WESTERN AUSTRALIAN DEPARTMENT OF AGRICULTURE

technical bulletin

No. 26

ISSN 0083-8675
WAGDEX 142/06

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Manuscript received March 25, 1974.

LUPINS OF THE MEDITERRANEAN REGION AND AFRICA

by J. S. Gladstones

SUMMARY

Twelve European and African species of *Lupinus* are recognized, including one new species *L. atlanticus.* A key is given, followed by a more detailed description of each species, its synonymy, and comments on its natural distribution, ecology, and range of variability. Selected herbarium specimens in the collection of the Royal Botanic Gardens, Kew (all seen by the author) are cited for each taxon.

Because of the extreme confusion in the literature regarding some species, full lists of literature references are given where identity could reasonably be established. Pre-Linnaean synonyms and references are included for their historical interest and because in some cases they bear directly on later taxonomic problems.

The possible phylogenetic history of lupins in the Mediterranean region and Africa is discussed, together with evidence on their more recent evolution. It is suggested that lupins are of ancient use as food plants, both by pre-agricultural and proto-agricultural communities, but that since the neolithic revolution they have been by-passed in favour of other leguminous genera better adapted to fertile soils and more amenable to domestication. With the present growing need to farm the world's poorer soil types, lupins may again come into prominence as a food crop in climatically suitable regions.

Technical Bulletin No. 26, December, 1974.

Department of Agriculture of Western Australia.

INTRODUCTION

The taxonomy of *Lupinus* in Europe and Africa has long been in confusion. As far as I am aware no serious attempt has been made in modern times to resolve this. Zhukovsky's (1929) account of the group is the most complete and authoritative available, but does not attempt any basic taxonomic revision, and being in Russian has not been readily accessible to most Western workers. The various regional floras of the last 150 years cover only restricted numbers of species. The recent Flora Europaea (Vol. 2, 1968) gives a more complete coverage (several solely African species are excluded), and does make some taxonomic amendments. However certain of these, in my opinion, are wrong and compound past mistakes.

It became clear in the course of the study that much of the present taxonomic disagreement derives from mistakes and misunderstandings going back to the earliest years of Linnaean taxonomy. These were traced as far as possible, in some cases into the pre-Linnaean literature, to give a historical as well as cytotaxonomic basis for the revisions proposed. Examination of the pre-Linnaean literature also made possible a brief account of the early history of lupin taxonomy and cultivation in Europe.

The growing importance of the large-seeded lupins as a source of edible protein (Gladstones, 1970) makes it imperative that their taxonomy be clarified, and the natural distribution and ecological ranges of the different species established. Only on such a basis can meaningful studies be carried out on their genetics, inter-specific relations, potential ranges of agronomic adaptation, and potential for further improvement as agricultural plants. The present study was carried out principally to fill this need.

KEY TO THE MEDITERRANEAN AND AFRICAN SPECIES OF LUPINUS

1. Seeds smooth.
    2. Lower flowers of inflorescences alternate.
        3. Upper lip of calyx entire; seeds ± square, compressed; flowers white to violet-blue. Native in Balkan Peninsula, cultivated throughout Mediterranean and elsewhere.
        1. L. albus L.
        3. Upper lip of calyx deeply 2-partite; flowers normally blue.
            4. Leaflets linear; lower lip of calyx entire to slightly 3-toothed; seeds round; plant sparsely sericeous. Mediterranean and S.W. France, elsewhere cultivated and naturalized.
            2. L. angustifolius L.
            4. Leaflets short and broad; lower lip of calyx deeply 3-toothed; seeds lenticular or compressed, brownish; plant coarsely hirsute. Mediterranean.
            3. L. micranthus Guss.
    2. Flowers fully verticillate.
        5. Flowers golden yellow, scented; upper surface of leaflets villous. Mainly W. Mediterranean, elsewhere cultivated and naturalized.
        4. L. luteus L.
        5. Flowers cream to mauve, not scented; upper surface of leaflets ± glabrous. S, Central, W and N.W. Spain, Portugal.
        5. L. hispanicus Boiss. et Reuter

1\. Seeds rough; flowers subverticillate to verticillate, usually blue.

6\. Hairs on stems ≲ 1 mm; pedicels ≲ 1/3 length of calyx, rigid; both surfaces of leaflets sericeous.

7\. Lower lip of calyx shallowly 3-toothed; tip of keel blunt, pigmented blue; seeds about 8 x 6 x 3 mm, brown or greyish with blackish markings. N.W. Africa and W. Mediterranean, coastal districts only; cultivated and naturalized in W. and S. Australia.

6. L. cosentinii Guss.

7\. Lower lip of calyx ± entire; tip of keel pointed, not pigmented blue.

8\. Pods 9-12 mm broad; seeds about 7 x 6 x 3 mm, mottled reddish brown with a smooth hump over the hilum. Egypt, Central and Western Sahara, Senegal.

7. L. digitatus Forskål

8\. Pods 16-18 mm broad; seeds about 10 x 8 x 4 mm, mottled reddish brown on pale yellow. E. African Highlands.

8. L. princei Harms

6\. Hairs on stem > 1 mm; lower lip of calyx entire.

9\. Hairs on stem 3-4 mm; pedicel ≳ ½ length of calyx, lax.

10\. Flowers very large, deep blue (rarely pink) with a white band up the centre of the standard; leaflets softly villous; seeds 10-14 x 9-12 x 6-8 mm, mottled brownish red; plants erect. E. Mediterranean, elsewhere occasionally cultivated.

9. L. pilosus Murray

10\. Flowers pale yellow to pale pink, tinged with blue; leaflets sericeous; seeds slightly smaller than 9, mottled brown; plants rosetted. S. Israel and Sinai Peninsula.

10. L. palaestinus Boiss.

9\. Hairs on stem 1-2 mm; pedicel ≲ ½ length of calyx, rigid.

11\. Leaflets sericeous; pedicel ≲ ⅓ length of calyx; standard with a central white band, broadening towards the upper margin; seeds about 8-11 x 6-8 x 5 mm, mottled brown to pinkish brown with a smooth hump over the hilum. N.W. Africa, in the High Atlas foothills and Anti Atlas.

11. L. atlanticus Gladstones

11\. Upper surface of leaflets glabrous; pedicel about ½ length of calyx; rounded white spot on standard, not approaching the upper margin. Highlands of Somaliland, possibly Ethiopia.

12. L. somaliensis Baker

1. L albus L.

L., *Sp. Pl.* 721 (1753); **Kniphof, *Herb. Viv.* t.667 (1761); Murray in L., *Syst. Veg.* ed.13, 545 (1774); Desr. in Lam., *Encycl. Méth. Bot.* 3:621 (1791); Willd., *Sp. Pl.* ed.4, 3:1022 (1803); Brot., *Fl. Lusit.* **2**:132 (1804); Lam. & DC., *Fl. Fr.* ed.3, 4:506 (1805); DC., *Prodr.* **2**:407 (1825); Guss., *Fl. Sic. Prodr.* **2**:396 (1828); Reichenb., *Fl. Germ. Excurs.* 539 (1832); Mutel, *Fl. Fr.* **1**:315 (1834); Agardh, *Syn. Gen. Lup.* 9 (1835); Ten., *Fl. Nap.* 5:99 (1835); Bertol., *Fl. Ital.* 7:412 (1847); Pouzolz, *Fl. Gard* 1:213 (1856); Boiss., *Fl. Or.* 2:29 (1872); Willk & Lange, *Prodr. Fl. Hisp.* 3:466 (1880); Arcangeli, *Comp. Fl. Ital.* 154 (1882); Colmeiro, *Pl. Hisp. Lusit. Bal.* **2**:82 (1886); Tornabene, *Fl. Aetnea* **2**:15 (1890); *Lojac., Fl. Sic.* **1** (2):32 (1891); Caruel in Parl., *Fl. Ital.* **10**:111 (1894); Rouy & Fouc., *Fl. Fr.* **4**:191 (1897); *Fiori & Paol., *Fl. Anal. Ital.* **2**:10, fig. 1864 (1899); *Coste, *Fl. Fr.* **1**:308 (1901); Halácsy, *Consp. Fl. Graec.* **1**:341 (1901); Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* **22**:36, t.10, II (1903); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):229 (1907); Briq., *Prodr. Fl. Corse* **2**:233 (1913); Coutinho, *Fl. Port.* 314 (1913); **Bonnier, *Fl. Compl. Fr.* **3**:8, t.638 (1914); Thompson, *Fl. Pl. Riviera* 76 (1914); Cadevall, *Fl. Catalunya* **2**:52 (1915); Hegi, *Ill. Fl. Mitteleur.* **4**:1153, fig. 1307 (1923); Bailey, *Man. Cult. Pl.* 408 (1924); Fiori, *Nuov. Fl. Anal. Ital.* **2**:804 (1925); *Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:270, figs. 13, 13a (1929); Foury, *Cah. Rech. Agron.* **3**:59 (1950); Gladstones, *J. Roy. Soc. W. Aust.* **41**:31 (1958a); *Hanelt, *Lupinen* 10, figs. 2-4, 12 (1960); *Abbe, *Pl. Virg. Georg.* 121 (1965); Franco & Silva, P. in Tutin *et al.*, *Fl. Europ.* **2**:105 (1968); Chamberlain in Davis, *Fl. Turkey* **3**:38 (1970); *Gladstones, *Lup. W. Aust.* 29 (1972); *Zohary, *Fl. Palaestina* **2**:42, t.55 (1972).

Holotypus: Linnaean Collection 898.2 (Linn).

L. Termis Forskål, *Fl. Aegypt* 131 (1775); Willd., *Sp. Pl.* ed.4. **3**:1023 (1803); Guss., *Fl. Sic. Prodr.* **2**:397 (1828); Agardh, *Syn. Gen. Lup.* 10 (1835); Ten., *Fl. Nap.* **5**:99 (1835); Moris, *Fl. Sard.* **1**:596 (1837); Bertol., *Fl. Ital.* **7**:411 (1847); Gren. & Godron, *Fl. Fr.* **1**:365 (1848); Lowe, *Man. Fl. Madiera* 119 (1868); *Cusin & Ansberque, *Herb. Fl. Fr.* **6**, t.967 (1870); Oliver, *Fl. Trop. Afr.* **2**:44 (1871); Boiss., *Fl. Or.* **2**:29 (1872); Tornabene, *Fl. Aetnea* **2**:18 (1890); Lojac., *Fl. Sic.* **1**(2):32 (1891); Post, *Fl. Syr. Pal. Sin.* 213 (1896); Halácsy, *Consp. Fl. Graec.* **1**:341 (1901); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):230 (1907); Muschler, *Man. Fl. Egypt* 474 (1912); Baker, *Leg. Trop. Afr.* **1**:60 (1926); Bouloumoy, *Fl. Lib. Syr.* 77 (1930); Thiébaut, *Fl. Lib.-Syr.* **2**:7 (1940); Montasir & Hassib, *Man. Fl. Egypt* 231 (1956); Plitmann, *Isr. J. Bot.* **15**:26 (1966).

Typification: "In Delta ad pagum Nedjel. Copiose in agris, an spontaneus, nescio." Type not seen.

