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THE INFRAGENERIC STRUCTURE OF LATHYRUS

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Dedicated to Professor P. H. Davis

ABSTRACT. The Old World members of *Lathyrus* (Leguminosae) are included in a sound taxonomic framework, but the New World species have never been brought into this system. This paper traces the historical development of the infrageneric structure of *Lathyrus*; surveys the variable characters, emphasising those of taxonomic significance; presents a comprehensive classification in which three of the 13 sections are described as new; and discusses the evolution of the genus.

INTRODUCTION

This paper is a sequel to my treatment of *Vicia* (Kupicha, 1976). The genus *Lathyrus* is equal in size to *Vicia* but easier to comprehend, because it exhibits more dramatic and better correlated vegetative characters than the latter, in addition to having interesting floral variation similar to that of *Vicia*. Moreover, the morphology and taxonomy of *Lathyrus* have recently been studied by several workers, notably Bässler (1966, 1973 & 1981), whose broad use of characters has led to a great improvement in the infrageneric classification. Nevertheless, there is still no world-wide account of the genus. This paper includes a very brief review of past taxonomic treatments of *Lathyrus*, a survey of its variable characters, a classification comprising 13 sections, and a short discussion on their evolution.

HISTORICAL BACKGROUND

Table 1 is a simplified diagram illustrating the taxonomic development of *Lathyrus*. Five historically significant treatments are aligned to show how the generic classification has evolved to the present, while my own system is given for comparison in the right-hand column.

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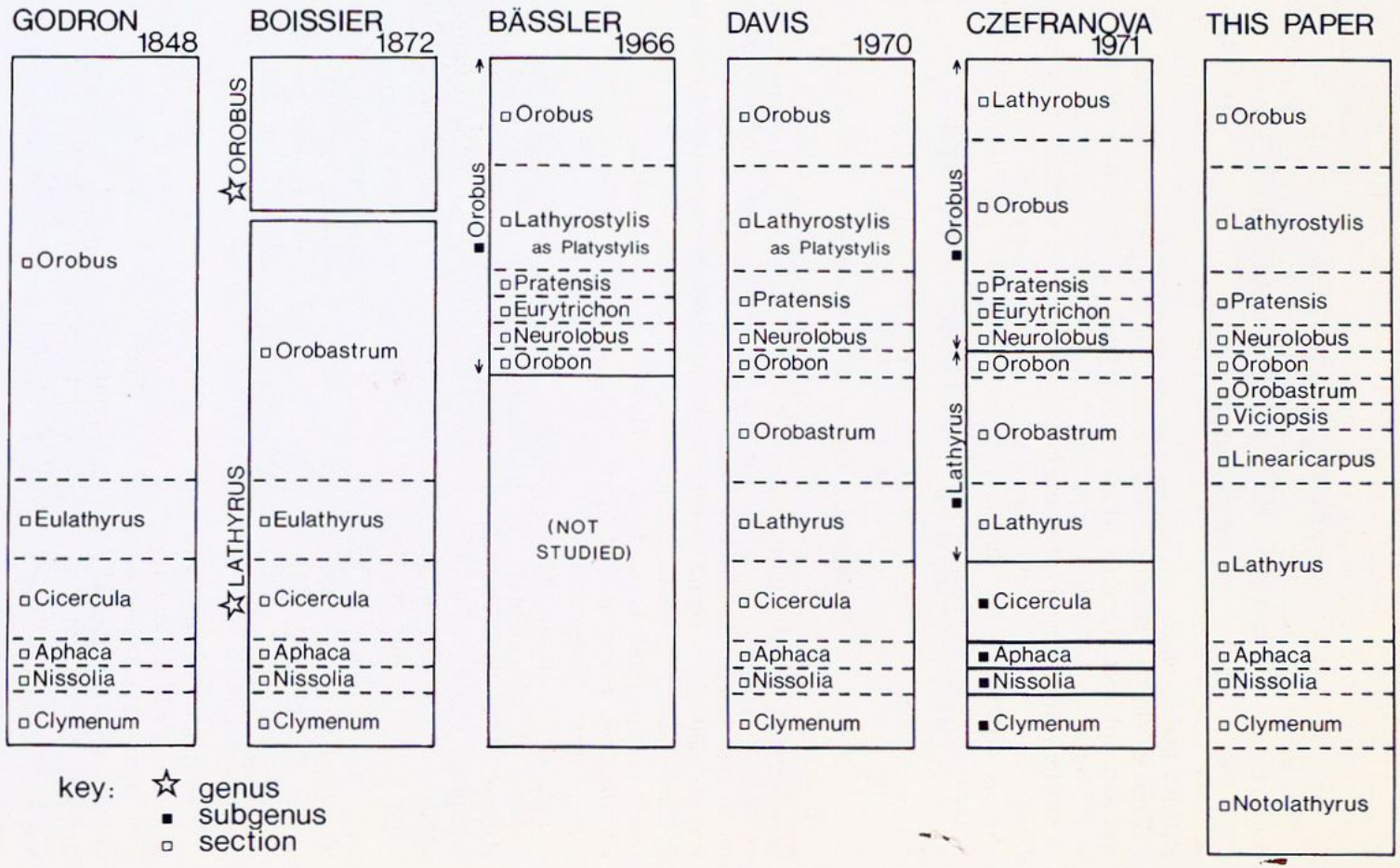
TABLE 1. Comparison of six different classifications of *Lathyrus*



Until the classification of Godron (1848), botanists had accepted the two Linnaean genera *Lathyrus* and *Orobus*, which were, however, separated on different criteria by different authors. Godron united the two into *Lathyrus*, and stated that this genus is characterised by a dorsally compressed style pubescent on the adaxial face, thereby excluding the 'oroboid' members of *Vicia* (Kupicha, 1981). Godron recognised six sections within *Lathyrus*: *Eulathyrus, Cicercula, Clymenum, Nissolia, Aphaca* and *Orobus*.

Boissier (1872) reinstated *Orobus* as a distinct genus to include those members of sect. *Orobus* which lacked tendrils. The remaining species which possessed tendrils were placed in *Lathyrus* sect. *Orobastrum*.

Bässler (1966) recently published a taxonomic study of '*Lathyrus* subgen. *Orobus* (L.) Baker', a unit comprising all the perennial members of sect. *Orobus sensu* Godron. Bässler recognised the following sections within subgen. *Orobus*: *Orobus, Lathyrostylis* (as *Platystylis*), *Orobon, Pratensis, Eurytrichon* and *Neurolobus*. The annual species which were excluded from subgen. *Orobus* formed, by implication, the small and fairly well defined sect. *Orobastrum*, as in Davis (1970).

The most recent classification is that of Czefranova (1971), who again dealt only with Eurasian species of *Lathyrus*. She divided the genus into six subgenera: *Orobus, Lathyrus, Clymenum, Nissolia, Cicercula* and *Aphaca*. Subgen. *Orobus* contained five sections, as follows: sect. *Orobus*, including members of sect. *Lathyrostylis* as well as *L. linifolius, L. montanus, L. vernus* and *L. venetus*; sect. *Lathyrobus*, including the 'oroboid' species—i.e. those perennials with multijugate leaves, broad pinnate-veined leaflets, no tendrils and many-flowered inflorescences; and sects *Eurytrichon, Pratensis* and *Neurolobus*. Subgen. *Lathyrus* contained the three sections *Lathyrus, Orobon* and *Orobastrum sensu* Davis.

This survey shows that the Eurasian species have been classified in a broadly similar manner by all authors. The five groups *Clymenum, Aphaca, Nissolia, Cicercula* and *Lathyrus* (which, except the last, are composed entirely of annuals) are generally accepted, while the remaining species, mostly perennials, have been assigned to progressively smaller, more numerous and better-defined sections.

Lathyrus is well represented in the New World by two separate endemic groups in N and S America. They have never been included in an infrageneric classification, but both groups have been revised on a regional basis (Hitchcock, 1952; Burkart, 1935, 1942) and their vegetative and floral characters are described in recent surveys (Simola, 1968; Gunn & Kluve, 1976).

I consider that *Lathyrus* is a compact genus, well-structured at the sectional level but not strongly polarised by correlated characters into units that demand subgeneric recognition. There are indeed associations of character-states, especially among vegetative features, but as will be shown these have been reproduced by parallel evolution in different parts of the genus and serve to unite, rather than divide it.

Lathyrus L., Sp. Pl. 729 (1753).

Perennial and annual herbs with erect or more usually climbing or sprawling habit; rootstock occasionally tuberous. Stems winged or

unwinged, always with complete replacement of cortical vascular bundles at the nodes. Leaves hypostomatic to epi-amphistomatic, paripinnate (except in the phyllodic *L. nissolia* and in adult leaves of members of sect. *Aphaca*), tendrillous or mucronate; leaflets unijugate to multijugate; leaves occasionally phyllodic or reduced to stipules and a tendril; stipules semisagittate or hastate; vernation of leaflets supervolute; venation brochidodromous, veins pinnate or parallel. Inflorescence racemose, 1–many-flowered. Calyx usually actinomorphic, sometimes with oblique mouth and teeth of unequal length. Standard oblong to stenonychioid, usually bossed or pouched at the fold. Wings very rarely with 'pleat' in upper edge of limb. Staminal tube usually truncate at apex, rarely oblique. Style dorsally compressed, pubescent on adaxial face, sometimes spathulate and/or contorted; stigma sometimes double. Legume compressed, sessile, rarely stipitate, sometimes winged, occasionally bearing glandular or tuberculate hairs, rarely villous, rarely with membranous or woolly partitions between the seeds. Seeds with long to short hilum; testa smooth or rough; lens always near hilum; free amino acid canavanine absent, lathyrine often present. $x = 7$, polyploidy rare.

Lectotype: *L sylvestris* L. [*Lathyrus* has been lectotypified twice, by *L. sativus* L. (Britton & Brown, 1913:412) and by *L. sylvestris* (Green, 1929:175); no reason was given for the first choice and the second is preferred because *L. sativus* is the type of the segregate genus *Cicercula* Medik. (1787) whereas *L. sylvestris* has invariably been treated as part of sect. *Lathyrus* (*Eulathyrus*)].

Lathyrus, which includes some 150 species, is distributed throughout temperate regions of the northern hemisphere and extends into tropical E Africa and into S America. Its main centre of diversity is in the Mediterranean and Irano-Turanian regions, with smaller centres in N and S America.

TAXONOMIC CHARACTERS

The characters discussed here are those whose variation has been found to be of particular taxonomic importance within *Lathyrus*; they form the basis of the present classification. The residue of variable characters is mentioned more briefly at the end of this section. These secondary characters, which vary more or less independently of each other and of the main characters, tend to provide the differences between closely related species.

Stipules and nodal anatomy. Most species of *Lathyrus* have semisagittate stipules (fig. 1a), but hastate stipules (fig. 1b) occur in four sections: they are characteristic of sects *Pratensis* and *Aphaca,* common in sect. *Notolathyrus* and confined to two species, *L. japonicus* and *L. pisiformis,* in sect. *Orobus.* I found that in seedlings of *L. pratensis, L. aphaca, L. japonicus* and *L. nervosus* semisagittate stipules are produced at the earliest nodes, and the adult hastate form appears in about the third or fourth leaf. The two members of sect. *Aphaca* are very remarkable in the form of the adult leaf, which has no petiole or leaflets but only a pair of large stipules and a tendril.

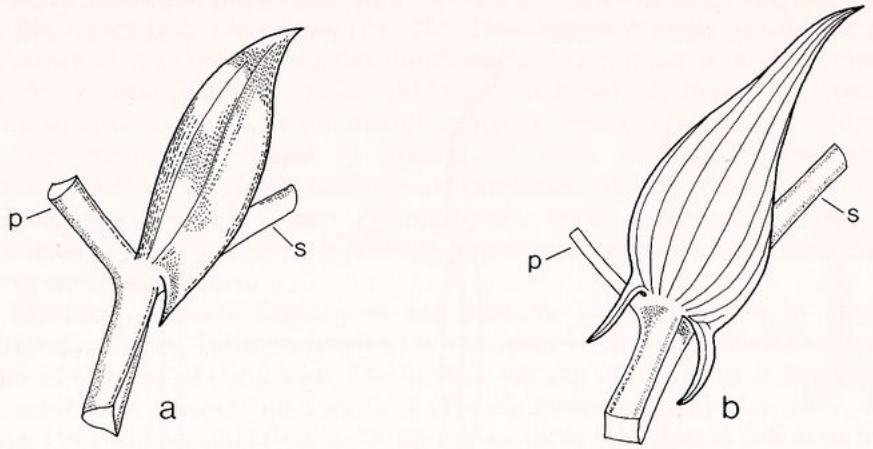


FIG. 1. *Lathyrus* stipules: a, semisagittate (*L. tingitanus*); b, hastate (*L. pratensis*). p = petiole, s = stem. Not to scale; only the front stipule is shown.

