

Taxonomy of the *Linum perenne* group in Europe

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ABSTRACT

A new taxonomic treatment of the *Linum perenne* group in Europe is presented, based on a detailed biosystematic study. *L. alpinum* Jacq., *L. extraaxillare* Kit. and *L. montanum* Schleicher ex DC. are treated as subspecies of *L. perenne* L., and *L. collinum* Guss. as a subspecies of *L. austriacum* L. Previous confusion between *L. perenne* subsp. *anglicum* (Miller) Ockendon and *L. leonii* Schultz has been resolved. The morphological variation within each subspecies is described and interpreted in terms of its distribution. Most of the morphological characters which have been used in the past have proved to be taxonomically unreliable because they vary almost continuously within the group and show considerable phenotypic plasticity. Chromosome number, heterostyly and pollen characters are taxonomically more reliable than the quantitative morphological characters. The pattern of variation within the *L. perenne* group is discussed in relation to its rarity, disjunct distribution, ecology and breeding system.

INTRODUCTION

The taxonomic difficulty of the *Linum perenne* group was mentioned in 1848 by Planchon and has been recognised by many taxonomists since then. A two-fold approach was made to the problem. The morphological characters which had been used in the past were examined in detail to see which were taxonomically reliable, and an attempt made to build up a general picture of the morphological variation in the group. Further taxonomic characters were sought, including those derived from a study of the cytology, pollen morphology, breeding system and artificial hybridization of the group. This work is published in detail elsewhere (Ockendon 1968a), but the results of it will be used here in-so-far as they affect the classification of the group. The taxonomic account given here is essentially the same as that in *Flora Europaea*, vol. 2 (Ockendon & Walters 1968). The opportunity is taken here to give the evidence on which this account is based and to discuss the taxonomic decisions taken.

The *L. perenne* group occurs in Asia, Europe and North America. All the North American plants can be referred to the single homostylous species *L. lewisii* Pursh. Most of the Asian members of the group have been dealt with by Juzepczuk (1949) and Davis (1967). This paper deals only with the European members of the group. A large number of populations have been studied in the field and considerable quantities of material were cultivated at Cambridge University Botanic Garden. All the known extant British populations were visited, plus about 70 per cent of those in France and Germany, and others in Austria, Czechoslovakia, Italy, Yugoslavia and Spain. Material from the following herbaria has been examined: British Museum (BM), Bruxelles (BR), Cambridge (CGE), Edinburgh (E), Florence (FI), Geneva (G), Kew (K), Manchester (MANCH), Paris (P) and Vienna (W). The coverage of material from most of western and central Europe is fairly complete, but that for southern and eastern Europe is less so.

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TAXONOMY

DESCRIPTION OF THE *L. PERENNE* GROUP

Glabrous perennials, sometimes caespitose and woody at base; stems up to 80 cm, erect, ascending, decumbent or procumbent. Leaves 1–3 (–5) mm wide, linear or linear-lanceolate, entire, 1- to 3-veined. Sepals 3.5–6 mm, unequal, with three main veins; the outer sepals narrower than the inner and with an acute or acuminate apex, the inner with a rounded or mucronate apex and entire, scarious margins. Petals blue, 3–4 times as long as the sepals, obovate or obovate-lanceolate, tapering gradually to a yellow, pubescent claw. Stamens 5, alternating with 5 rudimentary staminodes. Stigmas capitate. Capsules 3.5–7 (–8) mm, subglobose.

The *L. perenne* group is sometimes confused with *L. bienne* Miller. The latter has linear or clavate stigmas and subequal sepals with a single prominent mid-vein, in contrast to the capitate stigmas and unequal sepals with three main veins of the *L. perenne* group.

GENERAL FEATURES OF THE *L. PERENNE* GROUP

The following general features of the *L. perenne* group should be borne in mind when considering the taxonomic treatment which follows.

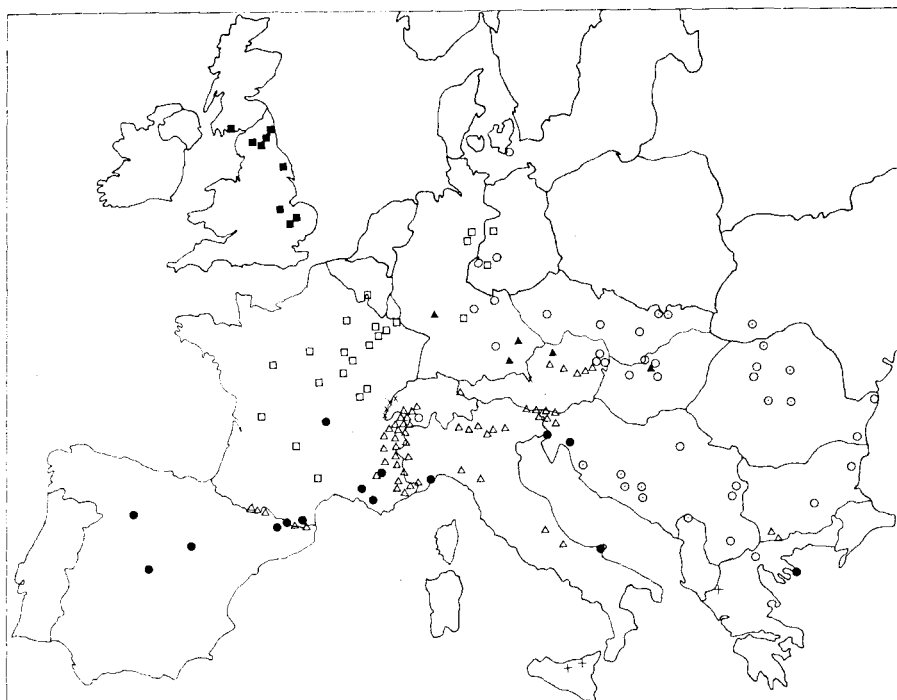


FIGURE 1. Distribution of the *Linum perenne* group in Europe. Δ *L. perenne* subsp. *alpinum*; \blacksquare *L. perenne* subsp. *anglicum*; \times *L. perenne* subsp. *montanum*; \blacktriangle *L. perenne* subsp. *perenne*; \odot *L. perenne* subsp. *extraaxillare*; \circ *L. austriacum* subsp. *austriacum*; \bullet *L. austriacum* subsp. *collinum*; \square *L. leonii*; $+$ *L. punctatum*.

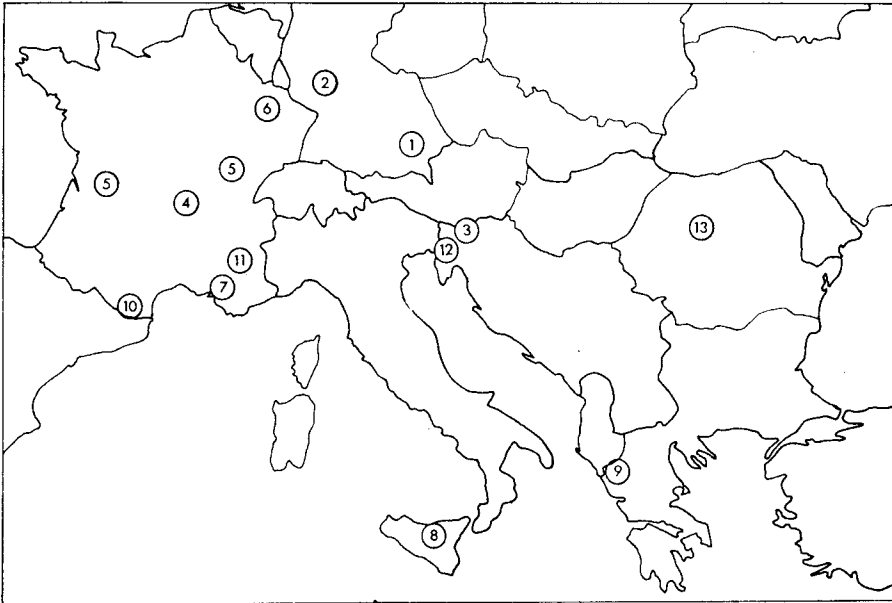


FIGURE 2. Distribution of binomials associated with limited areas. 1. *L. bavaricum* Schultz; 2. *L. darmstadinum* Alefeld; 3. *L. julicum* Hayek; 4. *L. limanense* Lamotte; 5. *L. loreyi* Jordan; 6. *L. petryi* Beyer; 7. *L. provinciale* Jordan; 8. *L. punctatum* Presl; 9. *L. pycnophyllum* Boiss.; 10. *L. ruscinonense* Timbal-Lagrange; 11. *L. saxicola* Jordan; 12. *L. tommasinii* (Reichb.) Nyman; 13. *L. trinervium* Freyn.

1. The *L. perenne* group is a natural group of very closely related species which can be easily separated from all other species of *Linum* by the combination of characters given above. Species within the group tend to be recognised on the basis of single characters which do not correlate well with other characters.

2. The characters showing most variation within the group are habit, stem length, leafiness of stem, leaf width, inflorescence size, sepal size and shape, petal size and colour, position of fruiting pedicels and capsule size. The majority of these characters are quantitative and show almost continuous variation. Apparent discontinuities in the variation (which are found) are liable to disappear when more material is examined.

3. The distribution of the group in Europe is markedly disjunct, especially in lowland areas (Fig. 1). Fieldwork in western Europe has shown that the discontinuities in the distribution are not an artifact of uneven collecting but are real, and that considerable extinction has occurred in the last hundred years.

4. Most of the subspecies in the group are local or rare and many of the populations are limited in extent (Appendix). Repeated collections have been made, over long periods of time, from single topodemes such as those at Puy Crouel, Clermont-Ferrand and at Mt. Spaccato near Trieste. Certain binomials have long been associated with plants coming from a very limited geographical area, e.g. *L. limanense* Lamotte – area around Clermont-Ferrand; *L. tommasinii* (Reichb.) Nyman – an area near Trieste. So constant is the association between some binomials and particular geographical areas that it is possible to map the areas in which the binomials have generally been applied (Fig. 2). Members of the *L. perenne*

group have commonly been identified on the basis of their locality rather than by their morphological characters. The strong geographical emphasis in the taxonomy of the group is reflected in names such as *L. anglicum* Miller, *L. bavarium* Schultz and *L. provinciale* Jordan.

PREVIOUS ACCOUNTS OF THE *L. PERENNE* GROUP

In the second edition of *Species Plantarum* (1762) Linnaeus recognised three species in the *L. perenne* group, namely *L. alpinum* Jacq., *L. austriacum* L. and *L. perenne* L. These three species are still widely recognised.

Reichenbach (1837) treated the *L. perenne* group as the genus *Adenolinum*. Planchon (1848) and Juzepczuk (1949) recognised *Adenolinum* as a section of *Linum*. There is very little to be said for treating *Adenolinum* as a genus and it is probably better to treat it as a sub-section rather than as a section of *Linum*.

Planchon (1848) considered the *L. perenne* group on a world-wide basis and treated it as a single species with 9 varieties.

Ascherson & Graebner's (1914) full account of most of the European members of the *L. perenne* group is apparently based on the work of H. Holzer, who determined quantities of herbarium material but did not publish his work. Their account may be summarised as follows:

<i>L. alpinum</i> Jacq.	<i>L. perenne</i> L.	<i>L. austriacum</i> L.
subsp. A <i>eualpinum</i>	subsp. A <i>perenne</i>	subsp. A <i>austriacum</i>
B <i>montanum</i>	B <i>extraaxillare</i>	B <i>squamulosum</i>
C <i>anglicum</i>	C <i>petryi</i>	C <i>collinum</i>

They included *L. leonii* with subsp. *anglicum*, while *L. loreyi* was included with subsp. *collinum*. Their detailed account of the infraspecific taxa gives a good impression of the morphological variability and taxonomic confusion of the group. Hegi's (1924) account is largely based on that of Ascherson & Graebner.