L. sativus Gaterau, *Descr. Pl. Montauban* 126 (1789).
L. prolifer Desr. in Lam., *Encycl. Méth. Bot.* **3**:622 (1791); Brot., *Fl. Lusit.* **2**:132 (1804).
L. bivonii Presl, *Fl. Sic.* **1**:24 (1826).
L. thermis Gaspar., *Atti Acc. Nap.* **6**:229, t.10 (1851).
L. thermus St. Lager, *Ann. Soc. Bot. Lyon* **7**:129 (1880).
L. hirsutus auct. non L.: Eichwald. *Plant. Casp. Cauc.* 23 (1833).
L. varius auct. non L.: Lojac., *Fl. Sic.* **1**(2):34 (1891); Arcangeli, *Comp. Fl. Ital.* ed.2, 479 (1894).

Pre Linnaean Synonyms

Sativus lupinus—*Lob., *Obs.* 514 (1576).
Lupinus sativus—*Dod., *Hist.* part 4 Book II, 520 (1583); **Cam., *Kreut.* 125 (1611); *Ger., *Herb.* 1217-8 (1633); Ray. *Hist.* **1**:906 (1686).
Lupinus—*Tab., *Kreut.* **2**:198 (1591); *Bauh., *Matth.* 344 (1598); **Blackw., *Herb.* **3**, t.282 (1757); *Ludw., *Egypta Veg.* t.191 (1760).
Lupinus sativus albo flore—*Clus., *Hist.* CCXXVIII (1601).
Lupinus vulgaris flore albo—*Besl., *Eyst.* **2** ord. 13, 4 (1613).
Lupinus sativus flore albo—Bauh., *Pin.* 347 (1623); Herm., *Lugd.* 386 (1687); Cup., *Hort. Cath.* 117 (1696); Tourn. *Inst.* 392 (1719); Boerh., *Lugd.* **2**:48 (1720); Miller, *Dict.*, no 6 (1754); Quer, *Fl. Espanola* **5**:373 (1784).
Lupinus sativus albus—Park., *Paradisus* 335 (1629); *Park., *Theat.* 1073-4 (1640).
Lupinus alter albus—Park., *Theat.* 1073 (1640).
Lupinus vulgaris semine et flore albo, sativus—*Bauh., *Hist.* **2**:288 (1651); Magnol, *Hort. Monsp.* 124 (1697).
Lupinus albus sativus flore & semine albo—Morison, *Hist.* **2**:88 (1680).
Lupinus flore albo—*Riv., *Tetrap.* t.151 (1691).
Lupinus caule composito—Linn., *Hort. Cliff.* 359 (1737).
Lupinus calycibus alternis absque appendiculatis—Linn., *Hort. Cliff.* 499 (1737); Ferber, *Hort. Ager.* 56 (1739); Linn.. *Hort. Ups.* 209 (1748).
Lupinus calycibus alternis, appendiculis lateralibus nullis—Roy., *Lugd.* 366 (1740).

Annual 30-120 cm high, at flowering branching from ± 3 nodes immediately below the inflorescences. Stems and petioles sparsely sericeous. Stipules subulate, setaceous, concrescent with the petioles over 1/3 of their length. Leaflets 5-9, 20-60 x 12-20 mm, oblong-obovate, mucronulate, ± glabrous above, villous below, margins ciliate. Racemes subsessile, 5-30 cm long; lower flowers alternate, upper flowers subverticillate, on short (1-2 mm) pedicels; bracts caducous, bracteoles small or absent. Calyx lobes of almost equal length, upper lip entire, lower lip entire or slightly 3-toothed. Corolla 15-16 mm long x 12-14 mm high, white

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* Indicates black and white illustration. ** Indicates coloured illustration.

variably tinged with blue or violet, or violet blue with a white centrobasal spot on the standard; not scented. Pods 70-150 x 12-20 mm, villous, glabrescent and longitudinally rugulose when drying, 3-6 seeded. Seeds 8-14 x 6-12 x 2-5 mm, ± square, compressed; testa smooth, white variably tinged salmon pink, or mottled dark brown.

Chromosome number n = 25.[1]

Corolla white variably tinged violet or blue; pods non-shattering at maturity; seeds pinkish white or white, with permeable testa.

1a. var. albus

Corolla dark violet-blue with white centrobasal spot on standard; pods shattering at maturity; seeds mottled dark brown with impermeable testa.

1b. var. graecus

1a. var. **albus**

Erect-growing plants. Corolla white variably tinged violet or blue. Pods very large, 90-150 x 16-20 mm, non-shattering at maturity. Seeds very large, 10-14 x 8-12 x 3-5 mm, white variably tinged salmon pink, with permeable testa.

DISTRIBUTION: Cultivated, occasionally as a volunteer, throughout Mediterranean region, Upper Nile, Madeira and Canary Is.—Map 1, on mildly acid or neutral soils of light to medium texture. Occasionally cultivated in Central and S.E. Europe, Georgia (U.S.S.R.), S. Africa, Australia, S. America, and S.E. United States.

SPAIN: Algeciras, Willkomm 600.[2] PORTUGAL: Faro, Bourgeau 1818. CORSICA: Bastia, Mabille; Evisa, Reverchon 250. SICILY: Palermo, Todaro 753. CRETE: Rechinger fil. 13693. EGYPT: Bot. Mus. Zürich 309. SUDAN: Wadi Shellai, Schweinfurth 948. ABYSSINIA: Schimper 1536; Evans & Lythgoe 3. CANARY IS.: Sprague & Hutchinson 458.

Var. *albus* represents the cultivated section of the species and agrees well with the Linnaean type. It almost certainly developed under cultivation by selection from var. *graecus,* some time before Roman times (see discussion below).

1b. var. **graecus** (Boiss. & Spruner) J. S. Gladstones, stat. nov.

L. graecus Boiss. & Spruner in Boiss., *Diagn. Plant. Or. Nov.* **2**:15 (1843); Boiss., *Fl. Or.* **2**:30 (1872); Halácsy, *Consp. Fl. Graec.* **1**:341 (1901); Zhukovsky, *Bull. appl. Bot. Pl. Breed.* **21**:273 (1929).

Typification: "Hab. in cultis Graeciae, inter Spartam et Mistra legi Aprili 1842." Type not seen.

L. jugoslavicus *Kazimierski & Nowacki, *Genet. polon.* **2**:115 (1961).

L. vavilovi Atabekova & Maissurjan, *Izv. Timirjazev. sel'skohozjajstv. Akad.* **44**(1):239 (1962).

L. albus ssp. *graceus* (Boiss. & Spruner) Franco & Silva, P., *Feddes Repert.* **79**:52 (1968) and in Tutin et al., *Fl. Europ.* **2**:105 (1968); Chamberlain in Davis, *Fl. Turkey* **3**:39 (1970).

Growth rosetted prior to flower initiation, semi-erect thereafter. Corolla dark blue with centrobasal white spot on the standard. Pods 60-80 x 11-14 mm, shattering at maturity. Seeds 7-10 x 6-8 x 2-3 mm, mottled dark brown, with impermeable testa.

DISTRIBUTION: Greece and Crete, Albania, S. Yugoslavia, perhaps W. Asia Minor—Map 1.

GREECE: Laconia near Platanos, Orphanides 619; Macedonia, Gamble 30836. ALBANIA: above Gjinokastrë, Alston and Sandwith 1504.

Although *L. termis* Forskål is now generally accepted as synonymous with *L. albus* L., the taxonomic status of var. *graecus* has remained undecided. Most authors using the name *L. graecus* have regarded it as a distinct species. Franco and da Silva (1968a, 1968b) accord it subspecific status. However, even this is

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[1] Recorded chromosome numbers for the different species are tabulated in Appendix 1.

[2] The selected specimens cited for each taxon are all present in the herbarium collection by the Royal Botanic Gardens, Kew, and have been seen by the writer.

probably not justified, despite a superficially different appearance and distribution. Var. *albus* has become distributed as a cultivated plant, and persists only as a very transient escapee from cultivation in most areas. No "natural" distribution has been established, beyond the fact that its common name "turmus" (or some variant of it) is more or less universal throughout the Middle East and probably derives from the Greek "thermos", which points to a Greek origin. The morphological and physiological differences which distinguish var. *albus* from var. *graecus* are such as would have been selected during domestication: non-shattering pods, permeable seed coats, larger and lighter-coloured seeds, and more erect growth and earlier flowering. Parallel changes have been wrought in other lupin species by plant breeders in recent years and are simply inherited (for review see Gladstones 1970). Most of the differences between *L. albus* and *"L. jugoslavicus"* have been shown by Kazimierski (1960, 1961, 1963, 1964a) to be simply inherited and under the control of relatively few genes. Nor has any sign of sterility been found in the hybrids.

Such changes in no way meet the normal botanical criteria for subspeciation. In the botanical sense we are here dealing merely with two varieties within the species, var. *albus* representing the cultivated form and var. *graecus* the wild ancestral form.

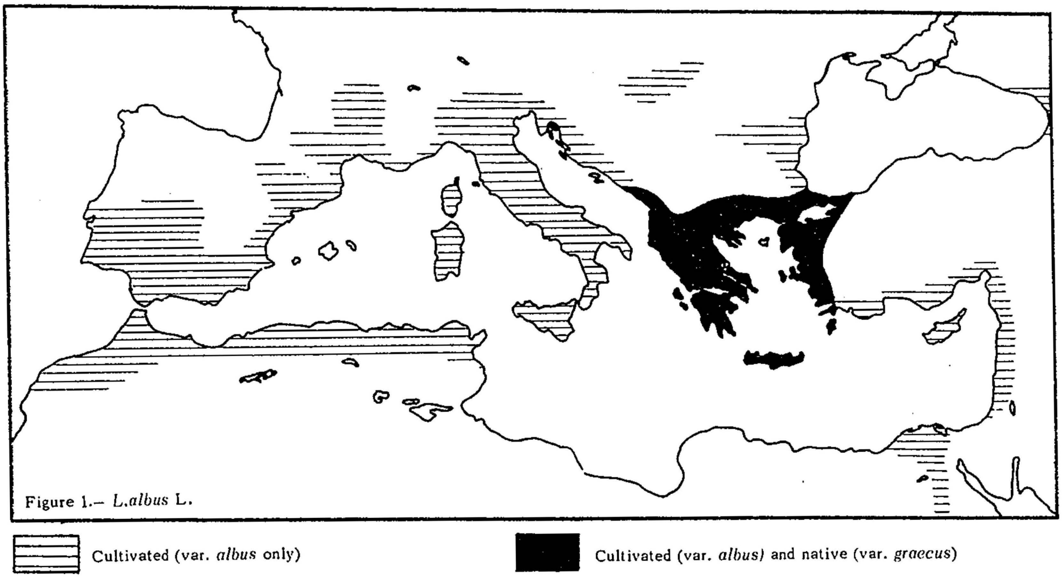
Figure 1.– *L.albus* L.

Subdivision of the wild Balkan types into two "oecospecies", *L. jugoslavicus* (= *vavilovi*) and *L. graecus* (Kazimierski 1963; Aniol, Kazimierski and Nowacki 1968), appears to be based on a misconception. These authors characterize *jugoslavicus* as having brown-mottled seeds, and *graecus* as similar but with white seeds. In fact, available descriptions of *"L. graecus"* which include seed characteristics (Halácsy 1901; Zhukovsky 1929) show it clearly to have mottled seeds. *"L. jugoslavicus"* is therefore essentially identical with *"L. graecus"*. The white-seeded form referred to by Aniol, Kazimierski and Nowacki is presumably an intermediate between var. *graecus* and var. *albus.* The presence of such intermediates in the Balkan Peninsula would not be surprising, in view of the probable very recent origin there of the cultivated forms of *L. albus,* together with the lack of any sterility barriers and the fact that *L. albus* undergoes a considerable amount of natural cross-pollination (author's field observation).

