo Y.-H. (1999) Biochemistry of the *Lathyrus* toxins. In: Mathur P.N., Ramanantha Rao V. & Arora R.K. (eds) Lathyrus *Genetic Resources Network Proceedings of an IPGRI–ICARDA–ICAR Regional Working Group Meeting.* International Plant Genetic Resources Institute (Office for South Asia), New Delhi.

Larrañga D.A. (1923) *Lathyrus*. *Escritos Publico de la Instituto Histórico de Geografia del Uruguay* **2**: 229–230.

Larrañga D.A. (1927) *Lathyrus*. In: Larrañga D.A. (ed.) *Atlas Instituto Botanico de Lámarck*, vol. 86, Edición Nacional, Montevideo, pp. 89–121.

Lavin M. & Delgado S.A. (1990) Pollen brush of Papilionoideae (Leguminosae): morphological variation and systematic utility. *American Journal of Botany* **77**: 1294–1312.

Lavin M. & Luckow M. (1993) Origins and relationships of tropical North America in the context of the boreotropics hypothesis. *American Journal of Botany* **80**: 1–14.

Lavin M., Doyle J.J. & Palmer J.D. (1990) Evolutionary significance of the loss of the chloroplast DNA inverted repeat in the Leguminosae subfamily Papilionoideae. *Evolution* **44**: 390–402.

Lavin M., Schrire B.D., Lewis G.P., Pennington R.T., Delgado Salinas A., Thulin M., Hughes C.E., Beyra Matos A. & Wojciechowski M. (2004) Metacommunity processes rather than continental history better explains geographically structures phylogenies in legumes. *Philosophical Transactions of the Royal Society series B – Biological Sciences* **359**: 1509–1522.

Lavin M., Herendeen P.S. & Wojciechowski M. (2005) Evolutionary rates analysis of Leguminosae implicates a rapid diversification of lineages during the Tertiary. *Systematic Biology* **54**: 575–594.

Lawson P. (1852) Synopsis of the vegetable products of Scotland. Peter Lawson, Edinburgh.

Leaché A.D. & Reeder T.W. (2002) Molecular systematics of the Eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony, likelihood and Bayesian approaches. *Systematic Biology* **52**: 44–68.

Ledebour C.F (1831) *Flora Altaica*, vol. 3. G Reimer, Berlin.

Ledebour C.F (1842) *Flora Rossica Sive Enumerato Plantarum in Totius Imperii Rossici*, vol. 1. E. Schwizerbart, Stuttgart.

Lee N.S., Sang T., Crawford D.J., Yeau S.H. & Kim. S.-C. (1996) Molecular divergence between disjunct taxa in eastern Asia and eastern North America. *American Journal of Botany* **83**: 1373–1378.

Leht M. & Jaaska V. (2002) Cladistic and phenetic analysis of relationships in *Vicia* subgenus Vicia (Fabaceae) by morphology and isozymes. *Plant Systematics and Evolution* **232**: 237–260.

Lev Yadun S. & Inbar M. (2002) Defensive ant, aphid and caterpillar mimicry in plants? *Biological Journal of the Linnaean Society* **77**: 393–398.

Lewis G., Schrire B., Mackinder B. & Lock M. (2005) *Legumes of the World.* Royal Botanic Gardens, Kew, Richmond.

Lewis P.O. (2001) Phylogenetic systematics turns over a new leaf. *Trends in Ecology and Evolution* **16**: 30–37.

Li J., Bogle L. & Klein A.S. (1999) Phylogenetic relationships of the Hamamelidaceae inferred from sequences of internal transcribed spacers (ITS) of nuclear ribosomal DNA. *American Journal of Botany* **86**: 1027–1037.

Li S. & Adair K.T. (1994) Species pools in eastern Asia and North America. *SIDA* **16**: 281–299.

Lindqvist C. & Albert V. (2002) Origin of the Hawaiian endemic mints within North American *Stachys* (Lamiaceae). *American Journal of Botany* **89**: 1709–1724.

Linnaeus C. (1753) *Species Plantarum*, vol. 2. Salvius, Stockholm.

Lock J.M. & Simpson K. (1991) *Legumes of West Asia, a Check-list.* Royal Botanic Gardens, Kew, Richmond.

Lock M. & Maxted N. (2005) Tribe Fabeae. In: Lewis G., Schrire B., Mackinder B. & Lock M. (eds) *Legumes of the World*. Royal Botanic Gardens, Kew, Richmond.

Luckow M. (1995) Species concepts: assumptions, methods and applications. *Systematic Botany* **20**: 589–605.

Luckow M., Miller J.J., Murphy D.J., & Livshultz, T. (2003) A phylogenetic analysis of the Mimosoideae (Leguminosae) based on chloroplast DNA sequence data. In: Klitgaard B.B. &Bruneau, A. (eds.)Advances in Legumes Systematics, part 10, higher level systematics. Royal Botanic Gardens, Kew, UK.

Lutzoni F., Wagner P., Reeb V. & Zoller S. (2000) Integrating ambiguously aligned regions of DNA sequences in phylogenetic analyses without violating positional homology. *Systematic Biology* **49**: 628–651.

Lutzoni F., Pagel M. & Reeb V. (2001) Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* **411**: 937 – 940.

Mabberley D.J. (2000) *The Plant-Book*, 2nd edn. Cambridge University Press, Cambridge.

MacBride J.F. (1943) *Lathyrus* in *Flora of Peru*. *Fieldiana* **13**: 352–355.

McKenna M. (1975) Fossil mammals and early Eocene North Atlantic land continuity. *Annals of the Missouri Botanical Garden* **62**: 335–353.

McKenna M.C. (1983) Holarctic landmass rearrangement, cosmic events and Cenozoic terrestrial organisms. *Annals of the Missouri Botanical Garden* **70**: 459–489.