This variation in stipule shape is accompanied by variation in the pattern of nodal vasculature, as described earlier (Kupicha, 1975). In *Lathyrus* there are three different patterns of leaf-trace behaviour at the node, type 1 being characteristic of species with semisagittate stipules and types 2 and 3 found in species with hastate stipules (Table 2). It is clear that the hastate form of stipule has evolved more than once within *Lathyrus,* accompanied in each case by the establishment of a pattern of vasculature in which the median leaf-trace contributes to the stipular supply. Type 3, where the median and lateral leaf-traces contribute to both the stipules and petiole, is found in sects *Orobus* and *Notolathyrus,* and also in the genus *Pisum* L. It has certainly evolved independently in all three groups. Type 2, where the petiole (or tendril, in sect. *Aphaca*), is supplied only by the median trace, is the most extreme modification of the normal type 1, and is characteristic of sects *Pratensis* and *Aphaca*. This suggests that these sections may be closely related, and also provides a clue as to how the unusual leaf of *L. aphaca* could have evolved, since members of sect. *Pratensis* have a pattern of nodal anatomy preadapted for the foliar modification seen in sect. *Aphaca.*

TABLE 2. Leaf-trace behaviour in *Lathyrus*

	Species with semi-sagittate stipules (the majority)	Species with hastate stipules	
		L. pratensis	*L. japonicus*
		L. laxiflorus	*L. hookeri*
		L. aphaca	*L. nervosus*
			L. pusillus
	TYPE 1	TYPE 2	TYPE 3
Stipules supplied by	lateral traces	median and lateral traces	median and lateral traces
Rest of leaf supplied by	median and lateral traces	median trace	median and lateral traces

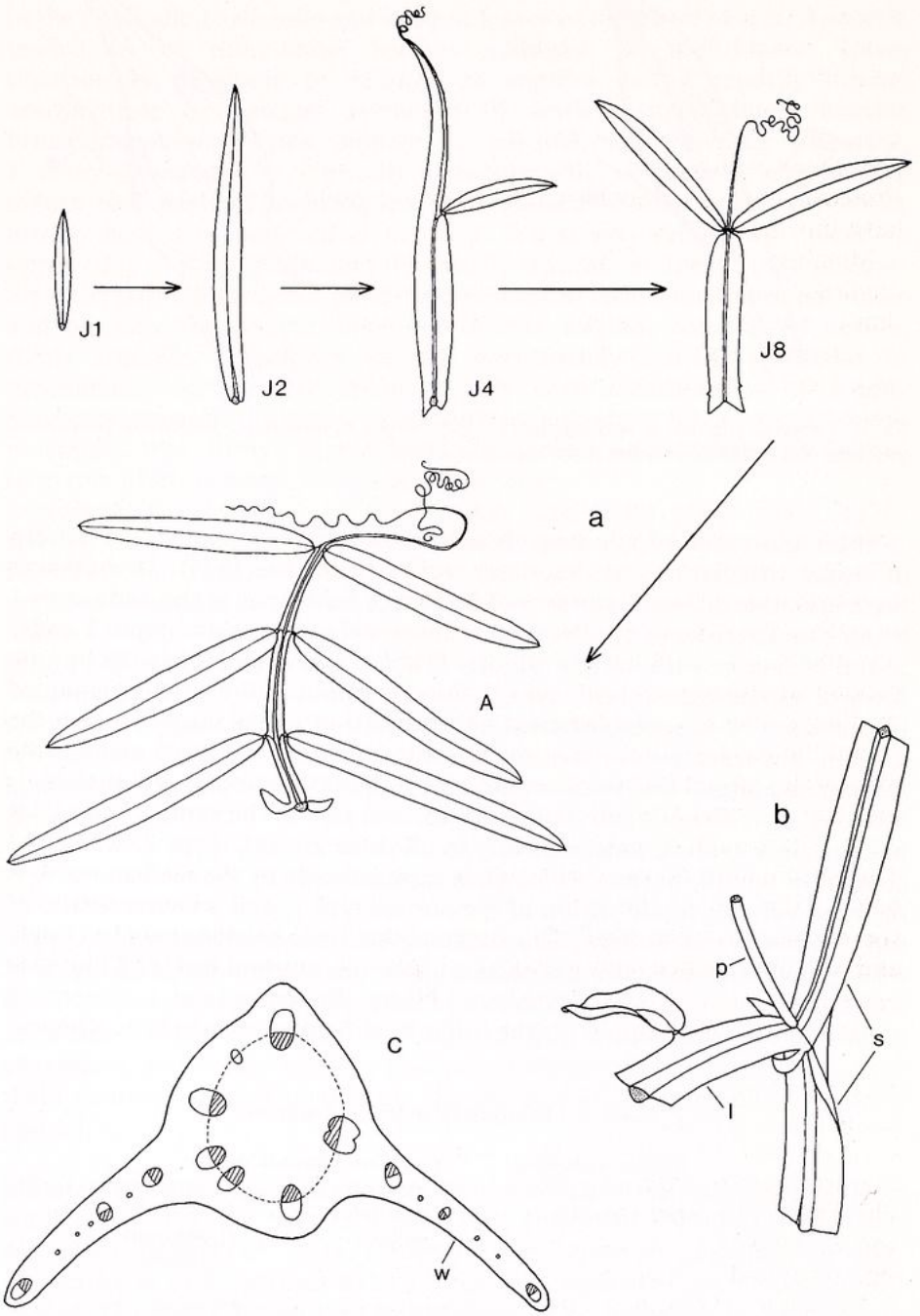


FIG. 2. *Lathyrus clymenum,* a species with strongly winged stems and phyllodic juvenile leaves: a, ontogenetic leaf series (J1, J2, J4, J8, first, second, etc. juvenile leaves; A, adult leaf); b, part of stem (s) at a node showing base of adult leaf (l) and peduncle (p); c, transection through internode showing the central stele comprising a ring of vascular bundles and the wings (w) containing cortical vascular bundles. a × ⅔; b, c not to scale.

Winged stems and phyllodes. Many species of *Lathyrus* have winged stems, as illustrated in *L. clymenum* (fig. 2b). This feature is made possible by the presence of the cortical vascular bundles (fig. 2c) that occur in all members of the Vicieae (Kupicha, 1975, 1977) although only *Lathyrus* has species with winged, as distinct from merely quadrate, stems. More or less strongly winged stems are found in species of sects *Lathyrus, Clymenum, Orobastrum* and *Neurolobus,* in some members of sect. *Orobus* and in a few representatives of sect. *Notolathyrus*. Sects *Lathrostylis, Orobon, Pratensis, Aphaca, Viciopsis, Linearicarpus* and *Nissolia* characteristically have unwinged stems.

Members of sects *Clymenum* and *Nissolia* are remarkable in having phyllodic leaves. In these species the ontogeny is strikingly different from that of the rest of the genus. The normal pattern of ontogeny is illustrated by a series of leaves from a seedling of *Vicia melanops* (Kupicha, 1977, fig. 4A). Here the plumule first produces two or three scale-leaves followed by a series of true leaves, the first of which is unijugate and mucronate. In species of *Lathyrus* where the adult form of leaf is also unijugate and mucronate (e.g. *L. roseus, L. laxiflorus*), successive seedling leaves are simply larger; in species where adult leaves are multijugate and/or tendrillous the adult form is reached through a series of intermediate stages. The ontogenetic sequence in *L. clymenum* is shown in fig. 2a. The seedling produces two or three scale-leaves, followed by a series of true leaves. Initially these organs consist of a grass-like phyllodic blade (J1, J2); after a few nodes, the phyllodes are terminated by a simple tendril and leaflets are produced, either at the apex or lower down (J4, J8). The stem apex of the seedling is enclosed by a number of young phyllodes, the older blades curled round the younger. The adult form of leaf (A) is attained after an unusually long series of intermediate stages. It is no longer phyllodic, but has a moderately-winged petiole and rhachis and several pairs of leaflets (fig. 2aA). The development of *L. gloeospermus* resembles that of *L. clymenum*. The pattern in *L. ochrus* is also similar, but leaves with leaflets are produced only at the end of the plant's life-cycle. During most of its growth this species bears simple, phyllodic leaves, often curiously divided at the apex and with unbranched tendrils from each point. *L. nissolia* is very similar in its ontogeny to species of sect. *Clymenum,* but unlike them it undergoes no change in leaf-construction during growth; no tendrils or leaflets are produced.

Number of leaflets. The genus *Lathyrus* shows a marked tendency towards reduction in leaflet number. Thus, about half of its species have leaves with a single pair of leaflets, and multijugate leaves are confined to, and characteristic of, sects *Orobus, Lathyrostylis, Clymenum* and *Viciopsis*. There are a few other species with two or more pairs of leaflets: *L. cirrhosus* and *L. mulkak* (sect. *Lathyrus*), *L. vinealis* (sect. *Linearicarpus*), and *L. macropus* and *L. multiceps* (sect. *Notolathyrus*).

As Bässler (1966) and Simola (1968) have pointed out, the multijugate leaf is the primitive form as it is found throughout *Vicia* and is typical of the Papilionoideae. The trend towards reduction in leaflet number may be regarded as an example of paedomorphosis, since the first leaves of the seedling are always unijugate (cf. Kupicha, 1977, fig. 4A), except in phyllode-bearing species.

Leaf venation. The venation of leaflets in *Lathyrus* is brochidodromous as in the rest of the Vicieae (Kupicha, 1977), but the orientation of the lateral veins varies so strongly that the venation can be described as pinnate or parallel, with some intermediates (Bässler, 1966; Simola, 1968). Parallel venation is characteristic of all members of sects *Lathyrostylis, Notolathyrus, Pratensis, Linearicarpus, Orobastrum* and *Neurolobus*. The venation of the leaflets of the first two seedling leaves of *L. aphaca,* and the phyllodes of *L. nissolia,* is also parallel. Sects *Orobus* and *Lathyrus* both show the whole range of venation types; in the latter, parallel venation is associated with annual life-form. The three small sections *Orobon, Clymenum* and *Viciopsis* have pinnate venation.

Bässler and Simola agree that pinnate venation is the more primitive state within *Lathyrus,* because of its occurrence throughout the rest of the Vicieae and its correlation with other relatively primitive characters, e.g. multijugate leaves. It is clear from its sectional distribution that parallel venation has evolved several times within the genus. As Simola has remarked, its adaptive significance is obscure; it does not seem to be linked with a particular type of habitat, being found in both xerophytic groups (e.g. sect. *Lathyrostylis*) and mesophytic ones (sect. *Notolathyrus*).

Parallel-veined leaflets tend to be proportionally narrower than pinnate-veined ones, but there are exceptions: for example, *L. laxiflorus* has parallel-veined, broad leaflets, while *L. clymenum* has pinnate-veined, narrow ones. Bässler (1966) implies that parallel venation in *Lathyrus* was induced by an evolutionary trend towards narrower leaflets. This may be so, but the two attributes are not linked by necessity, since *Vicia* has many species with extremely tenuous leaflets but none is parallel-veined.

Epidermal structure of leaves. The shape of the epidermal cells, and the distribution of stomata on upper and lower leaf surfaces, both vary in a manner that is taxonomically significant. This was first demonstrated by Bässler (1966), who described three different epidermal types in *Lathyrus,* characterised as follows:

1. leaves hypostomatic; epidermal cells isodiametric, with strongly wavy walls; e.g. *L. davidii, L. humilis, L. vernus, L. linifolius, L. niger, L. pisiformis, L. palustris* subsp. *palustris, L. roseus, L. laxiflorus*;
2. leaves amphistomatic; epidermal cells isodiametric or slightly elongated, with wavy or straight walls; e.g. *L. palustris* subsp. *nudicaulis, L. japonicus, L. incurvus, L. quinquenervius, L. pratensis, L. hallersteinii, L. czeczottianus, L. rotundifolius, L. ochroleucus, L. vestitus, L. parvifolius, L. venosus, L. polyphyllus, L. nevadensis, L. jepsonii, L. sulphureus*;
3. leaves amphistomatic; epidermal cells of upper leaf surface slightly elongated and usually wavy-walled, epidermal cells of lower leaf surface elongated, with straight walls; e.g. sect. *Lathyrostylis*; *L. setifolius, L. sphaericus, L. angulatus, L. clymenum, L. cassius, L. cicera, L. marmoratus, L. stenophyllus, L. amphicarpos, L. blepharicarpus, L. gorgoni, 'L. pulcher', L. pusillus, L. berterianus, L. subulatus.*

In his more recent papers on sect. *Orobus* (1973) and sect. *Lathyrostylis* (1981), Bässler has reinforced this earlier survey with a detailed investigation of the epidermis of almost every species in these sections. His

three papers include illustrations of 43 species. Simola (1968) also studied epidermal characters, especially of the New World species, and her results are comparable with those of Bässler.

In my own survey of the genus I found that the most useful characteristic of the epidermis is the relative distribution of stomata on the two sides of the leaflet, which can be expresed in a single figure by dividing the Stomatal Index of the upper leaf surface by that of the lower; this is explained in more detail in Kupicha (1976). My findings are summarised in Table 3. Bässler and Simola both used the Stomatal Index as a expression of stomatal density, and their results are included in Table 3, partly to make it more complete and partly to show how similar were the results obtained by three independent workers. Stomatal frequency is clearly a very constant specific character.

Table 3 shows that many Old World species in sect. *Orobus* and *L. roseus* (sect. *Orobon*) are hypostomatic, while the rest of the genus is amphistomatic. The North American species of sect. *Orobus,* and sects *Lathyrus, Pratensis* and *Clymenum,* are characterised by hypo-amphistomatic leaves. Sections *Lathyrostylis, Orobastrum, Viciopsis, Linearicarpus* and *Notolathyrus* have epi-amphistomatic leaves. This division of the genus into three groups has partial equivalence with Bässler's three categories: species of type 1 are hypostomatic, those of type 2 are hypo-amphistomatic, and the epi-amphistomatic species belong to type 3; but the latter also includes some hypo-amphistomatic species.

It is perhaps unnecessary to go further than this in the attempt to classify epidermal variation, since it seems clear that the different character-states do not define taxa but are evidence of a trend which has recurred several times during the evolution of *Lathyrus.* I agree with Bässler (1966) and Simola (1968) that the hypostomatic or strongly hypo-amphistomatic leaf with wavy-walled, isodiametric cells is the most primitive type; these characters are associated with other relatively primitive features such as multijugate leaves and pinnate venation. Conversely, epi-amphistomatic leaves with straight-walled, elongated cells are relatively advanced, being associated with parallel venation, and, to a lesser degree, with the unijugate condition. Hypo-amphistomatic species with nearly as many stomata on the upper leaf surface as below, which have moderately wavy to straight-walled, isodiametric to slightly elongated epidermal cells, represent intermediates in respect to this trend.