Alefeld (1867) described 4 new species belonging to the *L. perenne* group, but his treatment of the group as a whole is not very systematic. The importance of his work is that he was the first to appreciate the value of heterostyly as a taxonomic character, although he was apparently unaware of its biological significance. He recognised dimorphous and trimorphous species, the latter including 'mid-styled' in addition to the long- and short-styled forms. However, the 'mid-styled' forms in the *L. perenne* group are self-fertile and not comparable with the mid-styled, self-sterile forms of tristylous species of *Oxalis* and *Lythrum* (Fig. 3). Thus in the *L. perenne* group the basic distinction is between homostylous and heterostylous species.

The importance of Alefeld's work was recognised by Juzepczuk (1949), whose treatment of the section *Adenolinum* in Russia can be summarised as follows:

- Group 1. Homomorpha – Homostylous
 - Series 1. Pallescentes – Pedicels erect
 - Series 2. Mesostyla – Pedicels deflexed
- Group 2. Heteromorpha – Heterostylous
 - Sub-group 1. Trimorpha
 - Sub-group 2. Dimorpha
 - Series 1. Perennia – Pedicels erect
 - Series 2. Austriaca – Pedicels deflexed

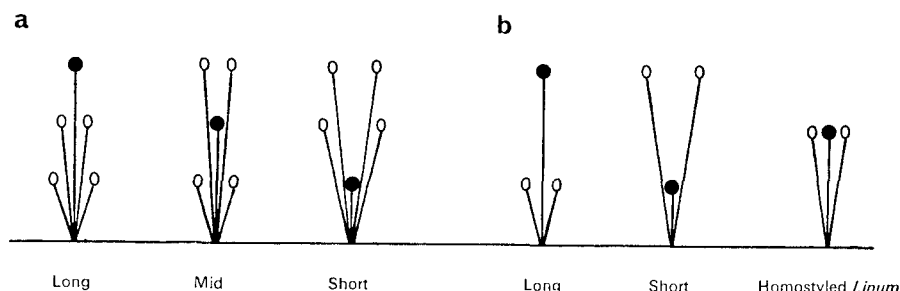


FIGURE 3. Tristyly in (a) *Oxalis* compared with distyly in (b) *Linum*.

The sub-group Trimorpha contains a single, poorly known species from the Caucasus, *L. subbiflorum* Juz. The claim that this species contains long-, short- and mid-styled forms needs to be substantiated. If it is confirmed, it will be the only known example of the occurrence of both heterostyled and homostyled forms within a single species of *Linum*.

Juzepczuk recognises a total of 18 species, of which 6 are homostylous. No infraspecific taxa are given, but it is admitted that the species recognised can be grouped into series of forms which replace one another geographically. Juzepczuk's account is valuable because it emphasises the taxonomic importance of heterostyly and pedicel position in the *L. perenne* group.

TYPIFICATION

The search for type specimens has not been exhaustive but most of those still in existence have been examined. The holotypes of the species described by Alefeld, Beyer and Schultz appear to have been lost, but a lectotype is available for *L. leonii* Schultz. The lack of some type specimens is not a serious handicap, because the precise type locality can be ascertained in almost every case and further material from the type locality is usually available. The chief exception to this is *L. laeve* Scop., for which the type locality ('in montanis Carnioliae calidoris') is not very precise and the type specimen is not available. Neither the original description nor the illustration of *L. laeve* are sufficiently detailed to ascertain the taxon to which this name was originally applied. Since then the name *L. laeve* has been used for several taxa, both within and outside the *L. perenne* group, and to avoid further confusion should now be rejected.

For species described before 1800, the specimens selected as type specimens are perhaps better considered as representative specimens because of the difficulty of verifying with certainty the specimens (if any) from which the original descriptions were made. *L. perenne* L. is typified by a specimen from the Linnaean Herbarium (396/8) labelled '2 H.U. perenne' by Linnaeus. This specimen was most probably in Linnaeus' possession at the time he wrote the first edition of *Species Plantarum*, as indicated by the number '2' written on the sheet, corresponding to the number this species has in *Species Plantarum*.

Neither of the specimens of *L. austriacum* in the Linnaean Herbarium (396/22 and 23) were numbered by Linnaeus and both were probably acquired by him subsequent to the writing of *Species Plantarum*. However, there is a specimen

of *L. austriacum* in Burser's Herbarium (Juel 1936) bearing the inscription 'In Austria inferiori', corresponding to 'Habitat in Austria inferiore' given for *L. austriacum* in *Species Plantarum*. As Linnaeus is known to have used Burser's Herbarium when writing *Species Plantarum* (Stearn 1957), the Burser specimen has been selected as the type of *L. austriacum*.

KEY AND DESCRIPTIONS

1. Homostylous, with anthers and stigmas at about the same height
4. *L. leonii*
1. Heterostylous, with anthers and stigmas at different heights
 2. Leaves very crowded, 6 mm long or less 3. *L. punctatum*
 2. Leaves moderately crowded, the longest at least 10 mm long
 3. Pedicels deflexed or patent 2. *L. austriacum*
 3. Pedicels erect, \pm straight 1. *L. perenne*

1. *L. PERENNE* L., Sp. Pl., p. 277 (1753). Type in Linnaean Herbarium, sheet number 396/8 (LINN).

Stems 10–80 cm, decumbent, ascending or erect. Inflorescence few- to many-flowered. Inner sepals acute or obtuse. Pedicels erect. Capsules 5–8 mm. Heterostylous. Central and Eastern Europe, extending locally westwards to Britain and the Pyrenees.

1. Middle cauline leaves usually more than 2.5 mm wide subsp. *extraaxillare* (e)
1. Middle cauline leaves usually less than 2.5 mm wide
 2. Inner sepals very obtuse, longer than the outer (lowlands)
 3. Stems erect, or ascending just at the base; pollen grains with furrows subsp. *perenne* (a)
 3. Stems decumbent or ascending below; pollen grains with pores subsp. *anglicum* (b)
 2. Inner sepals acute or obtuse, equalling the outer (mountains)
 4. Pollen grains with furrows subsp. *alpinum* (c)
 4. Pollen grains with pores subsp. *montanum* (d)

1a. *L. PERENNE* subsp. *PERENNE*

L. bavaricum F. W. Schultz, Flora (Regensb.), **21**: 643 (1838). Type not located.

L. darmstadtinum Alefeld, Bot. Zeit., **25**: 252 (1867). Type probably lost.

Stems (20–) 30–80 cm, ascending or erect. Middle cauline leaves 1–2.5 mm wide. Inflorescence 5- to 25-flowered. Inner sepals 4.5–5.5 mm long, obtuse or very obtuse, exceeding the outer sepals by 0.5–1 mm. Petals 12–20 mm long, pale blue or mauvish blue. Capsules 5–7 mm long. Pollen grains with three furrows. $2n=18$. Light sandy or gravelly soils, often near large rivers. Central Europe, extending westwards to west Germany.

1b. *L. PERENNE* subsp. *ANGLICUM* (Miller) Ockendon, Reprium nov. Spec. Regni veg., **74**: 20 (1967a).

L. anglicum Miller, Gard. Dict., 8th: no. 5 (1768). Type: 'Linum perenne majus caeruleum capitulo majore' Chelsea Physick Garden No. 1976 (BM).

Stems (15–) 20–70 cm, decumbent, ascending or erect from an ascending base. Middle cauline leaves 1–2.5 (–3.5) mm wide. Inflorescence 5- to 20-flowered.

Inner sepals 4.5–6.5 mm long, obtuse or very obtuse, exceeding the outer sepals by 0.5–1 mm. Petals 14–20 mm long, pale blue or mauvish blue. Capsules 5.5–7.5 mm. Pollen grains with six pores. $2n=36$. Usually in chalk or limestone grassland but occasionally on light sandy soils. Endemic to Britain.

1c. *L. PERENNE* subsp. *ALPINUM* (Jacq.) Ockendon, *Reprim* nov. Spec. Regni veg., **74**: 20 (1967a).

L. alpinum Jacq., Enum. Stirp. Vindob., **54**: 229 (1762). Type: Austria, 'Schneeberg', *Jacquin* (BM).

L. julicum Hayek, Abh. Zool.-Bot. Ges. Wien, **4**(2): 109 (1907). Type: Austria, 'Steiermark: Sannthaler Alpen, im Felschutt am Fuss der Merzlagora nächst der Okreselhütte, 1400 m', 31/8/1904, *A. Hayek* (GB).

Stems 5–30 (–40) cm, ascending or decumbent, often numerous and slender. Middle cauline leaves 1–3 (–5) mm wide. Inflorescence (1–) 3- to 12-flowered. Inner sepals 4.5–6 mm long, acute or obtuse, equaling the outer sepals. Petals 10–22 mm long, pale blue or bright blue. Pedicels usually erect but occasionally flexuous or patent. Capsules 5–7 mm long. Pollen grains with three furrows. $2n=18$. Alpine grassland and stabilised scree slopes, usually above 1500 m but occasionally descending to 800 m. Pyrenees, Alps, Apennines, Pirin Mountains.

1d. *L. PERENNE* subsp. *MONTANUM* (Schleicher ex DC.) Ockendon, *Reprim* nov. Spec. Regni veg., **74**: 20 (1967a).

L. montanum Schleicher ex DC., Prodr. Syst. Nat., vol. 1, p. 427 (1824). Type in Herbarium De Candolle (G-DC).

Stems 15–40 cm, ascending or erect from an ascending base. Middle cauline leaves 1–2.5 mm wide. Inflorescence 3- to 10-flowered. Inner sepals 5–6.5 mm long, acute or obtuse, equalling the outer sepals. Petals 15–20 mm long, pale blue. Capsules 5–7 mm long. Pollen grains with six pores. $2n=36$. Basic grassland, usually above 1500 m. Confined to the Jura and northern Alps.

1e. *L. PERENNE* subsp. *EXTRAAXILLARE* (Kit.) Nyman, *Consp. Fl. Europ.*, Suppl., vol. **2**(1): 71 (1889).

L. extraaxillare Kit., *Linnaea*, **32**: 573 (1864). Type in Prague (PR).

Stems 25–50 cm, erect from an ascending base. Middle cauline leaves 2–4 mm wide. Inflorescence 5- to 15-flowered. Inner sepals 5–6.5 mm long, acute, equaling the outer sepals. Petals 14–18 mm long, pale blue. Capsules 6.5–8 mm long. Pollen grains with three furrows. $2n=18$. Basic alpine grassland, usually above 1500 m. Carpathians and mountains of the Balkan Peninsula.

2. *L. AUSTRIACUM* L., *Sp. Pl.*, p. 278 (1753). Type in Burser's Herbarium, number XII. 44: 'Linum Syl. angustifolium, foliis rarioribus Bauh. Linum syl. II. Tab. In Austria inferiori' (UPS).

Stems (6–) 10–60 cm, erect or ascending. Middle cauline leaves 0.5–2 mm wide. Inflorescence many-flowered. Inner sepals 3.5–6 mm long, acute. Petals 10–18 mm long, deep blue. Pedicels deflexed or patent. Capsules 3.5–7.5 mm. Pollen grains with three furrows. Heterostylous. Central and eastern Europe.

Capsules 3.5–5 mm	subsp. <i>austriacum</i>	(a)
Capsules 5–7.5 mm	subsp. <i>collinum</i>	(b)

2a. *L. AUSTRIACUM* subsp. *AUSTRIACUM*

L. trinervium Freyn, Öst. bot. Z., **26**: 228 (1876). Type: Romania, 'Siebenbürgen, comitat Torda. Wiesen im Viragosthal, 350 m', 14/6/1871, *J. Freyn* (BRNM).

Stems (20–) 30–60 cm. Inflorescence 10- to 40-flowered. Capsules 3.5–5 mm long, usually rounded at the apex. $2n=18$. Dry rocky limestone soils or light sandy soils. Central Europe, extending to West Germany and Switzerland where it may have been introduced.