MacKloskie G. (1905) *Reports of the Princeton University Expedition to Patagonia, 1896–1899*, vol. 8. *Botany*. Schweizerbartsche Verlagshandlung, Stuttgart.

MacKloskie G. & Dusen P. (1914) *Revision of Flora Patagonica Reports Princeton Expedition 1896–1899*, vol. 8 (suppl.). Schweizerbartsche Verlagshandlung, Stuttgart, pp. 161–162.

Maddison D.R. & Maddison W.P. (2003) *MaClade*, version 4.06. Sinauer Associates, Sunderland.

van der Maesen L.J.G. & Somaatmadja S. (eds) (1989) *Plant Resources of South-East Asia*, no. 1. Pulses Pudoc, Wageningen.

Magallón S. & Sanderson M.J. (2001) Absolute diversification rates in Angiosperm clades. *Evolution* **55**: 1762–1782.

Makino T. (1931) Contributions to the Flora of Nippon. *Journal of Japanese Botany*

7: 13.

Malme G.O.A. (1936) Die in Rio Grandedo Sul vorkommenden Spezies der gattung *Lathyrus*. *Revista Sudamericana de Botanica* 3: 8–16.

Manchester S.R. (1999) Biogeographical relationships of North American Tertiary Floras. *Annals of the Missouri Botanical Garden* **86**: 472–522.

Manchester S.R. & Tiffney B. (2001) Integration of paleobotanical and neobotanical data in the assessment of phytogeographic history of Holarctic angiosperm clades. *International Journal of Plant Sciences* **162** (suppl.): S19–S27.

Marincovich L. & Gladenkov A.Y. (1999) Evidence for an early opening of the Bering Strait. *Nature* **397**: 149–151.

Maslin B.R., Miller J.T. & Seigler D.S. (2003) Overview of the generic status of Acacia (LEguminosae: Mimosoideae) *Australian Systematic Botany* **16**: 1 – 18.

Mathur P.N., Ramanantha Rao P.N. & Arora R.K. (eds) (1999) Lathyrus *Genetic Resources Network Proceedings of an IPGRI–ICARDA–ICAR Regional Working Group Meeting*. International Plant Genetic Resources Institute (Office for South Asia), New Delhi.

Matsumura J. (1902) A conspectus of the Leguminosae found growing wild or cultivated in Japan, Loochoo and Formosa (part 48 – *Lathyrus*). *Botanical Magazine of Tokyo* 181: 28–30.

Maximowicz C.J. (1873) Diagnoses des nouvelles plantes du Japon et de la Mandjourie Decade, vol. XIV. *Bulletin de L'Academie Imperiale des Sciences de St.-Petersbourg* **18**: 390–393. [Facsimile edition, Tokyo, 1943]

Maxted N. (1993) A phenetic investigation of *Vicia* L. subgenus *Vicia* (Leguminosae, Vicieae). *Botanical Journal of the Linnaean Society* **111**: 155–182.

Maxted N. & Bennett S. (eds) (2001) *Plant Genetic Resources of Legumes in the Mediterranean.* Kluwer, Dordrecht.

Maxted N. & Goyder D.J. (1988) A new species of *Lathyrus* sect. Lathyrus (Leguminosae–Papilionoideae) from Turkey. *Kew Bulletin* **43**: 711–714.

Mayr E. (1982) The growth of biological thought: systematics and evolution. In: Otte D. & Endler J.A. (eds) *Speciation and its Consequences*, Sinauer Associates, Sunderland, pp. 60–81.

Melville R. (1981) Vicarious plant distributions and paleogeography of the Pacific region. In: Nelson G. & Rosen D.E. (eds) *Vicariance Biogeography: a Critique.*

Columbia University Press, New York.

Meulenkamp J.E. & Sissingh W. (2003) Tertiary paleogeography and tectonostratigraphic evolution of the Northern and Southern Peri–Tethys platforms and the intermediate domains of the African–Eurasian convergent plate boundary zone. *Palaeogeography, Palaeoclimatology, Palaeoeclogy* **196**: 209–228.

Meyer M.S. & Bagga S.K. (2002) The phylogeny of *Lens* (Leguminosae): new insight from ITS sequence analysis. *Plant Systematics and Evolution* **232**: 145–154.

Miller P. (1768) *The Gardener's Dictionary*, 8th edn. Frances Rivington, London.

Möller M. & Cronk Q.C.B. (1997) Origin and relationships of *Saintpaulia* (Gesneriaceae) based on ribosomal DNA internal transcribed spacer (ITS) sequences. *American Journal of Botany* **84**: 956–965.

Moore D.M. (1972) Connections between cool temperate floras with particular reference to southern South America. In: Valentine D.H. (ed.) *Taxonomy, Phytogeography and Evolution.* Academic Press, San Diego, pp. 115–138.

Morain S. (1984) *Systematic and Regional Biogeography.* Van Nostrand Reinhold, New York.

Morley R.J. (2003) Interplate dispersal paths for megathermal angiosperms. *Perspectives in Plant Ecology, Evolution and Systematics* **6**: 5–20.

Munz P. & Keck D.A. (1968) *A California Flora*. University of California Press, Berkeley.

Murata J., Ohi T., Wu S., Darnaedi D., Sugawara T., Nakanishi T. & Murata H. (2001) Molecular phylogeny of *Aristolochia* (Aristolochiaceae) inferred from *matK* sequences. *Acta Phytotaxanomica et Geobotanica* **52**: 75–83.

Nakai T. (1952) A synoptical sketch of the Korean Flora. *Bulletin of the National Science Museum* **31**: 64.