L. albus is the oldest-established cultivated species among the Mediterranean and African lupins. The Greek writer Theophrastus (d. 287 B.C.) described in his Enquiry into Plants (Book 8.XI.8) its use at that time in Greece, while Varro (Book 1.XXIII.3) and Columella (Book 2.X.2 and elsewhere) refer to its value and extensive use in Rome of the 1st centuries B.C. and A.D. The Ancients used *L. albus* for green manure, and the seeds for cattle feed and human consumption after steeping to remove the water-soluble alkaloids. Greek and various subsequent authors also describe extensive use of the seeds for medicinal and cosmetic purposes. Zhukovsky (1929) states that seeds of "*L. termis*" were found by Schiaparelli in 1868 in Egyptian tombs of the 12th Dynasty (about 2 000 B.C.). Probably the species was first cultivated in the Aegean area by early Greek or pre-Greek civilizations, and carried thence, together with its name, to surrounding regions.

Present-day use of *L. albus* in the Mediterranean region hardly differs from that described by the early Greek and Roman writers. It is now little used for green manuring, except under special conditions such as in irrigated rice fields. Elsewhere, cultivation is largely confined to poorer peasant farms, where it is commonly grown on small areas for domestic consumption. Some seed enters commerce for use (after steeping and salting) as an appetiser or snack in cafés and bars.

Some physiological variability is known to occur within var. *albus*. Cultivars from the northern and western Mediterranean have large seeds, large leaves and strong stems, and are relatively tall and late-flowering. Their flowers are more or less white. Cultivars from the South-East Mediterranean tend to be earlier-flowering, finer, smaller-seeded, and to have bluish-tinged flowers, thus conforming with the description of *L. termis* Forsk.

The recent history of *L. albus* in cultivation and its modern development as a crop plant have been described elsewhere (Gladstones 1970).

2. **L. angustifolius** L.

L., *Sp. Pl.* 721 (1753); Murray in L., *Syst. Veg.* ed.13, 545 (1774); Desr. in Lam., *Encycl. Méth. Bot.* **3**:624 (1791); Willd., *Sp. Pl.* ed.4, **3**:1024 (1803); Brot., *Fl. Lusit.* **2**:132 (1804); Lam. & DC., *Fl. Fr.* ed. 3, **4**:507 (1805); Later., *Fl. Bord.* ed.2, 315 (1821), & ed. 4, 159 (1846); DC., *Prodr.* **2**:407 (1825); Guss., *Fl. Sic. Prodr.* **2**:402 (1828); **Sibth. & Sm., *Fl. Graeca* **7**:78 & t.685 (1830); Reichenb., *Fl. Germ. Excurs.* 539 (1832); Mutel, *Fl. Fr.* **1**:315 (1834); Agardh, *Syn. Gen. Lup.* 12 (1835); Ten., *Fl. Nap.* **5**:99 (1835); Koch, *Fl. Germ. Helv.* 157 (1837); Moris, *Fl. Sard.* **1**:599 (1837); Noulet, *Fl. Sous-Pyr.* 176 (1837); Bertol., *Fl. Ital.* **7**:415 (1847); Gren. & Godron, *Fl. Fr.* **1**:367 (1848); Pouzolz, *Fl. Gard* **1**:214 (1856); **Cusin & Ansberque, *Herb. Fl. Fr.* **6**, t.970 (1870); Boiss., *Fl. Or.* **2**:28 (1872); Loret & Barrandon, *Fl. Montp.* 151 (1876); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:466 (1880); Arcangeli, *Fl. Ital.* 154 (1882); Colmeiro, *Pl. Hisp. Lusit. Bal.* **2**:84 (1886); Batt. & Trabut, *Fl. Algér.* (*Dicot.*) 208 (1889); Tornabene, *Fl. Aetnea* **2**:18 (1890); Lojac., *Fl. Sic.* **1**(2):35 (1891); Caruel in Parl., *Fl. Ital.* **10**:108 (1894); Post, *Fl. Syr. Pal. Sin.* 212 (1896); Rouy & Fouc., *Fl. Fr.* **4**:193 (1897); *Fiori & Paol., *Fl. Anal. Ital.* **2**:10, fig. 1863 (1899); Halácsy, *Consp. Fl. Graec.* **1**:340 (1901); *Coste, *Fl. Fr.* **1**:308 (1901); Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* **22**:37, t.10, I (1903); Merino, *Fl. Galic.* **1**:410 (1905); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):231 (1907); Muschler, *Man. Fl. Egypt* 474 (1912); Briq., *Prodr. Fl. Corse* **2**:233 (1913); Coutinho, *Fl. Port.* 315 (1913); **Bonnier, *Fl. Compl. Fr.* **3**:9, t.641 (1914); Thompson, *Fl. Pl. Riviera* 76 (1914); Cadevall, *Fl. Catalunya* **2**:53 (1915); *Hegi, *Ill. Fl. Mitteleur.* **4**:1158, fig. 1312 (1923); Fiori, *Nuov. Fl. Anal. Ital.* **1**:804 (1925); *Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:267, figs. 12, 12a (1929); Bouloumoy, *Fl. Lib. Syr.* 77 (1930); Jahandiez & Maire, *Cat. Pl. Maroc* 348 (1932); Thiébaut, *Fl. Lib.-Syr.* **2**:8 (1940); Foury, *Cah. Rech. Agron.* **3**:59 (1950); Montasir & Hassib, *Man. Fl. Egypt* 231 (1956); Tackholm, *Stud. Fl. Egypt* 276 (1956); Gladstones, *J. Roy. Soc. W.Aust.* **41**:31 (1958a); Hanelt, *Lupinen* 46, figs. 14-16 (1960); **Polunin & Huxley, *Fl. Med.* 92, pl. 52 (1965); Plitmann, *Israel J. Bot.* **15**:26 (1966); Franco & Silva, P. in Tutin *et al.*, *Fl. Europ.* **2**:105 (1968); Chamberlain in Davis, *Fl. Turkey* **3**:39 (1970); *Zohary, *Fl. Palaestina* **2**:43, t.57 (1972); *Gladstones, *Lup. W. Aust.* 5-7, 28 (1972).

Holotypus: Linnaean Collection 898.7 (Linn).

L. varius L., *Sp. Pl.* 721 (1753) (*sensu* diagnosis and synonyms, not Linnaean specimens so labelled); Goüan, *Hort. Monsp.* 362 (1762), & *Fl. Monsp.* 183 (1765); Murray in L., *Syst. Veg.* ed.13, 545 (1774); Savi, *Fl. Pisana* **2**:178 (1798); Willd., *Sp. Pl.* ed.4, **3**:1023 (1803); Lam. & DC., *Fl. Fr.* ed.3, **4**:507 (1805); Laterrade, *Fl. Bord.* ed.1, 189 (1811), and ed.2, 315 (1821); Ten., *Fl. Nap.* **2**:141 (1820); Maratti, *Fl. Romana* **2**:120 (1822);

DC., *Prodr.* **2**:407 (1825); Balbis, *Fl. Lyon.* **1**:226 (1827); Reichenb., *Fl. Germ. Excurs.* 539 (1832); Mutel, *Fl. Fr.* **1**:315 (1834); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):227 (1907).

Typification: "Habitat: Messanae, Monspelii inter segetes." The two Linnaean specimens labelled *L. varius* are discordant with both diagnosis and synonyms and with each other. No. 898.3 is identical with *L. pilosus* Murr. and 898.4 with *L. micranthus* Guss. *sensu* this paper.

L. sylvestris Lam., *Fl. Fr.* **2**:627 (1778) (α only); All., *Fl. Pedem.* **1**:332 (1785).

L. linifolius Roth, ***Bot. Abh.* 14, t.5 (1787); Willd., *Sp. Pl.* ed.4, **3**:1025 (1803); Ten., *Fl. Nap.* **2**:141 (1820); Guss., *Fl. Sic. Prodr.* **2**:402 (1828); Reichenb., *Fl. Germ. Excurs.* 539 (1832); Agardh, *Syn. Gen. Lup.* 13 (1835); Boreau, *Fl. Cent. Fr.* ed.2, 152 (1849); Tornabene, *Fl. Aetnea* **2**:20 (1890); *Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* **22**:37, t.11 (1903).

L. reticulatus Desv., *Ann. Sc. Nat.* ser.2, **3**:100 (1835); Gren. & Godron, *Fl. Fr.* **1**:366 (1848); Boiss., *Fl. Or.* **2**:29 (1849); **Cusin & Ansberque, *Herb. Fl. Fr.* **6**, t.969 (1870); Loret & Barrandon, *Fl. Montp.* 151 (1876); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:467 (1880); Post, *Fl. Syr. Pal. Sin.* 212 (1896); *Coste, *Fl. Fr.* **1**:308 (1901); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):230 (1907); Tourlet, *Cat. Pl. Vasc. Indre-et-Loire* 114 (1908); Thompson, *Fl. Pl. Riviera* 76 (1914).

Typification: "Hab. in subulosis Andegavorum." Type not seen.

L. leucospermus Boiss., *Diagn. Pl. Or. Nov.* no. 9, 8 (1849); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:467 (1880).

L. philistaeus Boiss., *Diagn. Pl. Or. Nov.* no. 9, 9 (1849).

L. cryptanthus Shuttlew., ex Campbell, *Enum.* 8 (1872); Thompson, *Fl. Pl. Riviera* 76 (1914).

Typification: "Entre (?) Mobrierer & Bormes" (S.E. France).
Holotypus: K.

L. opsianthus Atab. et Maiss., *Bjull. glav. bot. Sad. Akad. Nauk. SSSR,* 1968, 75 (1968).

Pre-Linnaean Synonyms

Segetum sylvestris Lupinus flore purpureo—*Lob. *Kruydt.* **2**:74 (1581).
Lupinus sylvestris β—Dod. *Hist.* Part 4 Book II, 521 (1583).
Lupinus minor—*Tab. *Kreut.* **2**:198 (1591).
Lupinus caeruleo flore angustifolius—*Bauh., *Matth.* 345 (1598).
Lupinus flore coeruleo—*Clus., *Hist.* CCXXVIII (1601); *Ger. *Herb.* 1217-8 (1633).
Lupinus sylvestris flore coeruleo—**Cam., *Kreut.* 126 (1611).
Lupinus sylvestris angustifolius flore coeruleo—*Besl., *Eyst.* **2** ord. 13, 3 (1613).
Lupinus minimus—Bauh., *Prodr.* 148 (1620).
Lupinus sylvestris—Bauh., *Pin.* 348 (1623).
Lupinus caeruleus minor—Park., *Paradisus* 335 (1629); Ray, *Hist.* **1**:907 (1686).
Lupinus minimus caeruleus—Park., *Theat.* 1073 (1640).
Lupinus Gadensis marinus flore caeruleo—Park., *Theat.* 1075 (1640).
Lupinus sylvestris, purpureo flore, semine rotundo vario—*Bauh., *Hist.* **2**:290 (1651); Magnol, *Bot. Monsp.* 176 (1676); Miller, *Dict.*, no. 1 (1754); Quer, *Fl. Espanola* **5**:374 (1784).
Lupinus peregrinus minor sive angustissimo folio—Bauh., *Pin.* 348 (1671); Ray, *Hist.* **1**:908 (1686).
Lupinus sylvestris angustifolius flore caeruleo minore—Morison, *Hist.* **2**:88 (1680); Herm., *Lugd.* 386 (1687).
Lupinus angustifolius caeruleus elatoir—Ray, *Hist:* **1**:908 (1686); Tourn., *Inst.* 392 (1719); Miller, *Dict.*, no. 2 (1754).
Lupinus sylvestris purpureo flore semine rotundo vario, major & minore—Magnol, *Bot. Monsp. Append.* 301 (1686), and *Hort. Monsp.* 124 (1697).
Lupinus indicus, angustissimo folio—Herm., *Lugd.* 386 (1687).
Lupinus flore coeruleo minore—*Riv., *Tetrap.* t.153 (1691).
Lupinus sylvestris angustifolius—Cup., *Hort. Cath.* 117 (1696).
Lupinus angustifolius flore è candido purpureo—Cup., *Hort. Cath.* 117 (1696).
Lupinus sylvestris flore coeruleo—Boerh., *Lugd.* **2**:48 (1720).
Lupinus caule simplici ramoso (excl. γ)—Linn., *Hort. Cliff.* 359 (1737).
Lupinus calycibus alternis, utrinque appendiculatis—Linn., *Hort. Cliff.* 499 (1737); Ferber, *Hort. Ager.* 56 (1739); Roy., *Lugd.* 367 (1740); Linn., *Hort. Ups.* 209 (1748).