2b. *L. AUSTRIACUM* subsp. *COLLINUM* Nyman, Consp. Fl. Europ., p. 125 (1878).

L. collinum Guss., Fl. Sic. Syn., vol. 2, p. 808 (1845), nom. provis. Type: 'Linum collinum Guss. – perenne pr. fl. sic. non Lin. pedunculis fructiferis prope reflexi. Sicilia.' (BM).

Adenolinum tommasinii Reichb., Icon. Fl. Germ., vol. 6, p. 66 (1844). Type: 'Praires pierreuses du Mt. Spaccato dans les montagnes calcaires près de Trieste,' May–June, 1860, *M. de Tommasini* (K).

L. tommasinii (Reichb.) Nyman, Syll., p. 218 (1854).

L. saxicola Jordan, Cat. Jard. Dijon, p. 28 (1848). Type: France, 'de Gap', 1851, *A. Jordan* (K).

L. provinciale Jordan, Obs. Pl. Crit., vol. 7, p. 17 (1849). Type: France, 'Avignon, bords de la Durance', 1837, *A. Jordan* (LY).

L. ruscinonense Timbal-Lagrave, Bull. Soc. Bot. Fr., **7**: 509 (1860). Type: France, 'Font de Comps, Pyr. Or.', May, 1852. *P. M. E. Timbal-Lagrave* (P).

L. limanense Lamotte, Prod. Fl. Centr. Fr., vol. 1, p. 157 (1877). Type: France, 'Puy de Crouel', *M. Lamotte* (P).

Stems 6–40 cm. Inflorescence 3- to 20-flowered. Capsules 5–7.5 mm long, usually acuminate at the apex. $2n=18$. Dry rocky limestone soils, ascending to 1100 m in the Alps and 1300 m in the Pyrenees. Spain, south and central France, Italy, Jugoslavia, Greece and Sicily.

3. *L. PUNCTATUM* C. Presl in J. & C. Presl, Del. Prag., p. 58 (1822). Type in Prague (PR).

L. pycnophyllum Boiss. & Heldr. in Boiss., Diagn., Ser. 2, vol. 3(1), p. 97. Type: Greece, 'Rariforme in lapidosis reg. alpinae, m. Kyllenes. 6500 feet, 8/7/1848. *P. E. Boissier* (G).

Stems up to 15 cm, very crowded and densely leafy throughout. Leaves 3–5 (–7) mm long, narrowly ovate. Flowers solitary or in terminal groups of two or three. Inner sepals 5–6 mm long, obtuse. Pedicels erect or flexuous. Petals 8–12 mm long, pale blue. Capsules 5.5–7 mm long. Pollen grains with three furrows. Heterostylous. Restricted to a few mountains in Sicily (Madonie, Nebrodie 1400–1800 m), Greece (Mt Smolika 2000–2500 m) and Turkey.

4. *L. LEONII* F. W. Schultz, Flora (Regensb.), **21**: 644 (1838). Type: France, 'Pelouses sèches et pierreuses, champs de Sanfoin sur les hauteurs à calcaire oolithique aux environs de Metz, près d'Ancy, de Châtel et d'Onville', 15/7/1840, *Léo* 432 (K).

L. loreyi Jordan, Cat. Jard. Dijon, p. 27 (1848). Type not located.

L. petryi Beyer, Verh. Bot. Ver. Brand., **40**: 91 (1898). Type probably lost.

Stems 5–30 (–50) cm, erect when young, later often decumbent or reclinate.

Middle cauline leaves 0.5–2 mm wide. Inflorescence 1- to 6(–12)-flowered. Inner sepals 3.5–6 mm long, acute. Petals 8–14 mm long, deep blue. Pedicels erecto-patent, flexuous or patent. Capsules 5–7 (–8) mm long. Pollen grains with three furrows. Homostylous. $2n=18$. Dry rocky limestone soils, occasionally on chalk. Endemic to France and Germany.

The foregoing taxonomic account includes all the European members of the *L. perenne* group except those which are confined to Russia. These are omitted because I have not been able to grow these plants and know them only in the form of limited herbarium material.

DISCUSSION OF INDIVIDUAL TAXA

1a. *L. perenne* subsp. *perenne*. This subspecies has often been confused with the commoner *L. austriacum* subsp. *austriacum* and its precise distribution in eastern Europe is not known. It is rarer than has formerly been supposed and many of the earlier records need to be checked. It occurs in south Germany, Austria, Hungary, Romania and Russia, but is probably absent from East Germany, Czechoslovakia and the Balkan Peninsula. In Germany and Austria subsp. *perenne* and *austriacum* are readily distinguishable both by their morphology and ecology, but in Eastern Europe the distinction is not very clear. There are plants from Romania and Russia which have the erect pedicels of subsp. *perenne* but the small capsules of subsp. *austriacum*. Some of these plants have been referred to *L. euxinum* Juz. and *L. marschallianum* Juz. by Juzepczuk (1949), but their true affinities are obscure.

L. perenne subsp. *perenne* has become extinct in many of its localities during the last hundred years and now has a very disjunct distribution. Some of the topodemes are morphologically distinct, as in south Germany where there are three morphodemes, of which two have been given binomials (*L. darmstadinum* Alefeld and *L. bavaricum* Schultz). The Darmstadt topodeme has stems 30–70 cm long and very pale blue flowers. Topodemes along the Danube from Regensburg to Plattling consist of small plants with stems up to 30 cm long and deep blue flowers. The topodeme near Munich is intermediate, with a stem length of 25–50 cm and medium-blue flowers. It is of interest that most of the Central European topodemes of subsp. *perenne* are associated with the Danube or its tributaries (apart from the Darmstadt topodeme which is near the Rhine). This suggests that these topodemes may have been derived from *L. perenne* subsp. *alpinum* by seeds being carried down from the mountains. If topodemes of subsp. *perenne* were derived independently in this way, this would help to explain the morphological differences between them.

1b. *L. perenne* subsp. *anglicum*. Confined to eastern and northern England with one topodeme in southwest Scotland. The latter is unique in being no more than 30 m from the shore line. *L. perenne* subsp. *anglicum* is less disjunct and less variable than subsp. *perenne*. Morphological separation of these two subspecies is difficult, but they can readily be distinguished by the fact that subsp. *anglicum* is tetraploid and has pollen grains with six pores, while subsp. *perenne* is diploid and has pollen grains with three furrows. A fuller account of subsp. *anglicum* is given in Ockendon (1968b).

1c. *L. perenne* subsp. *alpinum*. Locally common in the western and south-eastern Alps, less common in the eastern and southern Alps and absent from

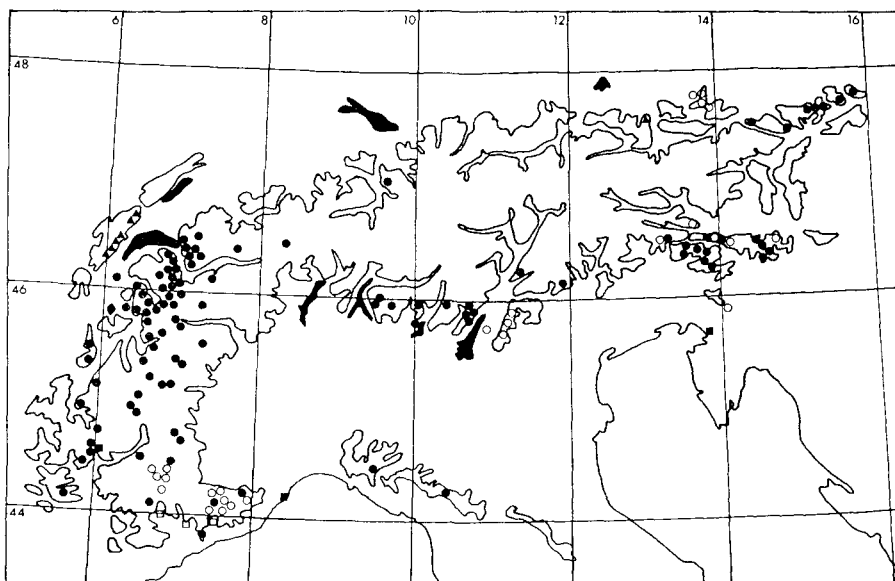


FIGURE 4. Distribution of the *Linum perenne* group in the Alps. Solid figures – herbarium records; open figures – literature records. ○● *L. perenne* subsp. *alpinum*; △▲ *L. perenne* subsp. *montanum*; □■ *L. austriacum* subsp. *collinum*. The contour line indicates the main land masses above 900m.

most of the north and central Alps. Scattered in the eastern and central Pyrenees and rare in the Apennines. This is the most variable subspecies of *L. perenne*, comprising a series of forms which replace one another geographically. Some of these forms may deserve taxonomic recognition but it is virtually impossible to key them out satisfactorily.

The distribution of *L. perenne* subsp. *alpinum* in the Alps is far from continuous (Fig. 4) and four main areas of its occurrence can be recognised. The largest of these is in the western Alps where it is scattered from Lake Geneva to the Alpes Maritimes. In the southern Alps it occurs in the mountains of Trentino and Bergamo, in the southeastern Alps mainly in the Julian, Karawanken and Steiner Alps, and in the eastern Alps mostly in the Styrian Alps. Three of these four topodemes have been given binomials. *L. alpinum* Jacq., originally described from the Schneeberg in the eastern Alps (Jacquin 1762), has short, decumbent or ascending stems up to 15 cm long, pale blue petals and erect or erecto-patent pedicels. *L. julicum* Hayek, originally described from the Sannataler Alps (Hayek 1907), has ascending or erect stems up to 30 cm long, deep blue petals and flexuous or deflexed pedicels. The topodeme from the western Alps, which has often been called *L. montanum* Schleicher, is rather heterogeneous, but generally has ascending stems up to 30 cm long, pale or medium blue petals and erect or erecto-patent pedicels. The topodeme from the southern Alps is similar to that of the western Alps except that it has deeper blue petals and patent pedicels.

Plants of *L. perenne* subsp. *alpinum* from the Pyrenees differ from those from the Alps in having longer stems and broader leaves. The stem length of Pyrenean

plants may reach 45 cm and is seldom less than 20 cm. Some of the Pyrenean topodemes show an unusually large amount of intrapopulation variation in leaf width and pedicel position and some plants are almost impossible to key out properly. The leaf width may be as much as 5 mm and such plants will key out as *L. perenne* subsp. *extraaxillare*. The pedicels may be flexous or patent and such plants are liable to key out to *L. austriacum* subsp. *collinum*. Confusion between *L. perenne* subsp. *alpinum* and *L. austriacum* subsp. *collinum* in the Pyrenees could be serious were it not for striking differences in their ecology. *L. perenne* subsp. *alpinum* occurs in closed mesic habitats, usually above 1500 m, with species such as *Anthoxanthum odoratum*, *Briza media*, *Helictotrichon pubescens*, *Lotus corniculatus*, *Plantago lanceolata* and *Primula veris*. *L. austriacum* subsp. *collinum* occurs in open, much more xeric habitats, often on rocky slopes with species such as *Helictotrichon bromoides* (Gouan) C. E. Hubbard, *Koeleria vallesiana* (Honck.) Bertol., *Stipa pennata* L., *Teucrium polium* L. and *Thymus vulgaris* L.

Topodemes of *L. perenne* subsp. *alpinum* from the northern Apennines are similar to those from the western Alps, but topodeme F50* from the central Apennines near L'Aquila shows several differences, notably the lack of sterile axillary shoots normally characteristic of this subspecies, and the short, appressed, glaucous leaves. This topodeme seems to vary in the direction of *L. austriacum* subsp. *collinum*, both in its morphology and ecology. There is considerable variation in subsp. *alpinum* in the Apennines and more samples are needed to see if this variation has a north-south pattern.

The Bulgarian topodeme of subsp. *alpinum*, which is confined to the Pirin Mountains and Slavianka, resembles the topodeme from the eastern Alps in having erect stems up to 20 cm long, narrow leaves, medium blue flowers and erect pedicels.