Inflorescence. In *Lathyrus* the inflorescence is usually few-flowered. Only a few members of sect. *Orobus* (e.g. *L. aureus*) have dense racemes, and this character, being associated with a bushy habit, etendrillous leaves and broad leaflets, contributes towards the 'oroboid' facies which occurs in both *Lathyrus* and *Vicia.* The remaining members of sect. *Orobus* have several flowers per raceme (i.e. about 5 to 10), and this is also typical of sects *Lathyrostylis* and *Notolathyrus.* Members of other sections usually have few- to 1-flowered racemes. Thus in *Lathyrus,* as in *Vicia,* the evolution of annual groups has been accompanied by a decrease in flower number. Unlike *Vicia,* where bracteoles are very uncommon, small, deciduous bracteoles are frequently present in perennial species of *Lathyrus.*

TABLE 3. Stomatal Index Ratios in *Lathyrus*

	A	B	C
Sect. Orobus			
L. davidii	0.0	0.0	0.0
L. gmelinii		0.0	
L. emodi		0.0	
L. libani		0.0	
L. aureus	0.0	0.0	
L. occidentalis		0.0	
L. laevigatus		0.0	
L. transsylvanicus		0.0	
L. humilis		0.0	
L. vernus		0.0	
L. frolovii		0.0	
L. komarovii		0.0	
L. venetus	0.0	0.0	
L. alpestris		0.0	
L. incurvus	0.7	0.8	
L. niger	0.0	0.0	0.4
L. japonicus	0.6	0.6	0.7
L. pisiformis	0.0	0.0	0.0
L. palustris	0.4	0.1	0.4
L. quinquenervius		1.3	
L. linifolius	0.7	0.4	0.7
L. arizonicus			1.0
L. brachycalyx			0.9
L. holochlorus			0.1
L. jepsonii	0.8		
L. laetiflorus			0.6
L. lanszwertii			0.9
L. leucanthus			1.4
L. nevadensis			0.0
L. pauciflorus	0.7		0.7
L. polymorphus	0.1		
L. polyphyllus			0.0
L. rigidus			1.1
L. sulphureus			0.9
L. venosus	0.6		
L. vestitus			0.0
Sect. Lathyrostylis			
L. ledebouri		1.8	
L. pannonicus	1.7	1.5	1.2
L. pallescens		1.5	
L. pancicii		1.7	
L. brachypterus		1.5	
L. bauhinii		1.4	
L. filiformis		1.3	
L. satdaghensis		1.3	
L. karsianus	1.1	1.1	
L. cyaneus		1.2	
L. digitatus		1.4	
L. armenus		1.2	
L. nivalis		1.1	
L. tukhtensis		1.5	
L. variabilis		1.1	
L. spathulatus	1.2	1.2	
L. elongatus		1.0	
L. cilicicus		0.9	
L. boissieri	1.0	1.0	
Sect. Lathyrus			
L. cirrhosus	0.8		0.8
L. grandiflorus	0.4		
L. rotundifolius	0.2		0.1
L. tuberosus	0.7		0.8
L. heterophyllus			1.1
L. latifolius	0.9		
L. sylvestris	0.8		0.9
L. tingitanus	0.7		0.8
L. odoratus	1.0		1.0
L. hirsutus	0.8		
L. sativus	0.8		
L. blepharicarpus	0.9		
L. amphicarpos			1.1
Sect. Orobon			
L. roseus	0.0		
Sect. Pratensis			
L. laxiflorus	0.4		
L. pratensis	0.6		
Sect. Aphaca			
L. aphaca	(0.4)		
Sect. Clymenum			
L. clymenum	0.9		0.7
L. ochrus	0.9		
Sect. Orobastrum			
L. setifolius	1.0		
Sect. Viciopsis			
L. saxatilis	1.4		
Sect. Linearicarpus			
L. angulatus	1.1		
L. inconspicuus	1.2		
L. sphaericus	1.5		
Sect. Nissolia			
L. nissolia	(2.6)		(2.6)
Sect. Notolathyrus			
L. berterianus			1.8
L. cabrerianus	5.2		14.5
L. hookeri	1.5		1.1
L. macropus			1.5
L. macrostachys			1.9
L. multiceps	1.7		0.5
L. pusillus	1.4		
L. subulatus	1.8		

Column A, new records; B, from Bässler (1973) for Sect. *Orobus* and from Bässler (1981) for Sect. *Lathyrostylis*; C, from Simola (1968). The score for *L. aphaca* refers to the stipules and those for *L. nissolia*, the phyllodic leaf.

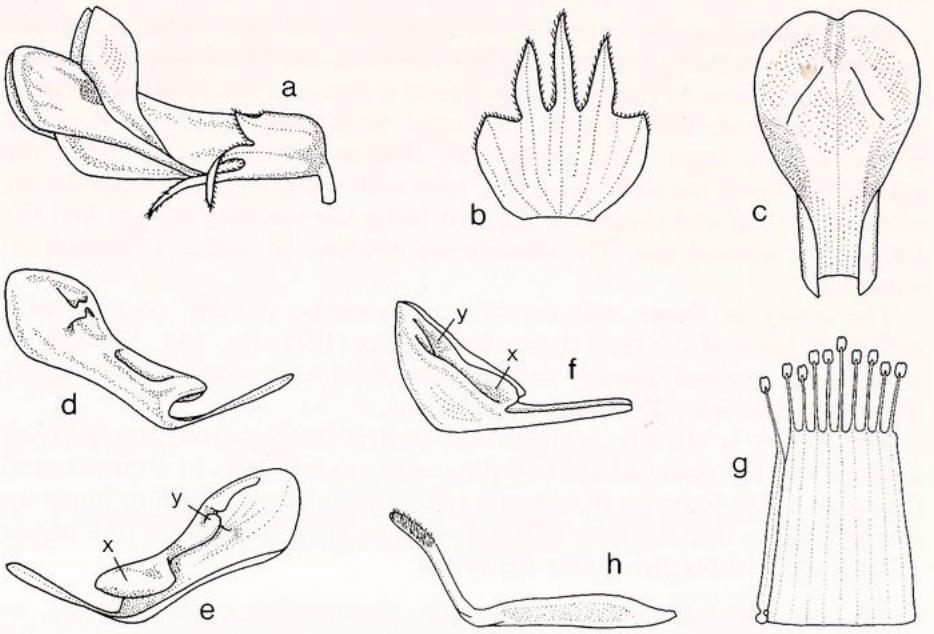


FIG. 3. *Lathyrus aureus*: a, flower; b, calyx; c, standard; d, wing from outside; e, wing from inside; f, keel (process 'x' of wing is united to hollow 'x' of keel, process 'y' of wing rests on keel at 'y'); g, androecium; h, gynoecium. All ×2.

In most species of *Lathyrus* with solitary flowers or few-flowered racemes the pedicel is articulated smoothly with the peduncle. A few species have a small projection at this point, suggesting that the axis is continuing past the flower (e.g. in *L. nissolia, L. aphaca, L. annuus* and *L. gorgoni*), while in others the scape actually ends in a long sterile process (e.g. in *L. sulphureus* and *L. chloranthus*; in the latter the length of the process is rather variable). Illustrations of these types are shown in fig. 5. Peduncle length may be regarded as one of the minor variable characters; *L. sphaericus, L. inconspicuus* and *L. gloeospermus* are unusual in having sessile flowers.

The flower. The general structure in *Lathyrus* may be illustrated by taking one species—*L. aureus*—and describing its flower in detail (fig. 3).

L. aureus. The calyx is gamosepalous, with unequal free lobes of which the uppermost are the shortest. The petals are intricately shaped, and fit together in a precise manner by which the flower forms a unit with a mechanism well adapted to pollination by bees. The lower edges of the two keel petals are united from their apex to half-way along the claw, forming the carina. The anthers are clustered around the end of the style, and are held closely in this position within the apex of the carina. The upper edges of the keel petals are free, and on each side there is a long groove. The wings correspond in shape with the carina: each wing has a thumb-like process (x in fig. 3e) whose papillate lower surface is firmly united with the keel at x, while the upper part of the wing is kinked to form a shelf (y) which rests on the upper part of the carinal groove at y. The standard turns back sharply from the wings, while its lower part grasps the claws of the keel and wings firmly in place round the staminal tube.

The androecium is basically diadelphous, but the filament of the uppermost (vexillary) stamen is lightly adnate to the staminal tube formed by the other nine. At the base, however, it is free and raised-up, leaving an opening on each side. Nectar, produced abundantly at the base of the ovary, exudes from these pores. All filaments become free from the staminal tube at the same level (the tube ends squarely). The stamens are alternately long and short, the shortest being the vexillary stamen and the longest the abaxial one. The anthers are introrse, of uniform size and all versatile.

The ovary is linear and compressed laterally, densely covered with glandular hairs of the type shown in Kupicha (1977: fig. 5A). The style is strongly compressed dorsally and has a brush of hairs near the apex on the inner (adaxial) side. The stigma is terminal.

The flower is slightly protandrous; pollen escapes from the bursting anthers into the pouched apex of the carina, and collects in a mass round the stigma. The hairs on the adaxial side of the style also help to brush up the pollen into this position, where it is ready to be transferred to a bee or other insect visiting the flower for nectar.

Calyx. Most members of *Lathyrus* have more or less regular calyces, as shown in *L. tuberosus* (fig. 4b). Flowers with unequal calyx lobes are typical of sect. *Orobus* (e.g. *L. aureus,* fig. 3b). They are also found in some members of sect. *Lathyrostylis*, e.g. *L. pannonicus, L. digitatus* and *L. satdaghensis,* and some representatives of sect. *Notolathyrus* (e.g. *L. magellanicus*).

Corolla. The flowers of *L. aureus, L. laevigatus* and other etendrillous members of sect. *Orobus* with broad leaflets have almost linear standards (fig. 3c) like the species of *Vicia* sects *Vicilla, Cassubicae* and *Atossa* (Kupicha, 1976: Table 2). However, in most species of *Lathyrus* the standard is stenonychioid, with a relatively wide banner and narrow claw. As in *Vicia,* this type is characteristic of species with few-flowered racemes. In all groups except sects *Lathyrus* and *Orobon* the standard has two more or less prominent pouches or bosses at the fold which carries the banner away from the wings. These processes rest against the wings and help to support the standard. *L. clymenum* and *L. ochrus* are characterised by a remarkably strong development of these pouches. (*L. gloeospermus,* the other member of sect. *Clymenum,* has reduced, cleistogamous flowers with undeveloped petals.) Sect. *Lathyrus* has flowers in which the tube is relatively short and the standard wide (e.g. *L. tuberosus*, fig. 4c). *L. roseus* (sect. *Orobon*) also has flowers of this type. The N American *L. sulphureus* (sect. *Orobus*) is distinctive in having a standard with the banner narrower than the claw.

The wings of most species resemble those of *L. aureus* (fig. 3d) in having a lower and an upper process but no pleat in the upper edge of the wings. A few species of sect. *Orobus* (e.g. *L. venetus, L. vernus*) do, however, have the latter feature which is more typical of *Vicia.* The wings of species of sects *Lathyrus, Orobon* and *Clymenum* are simpler in construction: only the lower process is present (fig. 4d). Members of sects *Pratensis* and *Aphaca* are unusual in having wings with a waist between the limb and the middle area that is united with the keel (Ross-Craig, 1954: plates 69 & 71).

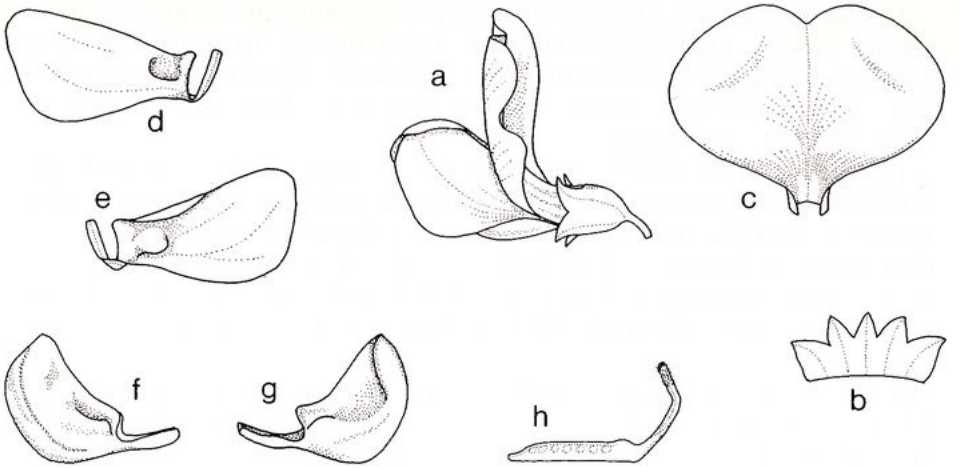


FIG. 4. *Lathyrus tuberosus*: a, flower; b, calyx; c, standard; d, wing from outside; e, wing from inside; f, keel, left side; g, keel, right side; h, gynoecium. All ×2.

Androecium. According to Gunn & Kluve (1976), *L. grandiflorus* and 11 New World species of *Lathyrus* have staminal tubes with an oblique apex instead of the truncate apex typical of the genus. I confirm Burkart's observation (1935) that the S American species *L. campestris* and *L. pusillus* have oblique-ended staminal tubes. Dr F. A. Bisby (pers. comm.) has supplied the following information for members of sect. *Notolathyrus*: the staminal tubes in *L. linearifolius, L. macropus, L. macrostachys* and *L. pubescens* are truncate; in *L. hasslerianus, L. hookeri, L. multiceps* and *L. pusillus* they are oblique; in *L. berterianus, L. cabrerianus, L. nervosus* and *L. paranensis* they are intermediate, and in *L. magellanicus* they vary from truncate to oblique.