Annual 20-150 cm high, erect with profuse lateral branching. Stems sparsely sericeous. Stipules linear-subulate. Leaflets 5-9, 15-35 x 1.5-4 mm in wild types, up to 50 x 6 mm in cultivated varieties, linear to linear-spathulate; upper surface glabrous, lower surface sparsely sericeous. Racemes subsessile, 5-20 cm long; lower flowers alternate, upper flowers ± subverticillate, on pedicels 2-4 mm long; bracts oblanceolate-obovate, caducous; bracteoles short, oblong. Upper lip of calyx deeply 2-partite, lower lip longer, entire or irregularly 2-3 toothed. Corolla 11-15 mm long x 10-14 mm high, light to dark blue tinged purple, especially at the tips of the wings, or rarely pink, purple or white (mainly in cultivated varieties); not scented. Pods 35-50 x 7-10 mm with 4-7 seeds in wild types or up to 60 x 15 mm with 3-5 seeds in cultivated varieties, villous. Seeds 4-6 x 3-5 x 3-4 mm in wild types or up to 8 x 7 x 6 mm in cultivated varieties, ± globular; testa smooth, variously coloured and patterned with cream spots and pale to dark brown or black reticulations on a cream, buff, greenish brown, brown or grey background.

Chromosome number n = 20.

DISTRIBUTION: ± circum-Mediterranean: Spain, Portgual, S. and W. France as far north as the Loire, Corsica, Sardinia, Sicily and islands, Italy, Albania, Greece, European Turkey and W. and S. Asia Minor, Syria, Lebanon, Israel, Egypt in the Nile Delta, Algeria, Morocco—Map 2. Distribution mainly coastal, but in Iberia and N. Africa extends inland to about 1 500 metres altitude; occurring especially as a weed of roadsides and cultivated fields, and confined to well-drained non-calcareous soils of mostly light-medium texture. Naturalized to a small extent in the Cape Province of S. Africa and S.W. Australia, cultivated there and in N. Europe, New Zealand, S.E. United States, and experimentally elsewhere.

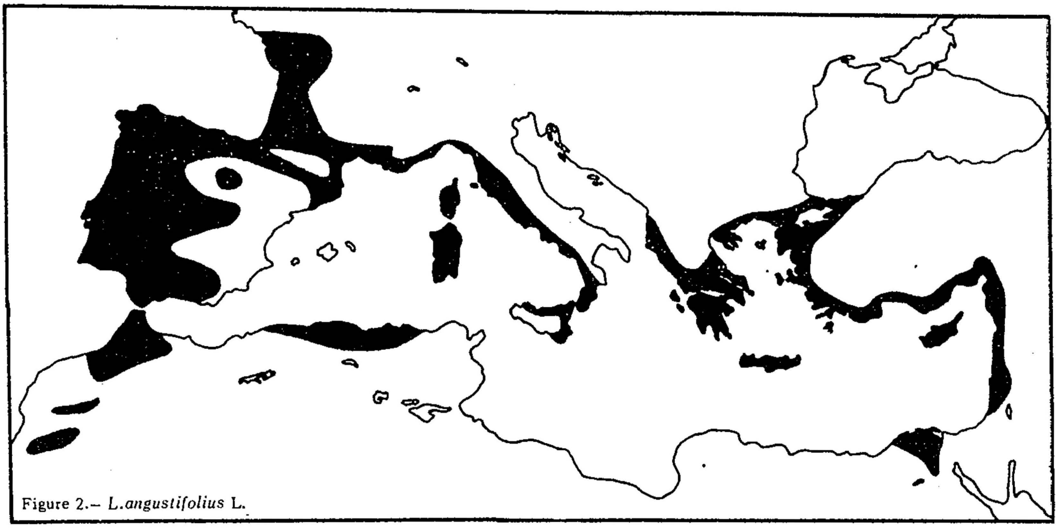

Figure 2.– *L.angustifolius* L.

SPAIN: Puerto Santa Maria, Bourgeau 148; Talavera-La-Reina, Bourgeau 2416; Cambrils, Tarragona, Sennen 3671; above Covarrubias, S.E. of Burgos, Sandwith 5675; Malaga, Boissier. PORTUGAL: Faro, Bourgeau 1817. FRANCE: Cheroulin, Gay; Loir-et-Chez, Cosson 1060. CORSICA: Serra di Scopamère, Reverchon 215; Vallée du Moulin près Ajaccio, Bourgeau 102. SARDINIA: Tempio, Reverchon 482. SICILY: Mt. Etna, Bornmüller 275; Catania, J. S. Mill. ITALY (Calabria): Reggio: Huter, Porta and Rigo 69. GREECE: Mulyani Is. opp. Pyrgos, Hill, Sandwith and Turrill 2625; Simonos Petra, Athos Peninsula, Hill, Sandwith and Turrill 2292; Mt. Malene nr. Hogios Petios, Orphanides 620; Kaisariani (Hymethus), Atcherley 472. CRETE: Le Canée, Reverchon 48. IS. CHIOS: Kampia, Platt 148. TURKEY: Gallipoli, Durham 58; Marmaris, Ol Mugla, Davis 25317; Bodrum, Ol Mugla, Davis 40906; Anamur, Prov. Mersin, Davis 25951. CYPRUS: Platres, Kennedy 545, 1844; Chakistra, Meikle 2724. PALESTINE: near Hakkuk, Lower Galilee, Hebrew Univ. 525. EGYPT: Kom Omboe, Muschler. ALGERIA: El Ancor, Faure;

Algiers, Bové; Jiaret, Munby. MOROCCO: Demnat near Marrakech, Richmond 8; Rabat, Trethewy 232; Tangier, Trethewy 387.

L. angustifolius is a fairly polymorphic species. Large-seeded, large-growing cultivated strains have been known and distinguished from "wild" types with smaller seeds, narrower pods, and smaller and finer leaflets for at least several hundred years (cf. Ray 1686; Magnol 1686, 1697). The Linnaean specimen of *L. angustifolius* is clearly of the larger type. Over the years, from Linnaeus onwards, a number of attempts have been made to draw a specific distinction between the two. The Linnaean epithet *varius* appears originally to have been applied to the small-seeded wild type (see later section on the problem of *"L. varius"*). Later epithets in distinction from *L. angustifolius* L. included *linifolius* Roth (1787), *reticulatus* Desv. (1835), and *philistaeus* Boiss. (1849).

The distinction has now fairly generally been abandoned, although Franco and da Silva (1968a) maintain it at subspecific level. Even this is unjustified in the light of present knowledge. No really clear-cut differences exist between large- and small-seeded, or between cultivated and wild forms such as occur in *L. albus.* Use of wild types as parents in breeding is tending to obliterate what differences do exist, apart from clearly defined characteristics such as presence or absence of alkaloids, pod shattering, and seed coat permeability. Mikolajczyk (1963), Forbes and Wells (1966) and the writer (unpublished) have crossed cultivated forms with wild types from Portugal, Spain, Italy, Greece and Israel without obvious infertility or other genetic disturbances. Most differences studied have been simply inherited. In Mikolajczyk's study the main difference in seed and plant size was shown to be controlled by a single gene.

Variation in seed and plant size and in other morphological and physiological characters is evident among wild strains and bears at least some relationship to region. Many collections from the Iberian Peninsula have long, lax inflorescences, which agree with the description of Willkomm and Lange (*Prodr. Fl. Hisp.* **3**:466, 1880). Lines from the western part of the distribution (France, Iberian Peninsula, North Africa) have mostly the "normal" seed coat pattern of brown reticulations and cream spots on a slate-grey to brownish background. In Italy, Sicily and Sardinia, light brown marbling on a cream background giving an overall buff colour (= *leucospermus* Boiss.?) is very common. Seed colours of the Eastern Mediterranean in general resemble those from the western part of the range.

Seed sizes do not show obvious systematic variation among the different regions, although undoubted differences do occur among wild strains as well as between the wild and "cultivated" types. Among presumed wild-type strains I have examined (both herbarium specimens and living material), the greatest variation in seed and plant size has been among those from the Iberian Peninsula and Morocco. The large-growing *Lupinus angustifolius caeruleus elatior* of Ray (1686, p. 908) was thought to have come from Cadiz ("semen hujus Lupini Gadensis titulo nobis communicatum est"). Magnol (1686, 1697) also recorded the existence of larger and smaller-seeded types at the Botanic Garden at Montpellier. More recently Plitmann (1966) drew distinction between naturally-occurring varieties in Israel with narrow leaflts and pods (and hence presumably small seeds) on one hand and one with broad leaflets and pods and large seeds (var. *basalticus*) on the other. By contrast, collections I have made in various parts of Southern Italy have all been small-seeded, albeit with some genetic variation in this respect.

Franco and da Silva (1968a) state that the large-seeded forms (their ssp. *angustifolius*) occur on inland loamy soils, whereas the small-seeded forms (their ssp. *reticulatus*) are found on maritime sands, and only rarely inland. This is only partly true. From my observations in Spain, Portugal and Morocco, the larger-seeded forms occur mainly on or near arable soils, which are indeed typically loamy and inland. The large-seeded, so-called "var. *basalticus*" of Zohary and Plitmann in Israel (Plitmann 1966) probably represents a parallel occurrence.

Although apparently wild, circumstantial evidence suggests that these forms may have originated in cultivation and become naturalized. Smaller-seeded forms, on the other hand, occur throughout, being the predominant type in non-arable coastal and rough or mountainous inland areas.

Whether variation in seed size among wild or semi-wild strains is due *ultimately* to natural selection or to artificial selection cannot be said with certainty, although cultivation of the species would undoubtedly have favoured selection and spread of larger-seeded types. There is no reason to think that variation in seed size is not itself ecologically adaptive. Mikolajczyk (1963) has suggested that small seeds and retarded early growth in the wild types may help confer an adaptation to drought and generally rigorous environmental conditions. On the other hand it might be envisaged that large seeds could be advantageous on very coarse sands of low water and nutrient-holding capacity, where large seed nutrient reserves and rapid root penetration should help seedling establishment.