Topodeme F42 from the central Pyrenees is particularly unusual. It has broader leaves than the other Pyrenean topodemes and is tetraploid ($2n=36$), while the three other Pyrenean topodemes investigated are diploid (Ockendon 1968a). Most of the pollen grains of F42 have three furrows, as do the diploid members of the *L. perenne* group, but a few of them have six furrows, resembling the pollen of the tetraploids. This is the sole exception to the rule that in the *L. perenne* group diploids have pollen with three furrows and tetraploids have pollen with six pores (Ockendon 1968a). Topodeme F42 is unusual in yet another respect, namely that it produces extremely few fertile seeds when open-pollinated or when artificially cross-pollinated. Meiosis was examined in two plants from this topodeme. Of 53 pollen mother cells, 42 per cent had one or more univalents and 35 per cent had one or more trivalents. Univalents and trivalents are normally absent or very rare in the meiosis of the tetraploid *L. perenne* subsp. *anglicum*. Thus the poor seed fertility of topodeme F42 may be accounted for by its meiotic irregularities. The evidence suggests that this topodeme has become tetraploid rather recently and has not been in existence as a tetraploid long enough for selection to have increased the fertility to the normal level.

1d. *L. perenne* subsp. *montanum*. Restricted to the Jura and one locality in the south-eastern corner of Bavaria on the Austrian border. This subspecies is morphologically very similar to subsp. *alpinum* from the western Alps and is

* See Appendix for details.

distinguished from it by its chromosome number and pollen morphology. Grenier (1865) thought that plants from the Jura differed from those from the western Alps but he was unable to describe any precise difference. The pollen morphology is more reliable than any other morphological character for distinguishing subsp. *montanum* from subsp. *alpinum*.

It should be noted that the name *L. perenne* subsp. *montanum* is being used here in a somewhat different sense from that in which the name *L. montanum* has been used in the past. The name *L. montanum* has been applied to plants from the Jura, the whole of the western Alps and the Pyrenees, while *L. perenne* subsp. *montanum*, as used here, applies only to the tetraploids in this area, the diploids being retained in subsp. *alpinum*. Neither the original descriptions of *L. montanum* (Candolle 1824) nor the type specimens in the Geneva Herbarium give any clear indication of the particular specimens to which the name should be applied, and as the description fits the tetraploids it was decided to call them *L. perenne* subsp. *montanum*.

It is a little surprising that there are no substantiated records of subsp. *montanum* between the single topodeme in Bavaria and the topodemes in the Jura, some 500 km away. The *L. perenne* group as a whole is largely absent from this area, apart from a record of *L. perenne* from Liechtenstein (Handel-Mazzetti 1911).

I have recently collected this plant from near Triesen in Liechtenstein and it has proved to be diploid rather than tetraploid. Hence it represents an interesting outlying locality for *L. perenne* subsp. *alpinum* and not another record for subsp. *montanum*.

1e. *L. perenne* subsp. *extraaxillare*. Scattered in the Carpathians and the mountains of Yugoslavia. *L. extraaxillare* was originally described from the Tatra and distinguished from *L. alpinum* by its broader leaves and longer stems. In Romania and Yugoslavia both broad- and narrow-leaved morphodemes occur, with the former predominating. Some of the Romanian plants have much shorter stems (10–20 cm) than the Czech plants (25–50 cm). Although leaf width separates subsp. *alpinum* and *extraaxillare*, it is not always reliable. The existence of broad-leaved forms of subsp. *alpinum* in the Pyrenees and narrow-leaved forms of subsp. *extraaxillare* in Romania could be used as an argument for treating these two subspecies as one. However, there are many subspecies which are incompletely separated by their morphology, and one can make a clear geographical separation between subsp. *alpinum* in the Alps and Pyrenees and subsp. *extraaxillare* in the Carpathians and mountains of Yugoslavia.

2a. *L. austriacum* subsp. *austriacum*. The commonest subspecies in central and eastern Europe. It has been questioned (Hegi 1924) whether it is native in its westernmost localities, which are in Germany and Switzerland. Known introductions are recorded for some localities, e.g. Friesener Warte, near Bamberg, Bavaria (Gauckler *in lit.*) and Møn, Denmark (Böcher 1946), but there are several other localities for which no such records exist. Topodemes such as F18 at Eichstätt, Bavaria are certainly fully naturalised if not actually native.

Capsule size, which is used to distinguish the two subspecies of *L. austriacum*, is not totally satisfactory, because some topodemes of subsp. *collinum* produce capsules as small as those of subsp. *austriacum*. Rather than applying a single taxonomic character rigidly, which would give an arbitrary separation between the two subspecies, a more satisfactory distinction can be made on the basis of

their geographical distributions. Subsp. *collinum* occurs in southern Europe south of the Alps while subsp. *austriacum* occurs in central and eastern Europe, north and east of the Alps. Nowhere do the two subspecies meet.

Subsp. *austriacum* in central Europe is much less variable than subsp. *collinum*, but in eastern Europe variants occur which have paler flowers, narrower leaves and more erect pedicels than is the case in central Europe. A broad-leaved variant of subsp. *austriacum* from Romania was described as *L. trinervium* by Freyn (1876).

2b. *L. austriacum* subsp. *collinum*. A morphologically heterogeneous and highly disjunct subspecies extending from northern Spain through southern France to Italy, Sicily, Yugoslavia and Greece. Most of the topodemes of subsp. *collinum* are very limited in extent (Table 1) and can be defined more easily by their distribution than by their morphology. The characters that vary most in subsp. *collinum* are stem length and capsule size (Table 1), but there is also variation in sepal shape, as shown by the topodeme from Trieste, which has long narrow sepals. The pattern and extent of variation in *L. austriacum* subsp. *collinum* is similar to that in *L. perenne* subsp. *alpinum* but the greater rarity of subsp. *collinum* has made the morphological differences between the topodemes more conspicuous.

The name *L. austriacum* subsp. *collinum* Nyman calls for some comment. *L. collinum* has been applied to plants in southern Europe which are similar to, but distinguishable from, *L. austriacum* subsp. *austriacum*. It has not been applied exclusively to a limited area, as have the binomials listed in Table 1, and hence is a suitable name for the subspecies as a whole. Nyman (1878) applied the name to plants from Spain, Sicily and Greece. Plants from France were treated by him as *L. provinciale* Jordan and are here included within subsp. *collinum*.

L. collinum Guss. is only a provisional name because Gussone (1845) was uncertain of the status of the Sicilian plants for which he suggested the name. Nevertheless, when Nyman (1878) published the combination *L. austriacum* subsp. *collinum* with precise reference to Gussone, he was both definitely accepting the taxon and validating the name by reference to Gussone's definition. Hence the name *L. austriacum* subsp. *collinum* Nyman is validly published.

Some mystery surrounds the plant named *L. ruscinonense* from Font-de-Comps, Pyrénées Orientales by Timbal-Lagrave (1860). This plant has never

TABLE 1. TOPODEMES OF *L. AUSTRIACUM* SUBSP. *COLLINUM*

Topodeme	Extant local populations	Binomial	Stem length cm	Capsule size mm
North Spain			30-50	5.5-7.0
Cerdagne, Pyrénées	4		15-40	5.5-7.0
Prades, Pyrénées	1	<i>L. ruscinonense</i>	25-40	7.0-8.0
Puy-de-Dôme	3	<i>L. limanense</i>	15-40	4.5-6.0
Hautes Alpes	1	<i>L. saxicola</i>	30-40	6.5-8.0
Vaucluse	0	<i>L. provinciale</i>	40-60	6.5-7.0
Capo di Noli, Liguria	1		40-50	5.0-6.0
Trieste	4	<i>L. tommasinii</i>	10-25	4.5-5.5
North Greece			20-30	5.0-5.5

been reported with certainty from any other site and I do not know precisely where Font-de-Comps is, although I do know that it is in the vicinity of Prades. *L. ruscinonense*, as described by Timbal-Lagrave, has short decumbent stems 5–8 cm long, bearing 1–4 flowers each. I visited Prades in 1966 and found only one population (F35) of the *L. perenne* group in the area. This was at about 1000 m. just above Villefranche-de-Confluent, at a place which could have been Font-de-Comps. However, F35 has ascending stems 25–40 cm long, with 10–20 flowers per stem, and is treated here as subsp. *collinum*. This probably is the population known by Timbal-Lagrave, but if so, why were the plants so much smaller in 1860 than 1966? Stem length in the *L. perenne* group is phenotypically highly plastic, and grazing may have been an important factor contributing to the very short stems produced in 1860. The habitat of topodeme F35 is very similar to that of other topodemes of subsp. *collinum* in the Pyrenees and quite different from that of *L. perenne* subsp. *alpinum*. Hence it appears that *L. ruscinonense* is simply a dwarf form of *L. austriacum* subsp. *collinum* and not a form of *L. perenne* subsp. *alpinum* as Timbal-Lagrave supposed.

Another dwarf member of the *L. perenne* group which is referable to *L. austriacum* subsp. *collinum* occurs at 600 m on Monte Calvo, Gargano, south Italy. It has stems 10–15 cm long with 2–4 flowers per stem. Herbarium specimens resemble the type specimens of *L. ruscinonense*. It was treated by Nyman (1878) as *L. punctatum*, and has some similarities to *L. tommasinii* from Trieste. It is geographically very isolated and needs further study.

The concept of *L. austriacum* subsp. *collinum* used here is an inclusive one. The topodemes which have been tested, though morphologically diverse, show fairly high interfertilities (Ockendon 1968a). Some of the morphodemes have been adequately characterised, but others are very poorly known and, until they are better known, any subdivision of subsp. *collinum* is liable to be arbitrary.

3. *L. punctatum*. A geographically isolated member of the *L. perenne* group confined to a few mountains in Greece, Sicily and Turkey. Formerly, the Greek and Turkish plants have been distinguished as *L. pycnophyllum* Boiss. et Heldr., but they are morphologically very similar to the Sicilian plants. Davis (1967) has treated the Turkish material as *L. pycnophyllum* subsp. *kurdicum*.

4. *L. leonii*. Endemic to western Europe, chiefly in east and central France and south and central Germany. Extending west to Charente, south to Aveyron, east to Thüringen and north to Niedersachsen (Fig. 5). At one time *L. leonii* was widespread in parts of eastern France, but as a result of extinction in many places it is now rather rare. It was almost unknown in Germany until recently but in the past ten years it has been reported from Bavaria (Gauckler 1964), Hessen (Nieschalk & Nieschalk 1963), Südniedersachsen (Lewejohann 1967) and Thüringen (Rauschert 1967). Rauschert's paper gives a full discussion of all the recent German records.