Gynoecium. All members of *Lathyrus* have a dorsally compressed style which is pubescent on the (developmentally) adaxial side. Within this basic unity of structure, variation in stylar shape provides important characters that have been heavily weighted in the past by taxonomists dealing with the Old World species. Gunn & Kluve (1976) recently published a survey of androecial and gynoecial variation in the Vicieae that mentions these features in *Lathyrus,* although their study was not strictly taxonomic, i.e. it was not slanted towards recognition of infrageneric species-groups.

Many species of *Lathyrus* have a twisted style, and this is a particularly valuable character. It is typical of the closely-related sections *Lathyrus* (which I regard as comprising the traditional sects *Lathyrus* and *Cicercula*) and *Orobon.* In these groups the style is twisted through 90–180 degrees, always in an anticlockwise direction as seen from above (fig. 4h). Twisted styles also occur in sect. *Lathyrostylis,* but as Bässler (1981) says, this is found only in species with broadened styles and is due to lack of space within the keel. The direction of twist is not constant and different specimens of the same species can show twisted or straight styles. Similarly, the N American *L. sulphureus* sometimes has a twisted style. As far as I know, in all other species the style is straight.

Distinctly widened, spathulate styles are characteristic of about half the species of sect. *Lathyrostylis* (Bässler, 1981: fig. 5). Spathulate styles are also found in some members of sect. *Lathyrus* (*L. hirsutus, L. gorgoni*), in sect. *Clymenum* and many members of sect. *Notolathyrus* (e.g. *L. cabrerianus, L. multiceps*).

In *L. clymenum* and *L. ochrus* (sect. *Clymenum*) the style ends in a mucro of non-stigmatic tissue that divides the stigma in two (Gunn & Kluve 1976: fig. 2). (The third species of sect. *Clymenum, L. gloeospermus,* has cleistogamous flowers with an undeveloped style.) This interesting feature recurs in some members of sect. *Notolathyrus*: *L. pubescens, L. subulatus* and *L. tomentosus* (Burkart, 1935, and my own observation).

Fruit. The range of legume shapes in *Lathyrus* is shown in fig. 5, and the letters in parentheses following the species cited here refer to these illustrations. Fruits of *Lathyrus* are typically linear and seldom stipitate. This contrasts with the situation in *Vicia,* where the larger subgenus *Vicilla* is characterised by stipitate pods. The etendrillous members of *Lathyrus* sect. *Orobus* can thus be distinguished from 'oroboid' species of *Vicia* by their fruits: compare *L. venatus* (a) with *V. crocea* (Kupicha, 1976: fig. 5a).

Fruit characters have some taxonomic value within *Lathyrus,* especially among annual groups. Members of sect. *Linearicarpus* are characterised by long, linear pods in which the valves are usually conspicuously veined, either in a 'herringbone' pattern as in *L. sphaericus* (d) or reticulately as in *L. vinealis. L. saxatilis* (sect. *Viciopsis*) has unusually short legumes; those of *L. setifolius* (c; sect. *Orobastrum*) are strongly stipitate. The fruits of *L. sphaericus* and *L. inconspicuus* are distinguished by the presence of membranous septa between the seeds, though in *L. sphaericus* the character is not always present. *L. nissolia* has linear fruits with a herringbone vein pattern very similar to that of *L. sphaericus,* and although they are normally non-septate I found a single specimen with partitions inside the pod, which is very suggestive of affinity between sects *Nissolia* and *Linearicarpus*. Some species of sect. *Notolathyrus*, e.g. *L. tomentosus,* have woolly partitions between the seeds.

In sect. *Clymenum* the legumes have wings which arise from the upper suture, as shown in *L. ochrus* (e). In *L. gloeospermus* (f) there are also narrow wings on the valves, parallel to the sutures.

Variation in fruit morphology is one of the main guides for specific identification among annuals of sect. *Lathyrus.* The legumes range from long and narrow, e.g. *L. annuus* (g), to short, e.g. *L. cicera* (l), while in some there are winged sutures, e.g. in *L. sativus* (h) and *L. blepharicarpus* (j). The pods may be conspicuously veined, as in *L. pseudo-cicera* (m), or tuberculate-pilose as in *L. chrysanthus, L. chloranthus* (n), *L. hirsutus* (o) and *L. basalticus. L. lentiformis* (k) has unique fruits which are very small, stipitate and subtorulose.

Minor variable characters. The presence or absence of tendrils was at one time thought to be a feature of particular significance; for example, it was used by Boissier (1872) to separate the genera *Lathyrus* and *Orobus*. However, Fritsch (1900) and more recently Simola (1968) and Bässler (1973) have shown that this character should not be given much weight. Fritsch

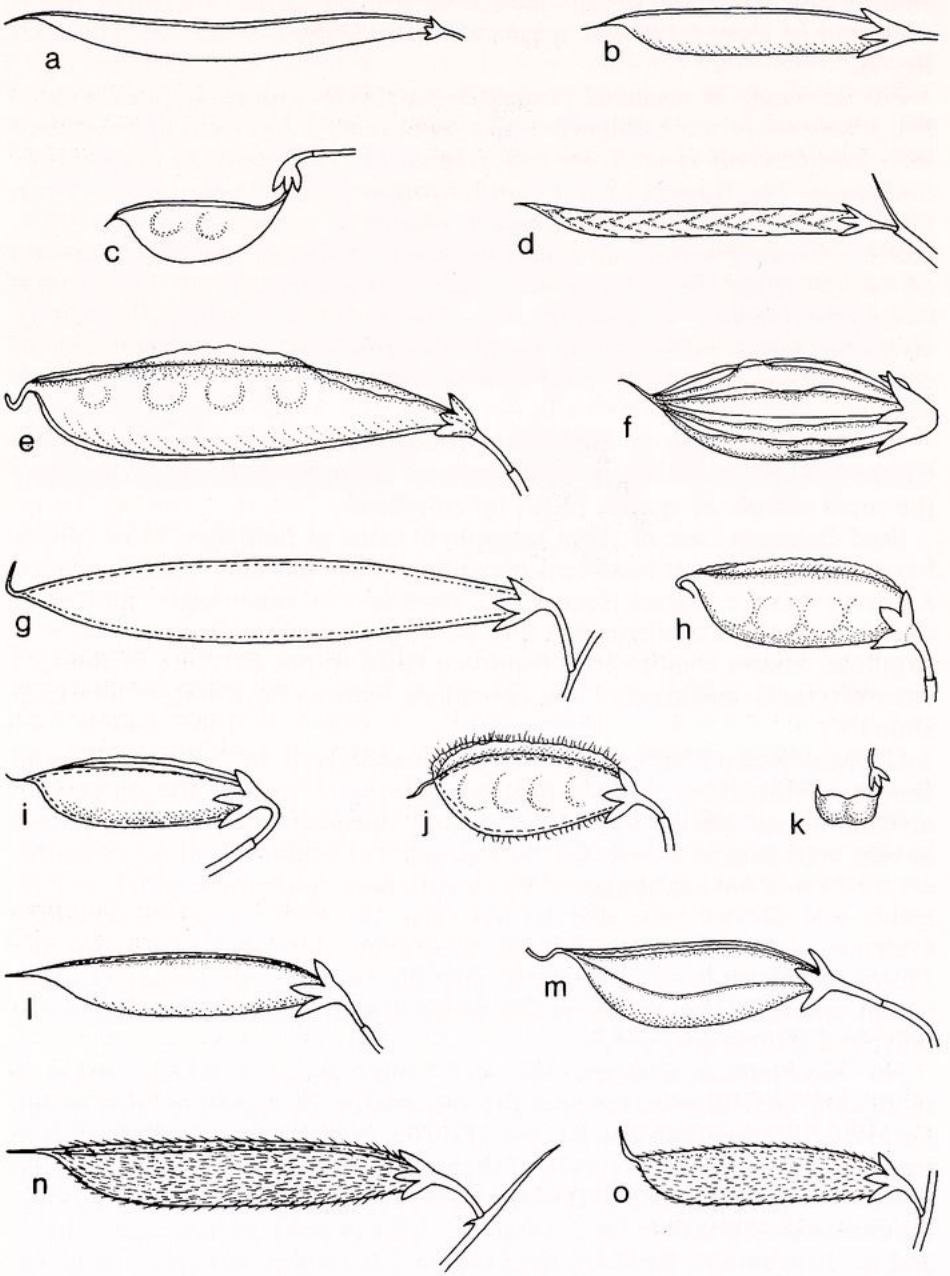


FIG. 5. *Lathyrus* fruits: a, *L. venetus*; b, *L. pratensis*; c, *L. setifolius*; d, *L. sphaericus*; e, *L. ochrus*; f, *L. gloeospermus*; g, *L. annuus*; h, *L. sativus*; i, *L. marmoratus*; j, *L. blepharicarpus*; k, *L. lentiformis*; l, *L. cicera*; m, *L. pseudo-cicera*; n, *L. chloranthus*; o, *L. hirsutus*. All natural size.

pointed out that there are several examples of closely related species pairs in which one species has tendrils and the other lacks them; similarly, normally tendrillous species sometimes have etendrillous forms and *vice versa*. Simola and Bässler agree that the primitive form of leaf in *Lathyrus* had tendrils and that these organs have been lost on various occasions in the evolution of more advanced species (Simola, 1968: fig. 22; Bässler, 1973: fig. 3).

Flower colour is no guide in identifying species groups within *Lathyrus* but is very useful in distinguishing between related species. The flowers of sect. *Lathyrostylis* range from pale sulphur (*L. pallescens*) to magenta (*L. tukhtensis*. The flowers of sect. *Lathyrus* may be yellow (*L. chrysanthus*), bluish (*L. hirsutus*), pink (*L. cassius*), orange (*L. pseudo-cicera*) or brick-red (*L. cicera*). The unusual colour brick-red occurs sporadically in the rest of *Lathyrus*, e.g. in *L. sphaericus* (sect. *Linearicarpus*) and *L. setifolius* (sect. *Orobastrum*). *L. aphaca* and *L. pratensis* have yellow flowers; *L. laxiflorus* (sect. *Pratensis*) is purple-flowered. In sect. *Clymenum*, *L. clymenum* has purplish or pink flowers while those of *L. ochrus* are pale yellow.

Pollen morphology in *Lathyrus* was studied by Gapotchka (1976) and Clarke & Kupicha (1976); no significant variation has been detected among the small sample of species so far investigated.

Seed characters are of slight taxonomic value in *Lathyrus*. Most species have smooth seeds (at hand-lens magnification), but many annuals of sect. *Lathyrus* have a rugose testa; in *L. nissolia* it is tuberculate, and in *L. angulatus* (sect. *Linearicarpus*) and *L. setifolius* (sect. *Orobastrum*) it is papillose. Hilum length varies from two-fifths to one-fifteenth of the seed circumference, and as in *Vicia* perennials tend to have longer hila than annuals.

Chromosome morphology has been investigated by Senn (1938) and Davies (1958). They found that most species have chromosomes with median or submedian centromeres, only members of sect. *Clymenum* having markedly asymmetrical chromosomes. *L. odoratus* and *L. hirsutus* are unusual in having no secondary constriction within the haploid complement, and Davies was able to hybridise these two species, providing evidence against their traditional separation into sects *Lathyrus* and *Cicercula*. Hybridisation is rarely possible in *Lathyrus* (Senn, Davies), except among N American species which are also unusual in often being polyploid (Hitchcock, 1952).

No biochemical evidence has yet been produced which makes a significant contribution towards the recognition of species groups within *Lathyrus*, although the distribution of different non-protein amino acids in seeds seems promising. A survey of the free amino acids in seeds of about 50 species was reported by Bell (1964) whose primary aim had been to discover the chemical responsible for the toxic syndrome known as 'neurolathyrism', and its distribution. Bell identified twelve different amino acids, of which the most common were arginine, homoarginine and lathyrine. The discontinuous and partially correlated distributions of the amino acids permitted the recognition of five groups of *Lathyrus* species. This chemically-based classification grouped together some closely-related species (e.g. the members of sect. *Clymenum*; many species of sect. *Lathyrus*), but in other

respects was discordant with the traditional classification. Simola (1968a) partly endorsed Bell's data but pointed out that interpretation of patterns of amino acid distribution is not straightforward, since the compounds are related by synthetic pathways, and when a particular amino acid is absent from the seed it may sometimes be detected in other organs. It would be interesting to make a fresh survey of the amino acids in seeds of *Lathyrus,* using authenticated seed and bearing in mind both the classification based on morphological characters and the interrelationships of the compounds. If these considerations were applied during the sampling and analysis, the results might have greater taxonomic meaning than in the past and shed light on the data already provided.

Robeson & Harborne (1980) have recently published a taxonomically important survey of the phytoalexins produced by the Vicieae. They found a major dichotomy within the tribe, *Lathyrus* and *Pisum* being characterised by the pterocarpans pisatin and related compounds in contrast to *Vicia* and *Lens* which produce wyerone and other furanoacetylenes. Thirty-one species of *Lathyrus* were tested, representing most of the sections. These responded rather uniformly to phytoalexin induction but two interesting results were the unique production by *L. odoratus* and *L. hirsutus* of the novel chromone lathodoratin and by *L. nissolia* of novel pterocarpans in place of pisatin.

CONSPECTUS OF TAXA WITHIN LATHYRUS

The following species-list is intended to include all currently recognised members of the genus, although since I have not studied the delimitation of species critically some may be omitted. Species are listed alphabetically in each section unless a more natural order has been achieved. This is explained, where relevant, in the following sectional descriptions.