Leaflet shape varies among wild and cultivated *L. angustifolius* varieties, although mostly within restricted limits. Over a wide range of leaflet sizes, the ratio of length : breadth varied between about 7 and 9 for material examined, apart from one distinct group of collections from the Aegean area, with relatively short, broad leaves and a length : breadth ratio of about 6. Examination of living material has also revealed differences in the flatness of the leaflets, some tending more than others to be angled at the midrib, forming in cross section a narrow "V".

Variation exists in the normal, blue flower colour of *L. angustifolius.* Certain races from Israel, Italy, and perhaps elsewhere have paler blue flowers than is usual for the species. The paleness is especially pronounced between the veins, giving the flowers a washed-out appearance. A few specimens have distinctly violet, rather than blue, flowers. Colour of the seeds is very variable in wild material, as already noted, but all colours are accompanied by flowers of some bluish shade and the presence of some anthocyanin pigmentation on stems, petioles bracts and calyces.

Numerous natural flower and seed colour mutations occur and have been selected from cultivated varieties of *L. angustifolius.* The flower colours include white, various shades of pale blue, pale and dark pink, and purple. They are usually accompanied by pleiotropic changes in anthocyanin pigmentation of the vegetative parts and in seed colour. Mutant seed colours cover a more or less continuous range from pale pearl-grey and white through light and dark brown, rust brown, buff, brownish grey, dark grey, and black, with varying combinations of presence or absence of marbling and pale spots. Individual flower and seed colour types of *L. angustifolius,* and their genetics, are described by Hallqvist (1921), Sypniewski (1925, 1930), Hackbarth (1957), Gladstones (1958b), and Mikolajczyk (1966a). Such types have value in breeding for genetic marking of cultivars, although the general absence of parallel variants persisting in nature raises questions as to their ecological fitness relative to the "wild" pigmentation types.

Some variation is known within wild populations of *L. angustifolius* in other characters of potential agronomic importance. An Israeli strain observed over several years has consistently flowered two or more weeks earlier under Australian conditions than strains from Greece, Italy, and Portugal. North African strains (not yet observed in cultivation) may very well do likewise. E. Mediterranean populations have already been used in Russian and Polish breeding of cultivated types (Mikolajczyk 1966b), and are now being used for breeding in Australia. Northern Mediterranean strains flower from about the same time as common cultivated types to substantially later.

I have noted a great deal of variation in seed setting among Mediterranean wild types when grown under Australian conditions, and am attempting to exploit this in breeding to improve seed setting and yield in commercial cultivars.

Forbes and Wells (1966) have shown that lines exist among wild Iberian lupins which are unusually resistant to low temperatures, while others carry genes for resistance to the fungal pathogens *Glomerella cingulata* and *Stemphylium* spp. These have been used in breeding forage varieties for the south-east United States and elsewhere.

L. angustifolius is not recorded as having been cultivated in classical Greece or Rome. Botanists of the 16th and 17th centuries called it *Lupinus sylvestris* (wild lupin), in contrast to *L. albus* which was known as *Lupinus sativus* (see pre-Linnaean synonyms). Nevertheless, there is evidence that seeds of wild or volunteer stands have probably been used casually for a long time. Bauhin (1651) and Savi (1798) record its common Italian name as "lupino salvatico", and Maratti (1822) as "fusaglia salvatico", presumably implying a role in times of need. Parkinson (1640), writing of the manifold pharmaceutical uses of *L. albus* in classical times, also noted that "the wilde Lupines are stronger and more effectuall to all purposes".

Some systematic cultivation appears to have taken place at least since the 18th century, and probably much earlier (see previous discussion). Miller (1754) and Tourlet (1908) clearly distinguished the large-seeded types of *L. angustifolius* as being cultivated, the small-seeded types as wild. In part at least, cultivation has been for use of the seeds as a coffee additive or substitute. The French botanists Boreau (1849) and Tourlet (1908) speak of it being cultivated in Anjou for that purpose under the names "pois à café", "café turc", and "café". Foury (1950) also gives "lupin à café" as a common name for *L. angustifolius* in Morocco. Hegi (1923) states that "*L. varius*" is grown as a coffee substitute in the Tyrol. But as Hanelt (1960) observes, "on the qualities of the resulting beverage the literature remains silent".

The modern use of *L. angustifolius* for green manure and to some extent for forage may be of fairly ancient origin. Klinkowski (1938) and the present writer have seen it used as a green manure or cover crop in orchards and olive groves in Morocco and Iberia, in what appears to be a traditional agricultural pattern. Hanelt (1960) cites Link's "Alterer Geschichte der Hülsenfrucht" (1820) as reporting its cultivation then for cattle fodder in the vicinity of Bordeaux. Oldershaw (1925) described use of *L. angustifolius* for both sheep feed and green manure in Suffolk (England) from at least as early as 1859.

Later spread of *L. angustifolius* in cultivation, and its recent development as a true crop plant are described elsewhere (Gladstones 1970).

3. **L. micranthus** Guss.

Guss., *Fl. Sic. Prodr.* **2**:400 (1828); Bertol., *Fl. Ital.* **7**:414 (1847); Halácsy, *Consp. Fl. Graec.* **1**:340 (1901); Franco & Silva, P. in Tutin *et al., Fl. Europ.* **2**:105 (1968); Chamberlain in Davis, *Fl. Turkey* **3**:39 (1970); *Zohary, *Fl. Palaestina* **2**:43, t.56 (1972).

Typification: "In collibus et planis aridis subarenosis Siciliae meridionalis: Castelvetrano, Marsala, Mazzara, Selinunte, da Vittoria a Siracusa." Type not seen.

L. hirsutus L. *Sp. Pl.* ed.2, 1015 (1763), non ed.1 1753; Murray in L., *Syst. Veg.* ed.13, 545 (1774); Desr. in Lam., *Encycl. Méth. Bot.* **3**:622 (1791); Willd., *Sp. Pl.* ed.4, **3**:1023 (1803); Brot., *Fl. Lusit.* **2**:133 (1804); Lam & DC., *Fl. Fr.* ed.3, **4**:508 (1805); Ten., *Fl. Nap.* **2**:142 (1820); DC., *Prodr.* **2**:407 (1825); Guss., *Fl. Sic. Prodr.* **2**:399 (1828); Mutel, *Fl. Fr.* **1**:315 (1834); Agardh, *Syn. Gen. Lup.* 5 (1835); Koch, *Fl. Germ. Helv.* 157 (1837); *Moris, *Fl. Sard.* **1**:407, t.72 fig. 1 (1837); Vis., *Fl. Dalm.* 272 (1842); Bertol., *Fl. Ital.* **7**:413 (1847); Gren. & Godron, *Fl. Fr.* **1**:365 (1848); *Cusin & Ansberque, *Herb. Fl. Fr.* **6**, t.968 (1870); Boiss., *Fl. Or.* **2**:28 (1872); Loret & Barrandon, *Fl. Montp.* 151 (1876); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:466 (1880); Arcangeli, *Fl. Ital.* 154 (1882); Colmeiro, *Pl. Hisp. Lusit. Bal.* **2**:83 (1886); Batt. & Trabut, *Fl. Agér. (Dicot.)* 208 (1889); Lojac., *Fl. Sic* **1**(2):33 (1891); Caruel in Parl., *Fl. Ital.* **10**:115 (1894); Post, *Fl. Syr. Pal. Sin.* 212 (1896); Rouy & Fouc., *Fl. Fr.* **4**:192 (1897); *Fiori & Paol., *Fl. Anal. Ital.* **2**:11, fig. 1866 (1899); *Coste, *Fl. Fr.* **1**:308 1901); Halácsy, *Consp. Fl. Graec.* **1**:340 (1901); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):226 (1907); Briq., *Prodr. Fl. Corse* **2**:230 (1913); Coutinho, *Fl. Port.* 315 (1913); **Bonnier, *Fl. Compl. Fr.* **3**:9, t.640 (1914); Thompson, *Fl. Pl. Riviera* 75 (1914); Knoche, *Fl. Balaer.* **2**:58 (1922); Fiori, *Nuov. Fl. Anal. Ital.* **1**:805 (1925);

Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:265 (1929); Bouloumoy, *Fl. Lib. Syr.* 77 (1930); Jahandiez & Maire, *Cat. Pl. Maroc* 348 (1932); Thiébaut, *Fl. Lib.-Syr.* **2**:7 (1940); Hanelt, *Lupinen* 89, t.88 (1960); **Polunin & Huxley, *Fl. Med.* 92, pl. 53 (1965).

Types: The two Linnaean specimens 898.5 and 898.6 labelled *L. hirsutus,* together with 898.4 labelled *L. varius* agree with Linnaeus' diagnosis of 1763 for *L. hirsutus,* but not with his diagnosis of 1753. The specimens were received from L. Gérard, probably between 1755 and 1757 (see further discussion below).

L. sylvestris β Lam., *Fl. Fr.* **2**:627 (1778).

L. gussoneanus Agardh, *Syn. Gen. Lup.* 5 (1835).

L. criticus *Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* **22**:36, t.12 (1903).

Typification: "Crescit in Dalmatia." Type not seen.

L. varius auct. non L.: Reichenb., *Fl. Germ. Excurs.* 539 (1832).

Pre-Linnaean Synonyms.

Lupinus exoticus hirsutissimus—Bauh., *Hist.* **2**:289 (1651).

Lupinus flore purpurascente, latifolius hirsutus—Magnol, *Bot. Monsp.* 167 (1676), & *Hort. Monsp.* 124 (1697).

Lupinus medius coeruleus—Ray, *Hist.* **1**:907 (1686).

Lupinus lanugifolius, latifolius, humilis, flore caeruleo purpurascente, stoloniferus—Cup., *Hort. Cath.* 117 (1696); Shaw, *Afr.,* no. 393 (1738).

Annual 10-50 cm high, rosetted at first, becoming erect with basal branching. Stems and petioles coarsely hirsute. Stipules linear-subulate, concrescent with the petiole over 2/3 of their length. Leaflets 5-7 (-9), 10-50 x 6-20 mm, obovate-cuneate to obovate-oblong, mucronate, coarsely hairy above and below. Racemes 3-12 cm long, shortly pedunculate, ovate in the bud stage; lower flowers alternate, upper flowers ± verticillate; bracts subulate, persistent; bracteoles linear. Upper lip of calyx short, deeply 2-partite, lower lip twice as long, deeply 3-lobed. Corolla varying greatly in size, from short and barely exceeding the calyx to twice as long, blue apart from a centrobasal white spot on the standard; standard relatively small and angled at about 45° to the wings (less erect than in other spp.); keel pointed, base white, distal 1/3-1/2 blue. Pods 30-50 x 9-12 mm, brownish, coarsely hirsute, 2-5 seeded. Seeds 5-8 x 4-6 x 3-4 mm, lenticular to subquadrangular compressed; testa smooth, light brown with darker brown marbling (darkest around the edges), sometimes with a dark brown arc around the hilum. Hairs of all plant parts are silver on the living plant but turn reddish brown in the dried specimen.

Chromosome number n = 25?