Past treatments of *L. leonii* have been very confused (Beyer 1898). It was treated as conspecific with *L. anglicum* by Ascherson & Graebner (1914) and Hegi (1924) and as a variety of *L. alpinum* by several French botanists. One reason for this confusion was the failure to recognise that *L. leonii* is homostylous whereas all the other European members of the *L. perenne* group are heterostylous. Small plants of *L. leonii* are highly characteristic and unlikely to be confused with anything except dwarf forms of *L. austriacum* subsp. *collinum*. They commonly have a single stem 5–10 cm long with one or two flowers and the cotyl-

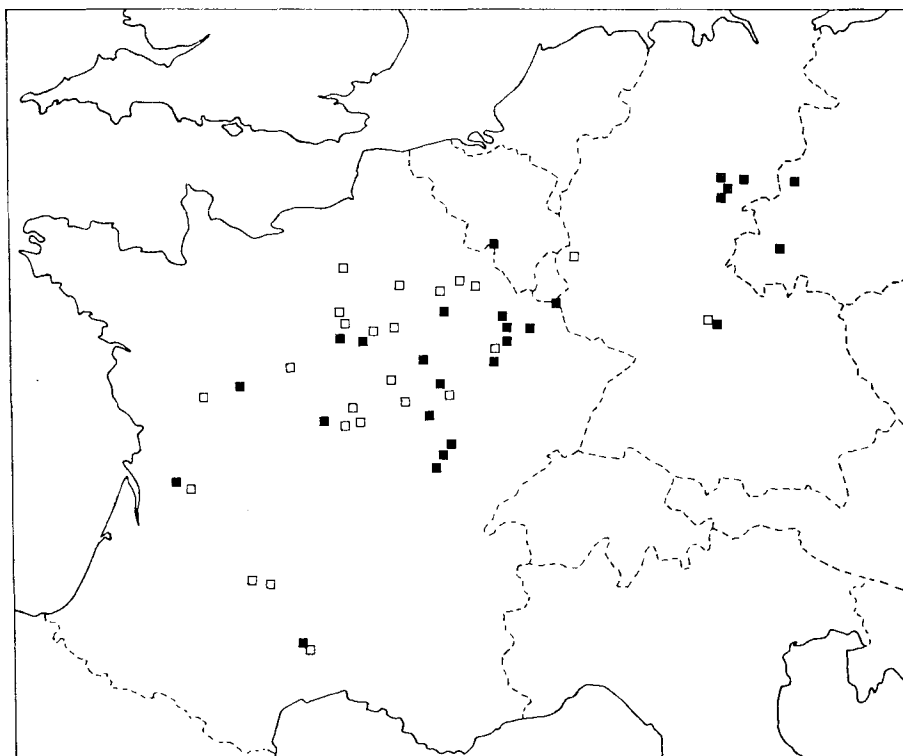


FIGURE 5. Distribution of *L. leonii*. ■ Records confirmed since 1955.
□ Old records not recently confirmed.

edons still present at the time of flowering. Large plants of *L. leonii* with stems 20–40 cm are sometimes found in populations consisting mainly of small plants. It was probably a robust plant of this sort which misled Beyer (1898) into describing *L. petryi* as a new species. *L. leonii* is a short-lived perennial which usually flowers in the first year, but the other European members of the *L. perenne* group are longer-lived and usually do not flower until the second or third year.

L. leonii is much less variable than *L. austriacum* subsp. *collinum* but does show variation in stem length. The topodemes of *L. leonii* from Côte d'Or and Charente consist mostly of robust plants with erect stems 20–50 cm long. This morphodeme corresponds to *L. loreyi* Jordan. As stem length is very variable within single populations of *L. leonii*, the robust morphodeme does not warrant treatment as a separate taxon. The two morphodemes of *L. leonii* are completely interfertile (Ockendon 1968a).

DISCUSSION OF THE TAXONOMIC TREATMENT

The taxonomic treatment given is an attempt to summarise the major features of the variation in the *L. perenne* group, but it is not intended as a detailed account of the morphological variation, this being given separately for each subspecies. The more detailed a taxonomic treatment of the group is, the more arbitrary is it likely to be. For this reason it has not been found desirable to use any taxonomic category below that of subspecies.

Some justification may be given for the decision to retain *L. perenne* and *L. austriacum* as species while treating *L. alpinum* as a subspecies of *L. perenne*. Although the morphological separation between *L. perenne* and *L. austriacum* is not completely clear in eastern Europe, there is no problem in central Europe. Furthermore, artificial hybrids between these two species are produced only with some difficulty and have reduced fertilities (Ockendon 1968a). The morphological separation between *L. alpinum* and *L. perenne* is incomplete because of intermediates such as *L. perenne* 351/65 from Bavaria and *L. perenne* subsp. *extraaxillare* from the Tatra. The cross *L. perenne* \times *alpinum* is highly fertile (Ockendon 1968a). *L. perenne* and *L. alpinum* may be thought of as ecological races and are conveniently treated as subspecies. The subspecific category has also been employed in the *L. perenne* group for widespread geographical races (*L. austriacum* subsp. *austriacum* and *collinum*) and for widespread cytological races (*L. perenne* subsp. *anglicum* and *montanum*) but has not been used for morphodemes of restricted distribution, which are not given formal taxonomic recognition.

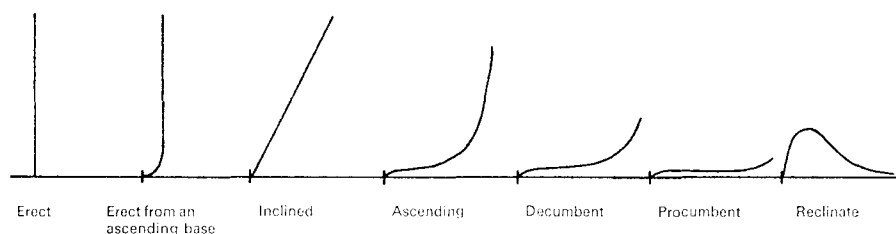
MORPHOLOGICAL VARIATION

Some of the morphological variation to be found within the different subspecies has already been described, but for a general consideration of the total variation of the *L. perenne* group it is useful to consider the variation character by character rather than subspecies by subspecies. For taxonomic purposes it is important to distinguish between those characters which can be modified by the environment to a large extent and those which are only slightly susceptible to environmental modification. An estimate of the phenotypic plasticity of the characters studied has been made by comparing the phenotypes produced in the field with those obtained by cultivation under various conditions. Phenotypically plastic characters are liable to be untrustworthy taxonomically, but may have to be used if more stable characters are lacking.

The morphological variation has been studied in terms of population samples rather than single herbarium specimens, because of the importance of assessing the amount of variation within populations and comparing this with the variation between populations. The local population is a particularly important unit in the *L. perenne* group because it is easy to define and the total number of local populations in western Europe is sufficiently small for a considerable proportion of them to be studied in detail. The sources of the material used here are given in Appendix 1.

HABIT AND STEM LENGTH

Both habit and stem length vary strikingly and have been used as taxonomic characters. Habit is difficult to describe accurately because of its complexity and because the different types of habit grade imperceptibly into one another. The descriptive terms used here are illustrated in Fig. 6. A further difficulty is that the habit of a plant may appear to change as it becomes older. Thus, early in the season the stems of *L. perenne* subsp. *anglicum* growing in open beds spread radially from the caudex and are procumbent or decumbent in habit. Further growth of these stems tends to be in a vertical rather than in a horizontal direction so that by the end of the season the habit is ascending or erect from an

FIGURE 6. Habit of the *L. perenne* group.

ascending base. This leads to a partial correlation between habit and stem length and hence it is convenient to consider these two characters together.

From Table 2 it can be seen that *L. perenne* subsp. *anglicum* growing in tall grass has long stems which are ascending or erect from an ascending base. Plants from short grass or open habitats have short procumbent, decumbent or ascending stems. In cultivation in open beds with a metre between each plant, the differences between these two forms largely disappear because the short-stemmed plants produce considerably longer stems in cultivation (Table 2). Small samples of *L. perenne* subsp. *anglicum* from different parts of the country do not show any marked differences in habit when cultivated. However, cultivation of a large sample from topodeme GB2 has shown marked variation in

TABLE 2. VARIATION IN HABIT AND STEM LENGTH OF
L. PERENNE SUBSP. *ANGLICUM*

Popu- lation	IN THE WILD			IN CULTIVATION	
	Habitat	Stem length	Habit	Stem length	Habit
GB1	Tall grass	30-70 cm	Erect from an ascending base or inclined	45-65 cm	Ascending or erect
GB1	Mown grass	20-40	Ascending or decumbent		
GB2	Tall grass	30-70 (-80)	Erect from an ascending base or ascending	50-75	Ascending or erect
GB3	Tall grass	30-80 (-100)	Erect from an ascending base or ascending		
GB5	Short grass	15-25	Decumbent or procumbent	60	Ascending
GB6	Tall grass	30-70(-90)	Erect from an ascending base	55-70	Ascending or erect
GB7	Short grass	15-30	Decumbent or procumbent		
GB11	Short grass	10-20	Ascending or decumbent	30-50	Decumbent or ascending
GB12	Medium grass	20-60	Erect from an ascending base or decumbent	45-60	Decumbent or ascending

habit, indicating that there is also a genetic component to the observed differences in habit. 89 plants had decumbent or ascending stems, while 15 had stems which were erect from an ascending base or completely erect. The habit of individual plants may vary from season to season. Five plants which were procumbent or decumbent in habit in 1966 were ascending in 1967.

In the field *L. leonii* is usually strikingly smaller than *L. perenne* subsp. *anglicum* but in cultivation this difference in stem length largely disappears (Table 3). There appears to be a correlation between stem length and soil depth in *L. leonii*. The smallest plants are invariably found in very shallow soils and large plants generally occur in much deeper soils. Large and small plants can occur in mixed populations as at Bourges (topodeme F9), where there are numerous small plants with stems 5–20 cm growing in soil 4–7 cm deep and a few larger plants with stems 25–35 cm growing in soil 15–20 cm deep. The correlation between stem length and soil depth has been confirmed by cultivation. Plants of *L. leonii* F4 grown in 10 cm pots produce stems up to 20 cm but when planted out in beds the stem length increases to 60 cm.

In *L. leonii*, both in the wild and in cultivation, short stems are usually erect but longer stems are usually ascending or reclinate. An exception is *L. leonii* F2, in which the stems are always procumbent. The unusual habit of this topodeme is presumably genetically determined.

Topodemes F17 and F25 of *L. perenne* subsp. *perenne* behave similarly in cultivation and in the field, having erect stems 40–80 cm long. Topodeme 351/65 from Bavaria is intermediate in habit and stem length between *L. perenne* subsp. *perenne* F17 and subsp. *alpinum* 80A/63. The stems of 351/65 are 30–45 cm long, thinner, more numerous and more flexuous than those of subsp. *perenne* F17, and in all these respects tend towards subsp. *alpinum*.

In cultivation the stem length of *L. perenne* subsp. *alpinum* 80A/63 from Haute Savoie reaches 45 cm compared with a maximum of about 25 cm in the wild. The long stems produced in cultivation differ from those of *L. perenne* subsp. *perenne* in being much branched below and in having long axillary shoots which overtop the inflorescences. Because of the short growing season in its natural habitats, a great development of axillary shoots does not normally occur in *L.*

TABLE 3. STEM LENGTH OF *L. LEONII*

Population	Wild	Cultivated in beds (maximum values)
F1	4–15 (–20) cm	
F2	7–30	50 cm
F3	30–35	60
F4	3–10	60
F8	5–20 (–25)	
F9	5–20 (–35)	45
F21	4–15 (–25)	55
F27	20–40	60
F28	25–55	
F43	30–50	90
F44	7–18	
329C/65		60

perenne subsp. *alpinum* in the wild. In cultivation, plants from the western Alps have a low compact habit with decumbent spreading, flexuous stems. Plants from the Pyrenees have more erect stems but retain a compact bushy habit. The bushy habit of *L. perenne* subsp. *alpinum* in cultivation is not normally seen in the wild. *L. perenne* subsp. *extraaxillare* and *montanum* share the typical bushy habit of subsp. *alpinum* when cultivated, but tend to have somewhat longer stems and inflorescence branches.

STEM LEAFINESS

In cultivation the alpine taxa *L. perenne* subsp. *alpinum*, *extraaxillare* and *montanum* commonly produce characteristic densely leafy sterile shoots with squarrose or deflexed leaves. Such shoots are not normally produced by the lowland subspecies in cultivation, but can occasionally occur when plants are growing vigorously under moist conditions. Furthermore, the densely leafy stems of the alpine taxa are often absent in the wild, especially when the plants are growing amongst tall vegetation. Although stem leafiness is a conspicuous character, which is sometimes useful for the purpose of recognition, it is generally too phenotypically plastic to be used diagnostically.