Nandini A.V., Murray B.G., O'Brien I.E.W. & Hammett K.R.W. (1997) Intra- and interspecific variation in genome size in *Lathyrus* (Leguminosae). *Botanical Journal of the Linnaean Society* **125**: 359–366.

Narayan R.K.J. (1982) Discontinuous variation in the evolution of plant species: the genus *Lathyrus*. *Evolution* **36**: 877–891.

Nature Conservancy (1996) Natural Heritage Central Database. Online. Available: http://www.natureserve.org/ 25 Aug 2006.

Nei M. (1987) *Molecular Evolutionary Genetics.* Columbia Press, New York.

Nelson E.C. (2000) *Sea Beans and Nickar Nuts.* BSBI handbook no. 10. Botanical Society of the British Isles, London.

Nelson G. & Platnick N.I. (1981) *Systematics and Biogeography: Cladistics and Vicariance*. Columbia University Press, New York.

Nelson G. & Rosen D.E. (eds) (1981) *Vicariance Biogeography: a Critique.* Columbia. University Press, New York.

Nelson G., Murphy D.J. & Ladiges P.Y. (2003) Brummitt on paraphyly: a response. *Taxon* 52: 295–298.

Nelson T.W. & Nelson J.P. (1983) Two new species of Leguminosae from Serpentine of Humboldt County, California. *Brittonia* **35**: 180–183.

Neubert E.E. & Miotto S.T.S. (2001) O gênero *Lathyrus* L. (Leguminosae–Faboideae) no Brasil. *Iheringia – Séries Botanico de Porto Alegre* **56**: 51–114.

Nixon K.C. & Carpenter J.M. (1996) On simultaneous analysis. *Cladistics* **12**: 221–242.

Nixon K.C. & Wheeler Q.D. (1990). An amplification of the phylogenetic species concept. *Cladistics* **6**: 211–223.

Norton S. (1996) Lathyrus*: Cousins of the Sweet Pea*. National Council for the Conservation of Plants and Gardens, Woking.

Ohashi H. (1979) Leguminosae. In: Hara H. & Williams L.H.J. (eds) *An Enumeration of the Flowering Plants of Nepal*, vol. 2. Trustees of the Natural History Museum, London.

Ohashi H. & Tateishi Y. (1977) Notes on *Lathyrus japonicus* in Japan. *Journal of Japanese Botany* **52**: 233–234. [In Japanese]

Oliver C. *Molecular genetics and the conservation of plants: two case studies*. PhD thesis, Royal Botanic Garden Edinburgh, Edinburgh–University of Glasgow, Glasgow.

Olmstead R.G. & Palmer J.D. (1994) Chloroplast DNA systematics: a review of methods and data analysis. *American Journal of Botany* **81**: 1205–1224.

Olmstead R.G. & Palmer J.D. (1997) Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. *Systematic Botany* **22**: 19–29.

Ooi K., Endo Y., Yokoyama J. & Murakami N. (1995) Useful primer designs to amplify DNA fragments of the plastid gene *matK* from Angiosperm plants. *Japanese Journal of Botany* **70**: 328–331.

Orchard, A.E. and Maslin, B.R. (2003). Proposal to conserve the name *Acacia* Mill. (Leguminosae: Mimosoideae) with a new type. *Taxon* **52**: 362 - 363.

Ortiz-Barrientos D. & Rieseberg L.H. (2006) Splitting when together. *Heredity* **97**: 2–3.

Osbaldeston T.A. & Wood R.P.A. (2000) *Dioscorides De Materia Medica. A New Indexed Version in Modern English.* IBIDS, Johannesburg.

Page R.D.M. & Holmes E.C. (1998) *Molecular Evolution: a Phylogenetic Approach.* Blackwell, Oxford.

Pagel M., Meads A. & Barker D. (2004) Bayesian Estimation of ancestral character states on phylogenies. *Systematic Biology* **53**: 673 – 684.

Palibin J. (1898) *Conspectus Florae Koreae.* [Version published in 1899 in *Acta Horti Petropolitani* **17**]

Palmer J.D., Osrio B., Aldrich J. & Thompson W.F. (1987) Chloroplast DNA evolution among legumes: loss of a large inverted repeat occurred prior to other sequence rearrangements. *Current Genetics* **11**: 275–286.

Pearce S.R., Knox M., Ellis T.H.N., Flavell A.J. & Kumar A. (2000) Pea Ty1-*copia* group retrotransposons: transpositional activity and use as markers to study genetic diversity in *Pisum*. *Molecular and General Genetics* **263**: 898-907.

Pennington R.T., Cronk Q.C.B., Richardson J.A. (2004) Introduction and synthesis: plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society of London series B – Biological Sciences* **359**: 1455–1464.

Philipe H., Lecointre G., Van lê H.L. & Guyader H.L. (1996) A critical study of homoplasy in molecular data with the use of a morphologically based cladogram, and its consequences for character weighting. *Molecular Biology and Evolution* **13**: 1174–1186.

Philippi F. (1881) *Catalogus Plantarum Vascularium Chilensium.* Imprente Nacional, Santiago.

Philippi R.A. (1856) Plantarum novarum Chilensium (Centuria Prima). *Linnaea* **28**: 609–655.

Philippi R.A. (1862). Nuevas plantas recojidas en Maule i Chillan. *Anales de la*

Universidade de Santiago de Chile **2**: 443–444.

Philippi R.A. (1864) Plantarum novarum Chilensium. *Linnaea* **33**: 1–309.

Philippi R.A. (1872) Descripcion de las nuevas plantas incorporadas úlitimamente en el Herbario Chileno. *Anales de la Universidade de Santiago de Chile* **41**: 694–695.

Philippi R.A. (1892) Bemerkungen über die Flora bei den Bädern von Chillan. *Verhandlungen Deutschen Wissenschaften Vereins zu Santiago (Chile)* **2**: 196–209.