DISTRIBUTION: Circum-Mediterranean: Spain, Portugal, S.E. France, Corsica, Sardinia, Sicily, Italy, Yugoslavia, Albania, Greece, Crete, Western Turkey, Cyprus, Syria, Lebanon, Israel, Lybia, Tunisia, Algeria, Morocco—Map 3. Coastal and inland to about 1 000 m, relatively rare, often on heavier and more calcareous soils than *L. angustifolius.*

SPAIN: Puerto Santa Maria, Bourgeau 151. PORTUGAL: Buarcos, Schultz 2427. MINORCA: Binisarmena, Porta and Rigo. FRANCE: Hyères, Joad. CORSICA: Bastia, Mabille 115. SARDINIA: Tempio, Reverchon 117; Golfo degli Aranci, Gamble 28297; Is. Maddalena, Fiori and Béguinot 1309. SICILY: Palermo, Lojacono 171. ISTRIA: Pola, Pichler. DALMATIA: Pichler. ALBANIA: (?) Celuga, Baldacci 331. GREECE: Is. Melos, Heldreich 1021; Is. Chios, Herb. Kew. 78; Mt. Kiurks, Atchley 619. CRETE: La Canée, Reverchon; Penins. Akrotiri, Rechinger fil. 13296. TURKEY: Gallipoli, Ingoldby

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[1] The diagnosis of *L. hirsutus* in *Species Plantarum* ed.1 describes *L. pilosus* Murray accurately except in giving the upper as well as the lower calyx lobe as entire. This would appear to have been an inadvertent mistake on Linnaeus' part, as he had previously published a correct diagnosis in the appendix to his Hortus Cliffortianus (1737, p. 499). The common synonymy of the two references and other corroborative evidence leave little doubt that the same species was intended.

[2] Correspondence on file, Linnaean Society, London. The specimens are not specifically mentioned, but since this is the only correspondence recorded between the two men they may reasonably be assigned to the same period.

160. CYPRUS: Meikle 2242; Merton 1879. LEBANON: Aïn Zehalteh, J. Ball. JORDAN: Hasbanis 267. LYBIA: Cyrenaica, Sandwith 2635. ALGERIA: Jamin 156; Algiers, Wolfe. MOROCCO: Trethewy 480.

This species has been known fairly generally as *L. hirsutus* L., with *L. micranthus* Guss. accepted as a later synonym. However, the epithet *hirsutus* is also applied by some, especially German writers, to *L. pilosus* Murr. The reason for this confusion lies in changes made by Linnaeus between the 1st and 2nd editions of *Species Plantarum,* and inconsistencies of the Linnaean specimens both with the published diagnosis and amongst themselves.

L. hirsutus L. as diagnosed in *Species Plantarum* ed.1 (1753) fairly clearly refers to the species here called *L. pilosus* Murr., although with one inaccuracy.[1] No Linnaean specimen labelled in this sense has survived. Instead, the two specimens labelled *L. hirsutus* (898.5 and 898.6) agree with the new and radically changed diagnosis for *L. hirsutus* in ed. 2 (1763), and with the later *L. micranthus* Guss. Linnaeus' change of mind presumably followed receipt of these specimens, apparently the first of their type to come into his possession, from L. Gérard, with whom he corresponded between 1755 and 1757.[2] The situation is further confused by the fact that an identical third Linnaean specimen (898.4) is labelled *L. varius.* The only Linnaean specimen conforming to *L. pilosus* Murr. (898.3) is also labelled *L. varius.* (The problem of "*L. varius*" is discussed fully in a later section.) Clearly the epithet *hirsutus* L. cannot validly be applied to *L. pilosus* Murr. in the absence of any Linnaean specimen of that species so labelled, together with the presence of one specimen of it labelled *L. varius* and the fact that the two specimens that are labelled *L. hirsutus* conform instead to the new diagnosis in *Species Plantarum* ed.2 (= *L. micranthus* Guss.). On the other hand to use "*hirsutus*" in the latter sense would be in obvious conflict with the diagnosis for *L. hirsutus* in *Species Plantarum* ed.1, as well as having an ambiguous basis in the Linnaean specimens. It may be concluded that either way *L. hirsutus* is a *nomen confusum,* and should be rejected in favour of the later but unequivocal epithet *micranthus* Guss. This agrees with the evident conclusion of Franco and da Silva (*Flora Europaea* **2**:105, 1968).

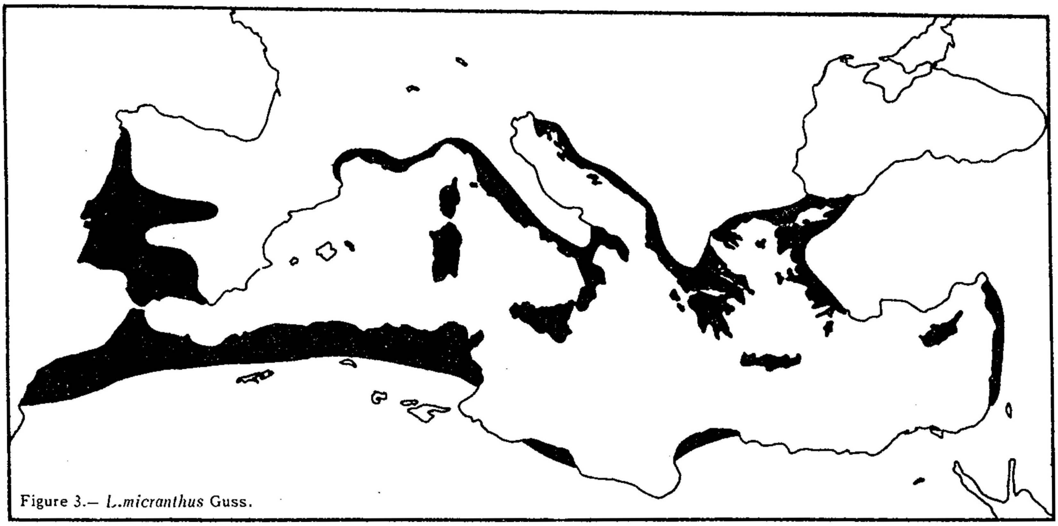
Figure 3.— *L.micranthus* Guss.

Gussone originally described *L. micranthus* in distinction from "*L. hirsutus*", *sensu* L. 1763, as being a smaller, more prostrate plant with a much smaller flower. Where subsequent writers have used the epithet they have usually done so in the same sense. However, as Briquet (1913) pointed out, the variation among specimens appears fairly continuous and provides no basis for delineating discrete groups. It seems likely, in fact, that *L. micranthus* parallels *L. angustifolius* in having small-seeded, smaller growing "wild" types, together with some intermediate and larger-seeded varieties. The smaller types, among which the Linnaean *"L. hirsutus"* specimens appear to belong, are probably the more universal.

A characteristic feature of *L. micranthus* is that in the dried specimens the hairs turn yellowish brown. In the living plant, however, they are silver.

After *L. angustifolius, L. micranthus* is the most widespread wild lupin of the Mediterranean region, although considerably less common. It is pan-Mediterranean in distribution, growing among grass and scrub, or as a weed of roadsides and cultivated fields: mainly in coastal districts, but also inland to altitudes of about 1 000 metres. The distribution suggests adaptation to neutral or even calcareous, rather than acid, soils, and tends to confirm the statement of Hegi (1923) that the species (as *L. hirsutus* L.)[1] is tolerant of calcareous soils. Zohary (1972) records its habitat in Israel as on both sandy and heavy soils. Limited observation by the writer in Morocco, where it was seen growing on a moderately alkaline clay loam together with *Medicago* spp., tends to confirm this.

L. micranthus is not known to be cultivated now to any extent, and has not been the subject of any recorded breeding in modern times. Nevertheless, it is reported (Hegi 1923) to have been widely used, since classical times, as a green manure plant in Italy and especially Greece, where it is said to be valued in comparison with other lupins for its tolerance of calcareous soils. A history of cultivation in this region would agree with the fact that the largest-growing and largest-seeded *L. micranthus* specimens seen in the present study were from Greece and Dalmatia.

4. L. luteus L.

L., *Sp. Pl.* 721 (1753); **Kniphof, *Herb. Viv.* t.665 (1761); Murray in L., *Syst. Veg.* ed.13, 545 (1774); Lam., *Fl. Fr.* **2**:627 (1778); **Curtis, *Bot. Mag.* **4**, t.140 (1791); Desr. in Lam., *Encycl. Méth. Bot.* **3**:624 (1791); Willd., *Sp. Pl.* ed4, **3**:1024 (1803); Brot., *Fl. Lusit.* **2**:134 (1804); Lam. & DC., *Fl. Fr.* ed.3, **4**:508 (1805); DC., *Prodr.* **2**:407 (1825); Guss., *Fl. Sic. Prodr.* **2**:401 (1828); **Sibth. & Sm., *Fl. Graeca* **7**:78, t.686 (1830); Reichenb., *Fl. Germ. Excurs.* 539 (1832); Agardh, *Syn. Gen. Lup.* 1 (1835); Ten., *Fl. Nap.* **5**:99 (1835); Moris, *Fl. Sard.* **1**:598 (1837); Bertol., *Fl. Ital.* **7**:416 (1847); Loret & Barrandon, *Fl. Montp.* 151 (1876); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:468 (1880); Arcangeli, *Fl. Ital.* 154 (1882); Colmeiro, *Pl. Hisp. Lusit. Bal.* **2**:86 (1886); Lojac., *Fl. Sic.* **1**(2):35 (1891); Caruel in Parl., *Fl. Ital.* **10**:117 (1894); Post, *Fl. Syr. Pal. Sin.* 213 (1896); Rouy & Fouc., *Fl. Fr.* **4**:189 (1897); *Fiori & Paol., *Fl. Anal. Ital.* **2**:11, fig. 1867 (1899); *Coste, *Fl. Fr.* **1**:307 (1901); *Reichenb. & Reichenb. fil., *Icon. Fl. Germ.* **22**:35, t.6 (1903); *Merino, *Fl. Galic.* **1**:410 (1905); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):228 (1907); Briq., *Prodr. Fl. Corse* **2**:232 (1913); Coutinho, *Fl. Port.* 315 (1915); **Bonnier, *Fl. Compl. Fr.* **3**:8, t.639 (1914); *Hegi, *Ill. F. Mitteleur.* **4**:1156, fig. 1310 (1923); Fiori, *Nuov. Fl. Anal. Ital.* **1**:805 (1925); *Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:260, figs. 9, 9a (1929); Jahandiez & Maire, *Cat. Pl. Maroc* 348 (1932); Thiébaut, *Fl. Lib.-Syr.* **2**:7 (1940); *Foury, *Cah. Rech. Agron.* **3**:67, 69 (1950); Gladstones, *J. Roy. Soc. W. Aust.* **41**:30 (1958a); *Hanelt, *Lupinen* 36, figs. 8-12 (1960); Franco & Silva, P. in Tutin *et al., Fl. Europ.* **2**:105 (1968); *Zohary, *Fl. Palaestina* **2**:44, t.58 (1972); *Gladstones, *Lup. W. Aust.* 7 and 28-9 (1972).

Holotypus: Linnaean Collection 898.8 (Linn).

Pre-Linnaean Synonyms

Lupinus flore, luteo—*Lob., *Kruydt.* **2**:75 (1581); Park,, *Paradisus* 335 (1629); *Ger., *Herb.* 1217-8 (1633); *Park., *Theat.* 1074 (1640); Ray, *Hist.* **1**:908 (1686); *Riv., *Tetrap.* t.151 (1691).

Lupinus sylvestris α—Dod., *Hist.* Part 4 Book II, 512 (1583).

Lupinus luteus—*Tab., *Kreut.* **2**:198 (1591).