LEAF WIDTH

Leaf width is the main character used to distinguish *L. perenne* subsp. *extraaxillare* from subsp. *alpinum*, and broad-leaved Romanian plants (*L. trinervium*)

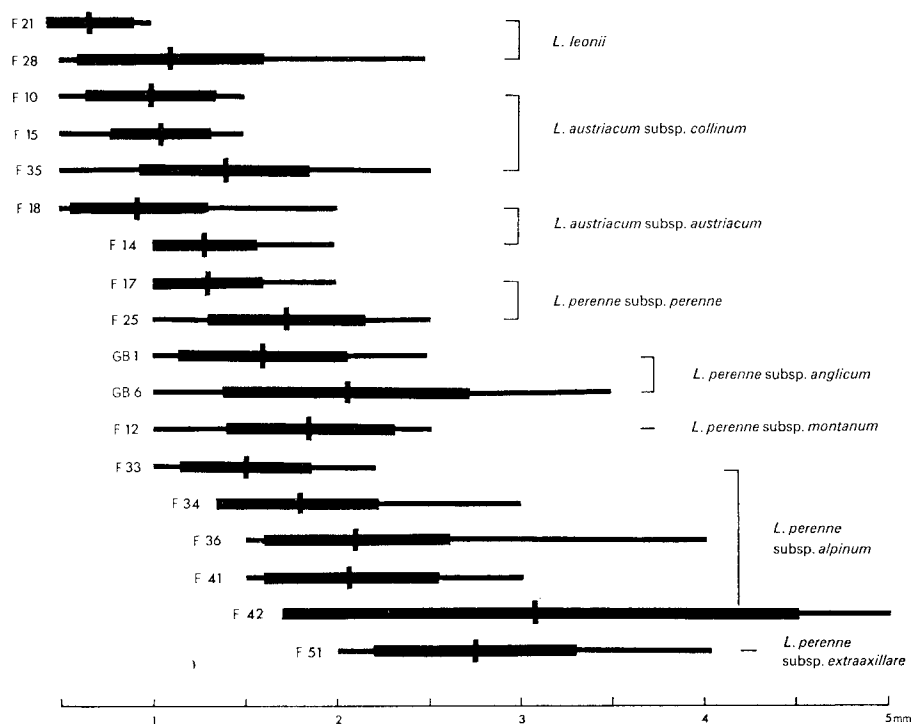


FIGURE 7. Leaf width of the *Linum perenne* group showing mean, range (thin line) and standard deviation (thick line) for population samples. For sources of material see Appendix.

of *L. austriacum* subsp. *austriacum* from the rest. Leaves on the branched part of the stem are commonly wider than those on the unbranched part and therefore a leaf from the middle of the stem was selected for measurement. The results in Fig. 7 are for samples of 20 stems collected in the wild. The amount of variation in leaf width in a single population ranges from very little in *L. leonii* F21 to a large amount in *L. perenne* subsp. *alpinum* F42. The leaves of *L. austriacum* and *L. leonii* tend to be a little narrower than those of *L. perenne* but there is a large amount of overlap. The sample with the narrowest leaves (*L. leonii* F21) also has the shortest stems, and it is not uncommon to find that large plants have wider leaves than small plants from the same population.

The greatest variation in leaf width occurs in *L. perenne* subsp. *alpinum*, especially in certain Pyrenean topodemes such as F42, which show almost as much variation in this character as the *L. perenne* group as a whole. Topodemes of this subspecies from the Alps have moderately narrow leaves similar to those of *L. perenne* subsp. *montanum* and *perenne*. *L. perenne* subsp. *extraaxillare* seldom has leaves less than 2 mm wide but does not produce leaves as wide as the widest produced by some Pyrenean topodemes of subsp. *alpinum*.

Leaf width shows some phenotypic plasticity. A few plants of topodeme F36 of *L. perenne* subsp. *alpinum* growing in partial shade had leaf widths of 2.5–4.5 mm compared with a range of 1.5–4.0 mm for the rest of the population. In cultivation several subspecies showed greater leaf widths than those found in wild material. This is partly a question of the greater vigour of plants in cultivation.

SEPAL SIZE AND SHAPE

The sepal dimorphism of the *L. perenne* group is highly characteristic. The two inner sepals have a much wider colourless scarious margin than the two outer sepals (Fig. 8). The fifth sepal is asymmetrical, with a wide margin on one side and a narrow margin on the other. The green parts of all five sepals have much the same shape, but because of the differences in the widths of the margins, the outer sepals are lanceolate or ovate-lanceolate, while the inner are ovate-lanceolate, ovate or obovate.

The variation in sepal size and shape is not easy to analyse because of the complex of characters involved. It is imperative that outer sepals be compared with outer and inner with inner. The only sepal character which can be recorded with precision directly from herbarium material is sepal length. For more

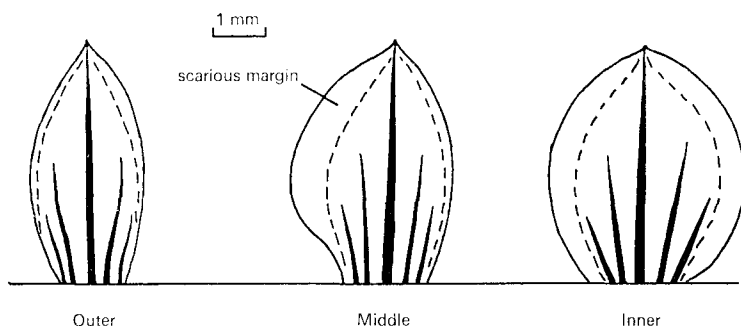


FIGURE 8. Sepal dimorphism of the *Linum perenne* group.

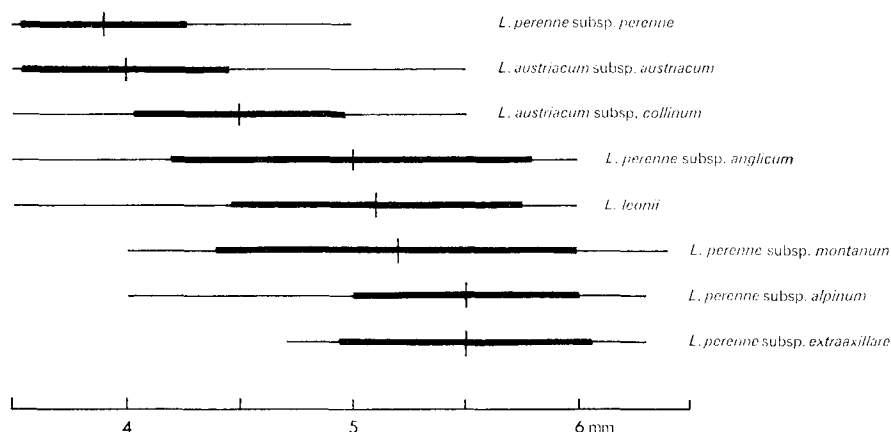


FIGURE 9. Length of inner sepals of the *Linum perenne* group showing mean, range (thin line) and standard deviation (thick line) for each taxon. For sources of material see Appendix.

detailed studies, sepals were dissected from the flower, mounted and examined under a binocular microscope.

The montane subspecies *L. perenne* subsp. *alpinum* and *extraaxillare* tend to have longer sepals than the lowland taxa, especially *L. perenne* subsp. *perenne* and *L. austriacum* subsp. *austriacum* (Fig. 9), and this has been used as a diagnostic character. However, the ranges for the different taxa overlap so much that this character is not very reliable. There is considerable variation in sepal length within populations. The range found for 10 plants of topodeme GB1 of *L. perenne* subsp. *anglicum* (4.1–5.8 mm) almost equals the total range for the subspecies.

The difference in length between the outer and inner sepals can be used to separate subsp. *anglicum* and *perenne* from the other subspecies of *L. perenne* (Fig. 10). In *L. perenne* subsp. *alpinum*, *extraaxillare* and *montanum* the outer and inner sepals are almost equal in length, never differing by more than 0.4 mm.

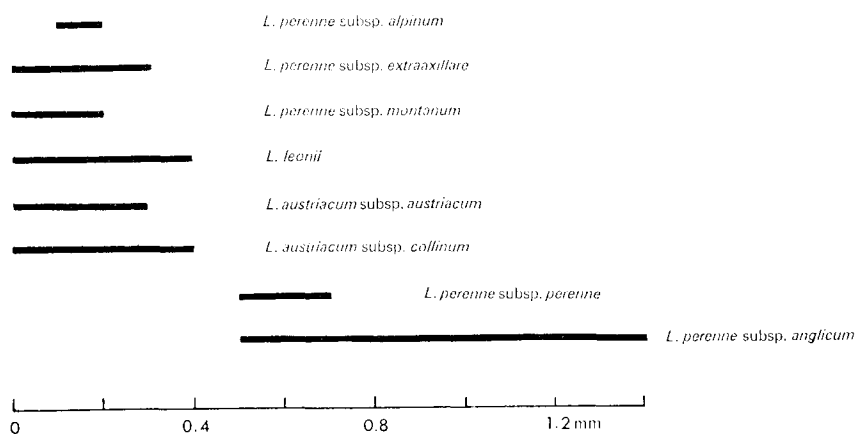


FIGURE 10. Difference in length between the outer and inner sepals, showing range for each taxon. For sources of material see Appendix.

In *L. perenne* subsp. *anglicum* and *perenne* the inner sepals exceed the outer by 0.5–1.4 mm. The difference in length between the sepals can usually be seen in herbarium material. Sepal shape can be expressed crudely in terms of length/breadth ratios but these do not give a much better separation between the subspecies than sepal length alone. The potential taxonomic value of sepal shape and size in the *L. perenne* group has not been realised despite detailed examination of these characters.

PETAL SIZE

The petals of the *L. perenne* groups are broadly obovate or obovate-lanceolate with a very obtuse or slightly emarginate apex. They taper gradually to a short yellow, pubescent claw. They are flimsy and fugacious. In hot weather few petals remain on the plant after midday. A new set of flowers opens each morning. Petals were collected in the morning and spread out carefully before pressing.

Petal length shows rather less intrapopulation variation than petal width and therefore was chosen as a possible taxonomic character. Fig. 11 shows that there is continuous variation in the petal length of the *L. perenne* group. *L. leonii* has the shortest petals and could be distinguished from *L. perenne* subsp. *anglicum* and *alpinum* by its petal length, but otherwise this character has little taxo-

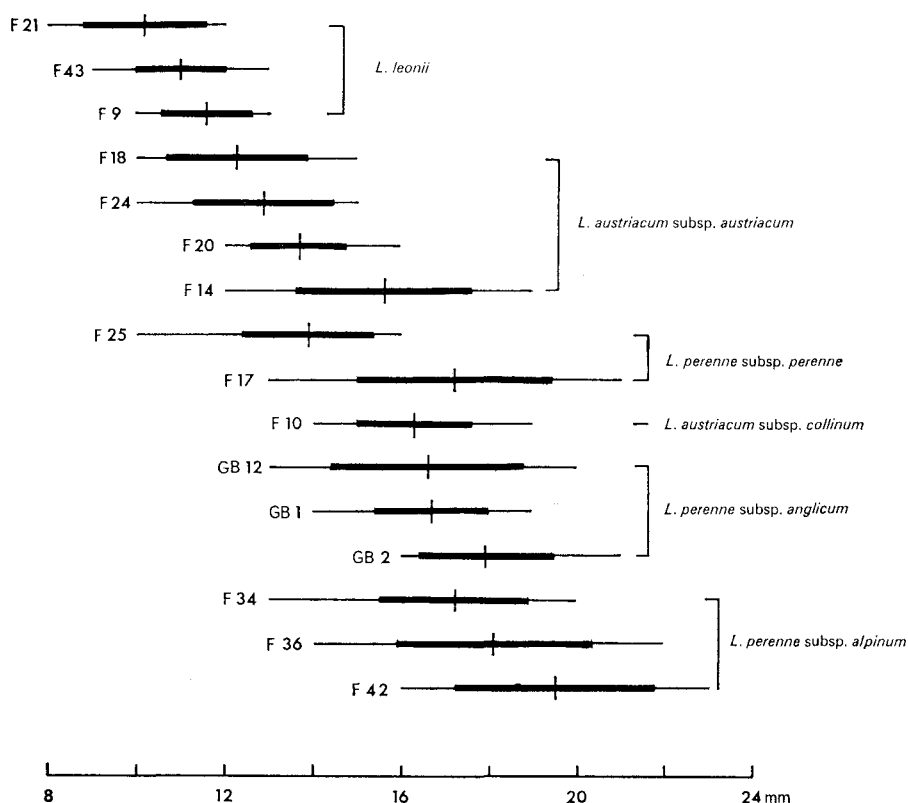


FIGURE 11. Petal length in material from the wild, showing mean, range and standard deviation. For sources of material see Appendix.