Philippi R.A. (1893) Plantas Nuevas Chilenas. *Anales de la Universidade de Santiago de Chile* **84**: 278–281.

Phillips M. (1983) *Wild Foods.* Pan, London.

Pittier H. (1938) Dos Plantas Nuevas para la Flora de Venezuela. *Boletin Sociedad Venezolana de Cincias Naturales* **4**: 345–347.

Platnick N.I. (1979) Philosophy and the transformations of cladistics. *Systematic Zoology* **28**: 537–546.

Plitmann U. & Kislev M.E. (1989) Reproductive changes induced by domestication. In: Stirton C.H. & Zarrucchi J.L. (eds) *Advances in Legume Biology.* Missouri Botanical Gardens, St Louis.

Plunkett G.M., Soltis D.E. & Soltis P.S. (1997) Clarification of relationships between Apiaceae and Araliaceae based on *matK* and *rbcL* sequences. *American Journal of Botany* **84**: 565–580.

Polhill R.M (1981) Papilionoideae. In: Polhill R.M. & Raven P.H. (eds) *Advances in Legume Systematics*, part 1. Ministry of Agriculture, Fisheries and Food, London, pp. 191–208.

Polozhij A.V. & Malyschev L.I. (1994) *Flora Sibiriae*, vol. 9. Nauka, Novosibirsk.

Porter T.C. & Coulter J.M. (1874) *Synopsis of the Flora of Colerado.* Government Printing Office, Washington.

Posada D. & Crandall K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.

Posada D. & Buckley T.R. (2004) Model selection and model averaging in phylogenetics: advantages of Akike Information Criterion and Bayesian approaches over Likelihood Ratio Tests. *Systematic Biology* **53**: 793-808.

Prajapati S. & Kumar S. (2002) Interaction of UNIFOLIATA–TENDRILLED ACACIA gene with AFILA and TENDRIL–LESS genes in the determination of leaf blade growth in pea *Pisum sativum. Plant Science* **162**: 713–721.

Prince L.M & Parks C.R. (1998) An evaluation of tribal and generic classification of Theoideae (Theaceae) based on DNA sequence data. *American Journal of Botany* **85**: 152–153.

Qian H. (2001) Floristic analysis of vascular plant genera of North America north of Mexico: spatial patterning of phytogeography. *Journal of Biogeography* **28**: 525–534.

Qian H. & Ricklefs R.E. (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature* **407**: 180–182.

Qian H., Song J.-S., Krestov P., Guo Q., Wu Z., Shen X. & Guo X. (2003) Large scale phytogeographical patterns in East Asia in relation to latitudinal and climatic gradients. *Journal of Biogeography* **30**: 129–141.

de Queiroz A. (2005a) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution* **20**: 68–73.

de Queiroz A. (2005b) Ernst Mayr and the modern concept of species. *Proceedings of the National Academy of Sciences of the USA* **102**: 6600–6607.

Radford A. & Bell C.R. (1964) *Manual of the Vascular Flora of the Carolinas.* University of Carolina Press, Chapel Hill.

Raji A.D. (1971) Evolution of the genera of the tribe Vicieae Adans. *Botanical Journal (Moscow)* **56**: 978–981. [In Russian]

Raloff J. (2000) Detoxifying desert's manna. *Science News* **158**: 74.

Ramstein G., Fluteau F., Besse J. & Joussaume S. (1997) Effect of orogeny, plate motion and land–sea distribution on Eurasian climate change over the past 30 million years. *Nature* **386**: 788–795

Raven P. (1972) Plant species disjunctions – a summary. *Annals of the Missouri Botanical Garden* **59**: 234–246

Rechinger K.H. (1979) *Lathyrus*. In: Chrtkova-Zertova A., van der Maesen L.J.G. & Rechinger K.H. *Flora Iranica*, no. 140. *Papillionaceae*, vol. I. *Vicieae*. Akademische Druck und Verlagsanstalt, Graz.

Rees H. & Narayan R.K.J. (1989) Biological implications of genome evolution. In: Stirton C.H. & Zarrucchi J.L. (eds) *Advances in Legume Biology.* Missouri Botanical Gardens, St Louis.

Regel E. (1862) *Versuch einer Flora des Ussuri–Gebeits*. [In Russian]

Reiche K. (1898) *Estudios Críticos Sobre la Flore de Chile*, vol. 2. Imprente Cervantes, Santiago.

Reichenbach (1832) *Flora Germanica excursiora*, vol. 2. Carl Cnobloch, Leipzig.

Renfrew J.M. (1973) *Palaeoethnobotany. The Prehistoric Food Plants of the Near East and Europe.* Methuen, London.

Renner S.S. (2004) Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences* **165** (suppl.): S23–S33.

Richardson J.E., Fay M.F., Cronk Q.C.B., Bowman D. & Chase M. W. (2000) A phylogenetic analysis of Rhamnaceae using rbcL and trnL–F plastid DNA sequences. *American Journal of Botany* **87**: 1309–1324.

Richardson J.E., Pennington R.T., Pennington T.D. & Hollingsworth P.M. (2001a) Rapid diversification of a species-rich genus of Neotropical rain forest trees. *Science* **293**: 2242–2245.

Richardson J.E., Weitz, F.M., Fay M.F., Cronk Q.C.B., Linder P.H. & Chase M.W. (2001b) Phylogenetic analysis of *Phylica* L. (Rhamnaceae) with an emphasis on island species: evidence from plastid trnL–F and nuclear internal transcribed spacer (ribosomal) DNA sequences. *Taxon* **50**: 405–427.

Ricklefs R.E. & Latham R.E. (1992) Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *American Naturalist* **139**: 1305–1321.