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[1] Some possibility exists that Hegi was referring in fact to *L. pilosus* Murray, or perhaps to the two species together, as his diagnosis of *"L. hirsutus* L." shows signs of confounding with *L. pilosus.* I am inclined to accept that his reference at least encompasses *L. micranthus* Guss.

Lupinus sylvestris luteus—Bauh., *Matth.* 344-5 (1598).

Lupinus flavo flore—*Clus., *Hist.* CCXXVIII (1601); Herm., *Lugd.* 386 (1687); Cup., *Hort. Cath.* 117 (1696).

Lupinus sylvestris flore luteo—**Cam., *Kreut.* 126 (1611); Bauh., *Pin.* 348 (1623); Morison, *Hist.* 2:88 (1680); Magnol, *Hort. Monsp.* 124 (1697); Tourn. *Inst.* 393 (1719); Boerh., *Lugd.* 2:48 (1720); Miller, *Dict.*, no. 3 (1754); Quer, *Fl. Espanola* 5:375 (1784).

Lupinus sylvestris flore luteo odorato—*Besl., *Eyst.* 2: ord. 13, 3 (1613).

Lupinus luteo flore, semine compresso, vario—Bauh., *Hist.* 2:290 (1651); Magnol, *Bot. Monsp.* 167 (1676).

Lupinus caule simplici ramoso (γ only)—Linn., *Hort. Cliff.* 359 (1737).

Lupinus calycibus verticillatis: labio inferiore trifido—Linn., *Hort. Cliff.* 499 (1737); Ferber, *Hort. Ager.* 56 (1739); Roy., *Lugd.* 367 (1740); Linn., *Hort. Ups.* 209 (1748).

Herbaceous annual 20-80 cm high, rosetted at first, becoming erect with vigorous basal branching. Stems hirsute. Stipules of rosette leaves about 8 x 2 mm, subulate, those on elongated stems 20-40 x 2-5 mm, linear-obovate. Leaflets 7-9 (-11), 30-60 x 8-15 mm, obovate-oblong, mucronate, villous above, sparsely sericeous below. Racemes 5-25 cm long on a 5-12 cm peduncle; flowers regularly verticillate in rather distant whorls on short (2 mm) pedicels; bracts obovate, caducous, bracteoles linear. Upper lip of calyx very deeply 2-partite, lower lip about the same length, shallowly 3-toothed. Corolla 14-16 mm long x 14-16 mm high, bright golden yellow, sweetly scented. Pods 40-60 x 10-14 mm, densely villous, 4- 6 seeded. Seeds 6-8 x 5-7 x about 3 mm, orbicular-quadrangular compressed; testa smooth, mottled brown to black on a whitish background, often with a light-coloured arc around the hilum, or pure white in some cultivars.

Chromosome number n = 26.

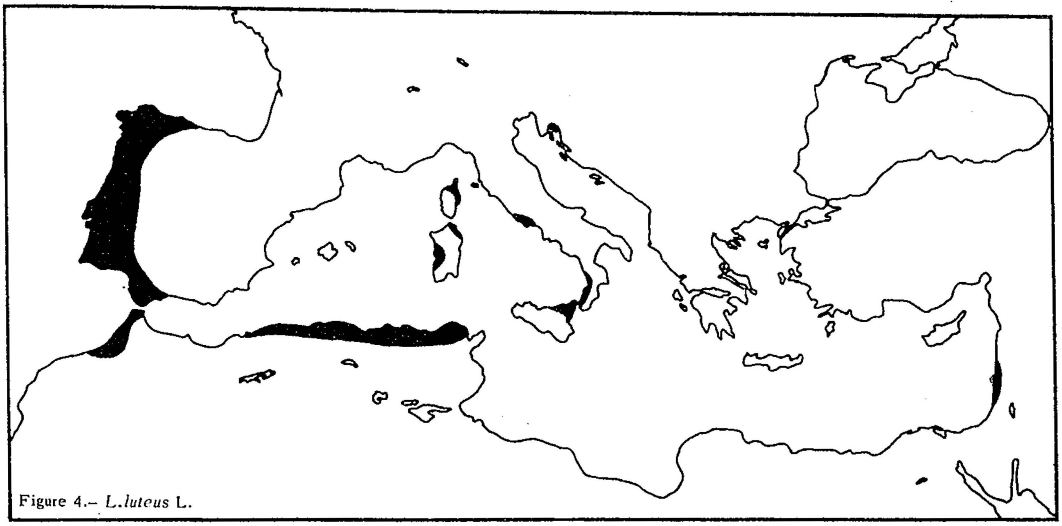

Figure 4.– *L. luteus* L.

DISTRIBUTION: Western coastal region of the Iberian Peninsular; doubtfully native (perhaps naturalized) in scattered parts of inland W. Iberia, coastal Morocco, Algeria and W. Tunisia, Corsica, Sardinia, Sicily, S. Italy, Lebanon and Israel—Map 4. Confined to neutral to acid soils. Cultivated on acid and usually sandy soils in N. Europe and to smaller extents in S. Africa, Australia and elsewhere as a field crop and ornamental.

SPAIN: Algeciras, Reverchon 78; Algeciras, Ellman and Hubbard 495. PORTUGAL: Faro, Bourgeau 1816. CORSICA: Pineto, near Bastia, Mabille 114. SARDINIA: Golfo degli Aranci, Gamble 28296. SICILY: Messina, Fiori and Béguinot 1308; Messina: Huter, Porta and Rigo 130; du Pavillon 78. IS. PANTELLARIA: Todaro. PALESTINE: Even Yehuda, Davis 4062; Sharon, Hebrew Univ. 526.

L. luteus probably originated in Western Spain and Portugal and spread from there as a cultivated plant, perhaps mainly as an ornamental because of its attractive sweetly scented, golden flowers, and also probably as a green manure and forage crop. In the Spanish province of Galicia, Merino (1905) noted that *L. luteus* is found principally around settlements, which underlines the role of cultivation in spread of the species even within its present natural range. Semi-naturalization of once-cultivated populations has been reported in Madeira (Lowe 1868) and the South of France (Thellung 1912), while populations of plants escaped from gardens and field sowings have persisted for many years in South Africa and Western Australia.

Natural variation within *L. luteus* is poorly documented. Living collections by the writer from populations growing wild in Calabria (S. Italy) conform fairly closely to the cultivated type. Many collections from the Iberian Peninsula are later-flowering and smaller seeded than the commonly cultivated types, and presumably represent the wild population from which the latter were developed (see also discussion below on *L. hispanicus*).

L. luteus was cultivated in Northern Europe as an ornamental at least as early as the 16th century. Bauhin (1598) wrote that in Germany it was known as the Turkish violet. It appears to have enjoyed some popularity in England during the 17th and 18th centuries (Parkinson 1629; Curtis 1791). Later cultivation of L. luteus and its modern development as a crop plant are described by Gladstones (1970).

5. **L. hispanicus** Boiss. & Reuter

Boiss. & Reuter, *Diagn. Pl. Nov. Hisp.* 10 (1842); Boiss., *Fl. Or.* **2**:28 (1872); Willk. & Lange, *Prodr. Fl. Hisp.* **3**:467 (1880); Colmeiro, *Pl. Hisp. Lusit* **2**:85 (1886); Merino, *Fl. Galic.* **1**:411 (1905); Coutinho, *Fl. Port.* 315 (1913); Zhukovsky, *Bull. appl. Bot. Pl. Breed, Leningrad* **21**:265 (1929); Silva, P., *Agron. Lusit.* **33**:10 (1971).

Typification: "Hab. in collibus dumosis ad radices Sierra de Guadarrama propè El Escorial et Colmenar Viejo."

Isotypus: K, "In pascuis arenosis, ad radicis Sa. de Guadarrama, prope Escorial et Colmenar."

Lupinus sylvestris, flore subrubente—Quer, *Fl. Espanola* **5**:374 (1784).

Herbaceous annual resembling *L. luteus,* differing in the following respects. Upper surface of leaflets ± glabrous. Flowers cream to lilac or violet, not scented. Pods 40-60 x 6-12 mm, 4-7 seeded. Seeds equal or slightly larger to substantially smaller than those of *L. luteus;* white, olive brown, or cream to light reddish or greenish brown with variable darker brown speckling and arc around the hilum.

Corolla violet; upper surface of leaflets glabrous; pods 9-12 mm broad, 3-6 seeded; seeds moderately large, pure white or olive brown, slightly tuberculate.
5a. ssp. hispanicus

Corolla cream becoming lilac; upper surface of leaflets sparsely villous near margins; pods 6-8 mm broad, 5-7 seeded. Seeds smaller, cream to light reddish or greenish brown with variable darker brown markings, or occasionally pure white; smooth.
5b. ssp. bicolor

5a. ssp. **hispanicus**

Corolla palish violet. Upper surface of leaflets glabrous, lower surface sparsely sericeous. Pods 9-12 mm broad, moderately villous, 3-6 seeded. Seeds at least equalling those of *L. luteus* in size, pure white or olive brown, almost smooth to moderately tuberculate.

DISTRIBUTION: S. and Central Spain, in granite or schistose mountains to about 1 200 m—Map 5. On moderately to strongly acid soils.

SPAIN: Escorial, Boissier and Reuter; Escorial, Bourgeau 2417; Guadarrama Ra., Atchley; Talavera-la-Reinha, Bourgeau: Alrededores de Guadalupe (Cáceres), Caballero; Cordoba, Ellman and Hubbard.

5b. ssp. **bicolor** (Merino) J. S. Gladstones, stat. nov.

L. luteus var. *bicolor* Merino, *Contr. Fl. Gal.* 72 (1905).
L. hispanicus var. *bicolor* Merino, *Fl. Gal.* 1:411 (1905).
Typification: "Abunda bastante en los terrenos labrados y en los vinedos de San Juan de Tabagon y en los arenales de la margen espanola del Mino á medio kilometro de la desembocadura." Type not seen.

L. bicolor (Merino) Rothmaler, *Cavan.* **7**:114 (1935), nom. illeg. non Lindley (1827).
L. rothmaleri *Klinkowski, *Züchter* **10**:124, fig. 17 (1938); Silva, P., *Agron. Lusit.* **33**:10 (1971). (?) Isotypus: K.

L. versicolor Caballero, *An. Jard. Bot. Madrid* **5**:507 (1945).
Typification: "hybr. *L. hispanicus* B. et R. x *L. luteus* L. Inter parentes copiosus. Floribus primum luteus, dein pupureo-violaceis, demum coerulescentibus." Type not seen.

L. hispanicus sensu auct. non Boiss. & Reuter: Franco and Silva, P. in Tutin *et al.*, *Fl. Europ.* **2**:105 (1968).
Pre-Linnaean synonym

(?)Lupinus obsoleto colore, lusitanicus, latifolius—Tourn., *Inst.* 392 (1719).

Corolla cream at first, becoming lilac. Upper surface of leaflets sparsely villous near margins, sometimes glabrescent; lower surface sparsely sericeous. Pods 6-7 mm broad, densely villous, 5-7 seedeed. Seeds smaller than in ssp. *hispanicus* or *L. luteus,* 4-5 x 3-4 x 2-3 mm, testa smooth, speckled and marbled greenish or reddish to blackish brown on a cream to light reddish brown background, including a distinct dark brown arc around the hilum, or occasionally pure white.