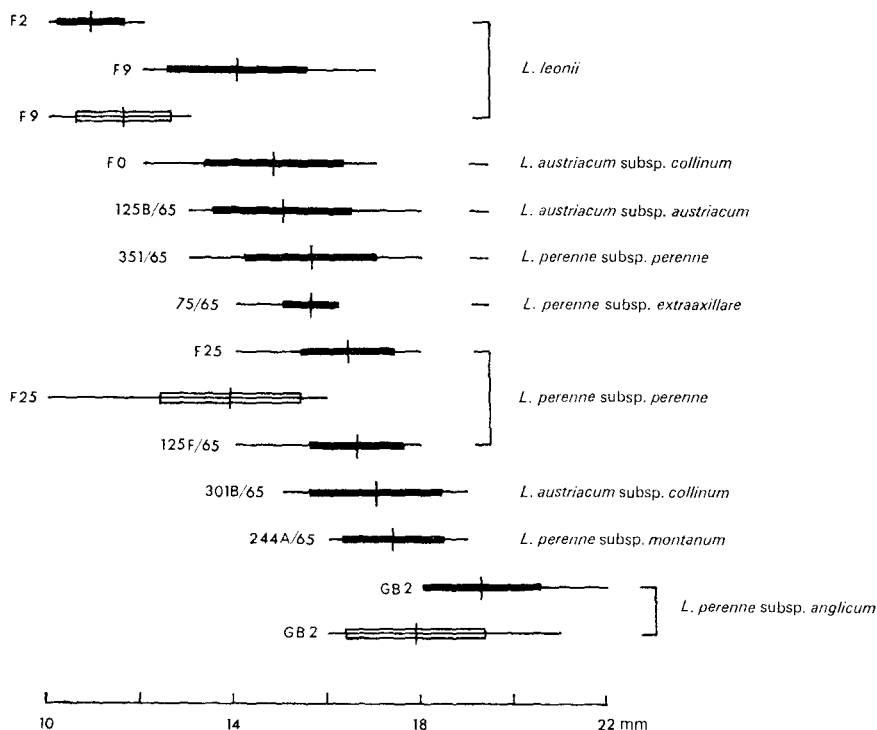


FIGURE 12. Petal length of cultivated material (solid figures) compared with that of wild material (open figures). For sources of material see Appendix.

nostic value. It is noteworthy that *L. leonii*, the only European member of the group which is not absolutely dependent on cross-pollination by insects, has the smallest petals.

The pattern of variation in petal length shown by the cultivated material is similar to that of the wild material, but if anything the differences between the taxa are less clear in cultivation (Fig. 12). In cultivation, the petal length of *L. leonii* remains shorter than that of *L. perenne* subsp. *anglicum*, indicating that there is a genetic basis to this difference. However, in the three cases in which direct comparisons can be made, the petal length of cultivated material is appreciably greater than that of wild material from the same source. This suggests that petal length is phenotypically plastic and is partially correlated with plant size.

PETAL COLOUR

Petal colour varies from pale blue to deep bright blue and has been used as a diagnostic character to distinguish *L. perenne* from *L. austriacum*, and *L. alpinum* from *L. julicum* (Hayek 1909). Occasional white-flowered variants occur in the wild and a single plant of *L. perenne* subsp. *perenne* 351/65 from Bavaria had deep purple flowers.

Petal colour is not a particularly good taxonomic character in the *L. perenne* group because it is difficult to measure accurately and because the colour fades

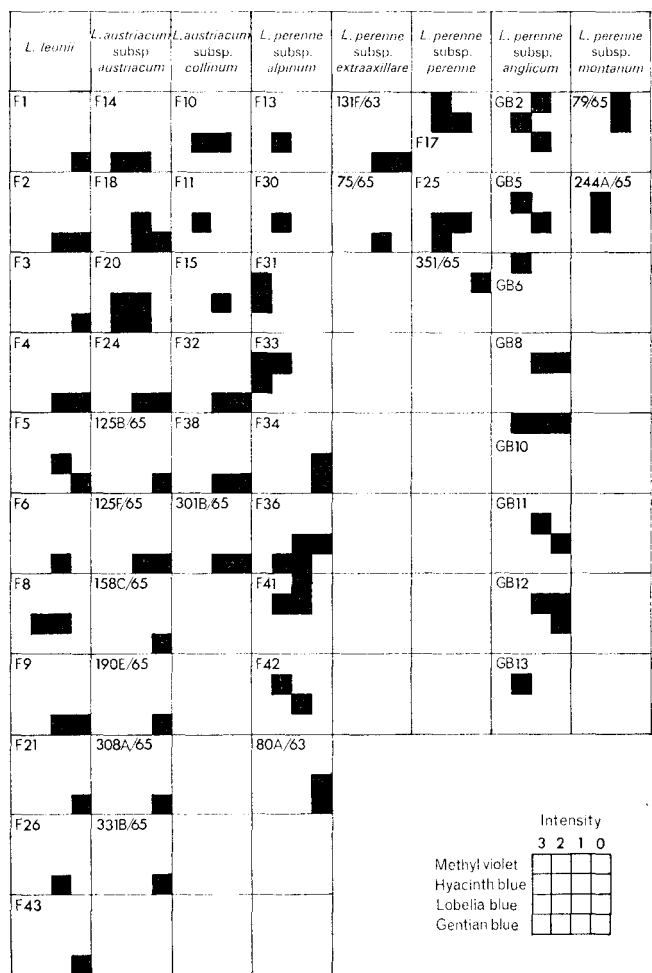


FIGURE 13. Petal colour as measured with the Horticultural Colour Chart. Each block diagram represents a single population. Four hues are recognised and each of these can exist at a range of intensities from 0 (most intense) to 3 (least intense). Squares in the bottom right of each diagram represent dark blue petals, while squares in the top left represent pale mauvish petals. For sources of material see Appendix.

on exposure to bright light. The colour was measured in terms of hue and intensity by means of the Horticultural Colour Chart and the results are summarised in Fig. 13. This shows that *L. leonii* and *L. austriacum* tend to have darker, bluer petals than *L. perenne*. Petal colour in *L. leonii* is fairly constant but is much more variable in *L. perenne* subsp. *alpinum*, ranging from deep blue in 80A/63 to pale mauvish blue in F41. The tetraploids *L. perenne* subsp. *anglicum* and *montanum* resemble subsp. *perenne* in having paler, mauvish petals. Petal colour is not sufficiently reliable to be a diagnostic character in the *L. perenne* group, but taxa which have been recognised on other grounds may show some differences in petal colour.

CAPSULE AND SEED SIZE

Each segment of the capsule is filled by a single seed. As seed and capsule length are closely correlated there is little to be gained by measuring both characters. Capsule length has the advantage that it can be measured directly on herbarium sheets, but the disadvantage that it is less easy to measure accurately than seed length. These characters should be measured on mature seeds or capsules. Population samples tend to show more variation in capsule length than in seed length:

subsp. <i>anglicum</i> GB1	Mean	Range	Standard deviation
100 capsules	6.16 mm	5.0–7.5	0.47
100 seeds	4.71 mm	4.0–5.3	0.23

For these reasons seed length was chosen for detailed study rather than capsule length.

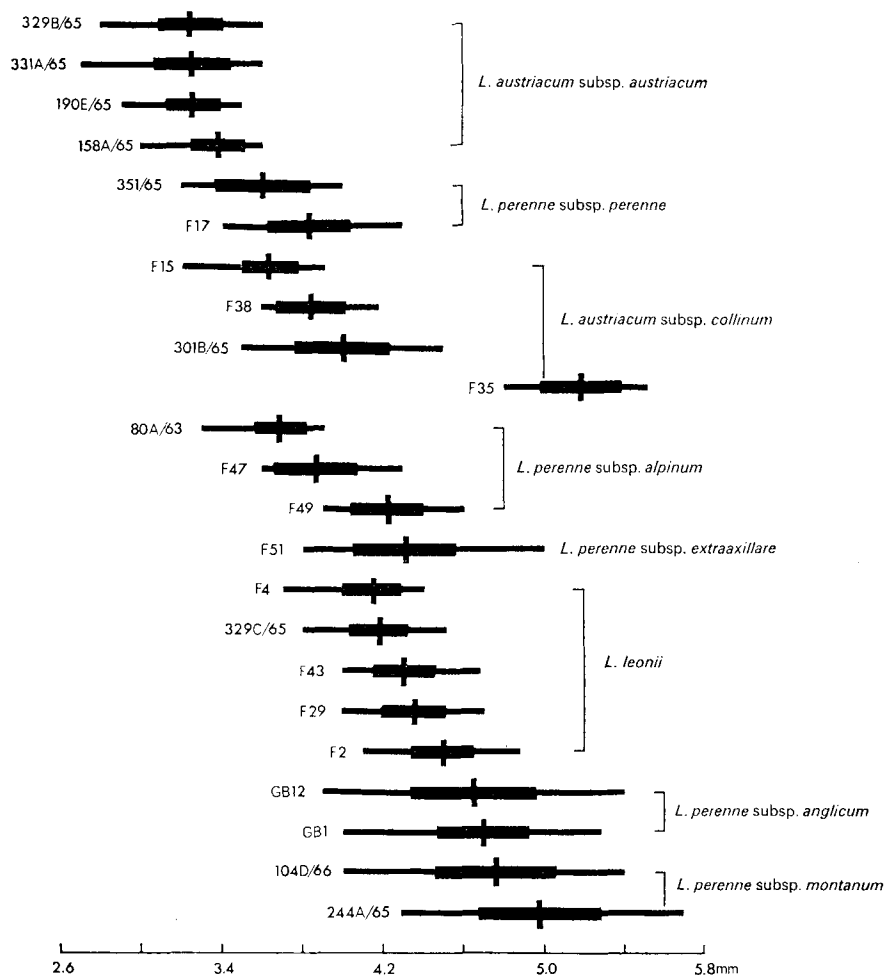


FIGURE 14. Seed length, showing mean, standard deviation and range for population samples of 50 seeds. For sources of material see Appendix.

Variation in seed length in the *L. perenne* group is virtually continuous, but the amount of variation within populations is relatively small and does not obscure the differences between populations (Fig. 14). Seed length is fairly constant in *L. austriacum* subsp. *austriacum* and *L. leonii* but varies considerably in *L. perenne* subsp. *alpinum*, and to an even greater extent in *L. austriacum* subsp. *collinum*. This parallels the marked variation between populations of *L. austriacum* subsp. *collinum* in other characters such as stem length and sepal shape. Seed length is less phenotypically plastic than most of the other morphological characters and is not correlated with overall plant size. Thus *L. leonii*, which has the shortest stem length, has relatively large seeds, while *L. perenne* subsp. *perenne* has long stems and small seeds.

Seed length can be used to distinguish *L. austriacum* subsp. *austriacum* from *L. perenne* subsp. *anglicum*, but other characters are easier to use for this. Capsule length is used in the key to separate the two species of *L. austriacum*, but as can be seen from Fig. 14, *L. austriacum* subsp. *collinum* F15 is intermediate in seed length between subsp. *austriacum* and the rest of subsp. *collinum*. *L. austriacum* subsp. *collinum* is a heterogeneous subspecies and is difficult to separate from subsp. *austriacum* in any simple way.