Ridley R. (2004). *A phylogeny of S. American* Lathyrus *(Leguminosae, Papilionoideae)*. MSc thesis, University of Edinburgh, Edinburgh.

Ritchie J.C. (1984) *Past and Present Vegetation of the Far Northwest of Canada.* University of Toronto Press, Toronto.

Ritchie M. & Tilman D. (1995) Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* **76**: 2648–2655.

Ronquist F., Huelsenbeck J.P. & van der Mark P. (2005) *MrBayes 3.1 Manual.* Online. Available: http://www.mrbayes.net/manual.php

Rønsted N., Chase M.W., Albach D.C. & Angelica Bello M. (2002) Phylogenetic relationships within *Plantago* (Plantaginaceae): evidence from nuclear ribosomal ITS and plastid *trnL–F* sequence data. *Botanical Journal of the Linnean Society* **139**: 323–338.

Roskov Y.R., Yakovlev G.P., Sytin A.K. & Jesniakowsky S.A. (1998) *Legumes of Northern Eurasia: Information Systems on Compact Disc.* International Legume Database and Information Systems, St Petersburg.

Rossow R.A. (1982) Notas sobre el género *Lathyrus* (Leguminosae). *Darwiniana* **24**: 489–495.

Rozas J. & Rozas R. (2001) *DNASP 3.51 DNA Sequence Polymorphism.* University of Barcelona, Barcelona.

Rozzi R. & Armesto J.J. (1989) Seed Dispersal Syndromes in the Rain Forest of Chiloe: Evidence for the Importance of Biotic Dispersal in a Temperate Rain Forest *Journal of Biogeography*, Vol. **16**: 219-226.

Salamin N., Chase M.W., Hodkinson T.R. & Savolainen V. (2003) Assessing internal support with large phylogenetic DNA matrices. *Molecular Phylogenetics and Evolution* **27**: 528–539.

Salazar G.A., Chase M.W., Soto Arenas M.A. & Ingrouille M. (2003) Phylogenetics of Cranichideae with emphasis on Spiranthinae (Orchidaceae Orchidoideae): evidence from plastid and nuclear DNA sequences. *American Journal of Botany* **90**: 777–795.

Samuel R., Stuessy T.F., Tremetsberger K., Baeza C.M. & Siljak-Yakovlev S. (2003) Phylogeneric relationships among species *Hypochaeris* (Asteraceae, Chicoreae) based on ITS, plastid *trnL* intron, *trnL–F* spacer and *matK* sequences. *American Journal of Botany* **90**: 496–507.

Sanderson M.J. (1989) Confidence limits on phylogenies: the bootstrap revisited. *Cladistics* **5**: 113–129.

Sanderson M.J. & Doyle J. (1993) Phylogenetic relationships in North American *Astragalus* (Fabaceae) based on chloroplast DNA restriction site variation. *Systematic Botany* **18**: 395–408.

Sanderson M.J. & Wojciechowski M.F. (2000) Improved bootstrap confidence limits in large-scale phylogenies, with an example from Neo-Astragalus (Leguminosae) *Systematic Biology* **49**: 672–685.

Sang T., Crawford D.J. & Stuessy T. (1997) Chloroplast DNA phylogeny, reticulate evolution and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* **84**: 1120–1136.

Savile, D.B.O. (1953) Splash-Cup Dispersal Mechanism in *Chrysosplenium* and *Mitella. Science*: **117**, No. 3036: 250-251.

Savolainen V., Cuénoud P., Spechiger R., Marinez M.D.P., Crèvecoeur M. & Manen J.-F. (1995) The use of herbarium specimens in DNA phylogenetics: evaluation and improvement. *Plant Systematics and Evolution* **197**: 87–98.

Schmidt G.J. & Schilling E.E. (2000) Phylogeny and biogeography of *Eupatorium* (Asteraceae, Eupatorieae) based on nuclear ITS data. *American Journal of Botany* 87: 716–726.

Schrire B.D., Lewis G.P. & Lavin M. (2005) Biogeoraphy of the Leguminosae. In: Lewis G., Schrire B., Mackinder B. & Lock M. (eds) *Legumes of the World.* Royal Botanic Gardens, Kew, Richmond, pp. 21–54.

Seberg O., Humphries C.J., Knapp S., Stevenson D.W, Petersen G., Scharff N. & Andersen N.M. (2003) Shortcuts in systematics? A commentary on DNA-based taxonomy. *Trends in Ecology and Evolution* **18**: 63–65.

Seijo J.G. & Fernandez A. (2003) Karyotype analysis and chromosome evolution in South American species of *Lathyrus* (Leguminosae). *American Journal of Botany* **90**: 980–987.

Senn H.A. (1938) Experimental data for a revision of the genus *Lathyrus*. *American Journal of Botany* **25**: 67–78.

Sewell M.M., Parks C.R. & Chase M.W. (1996) Intraspecific chloroplast DNA variation and biogeography of North American *Liriodendron* L. (Magnoliaceae). *Evolution* **50**: 1147–1154.

Sher A. (1999) Traffic lights at the Beringian crossroads. *Nature* **397**: 103–104.

Simmons M.P. & Ochoterena H. (2000) Gaps as characters n sequence-based phylogenetic analyses. *Systematic Biology* **49**: 369–381.

Simmons M.P., Ochoterena H. & Carr T.G. (2001) Incorporation, relative homoplasy and effect of gap characters in sequence-based phylogenetic analysis. *Systematic Biology* 50: 454–462.

Simola L.K. (1966) Chemical and morphological characteristics of some endemic species of *Lathyrus* (preliminary report). *Suomen Kemistilehti: the Finnish Chemical Journal* **B39**: 148–150.