Sections:

1. Orobus

Old World members

L. davidii Hance
L. gmelinii Fritsch
L. krylovii C. Serg.
L. emodi Fritsch
L. vaniotii Léveillé
L. libani Fritsch
L. aureus (Steven) Brandza
L. occidentalis (Fischer & Meyer) Fritsch
L. laevigatus (Waldst. & Kit.) Gren.
L. transsilvanicus (Sprengel) Reichb. f.
L. humilis (Ser.) Sprengel
L. vernus (L.) Bernh.
L. frolovii Rupr.
L. komarovii Ohwi
L. venetus (Miller) Wohlf.
L. alpestris (Waldst. & Kit.) Kit.
L. incurvus (Roth) Willd.
L. niger (L.) Bernh.
L. japonicus Willd.
L. pisiformis L.
L. palustris L.
L. dielsianus Harms
L. wilsonii Craib
L. quinquenervius (Miq.) Litv.
L. linifolius (Reichard) Bässler
L. dominianus Litv.

New World members

		L. arizonicus Britton	*L. littoralis* (Nutt.) Endl.
		L. bijugatus T. White	*L. nevadensis* S. Watson
		L. brachycalyx Rydb.	*L. ochroleucus* Hook. f.
		L. delnorticus C. Hitchc.	*L. parvifolius* S. Watson
		L. eucosmus Butters & St. John	*L. pauciflorus* Fern.
		L. graminifolius (S. Watson) T. White	*L. polymorphus* Nutt.
		L. hitchcockianus Barneby & Reveal	*L. polyphyllus* Nutt.
		L. holochlorus (Piper) C. Hitchc.	*L. rigidus* T. White
		L. jepsonii E. Greene	*L. splendens* Kellogg
		L. laetiflorus E. Greene	*L. sulphureus* Brewer
		L. lanszwertii Kellogg	*L. torreyi* A. Gray
		L. leucanthus Rydb.	*L. tracyi* Bradshaw
			L. venosus Mühlenb.
			L. vestitus Nutt.
			L. whitei Kupicha*
			L. zionis C. Hitchc.
2.	**Lathyrostylis**	*L. ledebouri* Trautv.	*L. armenus* (Boiss. & Huet) Čelak.
		L. pannonicus (Jacq.) Garcke	
		L. pallescens (M. Bieb.) K. Koch	*L. nivalis* Hand.-Mazz.
		L. pancicii (Jurišić) Adamović	*L. atropatanus* (Grossh.) Širj.
		L. brachypterus Čelak.	*L. tukhtensis* Czeczott
		L. bauhinii Genty	*L. variabilis* (Boiss. & Kotschy) Čelak.
		L. filiformis (Lam.) Gay	
		L. satdaghensis P. H. Davis	*L. spathulatus* Čelak.
		L. karsianus P. H. Davis	*L. elongatus* (Bornm.) Širj.
		L. cyaneus (Steven) K. Koch	*L. cilicicus* Hayek & Siehe
		L. digitatus (M. Bieb.) Fiori	*L. boissieri* Širj.
3.	**Lathyrus**	*L. mulkak* Lipsky	*L. chrysanthus* Boiss.
		L. cirrhosus Ser.	*L. trachycarpus* (Boiss.) Boiss.
		L. grandiflorus Sibth. & Smith	*L. lycicus* Boiss.
		L. rotundifolius Willd.	*L. phaselitanus* Huber-Mor. & P. H. Davis
		L. tuberosus L.	
		L. undulatus Boiss.	*L. sativus* L.
		L. heterophyllus L.	*L. amphicarpos* L.
		L. latifolius L.	*L. cicera* L.
		L. sylvestris L.	*L. stenophyllus* Boiss. & Heldr.
		L. tingitanus L.	*L. marmoratus* Boiss. & Blanche
		L. tremolsianus Pau	*L. blepharicarpus* Boiss.
		L. annuus L.	*L. ciliolatus* Rech. f.
		L. hierosolymitanus Boiss.	*L. hirticarpus* Mattatia & Heyn
		L. cassius Boiss.	*L. basalticus* Rech. f.
		L. odoratus L.	*L. lentiformis* Plitm.
		L. hirsutus L.	*L. gorgoni* Parl.
		L. chloranthus Boiss.	*L. pseudo-cicera* Pampan.
4.	**Orobon**	*L. roseus* Steven	
5.	**Pratensis**	*L. binatus* Pančić	*L. laxiflorus* (Desf.) Kuntze
		L. czeczottianus Bässler	*L. layardii* Ball ex Boiss.
		L. hallersteinii Baumg.	*L. pratensis* L.
6.	**Aphaca**	*L. aphaca* L.	*L. stenolobus* Boiss.
7.	**Clymenum**	*L. clymenum* L.	*L. ochrus* (L.) DC.
		L. gloeospermus Warb. & Eig	

* *Lathyrus whitei* Kupicha, nom. nov. Syn.: *L. longipes* T. White in Bull. Torrey Bot. Club 21: 453 (1894), non *L. longipes* Philippi (1856).

8.	**Orobastrum**	*L. setifolius* L.	
9.	**Viciopsis**	*L. saxatilis* (Vent.) Vis.	
10.	**Linearicarpus**	*L. angulatus* L.	*L. tauricola* P. H. Davis
		L. hygrophilus Taubert	*L. vinealis* Boiss. & Noë
		L. inconspicuus L.	*L. woronowii* Bornm.
		L. sphaericus Retz.	
11.	**Nissolia**	*L. nissolia* L.	
12.	**Neurolobus**	*L. neurolobus* Boiss. & Heldr.	
13.	**Notolathyrus**	*L. berterianus* Colla	*L. nervosus* Lam.
		L. cabrerianus Burkart	*L. nigrivalvis* Burkart
		L. campestris Philippi	*L. paraguayensis* Hassler
		L. hasslerianus Burkart	*L. paranensis* Burkart
		L. hookeri G. Don	*L. parodii* Burkart
		L. linearifolius Vogel	*L. pubescens* Hook. & Arn.
		L. lomanus I. M. Johnston	*L. pusillus* Elliott
		L. longipes Philippi	*L. subandinus* Philippi
		L. macropus Gillies	*L. subulatus* Lam.
		L. macrostachys Vogel	*L. tomentosus* Lam.
		L. magellanicus Lam.	*L. tropicalandinus* Burkart
		L. multiceps D. Clos	

KEY TO THE SECTIONS OF LATHYRUS

1. At least some of the leaves phyllodic; annuals 2
\+ None of the leaves phyllodic; annuals and perennials 3

2. All leaves phyllodic and without tendrils; phyllodes with parallel venation; stigma single; fruit not winged ..... sect. 11. *Nissolia*
\+ Lower leaves phyllodic, upper ones with leaflets and tendrils; phyllodes with pinnate venation; stigma double; fruits winged . sect. 7. *Clymenum*

3. Stipules hastate (in adult leaves) 4
\+ Stipules semisagittate 7

4. Leaves without leaflets, except in seedling ..... sect. 6. *Aphaca*
\+ All leaves with leaflets 5

5. Leaves with two or more pairs of pinnate-veined leaflets sect. 1. *Orobus* p.p.
\+ Leaves unijugate, leaflets parallel-veined 6

6. Plants of Old World; leaves hypo-amphistomatic; wing petals with 'waisted' limb ..... sect. 5. *Pratensis*
\+ Plants of New World; leaves epi-amphistomatic; wing petals not 'waisted' ..... sect. 13. *Notolathyrus* p.p.

7. Style contorted; standard always stenonychioid 8
\+ Style not contorted, or if so then limb of standard narrower than claw (*L. sulphureus*) 10

8. Tendrils absent; perennials 9
\+ Tendrils present or if absent then plants annual .. sect. 4. *Lathyrus* p.p.

9. Leaves unijugate, hypostomatic; leaflets broadly ovate, with pinnate venation ..... sect. 3. *Orobon*
\+ Leaves 1–7-paired, epi-amphistomatic; leaflets lanceolate, with parallel venation ..... sect 2. *Lathyrostylis* p.p.

10. Annuals 11
\+ Perennials 15

11. Leaves unijugate 12
\+ Leaves with two or more pairs of leaflets 13

12. Legumes strongly stipitate ..... sect. 8. *Orobastrum*
\+ Legumes not stipitate 14

13. Leaf venation pinnate ..... sect. 9. *Viciopsis*
\+ Leaf venation parallel ..... sect. 10. *Linearicarpus* p.p.

14. Stems winged; leaves hypo-amphistomatic (*L. gorgoni, L. pseudocicera*) ..... sect. 4. *Lathyrus* p.p.
\+ Stems not winged; leaves epi-amphistomatic sect. 10. *Linearicarpus* p.p.

15. Leaves unijugate 16
\+ Leaves with two or more pairs of leaflets 17

16. Stems strongly winged; flowers less than 1cm long; plants of Crete sect. 12. *Neurolobus*
\+ Stems not or only weakly winged; flowers more than 1.5cm long; plants of S America ..... sect. 13. *Notolathyrus* p.p.

17. Legumes tomentose; plants of S America ... sect. 13. *Notolathyrus* p.p.
\+ Legumes ±glabrous; plants of N America and Eurasia 18

18. Leaflets epi-amphistomatic, parallel-veined; leaf-rhachis etendrillous; stem not winged ..... sect. 2. *Lathyrostylis* p.p.
\+ Leaflets usually hypostomatic and pinnate-veined; leaf-rhachis tendrillous or etendrillous; stem winged or unwinged; if leaves epi-amphistomatic then stem winged and tendrils present; if leaves parallel-veined then stem winged and/or leaves hypostomatic ..... sect. 1. *Orobus* p.p.

SECTIONAL DESCRIPTIONS

1. Sect. **Orobus** (L.) Godron in Gren. & Godron, Fl. Fr. 1: 485 (1848).

Syn.: *Orobus* L., Sp. Pl. 728 (1753); *Lathyrus* subgen. *Orobus* (L.) Peterm., Deutschl. Fl. 155 (1849); *Lathyrus* sect. *Lathyrobus* (Tamamschjan) Czefr. in Novit. Syst. Pl. Vasc. (Leningrad) 8: 192 (1971).

Plants perennial, sometimes with tuberous rootstocks. Stems usually unwinged but occasionally winged. Leaves hypostomatic to amphistomatic, multijugate, with or without tendrils; leaflets broadly ovate to elliptic; venation pinnate or rarely parallel; stipules semisagittate or rarely hastate. Inflorescences many- to several-flowered, dense to comparatively lax (racemes 1–2-flowered in *L. torreyi*). Flowers brownish-yellow or bluish- or reddish-purple. Calyx teeth unequal; standard oblong to stenonychioid (in *L. sulphureus* the banner is narrower than the claw), usually bossed at the fold; wings rarely with a 'kink' in upper edge of limb; style not contorted (except in *L. sulphureus*), not spathulate. Legumes linear, not stipitate,

occasionally gland-dotted. Seeds smooth, with relatively long hilum.—54 species.

Lectotype: *L. linifolius* (Reichard) Bässler (*Orobus tuberosus* L.: see Green (1930) and Gunn (1969)).

Europe, NW Africa, Anatolia except the south-west, W Syria, N Iran, USSR, E Asia, Japan, N & C America.

The status of sect. *Orobus,* and its delimitation, have undergone many changes in the past. The genus *Orobus* L. originally contained only etendrillous perennial species. Later Döll (1843) considered that the group should comprise all members of the *Lathyrus* affinity which did not possess a twisted style, thus greatly widening its compass. This idea was followed to some extent by Boissier (1872), but he refined *Orobus* by excluding all tendrillous species. Much more recently Tutin (1956) made the novel suggestion, which has not been followed in practice, that *Orobus* should be a genus including only species with pinnate-veined leaflets. In the latest revision, that of Bässler (1973), sect. *Orobus* has the same delimitation as the genus *Orobus sensu* Boissier, with the exclusion of species with spathulate styles, the latter being placed in sect. *Lathyrostylis.* The N American species have never been dealt with taxonomically in the context of the whole genus, but Bässler (1966) has suggested a close relationship between them and the Old World members of sect. *Orobus.* The Eurasian species are listed here in the order of Bässler (1973), with the omission of his series, while the American species are arranged in alphabetical order.

Section *Orobus* contains a diversity of vegetative and floral forms and many of its members appear to be rather distantly related. The Old World representatives include a number of species characterised by an erect, bushy habit and leaves with few pairs of large, broad, pinnately-veined leaflets. The epidermal cells of the leaf are isodiametric, with very wavy walls, and stomata occur only on the lower leaf surface. This 'oroboid' syndrome is most complete in *L. aureus, L. libani, L. niger, L. transsylvanicus, L. gmelinii* and *L. laevigatus,* for these have etendrillous leaves and *Vicia*-like inflorescences in which the flowers are numerous, borne in a close, secund raceme, and the standard is oblong rather than stenonychioid. Species with this facies are linked to the rest of sect. *Orobus* by species with intermediate characteristics. Thus, *L. davidii* closely resembles *L. aureus,* but has strongly developed tendrils. *L. vernus* and *L. venetus* have typically oroboid leaves but laxer inflorescences in which the flowers are individually more attractive; however, these two species appear to be unique within *Lathyrus* in the possession of wing petals with a 'kink' in the upper edge, a feature otherwise associated with *Vicia.*

A few species which are included in sect. *Orobus* approach rather closely to members of sect. *Lathyrostylis.* The most problematic species of this type is *L. alpestris,* native to the Balkan peninsula, which has unwinged stems and etendrillous leaves with parallel-veined, narrowly elliptic leaflets; in facies it is thus very reminiscent of sect. *Lathyrostylis.* Bässler (1973) records that the leaves are hypostomatic (Table 3), and this provides support for its present taxonomic position. However, *L. quinquenervius,* a species nearly related to *L. palustris* and distinguished from members of sect. *Lathyrostylis* by its winged stems and tendrils, has epi-amphistomatic

leaves. The circumboreal *L. palustris* has winged stems, tendrillous leaves with an intermediate type of venation, a stenonychioid standard and a looser inflorescence than the oroboid species. In these characters it forms a link between the N American and the Old World members of sect. *Orobus*.