POSITION OF MATURE FRUIT PEDICEL

The difference between erect and patent or deflexed mature fruit pedicels (here referred to simply as 'pedicels') has long been the chief character for distinguishing *L. perenne* from *L. austriacum*. There is a complete series of pedicel positions in the *L. perenne* group but it is only feasible to distinguish a few main types (Fig. 15).

The position of the pedicel may alter considerably as the fruit matures and it is essential to compare the pedicels of mature fruits. A striking example of this is a specimen of *L. perenne* subsp. *anglicum* with immature fruit collected near Stamford on 4 July 1957, which has small capsules on patent pedicels looking just like those of *L. austriacum* subsp. *austriacum*. Specimens with mature fruit collected from the same site on 3 August 1965 have large capsules with erect pedicels.

Pedicel position is not noticeably altered by cultivation and there is no evidence of appreciable phenotypic plasticity. The species which is most difficult to recognise by its pedicels is *L. leonii*, which has erecto-patent, flexuous or patent pedicels and is intermediate between *L. perenne* and *L. austriacum* in this respect. Normally pedicel position is constant in a single plant but there are some exceptions. A single plant of *L. perenne* subsp. *alpinum* F41 has erecto-patent, flexuous and patent pedicels, this variation being almost as great as that

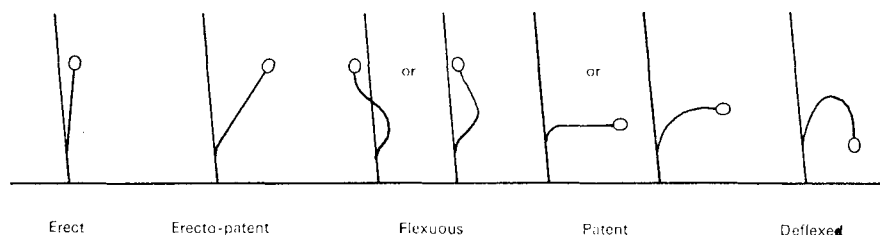


FIGURE 15. Fruiting pedicel position.

of the population from which the specimen came. Pedicel position does not correlate with any other character and is the only means of distinguishing all the subspecies of *L. perenne* from those of *L. austriacum*.

HETEROSTYLY

Although heterostyly is a morphological character, it is in some ways better considered as a morphological manifestation of the breeding system. The variation pattern shown by this character is totally different from that of the quantitative morphological characters previously considered. In the case of heterostyly there are two sharply contrasting character states, namely heterostyly, in which long- and short-styled plants occur in approximately equal numbers in a population, and homostyly, in which all plants have stigmas and stamens at about the same height. No population of *Linum* containing both heterostyled and homostyled plants has yet been reported in Europe and the character is not phenotypically plastic. It may be difficult to classify immature or malformed flowers as long-styled, short-styled or homostylous, but in the field there is no difficulty in determining whether a population is heterostylous or homostylous. As the character can be seen more easily in the field than in herbarium material, it is highly desirable that it be recorded in the field whenever a species of *Linum* is collected. Homostyly is by far the most reliable character for distinguishing *L. leonii* from *L. austriacum* and *L. perenne*. Heterostyly is an especially valuable taxonomic character in *Linum* and might well be used more in the other genera in which it occurs.

DISCUSSION

The evidence presented clearly shows that the majority of the morphological characters vary almost continuously. The minor discontinuities which are found tend to reflect discontinuities in the distribution or lack of adequate samples. Almost all the characters show some phenotypic plasticity, but this is more marked in the stem, leaf and flower characters than in seed size and pedicel position. In no case could the variation in any character be attributed to phenotypic plasticity alone, but the genetically controlled differences which do occur are often obscured by phenotypic plasticity. There is a partial correlation between the variation of some of the characters in so far that large plants tend to have longer stems, sepals and petals and broader leaves than small plants. Seed length is an exception to this in that it remains fairly constant despite wide variation in the size of the plant. The phenotypic plasticity of the *L. perenne* group may have considerable ecological significance because the group can behave as an opportunist coloniser of disturbed sites and often occupies unstable habitats where conditions such as soil depth and degree of competition are liable to change rapidly.

Differences in the amount of variation within single populations of the *L. perenne* group may be associated with particular geographical areas or with the type of breeding system. Geographically correlated differences of this type are exemplified by some of the Pyrenean populations of *L. perenne* subsp. *alpinum* which are exceptionally variable. This may have resulted from past hybridization between *L. perenne* subsp. *alpinum* and *L. austriacum* subsp. *collinum* in the Pyrenees. Artificial hybrids between these two subspecies can be made easily (Ockendon 1968a), but there is at present nowhere where they occur sufficiently

close together to produce natural hybrids. A correlation between the type of breeding system and the amount of variation within a population is exemplified by the inbreeding species *L. leonii*, which generally shows less variation within populations than do the obligatory outbreeding species *L. austriacum* and *L. perenne*.

A useful comparison can be made between the variation patterns of the *L. perenne* group in Europe and of *Hesperolinon* in California. The species of *Hesperolinon* are homostylous annuals and resemble the *L. perenne* group in occurring in highly disjunct and very localised populations and in having a restricted ecological tolerance (Sharsmith 1961). In contrast to the *L. perenne* group, the species of *Hesperolinon* can be assessed with a reasonable degree of assurance and, where two species occur sympatrically, hybridization is very rare. In *Hesperolinon* most of the populations are morphologically uniform but may be separable one from the next. The difference between the almost continuous variation in the *L. perenne* group and the clear discontinuities in *Hesperolinon* are a reflection of the fact that the former is outbreeding (except for *L. leonii*) while the latter is chiefly inbreeding.

The majority of characters which have been used in the *L. perenne* group are taxonomically unreliable because of phenotypic plasticity and genetically based variation within populations. Although statistically significant differences in these characters could often be demonstrated between populations, these are insufficient to assign a single plant to a particular population. Some characters are reliable in limited areas but break down when applied to other areas. Thus leaf width reliably separates *L. perenne* subsp. *extraaxillare* from the Tatra from subsp. *alpinum* from the Alps, but breaks down when material from Romania or the Pyrenees is considered. The morphological variation in the *L. perenne* group has arisen largely by the gradual differentiation of geographically isolated populations. This, together with widespread extinction, has given rise to the familiar situation of a series of forms which replace one another geographically, but in most cases the sharp geographical discontinuities are not marked by clear morphological discontinuities. A satisfactory taxonomic treatment of the *L. perenne* group has been achieved by rejecting many of the morphological charac-

TABLE 4. MAIN DIVISIONS OF THE *L. PERENNE* GROUP

Taxa	Breeding system	Ploidy level	Pollen type	Pedice position
<i>L. leonii</i>	Homostylous	2x	3 Furrows	Flexuous or patent
<i>L. austriacum</i>	Heterostylous	2x	3 Furrows	Patent or deflexed
<i>L. perenne</i> subsp. <i>alpinum</i> , <i>extraaxillare</i> and <i>perenne</i>	Heterostylous	2x	3 Furrows	Erect
<i>L. perenne</i> subsp. <i>anglicum</i> and <i>montanum</i>	Heterostylous	4x	6 Pores	Erect

ters which were used in the past, by emphasising the sharply discontinuous characters of the breeding system, chromosome number and pollen morphology, and by ensuring that the taxa recognised are valid in terms of their distribution and ecology. The main divisions within the group are summarised in Table 4.

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APPENDIX

L. austriacum subsp. *austriacum*

F14	Raron, Brig, Valais, Switzerland	(150)*
F18	Eichstatt, Bavaria, Germany	(400)
F20	Staffelberg, Staffelstein, Bavaria, Germany	(200)
F24	Randersacker, Würzburg, Bavaria, Germany	(600)
125B/65	Letea, Tulcea, Romania	
158C/65	Budapest, Hungary	
190E/65	Kyffhäuser, Thüringen, Germany	
308A/65	Hungary	
329B/65	Suad, Romania	
331A/65	Hovblege, Mön, Denmark	
331B/65	Illmitz, Burgenland, Austria	

L. austriacum subsp. *collinum*

F10	Puy Crouel, Clermont-Ferrand, Puy-de-Dôme, France	(300)
F11	Cournon d'Auvergne, near Clermont-Ferrand, France	(5)
F15	Mt. Spaccato, Trieste, Italy	
F32	Gap, Hautes Alpes, France	(20)
F35	Villefranche-de-Confluent, Pyrénées Orientales, France	(400)
F38	Bellver de Cerdàña, near Seo de Urgel, Spain	(1000)
301B/65	Capo di Noli, Liguria, N. Italy	

L. leonii

F1	Flohiment, Ardennes, France	(50)
F2	Thierville, near Verdun, Meuse, France	(30)
F3	Côte Quaraille, Noveant, near Metz, Moselle, France	(20)
F4	Montenach, near Sierck, Moselle, France	(100)
F5	St Mihiel, Meuse, France	(50)
F6	Bovée sur Barboure, Meuse, France	(3)
F8	Malesherbes, Loiret, France	(100)
F9	Chapelle-St-Ursin, near Bourges, Cher, France	(100)
F21	Böttingheim, Taubertal, Württemberg, Germany	
F26	Neuville-sur-Seine, near Troyes, Aube, France	(2)
F28	Gamay, near Chagny, Côte d'Or, France	(1000)
F29	Santannay, near Chagny, Côte d'Or, France	(1000)
F43	Chaumes de Souberac, near Jarnac, Charente, France	(60)

* Figures in brackets are approximate numbers of individuals at each locality.

L. perenne subsp. *alpinum*

- F13 Plateau d'Assy, near St. Gervais, Haute Savoie, France. 900 m
 F30 Lac du Crozet, near Revel, Isère, France. 1950 m
 F31 Col de Glaize, Gap, Hautes Alpes, France. 1950 m
 F33 Mt Charance, Gap, Hautes Alpes, France. 1800 m
 F34 Pic de Costabonna, Prats de Mollo, Pyrénées Orientales, France. 2000 m
 F36 Val d'Eyne, Pyrénées Orientales, France. 2000 m
 F41 Valle de Aran, near Tredos, Lerida, Spain. 2000 m
 F42 Mt. Ceciré, near Luchon, Haute Garonne, France. 2000 m
 F47 Mt. Maggiorasca, near Genova, Italy. 1800 m
 F49 Bansky suchodol, Pirin Mountains, Bulgaria. 2600 m
 F50 Val Fredda, Gran Sasso, Abruzzi, Italy. 1550 m
 80/63 Grenairon, near Martigny, Haute Savoie, France. 2100 m

L. perenne subsp. *anglicum*

- GB1 Gog Magog Hills, Cambridge, England (1000)
 GB2 Babraham Hall Estate, Cambridge, England (500)
 GB5 Lakenheath Warren, Suffolk, England (70)
 GB6 Great North Road, Stamford, Lincolnshire, England (30)
 GB8 Sherburn Wold, East Riding, Yorkshire, England (150)
 GB10 West Cornforth, Co. Durham, England (300)
 GB11 Tunstall Hill, Sunderland, Co. Durham (30)
 GB12 Brighthouse Bay, Kirkcudbrightshire, Scotland (500)
 GB13 Crosby Ravensworth, Westmorland, England (15)

L. perenne subsp. *extraaxillare*

- F51 Chalet Hvezdon, Tatra, Czechoslovakia. 1600 m
 131F/63 Orava, Czechoslovakia
 75/65 Košice, Czechoslovakia

L. perenne subsp. *montanum*

- F12 Le Rozet, Thoiry, Ain, France. 850 m
 79/65 Crozet, Ain, France. 1300 m
 244A/65 Mt Dôle, Vaud, Switzerland
 104D/66 Col de Crozet, Ain, France. 1500 m

L. perenne subsp. *perenne*

- F17 Garchinger Heide, Eching, Munich, Bavaria, Germany (600)
 F25 Pfungstädter Düne, near Darmstadt, Hessen, Germany (150)
 351/65 Pfatter, near Regensburg, Bavaria, Germany