Simola L.K. (1968a) Comparative studies on number of leaflets, veination, and epidermal structure in the genus *Lathyrus*. *Canadian Journal of Botany* **46**: 71–84.

Simola L.K. (1968b) Comparative studies on the amino acid pools of three *Lathyrus* species. *Acta Botanica Fennica* **81**: 4–62.

Simola L.K. (1986) Structural and chemical aspects of evolution of *Lathyrus* species. In: Kaul A.K. & Combes D. (eds) *Lathyrus and Lathyrism.* Third World Medical

Research Foundation, New York.

Simpson B.B. & Neff J.L. (1985) Plants, their pollinating bees, and the Great American Interchange. In: Stehli F.G. & Webb S.D. (eds) *The Great American Biotic Interchange.* Plenum, New York.

Simpson B.B. & Todiza C.A. (1990) Patterns and processes in the development of the high Andean flora. *American Journal of Botany* **77**: 1419–1432.

Small R.L., Ryburn J.A., Cronn R.C., Seelanan T. & Wendel, J. F. (1998) The tortoise and the hare: choosing between noncoding plastome and nuclear ADH sequences for phylogeny reconstruction in a recently diverged plant group. *American Journal of Botany* **85**: 1301–1315.

Soltis D.E. & Soltis P.S. (1998) Choosing an approach and appropriate gene for phylogenetic analysis. In: Soltis D.E., Soltis P.S. & Doyle J.J. (eds) *Molecular Systematics of Plants,* vol. II. *DNA Sequencing*. Kluwer, Boston.

Soltis D.E., Soltis P.S. & Doyle J.J. (eds) (1998) *Molecular Systematics of Plants*, vol. II. *DNA Sequencing.* Kluwer, Boston.

Soltis D.E., Tago-Nakazawa M., Xiang Q.Y., Murata J., Wakabayashi M. & Hibsch-Jetter C. (2001) Phylogenetic relationships and evolution in *Chrysosplenium* (Saxifragaceae) based on *mat*K sequence data. *American Journal of Botany* **88**: 883–893.

Sosef M.S.M. (1997) Hierarchical models, reticulate evolution and the inevitability of paraphyletic supraspecific taxa. *Taxon* **46**: 75–85.

Spegazzini C. (1897) Primitiae Florae Chubutensis. *Revista de la Facultad de Agronomia y Veterinaria de la Plata* **3**: 602–603.

Spegazzini C. (1902) Nova addenda ad floram Patagonicam IV. *Anales del Museo Nacional de Historia Natural de Buenos Aires* **7**: 279–281

Sprent J.I. & McKey D. (eds) (1994) *Advances in Legume Systematics*, part 5. *The Nitrogen Factor.* Royal Botanic Gardens, Kew, Richmond.

Stanford A.M., Harden R. & Parks C.R. (2000) Phylogeny and biogeography of *Juglans* (Juglandaceae) based on *matK* and ITS sequence data. *American Journal of Botany* **87**: 872–882.

Stankevich A.K., Roskov Y.R. (1998) New combinations in Northern Eurasian Leguminosae: Papilionoideae, Vicieae. *Kew Bulletin* **53**: 732.

Steele K.P. & Vilgalys R. (1994) Phylogenetic analyses of Polemoniaceae using nucleotide sequences of the plastid gene *mat*K. *Systematic Botany* **19**: 126–142.

Steele K.P. & Wojciechowski M.F. (2003) Phylogenetic analyses if tribes Trifoleae and Vicieae based on sequences of the plastid gene matK (Papilionoideae: Leguminosae). In: Klitgaard B.B. & Bruneau A. (eds) *Advances in Legume Systematics*, part 10. *Higher Level Classification*. Royal Botanic Gardens, Kew, Richmond.

Steudel E.T. (1841) *Nomenclator Botanicus*, 2nd edn. J.G. Cotta, Stuttgart.

Stevens P.F. (2006) An end to all things? Plants and their names. *Australian Systematic Botany* **19**: 115–133.

Stirton C.H. (1981) Petal sculpturing in papilionoid legumes. In: Polhill R.M. & Raven P.H. *Advances in Legume Systematics*, part 2. Royal Botanic Gardens Kew, Richmond.

Suc J.-P. (1984) Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* **307**: 429–432.

Suh Y., Thien L.B., Reeve H.E. & Zimmer E.A. (1993). Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of ribosomal DNA in Winteraceae. *American Journal of Botany* **80**: 1042–1055.

Suigura M. (1992) The chloroplast genome. *Plant Molecular Biology* **19**: 149–168.

Suzuki Y., Glazko G.V. & Nei M. (2002) Overcredibility of molecular phylogenies obtained by Bayesian phylogenetics. *Proceedings of the National Academy of Sciences of the USA* **99**: 16138–13143.

Swofford D.L. (2001) *PAUP: Phylogenetic Analysis Using Parsimony*, version 4.0β10. Sinauer Associates, Sunderland.

Taberlet P., Gielly L., Pautou G. & Bouvet J. (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* **17**: 1105–1109.

Takhtajan A. (1986) *Floristic Regions of the World.* Crovello T.J. (tr.), Cronquist A. (ed.) University of California Press, Berkeley.

Taylor S., Hofer J. & Murfet I. (2001) *Stamina pistilloida*, the pea ortholog of Fim and UFO is required for the normal development of flowers, inflorescences and leaves. *The Plant Cell* **13**: 31–46.

Tekle-Haimanot R.B., Abegaz E., Wuhib A., Kassina Y., Kidane N., Kebede T., Alemu T. & Spencer P.S. (1995) Nutritional neuro-toxicological surveys of *Lathyrus sativus* consumption in Northern Ethiopia. In: Yusuf H.K.M. & Lambein F. (eds) Lathyrus sativus *and Human Lathyrism: Progress and Prospects. Proceedings of the Second International Colloquium on* Lathyrus *and Lathyrism.* University of Dhaka, Dhaka, pp. 41–45.