L. linifolius (syn. *L. montanus* Bernh.) stands apart from other members of sect. *Orobus* in having a tuberous rootstock, winged stems and etendrillous leaves with parallel-veined, narrowly elliptic leaflets. *L. japonicus* and *L. pisiformis* comprise another somewhat isolated group, characterised by the presence of hastate stipules.

The American representatives of sect. *Orobus* number about 30, and although some morphologically distinct species are present (e.g. *L. splendens* with few, very large flowers; *L. torreyi* with mucronate, multijugate leaves and 1–2-flowered inflorescences), many of the taxa form complexes whose limits are confused by interspecific hybridisation, a phenomenon unusual within the Vicieae. Besides *L. palustris,* only *L. delnorticus* and *L. jepsonii* have winged stems. Most species are climbers, having tendrillous leaves with many pairs of broad, pinnately-veined leaflets. A few (e.g. *L. polymorphus* and *L. arizonicus*) are more bushy, lacking tendrils and having linear leaflets. The inflorescence usually comprises several to many, often showy flowers, with stenonychioid standards. *L. sulphureus* is unusual in having a twisted style. This character is variable within the species; sometimes the style is not contorted, and when twisting occurs the direction varies. It seems most unlikely that this species is at all closely connected with members of other sections (sects *Lathyrostylis, Lathyrus* and *Orobon*) in which a twisted style is sometimes or typically present. The flower of *L. sulphureus* is also very unusual in having a standard in which the claw is broader than the banner. In epidermal characters, N American members of sect. *Orobus* resemble the non-oroboid Eurasian species. The leaves are hypo-amphistomatic to amphistomatic, and the epidermal cells are elongate, with slightly wavy walls. This type of leaf is correlated with a loose inflorescence and the stenonychioid standard.

2. Sect. **Lathyrostylis** (Griseb). Bässler in Feddes Rep. 82: 443 (1971).

Syn.: *Platystylis* Sweet, Brit. Fl. Gard. ser. 1, 3: 239 (1828); *Orobus* sect. *Lathyrostylis* Griseb., Spic. 1: 74 (1843); *Lathyrus* sect. *Platystylis* (Sweet) Bässler in Feddes Rep. 72: 88 (1966).

Plants perennial, sometimes with tuberous rootstocks. Stems not winged. Leaves epi-amphistomatic, with 1–7 pairs of leaflets, pinnate to subdigitate, etendrillous; leaflets narrowly linear-lanceolate to elliptic; venation parallel; stipules semisagittate. Inflorescence lax, several-flowered. Flowers in a wide range of colours. Calyx teeth equal or unequal; standard stenonychioid, bossed; style linear or moderately to strongly spathulate at the apex, sometimes contorted. Legumes linear, not stipitate, not gland-dotted. Seeds rough or smooth, with relatively long hilum.—20 species.

Type: *L. digitatus* (Bieb.) Fiori & Paol., Fl. Anal. Ital. 2: 105 (1900). (*Orobus digitatus* Bieb., Fl. Taur.-Cauc. 2: 153 (1808)).

Central & S Europe (except the extreme W), NW Africa, Anatolia, W Syria, Iraq, W Iran, Caucasia, Russia.

Sect. *Lathyrostylis*, although fairly large, is remarkable for its relative uniformity; its species all share a distinctive habit and have several less obvious characteristics in common. Bässler (1981) finds it impossible to subdivide the section into series as he did in his earlier revision of sect. *Orobus*. Although sect. *Lathyrostylis* is undoubtedly a natural group it has only very recently been recognized (Bässler, 1966, 1981; Davis, 1970), because the majority of its members are endemic to SW Asia and have rarely been included in studies of the genus. Boissier (1872) divided those species which he knew between *Lathyrus* and *Orobus*, because some (*L. nervosus*—syn. *L. boissieri*) were found to have twisted styles, while others (*O. cyaneus* and *O. armenus*) had straight styles and no tendrils. The species are listed here in the order of Bässler (1981).

Members of sect. *Lathyrostylis* are perennials which grow erect, their rigid stems requiring no support from neighbouring vegetation. The rootstocks of *L. pannonicus*, and possibly other species, bear clusters of tubers. The leaves are always etendrillous. Most species have unijugate leaves in the lower part of the plant and bijugate ones above; *L. elongatus* is unusual in having uniformly unijugate leaves; while *L. ledebouri, L. pancicii, L. pannonicus* and *L. satdaghensis* have more numerous leaflets, in the latter up to eight pairs per leaf. The leaflets are narrowly elliptic to elliptic, with strongly parallel venation. The petiole and rhachis are frequently both very short so that the leaflets are crowded together, giving a subsessile, subdigitate leaf. Sect. *Lathyrostylis* is distinctive in having epi-amphistomatic leaves.

The inflorescence bears several flowers which are often large and beautiful; apart from the differences in leaf form, it is this part of the plant that provides the main source of variation between species. Flower colour varies from deep blue, through lilac, magenta and pink, to yellow and cream; the corolla is often bicoloured. In *L. boissieri* the leaves at the apex of the flowering stem are reduced in size, and secondary shoots arise in the axils of earlier peduncles. This condition suggests a transition towards a compound type of inflorescence, otherwise seen in the Vicieae only in some 'oroboid' members of *Vicia* sect. *Vicilla*. The form of the corolla of this group is similar to that found in the non-oroboid species of sect. *Orobus*: the standard is stenonychioid and bossed, and the wings are joined to the keel by a strongly-developed interlocking arrangement. In about half the species (e.g. *L. pallescens, L. elongatus* etc.) the style is spathulate, terminating in a wide stigma. In other species (*L. cyaneus, L. nivalis*) the style is almost parallel-sided as in sect. *Orobus*. Twisted styles are found occasionally in sect. *Lathyrostylis*, and it seems that this character is variable within most or all of the species where it occurs (as observed in *L. satdaghensis, L. boissieri, L. spathulatus* and *L. filiformis*). It is also probable that the contortion is irregular in direction, unlike the situation in sect. *Lathyrus*. The fruits of sect. *Lathyrostylis* are uniform in shape, and similar to those of sect. *Orobus*.

The limited geographical distribution and narrow range of variability of this section, combined with its large size, suggest that many of its species are of comparatively recent origin, and that the group is still actively evolving. The taxonomy of the section is difficult, and hybridisation is thought to occur between some of the species, e.g. *L. variabilis* and *L. spathulatus* (Davis, 1970; Bässler, 1981).

3. Sect. **Orobon** Tamamshjan in Takhtadjan, Fl. Armenii 4:316 (1962).

Erect perennial with unwinged stems. Leaves hypostomatic, unijugate, etendrillous; leaflets suborbicular, pinnate-veined; stipules semisagittate. Inflorescence few-flowered; flowers deep pink. Calyx teeth equal; standard stenonychioid, with very broad banner and short claw, not bossed; style contorted. Fruit linear. Seed smooth, with hilum of intermediate length.—Monotypic.

Type: *L. roseus* Steven in Mem. Soc. Nat. Mosc. 4: 52 (1813).

Crimea, Caucasia, E & NE Anatolia, N & NW Iran.

L. roseus is a beautiful species, unusual within the tribe Vicieae in its tall bushy habit; its twiggy shoots grow up to 1.5m, but die back each season. The flower and fruit characters agree entirely with those of sect. *Lathyrus,* and it is only the vegetative features that support the sectional isolation of *L. roseus*. The leaflets are similar in shape and venation to those of *L. grandiflorus* and *L. tuberosus,* and *L. roseus* probably has its closest relatives among the 'delicate' perennials of sect. *Lathyrus*. Its leaves are, however, distinguished by having stomata only on the lower surface and in being etendrillous. The correlation of these two characters in *L. roseus* is particularly interesting, since it parallels the situation found in the various 'oroboid' groups of the Vicieae (*Lathyrus* sect. *Orobus* pro parte, *Vicia* sects *Vicilla* pro parte and *Atossa* pro parte). As in these oroboid groups, the epidermal cells of *L. roseus* are isodiametric and very strongly wavy-walled; in species of sect. *Lathyrus* they are somewhat elongated and more faintly wavy-walled.

4. Sect. **Lathyrus**

Syn.: *Cicercula* Medikus in Vorles. Churpf. Phys. Ges. 2: 358 (1787); *Lathyrus* sect. *Cicercula* (Medikus) Godron in Gren. & Godron, Fl. Fr. 1: 481 (1848); *Lastila* Alef. in Bonplandia 9: 146 (1861); *N avidura* Alef., op. cit. 147; *Lathyrus* sect. *Lentiformia* Zoh. in Zoh., Flora Palaestina 2: 458 (1972).

Plants annual and perennial, sometimes with tuberous rootstock. Stems usually winged. Leaves hypo-amphistomatic, unijugate and tendrillous (rarely with 2–3 pairs of leaflets or etendrillous); leaflets suborbicular to narrowly lanceolate; venation pinnate, intermediate or parallel; stipules semisagittate. Inflorescence few- to 1-flowered. Flowers in a wide range of colours. Calyx teeth equal; standard stenonychioid, with very wide banner and short claw, not bossed; style contorted, always in the same sense, or very rarely straight. Legumes of variable shape, sometimes glandular, tuberculate-hairy or with winged sutures. Seeds often with rough testa; hilum long to short.—c. 33 species.

Lectotype: *L. sylvestris* L., Sp. Pl. 733 (1753).

Europe except Ireland, Canaries, N Africa, Anatolia, Caucasia, Palestine, Lebanon, Iraq, Iran, Afghanistan, Transcaspia, Russia.

Very broadly speaking, sect. *Lathyrus* includes three habit-types:

1. delicate, though often tall-growing, perennials with narrowly winged or unwinged stems and thin, suborbicular, pinnate-veined leaflets: e.g. *L. grandiflorus, L. tuberosus, L. rotundifolius*;

2. sturdy perennials and annuals with wide-winged stems and coarse, broadly elliptic leaflets with intermediate to parallel venation: e.g. *L. latifolius, L. sylvestris, L. mulkak, L. odoratus, L. trachycarpus*;
3. more delicate annuals with narrowly elliptic leaflets and parallel venation: e.g. *L. cicera, L. lentiformis.*

These habit-types are not well-defined; for example, *L. undulatus* and *L. lycicus* are intermediate between the first two, *L. annuus, L. hirsutus* and *L. sativus* between the second and third. Nevertheless, this informal grouping forms a useful background against which one can trace variation in many other characters, as follows.

All species have unijugate leaves with the exception of three perennials belonging to group 2: *L. mulkak, L. cirrhosus* and *L. heterophyllus.* Only *L. trachycarpus* has etendrillous leaves; apart from this sturdy species, it appears that the larger annuals and the perennials have the best-developed tendrils, while in the smallest annuals these organs are weak and unbranched. Leaflet shape varies quite regularly from very broadly ovate in the delicate perennials, through broadly lanceolate or elliptic in sturdy annuals and perennials, to narrowly elliptic in most annuals. The type of venation is strictly correlated with leaflet shape: suborbicular leaflets have pinnate venation, elliptic ones are parallel-veined, and broadly elliptic ones have an intermediate type.

The number of flowers in the inflorescences follows a parallel pattern of variation. The perennials and the sturdier annuals have both the largest flowers and the highest number of blooms per raceme. Among the perennials, examples include *L. rotundifolius* (with about eight flowers on each peduncle), *L. undulatus* (c. six), *L. mulkak* (c. three); among the annuals, *L. trachycarpus* (c. five), *L. chrysanthus* (c. four), *L. annuus* (c. three) and *L. hirsutus* (c. three). The more delicate annuals have only one or two flowers per inflorescence.

Flower colour is very variable within sect. *Lathyrus,* almost every shade being represented, from deep crimson in *L. tingitanus* to deep pink in *L. latifolius*, yellow in *L. chrysanthus,* blue in *L. hirsutus* and brick-red in *L. cicera.* The wild sweet pea, *L. odoratus,* has a purple standard and mauve wings, but its cultivated descendants have reproduced all the colours found in the rest of the section, except yellow. As far as I know, *L. odoratus* and *L. tuberosus* are the only members of the Vicieae with strongly scented flowers.

Legume shape shows considerable variation within sect. *Lathyrus,* especially among the annuals. All perennial species have large, parallel-sided linear pods like those of sects *Orobus* and *Lathyrostylis,* and the larger annuals, including *L. annuus* (fig. 5g), *L. chloranthus* (fig. 5n) and *L. cassius,* have fruits of a similar shape. In the smaller annuals, however, they are usually shorter and broader and often possess specifically distinct characteristics. Several species have pods with winged sutures (e.g. *L. sativus, L. marmoratus* and *L. blepharicarpus*—fig. 5h, i, j) and in *L. blepharicarpus,* as the name implies, the wings are ciliate. *L. amphicarpos* and *L. ciliolatus* are remarkable in having both aerial and subterranean fruits (Mattatia, 1977). The pods of *L. pseudo-cicera* have a prominent longitudinal vein on each valve (fig. 5m). Finally, the recently-discovered *L. lentiformis* takes this variation to an extreme, having very small, papery-valved and indehiscent fruits containing only one or two seeds (fig. 5k).