Tenore M. (1831) *Sylloge Plantarum Vascularum Flora Neapolitanae.* Fibreni, Naples.

Thompson J.D., Gibson T.J., Plewniak F., Jeanmougin F. & Higgins D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* **25**: 4876–4882.

Tiffney B.H. (1985a) Perspectives on the origin of the floristic similarity between Eastern Asia and eastern North America. *Journal of the Arnold Arboretum* **66**: 73–94.

Tiffney B.H. (1985b) The Eocene North Atlantic land bridge: its importance in Tertiary and modern phytogeography of the northern hemisphere. *Journal of the Arnold Arboretum* **66**: 243–273.

Tiffney B.H. & Manchester S.R. (2001) The use of geological and paleontological evidence in evaluating phylogeographical hypotheses in the northern hemisphere Tertiary. *International Journal of Plant Sciences* **162** (suppl.): S3–S17.

Torrey J. & Gray A. (1838) *A Flora of North America*, vol. 1. Wiley & Putnam, New York.

Troncoso de Burkart N.S. & Bacigalupo N.M. (1987) Leguminosae. In: Troncoso de Burkart N.S. & Bacigalupo N.M. *Flora Illustrada de Entre Ríos*, vol. III. Instituto Naçional de Tecnologia Agropecuaria, Buenos Aires.

Tsui H.-P. (1984) Materiae ad Floram Lathyrorum Sinensium. *Bulletin of Botanical Research* 4(1): 36–60. [In standard Chinese]

Tsui H.-P. (1998) *Lathyrus*. In: Tsui H.-P. (ed.) *Flora of China (Flora Reipublicae Popularis Sinicae)*, vol. 42. Chinese Academy of Sciences, Beijing, pp. 270–286. [In standard Chinese]

Turczaninow N. (1969) *Flora Baicalensi-Dahurica (1842–1845) seu descriptio plantarum in regionibus Cis – et Transbaicalensibus atque in Dahuria sponte nascentium*. A. Asher, Amsterdam.

Urban I. (1893) Biographische Skizzen – Friedrich Sellow. *Botanische Jahrbücher* **17**: 177–198.

Vershinin A.V., Allnutt T.R., Knox M.R., Ambrose M.J. & Ellis T.H.N. (2003) Transposable Elements Reveal the Impact of Introgression, Rather than Transposition, in *Pisum* Diversity, Evolution, and Domestication. *Molecular Biology and Evolution* **20**: 2067 - 2075.

Vogel J.R.T. (1839) De Vicieis Brasiliensibus. *Linnaea* **13**: 21–38.

Wakasugi T., Sugita M., Tsudzuki T. & Sugiura M. (1998) Updated gene map of tobacco chloroplast DNA. *Plant Molecular Biology Reporter* **16**: 231–241.

Walter K.S. & Gillett H.J. (eds) (1998) *1997 IUCN Red List of Threatened Plants*. IUCN World Conservation Monitoring Centre, Gland.

Wang X.-Q., Tank D.C. & Sang T. (2000) Phylogeny and divergence times in Pinaceae: evidence from three genomes. *Molecular Biology and Evolution* **17**: 773–781.

Waterman P.G. (1994) Costs and benefits of secondary metabolites to the Leguminosae. In: Sprent J.I. & McKey D. (eds) *Advances in Legume Systematics*, part 5. *The Nitrogen Factor.* Royal Botanic Gardens, Kew, Richmond, pp. 129–149.

Watson L.E., Sayed-Ahmed H. & Badr A. (2000) Molecular phylogeny of Old World *Trifolium* (Fabaceae) based on plastid and nuclear markers. *Plant Systematics and Evolution* **224**: 153–171.

Wen J. (1999) Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Annual Review of Ecology and Systematics* **30**: 421–455.

Wen J. & Shi S. (1999) A phylogenetic and biogeographic study of *Hamamelis* (Hamamelidaceae), an eastern Asian and eastern North American disjunct genus. *Biochemical Systematics and Ecology* **27**: 55–66.

Wen J. & Stuessy T.F. (1993) The phylogeny and biogeography of *Nyssa* (Cornaceae). *Systematic Botany* **18**: 68–79.

Wen J. & Zimmer E. (1995) Phylogeny and biogeography of *Panax* L. (the *Ginseng* genus, Araliaceae): inferences from ITS sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* **6**: 167–177.

Wen J., Jansen R.K. & Kilgore K. (1996a) Evolution of the eastern Asian and eastern

North American disjunct genus *Symplocarpos* (Araceae): insights from chloroplast DNA restriction site data. *Biochemical Systematics and Ecology* **24**: 735–747.

Wen J., Jansen R.K. & Zimmer E.A. (1996b) Phylogenetic relationships and DNA sequence divergence of eastern Asian and eastern North American disjunct plants. In: Nei M. & Takahata N. (eds) *Current Topics in Molecular Evolution.* Pennsylvania State University and Graduate School for Advanced Studies, Hayama, pp. 37–44.

Westerkamp C. (1993) The co-operation between the asymmetric flower of *Lathyrus latifolius* (Fabaceae–Viceae) and its visitors. *Phyton* **33**: 121–137.

White P.S. (1983) Eastern Asian–North American floristic relations: the plant community level. *Annals of the Missouri Botanical Garden* **70**: 734–747.

White T.G. (1894) A preliminary investigation of the genus *Lathyrus* in North and Central America. *Bulletin of the Torrey Botanical Club* **21**: 444–458

White T.J., Burns T., Lee S. & Taylor J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis M., Gelfand D., Sninsky J. & White T. (eds) *PCR Protocols: a Guide to Methods and Application.* Academic Press, San Diego, pp. 315–322.