A number of species have legumes that bear tuberculate hairs (i.e. simple unicellular smooth-walled hairs of the usual kind in the Vicieae (Kupicha, 1977: fig. 5A) but with a prominently swollen base). These include *L. hirsutus* (fig. 5o), *L. odoratus, L. trachycarpus, L. chrysanthus, L. chloranthus* (fig. 5n) and *L. lycicus.* This feature is not found elsewhere in *Lathyrus,* but occurs in *Vicia lutea. L. odoratus* and *L. cassius* are apparently unique within the tribe in possessing glandular hairs of the kind shown in Kupicha (1977: fig. 5B). In the former species they occur on the young shoots, in the latter on the fruit.

Many species in this section have seeds with a rough testa (e.g. *L. tuberosus, L. sylvestris, L. hirsutus, L. choranthus, L. annuus, L. lentiformis*). Probably about the same proportion of species have smooth seeds; these include *L. tingitanus, L. sativus* and *L. marmoratus.*

All members of sect. *Lathyrus* have a style which is contorted, always anticlockwise (fig. 4h), with the exception of the closely related species *L. gorgoni* and *L. pseudo-cicera.* In these two the style is straight and widened slightly below the stigma. The other characteristics of these species link them strongly with annuals of sect. *Lathyrus,* especially with *L. cicera* and *L. hierosolymitanus,* and there is little doubt of their taxonomic affinity.

The two sections *Lathyrus* and *Cicercula,* which are here reduced to synonymy, were originally separated by the type of style in each: in the former it was said to be arcuate, in the latter canaliculate (Godron, 1848). In practice this distinction, which is exaggerated in the dried flower, appears to reflect merely the robustness of the style and hence the size of the flower. Large-flowered annuals (*L. odoratus, L. trachycarpus* and *L. chloranthus*) have 'arcuate' styles similar to those of all perennials, while the more delicate annuals have 'canaliculate' styles which collapse on drying. A sectional classification whose limits are based strictly on this distinction is unnatural, and the wholly annual section *Cicercula* that results is probably not monophyletic but has more than one connection with the presumably older and more primitive sect. *Lathyrus.* For example, *L. odoratus* (sect. *Lathyrus*) and *L. hirsutus* (sect. *Cicercula*) have been successfully hybridised (Davies, 1958), an achievement rare in the Vicieae except between the most closely related taxa, and these two species share a unique phytoalexin (Robeson & Harborne, 1980). Again, *L. sylvestris* (sect. *Lathyrus*) and *L. annuus* (sect. *Cicercula*) are very similar in general morphology, arguing strongly for a close taxonomic relationship.

Sect. *Lathyrus* contains a particularly interesting and attractive assemblage of species. The many characters which vary throughout the group are partially correlated, suggesting trends which have been followed during its evolution. In the conspectus of taxa I have tried to arrange the species in a natural order, basing the sequence on the trends and characters mentioned above.

5. Sect **Pratensis** Bässler in Feddes Rep. 72: 90 (1966).

Syn.: *Lathyrus* sect. *Orobastrum* Boiss., Fl. Or. 2: 601 (1872) pro parte excl. typ.; *Lathyrus* sect. *Eurytrichon* Bässler, loc. cit.

Perennials, often pubescent to villous, sometimes with creeping or tuberous rootstock. Stems not winged. Leaves hypo-amphistomatic, unijugate, tendrillous or mucronate; leaflets broadly to narrowly elliptic,

with parallel venation; stipules hastate. Inflorescence several-flowered. Flowers yellow or bluish-purple. Calyx teeth equal; standard stenonychioid, bossed; wing petals with 'waist' in the limb; style linear, not contorted. Fruit linear, glabrous or hairy. Seeds smooth; hilum short.—c. 6 species.
Type: *L. pratensis* L., Sp. Pl. 733 (1753).
Europe, NW Africa, Ethiopia, Lebanon, N Iraq, Caucasia, eastwards to C Asia and Himalayas.

The members of this small section form a well-defined group, sharing several distinctive characteristics. Their leaves are always unijugate, with elliptic, parallel-veined leaflets. *L. pratensis* and the closely related *L. hallersteinii* have well-developed, branched tendrils, but in the remaining species the tendril is reduced: in *L. binatus* and *L. layardii* it is short and simple, in *L. czeczottianus* and *L. laxiflorus* absent. Members of sect. *Pratensis* are recognizable by the presence of large hastate stipules, and as described earlier they have a modified pattern of nodal vascular anatomy shared only with sect. *Aphaca*. The flowers of sect. *Pratensis* are also distinctive. In general they resemble those of sects *Orobus* and *Lathyrostylis,* but differ in presence of long, equal calyx segments and in the shape of the corolla wings. These petals are narrowed abruptly to a waist between the distal part of the limb and the region of attachment to the keel. *L. pratensis, L. hallersteinii* and *L. binatus* have yellow flowers; in the remaining species they are bluish-purple.

6. Sect. **Aphaca** (Miller) Dumort., Fl. Belg.: 103 (1827).
Syn.: *Aphaca* Miller, Gard. Dict. ed 4 (1754).

Glabrous annuals with unwinged stems. First two seedling leaves with a pair of elliptic, parallel-veined leaflets; leaves of adult plant without leaflets but with strong, simple tendril and large, hastate stipules. Inflorescence 1–2-flowered. Flowers bright yellow, cream or sulphur-coloured. Calyx teeth equal; standard stenonychioid, bossed; wing petals with 'waist' in the limb; style linear, not contorted. Fruit linear. Seeds smooth, hilum short.—Ditypic.
Type: *L. aphaca* L., Sp. Pl. 729 (1753).
W, C & S Europe, N Africa, SW & C Asia.

Sect. *Aphaca* comprises two species: *L. aphaca,* which is very variable and widespread, and the closely related *L. stenolobus,* endemic to the Amanus region of Turkey. The two are separated by their differently shaped stipules and fruit.

The remarkable ontogeny of *L. aphaca,* in which the photosynthetic functions of the leaf become delegated from the leaflets to the stipules, makes it one of the most interesting species in the Vicieae. Despite its apparent morphological distinctness, however, *L. aphaca* has several significant features in common with members of sect. *Pratensis.* Its earliest leaves are similar to theirs, having a pair of parallel-veined leaflets. In both sections the stipules are hastate, and the species share a unique pattern of nodal anatomy, which, as described earlier, provides a clue to understanding how the peculiar habit of *L. aphaca* has evolved. *L. aphaca* and *L. stenolobus* have flowers similar in shape to those of sect. *Pratensis,* sharing, in particular, the same wing-shape. Sect. *Aphaca* is kept separate from sect.

Pratensis because of its annual habit, and because sect. *Pratensis* is very uniform, containing little diversity. The addition of *L. aphaca* and *L. stenolobus* to this compact group would greatly increase its variability and an unbalanced, heterogeneous section would result.

7. Sect. **Clymenum** (Miller) DC. ex Ser. in DC., Prodr. 2: 375 (1825).
Syn.: *Clymenum* Miller, Gard. Dict. ed. 4 (1754); *Lathyrus* sect. *Gloeolathyrus* Warb. & Eig in Feddes Rep. 25: 351 (1928).

Annuals with strongly winged stems. Leaves hypo-amphistomatic; the juvenile entirely phyllodic and at first etendrillous, the later with several pairs of leaflets, tendrillous; leaflets broadly ovate to elliptic; venation (of leaflets and phyllodes) pinnate; stipules semisagittate or minute. In *L. clymenum* and *L. ochrus* inflorescence pedunculate, 1- to few-flowered; flowers purple, pink or yellow; standard stenonychioid, with two very prominent pouches at the fold; style spathulate at apex; stigma double, its halves separated by a sterile mucro or arista. In *L. gloeospermus* flower solitary, inconspicuous, sessile in leaf-axil, greenish-yellow, cleistogamous, with morphologically simple parts. Legume large, linear, broadly winged at sutures and sometimes on valves. Seeds smooth; hilum of medium length.—3 species.

Lectotype (see Gunn, 1969): *L. articulatus* L., Sp. Pl. 731 (1753) (syn. *L. clymenum* L.).

Mediterranean.

The members of this small section possess several remarkable morphological features. They share the unique pattern of ontogeny described earlier (p. 000). The flowers of *L. clymenum* and *L. ochrus* are distinctive in having hollow, finger-like pouches on the standard, instead of the shallow bosses found in sects *Orobus* and *Lathyrostylis*. These species also have an unusual type of style. It is spathulate, as in some members of sect. *Lathyrostylis*, but the apex is produced into a sterile fleshy mucro or arista which divides the stigma into two halves. In contrast, *L. gloeospermus* has very inconspicuous flowers; they are sessile, with rudimentary, greenish corollas and reduced sex organs, and they develop cleistogamously. The strong tendency towards winging of petioles and stems exhibited in the vegetative parts of these species is reflected also in their fruits. *L. clymenum* and *L. ochrus* have pods with winged sutures (*L. ochrus*, fig. 5e), while the legumes of *L. gloeospermus* (fig. 5f) have narrow, leafy laminae on the valves as well.

Although the flowers of *L. gloeospermus* are very different from those of *L. clymenum* and *L. ochrus*, all the differences can be attributed to a single factor, the adoption of cleistogamy in *L. gloeospermus*. This has obscured the normal floral features which the ancestors of this species must have possessed, and prevents a true comparison with the other members of the section. On the other hand the unusual ontogenetic sequence, and the presence of winged stems, winged fruits and hypo-amphistomatic, pinnate-veined, multijugate leaves, all provide evidence to support my decision to unite sects *Clymenum* and *Gloeolathyrus*.

8. Sect. **Orobastrum** Boiss., Fl. Or. 2: 601 (1872).

Annual, with narrowly winged stems. Leaves amphistomatic, unijugate, with an unbranched tendril; leaflets narrowly elliptic, parallel-veined; stipules semisagittate. Inflorescences 1-flowered. Flowers pedunculate, brick-red. Calyx teeth equal; standard stenonychioid, bossed; style not contorted. Legume rhomboidal, strongly stipitate. Seeds rugose, with short hilum.—Monotypic.

Lectotype (Czefranova, 1971): *L. setifolius* L., Sp. Pl. 731 (1753).

Mediterranean region, Crimea, Transcaucasia.

The delimitation of sect. *Orobastrum* has changed greatly since the group was first described by Boissier in 1872 (Table 1). In Boissier's sense it comprised tendrillous species of the *Lathyrus* affinity which did not belong to sects *Aphaca, Clymenum* or *Nissolia,* and were also excluded from sects *Lathyrus* and *Cicercula* by the absence of a twisted style. Since then this negative concept has been modified, notably by Bässler (1966) who removed the perennial species to sect. *Orobus* (*L. japonicus* and *L. pisiformis*) and sect. *Pratensis* (*L. pratensis*) leaving behind only small-flowered annuals: *L. setifolius, L. saxatilis, L. inconspicuus, L. sphaericus,* etc. Though small in number of species, this group embraces rather wide variation. Its members are highly evolved, showing reduction in several characters (in tendril development, number of leaflets, length of peduncle) and specialisation in others (diversity in legume shape, presence of septa between the seeds). While the majority of species form a group of undoubted affinity, *L. saxatilis* and *L. setifolius* are each isolated by the possession of several differential characteristics. I consider that this heterogeneity is properly reflected by the recognition of three sections rather than one, and since Czefranova has selected *L. setifolius* to be the type of sect. *Orobastrum,* this section, once the most diverse 'dustbin' group in *Lathyrus,* becomes monotypic.

In habit, *L. setifolius* resembles the members of sect. *Linearicarpus,* but has winged stems. It is thus very similar to some of the annual species in sect. *Lathyrus.* The flowers are brick-red, a colour occurring in both sect. *Linearicarpus* (e.g. *L. sphaericus*) and sect. *Lathyrus* (e.g. *L. cicera*). The standard is short-clawed like those of sect. *Lathyrus,* but is distinctly bossed. The strongly stipitate fruit of *L. setifolius* is its most characteristic feature (fig. 5c). Pods of this shape are common in *Vicia* subgen. *Vicilla,* but very unusual in *Lathyrus.* The species with the most similar fruit to that of *L. setifolius* is *L. lentiformis* (fig. 5k). Davies (1958) states that *L. setifolius* has a twisted style. According to my own observations the style is in fact straight, but if it were confirmed that this character is variable within the species the taxonomic position of sect. *Orobastrum* would have to be reconsidered, bearing in mind the almost equal phenetic similarity of *L. setifolius* with members of sects *Linearicarpus* and *Lathyrus*; it might be better placed within the latter.

9. Sect. **Viciopsis** Kupicha, **sect. nov.**

Syn.: *Lathyrus* sect. *Orobastrum* Boiss., Fl. Or. 2: 601 (1872), pro parte excl. typ.

Planta annua, caulibus exalatis. *Folia* stomatibus adaxialibus plus quam

abaxialibus, ecirrhosa, 1–3-juga; foliola ovata vel linearia, pinnatinervata; stipulae semisagittatae. *Inflorescentia* uniflora. *Flores* parvi, pedunculati, cremei. *Calyx* dentibus subaequalibus; vexillum obovato-spathulatum umbonatum; stylus non contortus. *Fructus* linearirhombeus, non stipitatus. *Semina* laevia, hilo brevi.

Annual, with unwinged stems. Leaves epi-amphistomatic, etendrillous, with 1–3 pairs of leaflets; leaflets ovate to linear, pinnate-veined; stipules semisagittate. Inflorescence 1-flowered. Flowers small, pedunculate, cream-coloured. Calyx teeth subequal; standard stenonychioid, bossed; style not contorted. Fruit linear-rhomboidal, not stipitate. Seeds smooth, with short hilum.—Monotypic.

Type: *L. saxatilis* (Vent.) Vis., Fl. Dalm. 3: 330 (1852) (*Orobus saxatilis* Vent., Hort. Cels. t. 94 (1802); *Vicia saxatilis* (Vent.) Tropea in Malpighia 21: 41 (1907)).

S Europe, E Anatolia, NW Africa.

L. saxatilis has had an unsettled taxonomic history. It was first described by Ventenat as a member of the genus *Orobus,* later being transferred to *Lathyrus* by Visiani and to *Vicia* by Tropea (see synonymy above). Fedtschenko (1948) placed it in *Vicia* sect. *Vicia.* The species is distinguished from all other annual species of *Lathyrus* by its leaves which have up to three pairs of *pinnate-veined* leaflets. The leaves produced early in the life-cycle have ovate, emarginate leaflets and are very similar to those of *Vicia* sects *Vicia* and *Hypechusa* (Kupicha, 1976). Leaflets of later shoots are quite different in shape, being narrowly linear, but they are still pinnate-veined. The style of *L. saxatilis* is dorsally compressed and pubescent on the adaxial side, confirming its position within *Lathyrus.* The legume is linear, but shorter and broader than those of sect. *Linearicarpus*; it resembles the fruit of some members of sect. *Lathyrus* (e.g. *L. cicera,* fig. 5l). In any future survey of chemical characters in *Lathyrus,* this would be one of the more important species to include, because one would be glad of more evidence to support its position in *Lathyrus*!

10. Sect. **Linearicarpus** Kupicha, **sect. nov.**

Syn.: *Graphiosa* Alef. in Bonplandia 9: 128 (1861); *Lathyrus* sect. *Orobastrum* Boiss., Fl. Or. 2: 601 (1872), pro parte excl. typ.; *Lathyrus* sect. *Linearicarpus* [Kupicha ex] Robeson & Harborne in Phytochemistry 19: 2360 (1980), nom. nud.

Plantae annuae, caulibus exalatis. *Folia* stomatibus in superficiebus amabus pariter dispositis, uni- vel bijuga, mucronata vel cirrho simplici; foliola anguste lanceolata, parallelinervia; stipulae semisagittatae. *Inflorescentia* uniflora. *Flores* subsessiles vel pedunculati, lateritii vel pallide purpurei vel lutei, parvi. *Calyx* dentibus aequalibus; vexillum obovato-spathulatum umbonatum; stylus non contortus. *Fructus* anguste linearis, interdum septis membraneis inter semina instructus; valvae interdum manifeste nervatae. *Semina* papillosa vel laevia, hilo brevi.

Annuals with unwinged stems. Leaves epi-amphistomatic, uni- or bijugate, mucronate or with simple tendril; leaflets narrowly lanceolate, parallel-veined; stipules semisagittate. Inflorescence l-flowered. Flowers subsessile to pedunculate, brick-red, pale purple or yellowish, small. Calyx

teeth equal; standard stenonychioid, bossed; style not contorted. Legume narrowly linear, sometimes with membranous septa between the seeds; valves sometimes prominently veined. Seeds rough or smooth, with short hilum.—7 species.
Type: *L. inconspicuus* L., Sp. Pl. 730 (1753).
S, W & C Europe, N Africa, E Tropical Africa, Anatolia, Caucasia, Palestine, W Syria, Iraq, Iran, Afghanistan.

The members of this section share a characteristic habit and appear to be closely related. The species are distinguished by the presence or absence of features such as tendrils, prominent veins on the legumes, and partitions between the seeds; by the length of the peduncle, and whether it is prolonged past the pedicel into an arista; and by flower colour.

11. Sect. **Nissolia** (Miller) Dumort., Fl. Belg.: 103 (1827).
Syn.: *Nissolia* Miller, Gard. Dict. ed. 4 (1754).
Annual with unwinged stems. Leaves phyllodic throughout life-cycle, lanceolate, parallel-veined, etendrillous, epi-amphistomatic; stipules minute. Inflorescence 1–2-flowered. Flowers pink to brick-red, pedunculate. Calyx teeth subequal; standard stenonychioid, bossed; style linear, not twisted. Legume linear, prominently veined, very rarely with septa between the seeds. Seeds tuberculate, with short hilum.–Monotypic.
Lectotype (Gunn, 1969): *L. nissolia* L., Sp. Pl.: 729 (1753).
W, C & S Europe, NW Africa, Crimea, Caucasia, Anatolia, N Iraq.

L. nissolia is unique within *Lathyrus* in having entirely phyllodic leaves. Although a parallel tendency is found in sect. *Clymenum*, there is little to indicate a close relationship between the two groups: the flower and fruit of *L. nissolia* are quite unlike those of sect. *Clymenum*. On the other hand, the vegetative and reproductive characteristics of *L. nissolia* both provide evidence suggesting a connection with sect. *Linearicarpus*. Thus, the stem is unwinged (despite the apparently contrary tendency which has led to the evolution of the phyllodic leaf), and the leaf itself is similar in shape, stomatal distribution and venation to the leaflets in *L. sphaericus, L. angulatus, L. inconspicuus,* etc. The leaf of *L. nissolia* is not strictly homologous with the leaflets of other species, but it seems permissible to compare their attributes. The flower of *L. nissolia* is similar in colour, shape and size to that of *L. sphaericus,* and its fruit, like that of the latter species, is long, parallel-sided and prominently veined in a 'herringbone' pattern. There are usually no partitions between the seeds, but I observed the presence of this character in a single case.

The relationship between *L. nissolia* and sect. *Linearicarpus* appears to parallel that of sects *Aphaca* and *Pratensis*. In each case, a mono- or ditypic section is defined entirely on the basis of a striking vegetative character, while data from other vegetative and reproductive features suggest an alliance with a larger neighbouring group.

12. Sect. **Neurolobus** Bässler in Feddes Rep. 72:91 (1966).
Perennial with broadly winged, slender stems. Leaves amphistomatic, unijugate, tendrillous; leaflets elliptic, parallel-veined; stipules semisagittate. Inflorescence 1–2-flowered. Flowers bluish-violet. Calyx teeth

subequal; standard stenonychioid, bossed; style not contorted or spathulate at apex. Fruit linear, with prominent longitudinal veins, without septa between the seeds. Seed smooth, with hilum c. one-sixth of the circumference.—Monotypic.

Type: *L. neurolobus* Boiss. & Heldr. in Boiss., Diagn. ser. 1(9): 125 (1849).

W Crete.

This little-known species appears to be of very isolated taxonomic position (Bässler, 1966). Its unijugate leaves and parallel-veined leaflets suggest a connection with sect. *Pratensis*; the wide-winged stems are reminiscent of sects *Lathyrus* and *Clymenum*; and the small flowers and strongly-nerved fruit resemble those of sect. *Linearicarpus*. None of these groups, however, has a convincing claim to particular affinity with sect. *Neurolobus*, and it is perhaps best regarded as a relict species.

13. Sect. **Notolathyrus** Kupicha, **sect. nov.**

Syn.: *Lathyrus* sect. *Notolathyrus* [Kupicha ex] Robeson & Harborne in Phytochemistry 19: 2360 (1980), nom. nud.

Plantae perennes (species *L. pusillus* annua excepta). *Caules* alati vel exalati. *Folia* stomatibus adaxialibus plus quam abaxialibus, plerumque unijuga, rare multijuga, plerumque cirrho valido ramoso; foliola late vel anguste elliptica, parallelinervia; stipulae semisagittatae vel hastatae. *Inflorescentia* pluri- vel pauciflora. *Flores* purpurei vel rosei vel lutei. *Calyx* dentibus aequalibus vel disparibus; vexillum obovato-spathulatum umbonatum; tubus staminum ad apicem truncatus aut obliquus; stylus non contortus, plerumque spathulatus; stigma interdum geminatum. *Fructus* interdum hirsuti, interdum seminibus septis segregatis. *Semina* hilo brevi vel modice longo.

Plants perennial (except for the annual *L. pusillus*). Stems winged or unwinged. Leaves epi-amphistomatic, usually unijugate, rarely multijugate, usually with a strong, branched tendril; leaflets broadly to narrowly elliptic, with parallel venation; stipules semisagittate or hastate. Inflorescence several- to few-flowered. Flowers purplish, pink or yellow. Calyx teeth equal or unequal; standard stenonychioid, bossed; staminal tube ending squarely or obliquely; style not contorted, often spathulate; stigma sometimes double. Fruits sometimes hairy, sometimes with septa between the seeds. Seeds with short to moderately long hilum.—c. 20 species.

Type: *L. magellanicus* Lam., Encycl. Méth. Bot. 2:708 (1788).

Temperate S America (Chile, Argentina, Paraguay & Uruguay); Brazilian highlands; Andes of Peru, Ecuador & Columbia; SE USA.

The S American species of *Lathyrus* (including *L. pusillus*, which extends into N America), form a fairly homogeneous group clearly distinct from members of sect. *Orobus* to the north. The most striking difference is that the leaves of N American species are multijugate while those of S American species are unijugate; but there are many other traits by which the southern group shows itself to be more highly evolved and specialised.

Members of sect. *Notolathyrus* have several features in common with the mainly Turkish section *Lathyrostylis*. For example, the leaflets are narrowly elliptic, have parallel venation and are epi-amphistomatic. The stems are

rarely winged. The style is often spathulate (e.g. in *L. cabrerianus*). However, unlike species of sect. *Lathyrostylis,* S American species have unijugate leaves (except for *L. multiceps* and *L. macropus*), usually with well-developed tendrils. Other interesting characters are found here. The calyx and fruit are frequently tomentose or sericeous (e.g. in *L. cabrerianus, L. macropus, L. pubescens* and *L. tomentosus*). The staminal tube is often oblique, rather than truncate, at the apex, a character traditionally used to separate *Vicia* from *Lathyrus*. The stigma is sometimes double (e.g. in *L. pubescens, L. subulatus* and *L. tomentosus*), although the style is not prolonged into a sterile mucro as in some members of sect. *Clymenum.* Some species have 'woolly' false septa between the seeds; examples are *L. pubescens, L. nervosus, L. subulatus* and *L. tomentosus.* The majority of species have semisagittate stipules, but in *L. nervosus, L. hookeri, L. magellanicus* and *L. pusillus* they are hastate.

Sect. *Notolathyrus* is an interesting group, both in itself and in the context of the whole genus. Its members share a relatively uniform habit which unites the section, but they possess a variety of highly specialised characteristics each of which would be given strong taxonomic weighting if found in Old World species of *Lathyrus.* Thus in Europe a species with parallel-veined, epistomatic leaflets and a spathulate style would be placed in sect. *Lathyrostylis*; the presence of a divided stigma is exclusive to sect. *Clymenum*; and septa between the seeds are found only in sects *Linearicarpus* and *Nissolia.*

Discussion

Concluding her excellent paper on the vegetative characters of *Lathyrus*, Simola (1968) wrote: 'Historical geology has created the major framework within which the genera and species have evolved, and I think that the most natural explanation of many problems of plant evolution is to be sought along these lines'; but she was hampered in her attempt to explain the evolution of *Lathyrus* because at that time 'no new paleogeographic atlas elucidating the connections between different continents and the distribution of sea and land in different geological eras has been published which takes account of continental drift'. In the absence of these necessary data, Simola made the suggestion, which is reasonable on morphological grounds, that during the period of alpine folding there was introgression of genetic material from S American *Lathyrus* into the Mediterranean *via* Africa. Mediterranean groups with parallel-veined leaflets such as sect. *Lathyrostylis* and the annuals of sect. *Lathyrus* could thus be more closely related to sect. *Notolathyrus* than to sect. *Orobus* in Eurasia and N America.

We are fortunate that there are now available palaeogeographic maps, of which the details may still be open to question but the main features are agreed (Smith & Briden, 1977). It is known (Raven, 1979) that S America separated from Africa 90 m.y. B.P., in the middle Cretaceous. Opportunities for migration between N and S America began at the end of the Eocene (38 m.y. B.P.), and improved dramatically in the Pliocene with the appearance of a terrestrial connection, the Panama isthmus (c. 5.7 m.y.

B.P.). Evidence from mammalian fossils shows that N America became effectively isolated from Europe in the middle Eocene, c. 45 m.y. B.P. (Hallam, 1981). From the late Cretaceous to the Palaeocene Africa rotated anti-clockwise and approached Europe, resulting in compression between the two continents and the creation of the Alpine system, whose development is thought to have been completed by the early Oligocene, c. 35 m.y. B.P.

In the light of this chronology, Simola's hypothesis regarding the evolution of Mediterranean *Lathyrus* species from S American ones is seen to be impossible. It is probable that *Lathyrus* originated at high latitudes in the Old World, in the Cretaceous or early Tertiary periods, as an inhabitant of the Boreal-Tertiary woodland flora. This primitive ancestral stock, having characteristics of sect. *Orobus,* migrated to the N American continent, either *via* Greenland or from Asia to Alaska. (At this time, S America was already isolated from other continents.) In Europe the Alpine orogeny and major climatic changes provided stimuli and opportunities for the evolution of the autochthonous Mediterranean flora, a development in which *Lathyrus* was profoundly involved. At the end of the Tertiary period, primitive *Lathyrus* representatives were able to migrate from N into S America, and in a burst of evolution gave rise to the complex which is sect. *Notolathyrus.*

The similarities between the S American and Mediterranean/Irano-Turanian *Lathyrus* must be due to parallel evolution. It seems that the ancestral *Lathyrus* stock possessed innate tendencies to evolve along certain lines: towards delegation of photosynthetic function from leaflets to winged stems, phyllodes and enlarged stipules; from many to few leaflets; from pinnate to parallel venation; and towards a flattened style. The advanced states of these characters are so striking, and their tendency to be correlated so marked, that it is difficult to accept that they could have arisen more than once. On the other hand, the almost perfect structural similarity between *Lathyrus* and its sister genus *Vicia*—both having c. 150 species, occupying the same geographical area, being centred in the same regions, and with their primitive representatives the most alike—lends extra support for the concept of evolutionary development just outlined; the same hypothesis holds good for both genera, and indeed for the whole tribe Vicieae.

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