Wilcox T.P., Zwickl D.J., Heath T.A. & Hillis D.M. (2002) Phylogenetic relationships of the dwarf boas and a comparison of Bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution* **25**: 361–371.

Will K.W. & Rubinoff D. (2004) Myth of the molecule: DNA barcodes for species cannot replace morphology for identification and classification. *Cladistics* **20**: 47–55.

Willdenow C.L. (1802) *Species Plantarum*, vol. 3, 4th edn. G.C. Nauk, Berlin.

Wojciechowski M.F., Sanderson M.J. & Hu J.-M. (1999) Evidence on the monophyly of *Astragalus* (Fabaceae) and its major subgroups based on nuclear ribosomal DNA ITS and chloroplast DNA trnL data. *Systematic Botany* **24**: 409–437.

Wojciechowski M.F., Sanderson M.J., Steele K.P. & Liston A. (2000) Molecular phylogeny of the 'temperate herbaceous tribes' of Papilionoid legumes: a supertree approach. In: Herendeen P.S. & Bruneau A. (eds) *Advances in Legume Systematics*, part 9. Royal Botanic Gardens, Kew, Richmond, pp. 277–298.

Wojciechowski M. F.; Lavin, M. & Sanderson M.J. (2004) A phylogeny of Legumes

(Leguminosae) based on analysis of the plastid *matK* gene resolves many well-supported subclades within the family. American Journal of Botany **91**: 1846 – 1862.

Wolfe J.A. (1975) Some aspects of plant geography of the northern hemisphere during the late Cretaceous and Tertiary. *Annals of the Missouri Botanic Garden* **62**: 264–279.

Wolfe J.A. (1981) Vicariance biogeography of angiosperms in relation to paleobotanical data. In: Nelson G. & Rosen D.E. (eds) *Vicariance Biogeography: a Critique*. Columbia University Press, New York.

Wolfe J.A. (1987) Late Cretaceous–Cenozoic history of deciduousness and the terminal Cretaceous event. *Paleobiology* **13**: 215–226.

Wolfe J.A. (1997) Relations of environmental change to Angiosperm evolution during the late Cretaceous and Tertiary. In: Iwatsuki K. & Raven P.H. (eds) *Evolution and Diversification of Land Plants*. Springer-Verlag Tokyo, Tokyo, pp. 269–290.

Xiang Q.-Y. & Soltis D.E. (2001) Dispersal–vicariance analyses of intercontinental disjuncts: historical biogeographical implications for Angiosperms in the Northern Hemisphere. *International Journal of Plant Science* **162** (suppl.): S29–S39.

Xiang Q.-Y., Crawford D.J., Wolfe A., Tang Y.-C. & DePamphilis C. (1998a) Origin and biogeography of *Aesculus* L. (Hippocastanaceae): a molecular phylogenetic perspective. *Evolution* **52**: 988–997.

Xiang Q.-Y., Soltis D.E. & Soltis P.S. (1998b) Phylogenetic relationships of Cornaceae and close relatives inderred from matK and rbcL sequences. *American Journal of Botany* **85**: 285–297.

Xiang Q.-Y., Soltis D.E. & Soltis P.S. (1998c) The eastern Asian, eastern and western North American floristic disjunction: congruent phylogenetic patterns in seven diverse genera. *Molecular Phylogenetics and Evolution* **10**: 178–190.

Xiang Q.Y., Soltis D.E., Soltis P.S., Manchester S.R. & Crawford D.J. (2000) Timing in the eastern Asian–eastern North American floristic disjunction: molecular clock corroborates paleontological estimates. *Molecular Phylogenetics and Evolution* **15**: 462–472.

Xu D.H., Abe J., Sakai M., Kanazawa A. & Shimamoto Y. (2000) Sequence variation of non-coding regions of chloroplast DNA of soybean and related wild species and its implications for the evolution of different chloroplast haplotypes. *Theoretical and Applied Genetics* **101**: 724–732.

Yakovlev G.P. (1988) *Plantae Asiae Centralis*, vol. 8a. V.L. Komarov Institute of Botany, St Petersburg. [In Russian]

Yamamoto K., Fujiwara T. & Blumenreich I.B. (1984) Karyotypes and morphological characteristics of some species in th [*sic*] genus *Lathyrus* L. *Japanese Journal of Plant Breeding* **34**: 273–284.

Yang G. (1998) On the best evolutionary rate for phylogenetic analysis. *Systematic Biology* **47**:125–133.

Yaxley J.L., Jablonski W. & Reid J. (2001) Leaf and flower development in pea (*Pisum sativum* L.): mutants *cochleata* and *unifoliata*. *Annals of Botany* **88**: 225–234.

Yoder A.D., Irwin J.A. & Payseur B.A. (2001) Failure of the ILD to determine data combinability for slow loris phylogeny. *Systematic Biology* **50**: 408–424.

Young N.D. & DePamphlis C.W. (2000) Purifying selection detected in the plastid gene *matK* and flanking ribozyme regions within a group II intron of nonphotosynthetic plants. *Molecular Biology and Evolution* **17**: 1933–1941.

Zhu Y.J. & Meng RX (1986) A new species of *Lathyrus* Linn. from China. *Acta Phytotaxanomica Sinica* **24**(5): 402–403.

Zubakov V.A. & Borzenkova I.I. (1990) *Global Paleoclimate of the Late Cenozoic.* Elsevier, Amsterdam.

Zuluoga F.O. & Morrone O. (1999) *Catálogo de las Plantas Vasculares de la República Argentina*, vol. II. Missouri Botanical Garden Press, St Louis.