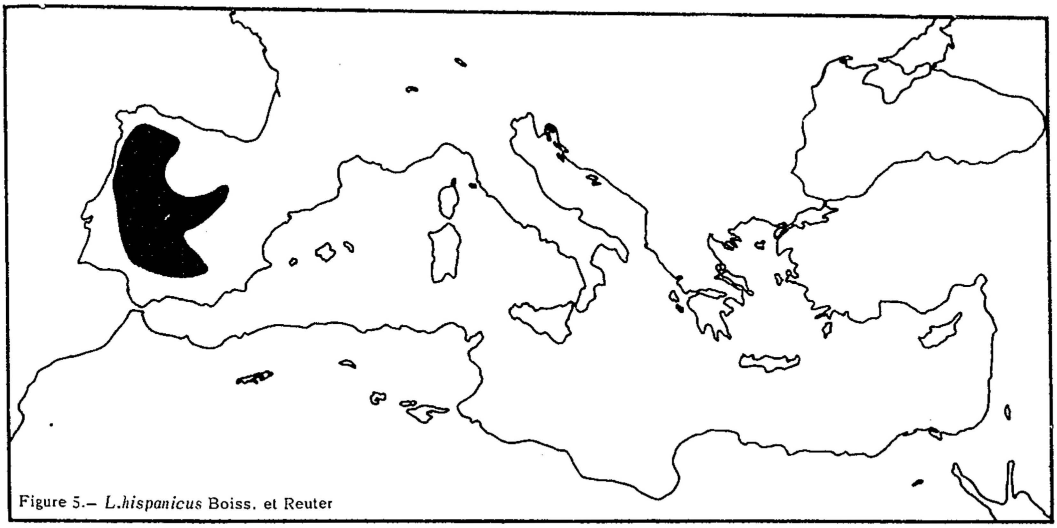
Figure 5.– *L.hispanicus* Boiss. et Reuter

Chromosome number n = 26.

DISTRIBUTION: Central and N.W. Spain, Central and N. Portugal—Map 5. Mainly on granite mountains and plateaus to 1 500 m. On sands to sandy loams, moderately to strongly acid, sometimes poorly drained.

SPAIN: El Escorial, Winkler. PORTUGAL: Fernandes and Sousa, Herb. Inst. Bot. Univ. Conimbr. 3263.

L. hispanicus is closely related to *L. luteus*. At least for ssp. *bicolor* the chromosome number n = 26 is the same as for *L. luteus* and the two can be crossed, albeit with much sterility in the hybrids (Lamberts 1958; Kazimierski and Kazimierska 1965, 1970b). Further, Nowacki and Prus-Glowacki (1971) have shown serological distinctions between *L. luteus* and *L. hispanicus* ssp.

bicolor. No chromosome count or crossing or serological data are available for ssp. *hispanicus*. Maintenance of the specific distinction between *L. hispanicus* and *L. luteus* appears justified on present genetic and morphological evidence, although there may be room for argument.

The relationship within *L. hispanicus* of sspp. *hispanicus* and *bicolor* has likewise so far been not fully resolved. Both are distinguished from *L. luteus* in having non-scented flowers, which are not gold in colour, and a more or less glabrous leaflet upper surface. Experimental crossing between the two subspecies, or between ssp. *hispanicus* and *L. luteus,* has not so far been reported.

According to Klinkowski (1938), ssp. *bicolor* (there *L. rothmaleri)* differs from ssp. *hispanicus* also in having a larger and coarser growth habit, more like that of *L. luteus*. The majority of herbarium specimens I have consulted have supported this view. However, inspection of naturally-occurring stands at or near maturity has indicated that all reach similar sizes.

The two subspecies of *L. hispanicus* together with *L. luteus* clearly form a closely related group, differing in distribution and to some extent ecology as well as in morphological characters. *L. luteus* in its true native state appears to be confined to fairly low altitude coastal districts of the W. and S.W. Iberian Peninsular and perhaps N.W. Africa, although plantings further inland have in some cases persisted for a while. *L. hispanicus* ssp. *hispanicus* occurs at intermediate altitudes and mainly in S. and central Spain. Boissier *(Fl. Or.* 28, 1872) and Chamberlain (Davis, *Fl. Turkey* 3:40, 1970) also record what may be naturalized ssp. *hispanicus* in western Turkey, growing in valleys up to 720 m, but I have been unable to confirm this directly. *L. hispanicus* ssp. *bicolor* extends to higher altitudes than ssp. *hispanicus,* and grows in the relatively cool and wet regions of central and N.W. Spain and N. Portgual. Of the three it shows the greatest adaptation to waterlogging-prone soils.

I have noted some evidence of introgression between ssp. *hispanicus* and ssp. *bicolor* where the two overlap in central Spain (e.g. *bicolor* with pure white seeds) and also seen a number of apparent hybrid swarms between ssp. *bicolor* and *L. luteus* in N.W. Spain and N. Portugal. The latter may have originated from field sowings of *L. luteus,* which have been harvested or died out, but which have resulted through cross-pollination in massive introgression of *L. luteus* characteristics into nearby *L. hispanicus* populations. The progeny of seed collections from these swarms are currently under study.

A more detailed cytogenetic study of the group would seem warranted in view of the potential value of *L. hispanicus* as a source of cold, waterlogging and perhaps disease resistance for incorporating into crop varieties of *L. luteus.*

6. **L. cosentinii** Guss.[1]

Guss., *Fl. Sic. Prodr.* **2**:398 (1828); Ten., *Fl. Nap.* **4**:emend. XI (1830), and **5**:100 (1835); Bertol., *Fl. Ital.* **7**:410 (1847); Cesati, Passer. & Gibelli, *Comp. Fl. Ital.* 729 (1867); Arcangeli, *Fl. Ital.* 154 (1882); Colmeiro, *Pl. Hisp. Lusit. Bal.* **2**:84 (1886); Tornabene, *Fl. Aetnea* **2**:19 (1890); Coutinho, *Fl. Port.* 315 (1913); Malheiros, *Agron. Lusit.* **4**:231 (1942); *Gladstones, *Lup. W. Aust.* 3-5, 29 (1972).

Typification: "In herbosis inter vulcanicos lapides: Catania (Cosentini)." Type not seen.

(?)*L. semiverticillatus* Desr. in Lam., *Encycl. Méth. Bot.* **3**:623 (1791).

L. pilosus ssp. *cosentini* (Guss.) Rouy & Fouc., *Fl. Fr.* **4**:190 (1897); Briq., *Prodr. Fl. Corse* **2**:232 (1913); Jahandiez & Maire, *Cat. Pl. Maroc* 348 (1932).

L. hirsutus auct. non L.: *Black, *Fl. S. Aust.* fig. 138 (1924) (excl. descr.); *Foury, *Cah. Rech. Agron.* 3, ill. pp. 63 and 65 (1950) (excl. descr.).

L. digitatus auct. non Forskål: Lojac., *Fl. Sic.* **1**(2):33 (1891); Arcangeli, *Fl. Ital.* ed.2, 480 (1894); *Gladstones, *J. Roy. Soc. W. Aust.* **41**:31, pl. 1, II (1958a); *Kazimierski & Nowacki, *Genet. polon.* **2**:115 (1961).

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[1] Originally *L. cosentini* Guss., after the Sicilian botanist F. Cosentini (1769-1840). I have added the genitive "i" to conform with accepted nomenclatural practice.

L. varius auct. non L.: Caruel in Parl., *Fl. Ital.* **10**:113 (1894); Bonnet & Barratte, *Cat. Pl. Vasc. Tun.* 97 (1896); *Reichenb. & Reichenb fil., *Icon. Fl. Germ.* **22**:35, t.8, I (1903); *Gardner & Bennetts, *Tox. Pl. W. Aust.* 101 (1956); *Hanelt, *Lupinen* 91, figs. 31, 33-5 (1960); *Kazimierski & Kazimierska, *Genet. polon.* **11**:208 (1970).

L. pilosus ssp. *digitatus* auct. non Forskål: Fiori & Paol., *Fl. Anal. Ital.* **2**:11 (1899); Fiori, *Nuov. Fl. Anal. Ital.* **1**:805 (1925); Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:263 (1929) (in part).

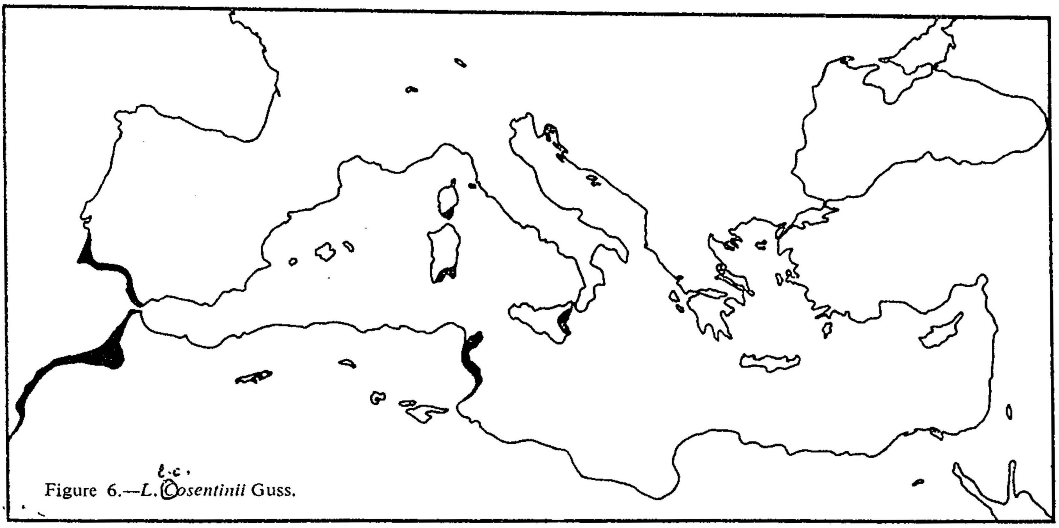
L. pilosus auct. non Murray: Black, *Fl. S. Aust.* 307 (1924); *Gardner & Elliott, *J. Dep. Agric. W. Aust.* (2)**6**:416, t.1 (1929).

L. varius ssp. *varius* auct. non L.: Franco & Silva, P., *Feddes Repert.* **79**:52 (1968) and in Tutin *et al.*, *Fl. Europ.* **2**:106 (1968).

Pre-Linnaean Synonym

Lupinus minoris caerulei Gadensis: Morison, *Hist.* **2**:87-8 (1680); Tourn., *Inst.* 393 (1719).

Robust annual, 20-120 cm, erect with vigorous lateral branching. Stems and petioles shortly villous, hairs ± 1 mm long. Stipules linear-subulate. Leaflets 9-11 (-13), 25-60 x 7-12 mm, oblong-oblanceolate, sericeous above and below. Racemes 5-15 cm long on short stout peduncles; flowers verticillate to rarely subalternate, on short pedicels ± 1/3 the length of the calyx; bracts lanceolate, caducous, bracteoles linear. Upper lip of calyx deeply 2-partite, lower lip longer, shallowly 3-toothed. Corolla 12-17 mm long x 14-19 mm high, bright blue apart from a centrobasal yellowish white spot on the standard, reaching to about 3 mm from the upper margin; keel blunt, tip pigmented dark blue; scent very slight (spicy) or absent. Pods 40-55 x 13-16 mm, densely villous to softly hirsute, 3-5 seeded. Seeds 6-9 x 4-7 x 3-4 mm, orbicular-quadrangular compressed; testa tuberculate, light grey or more commonly brown, with blackish markings including a narrow arc around the hilum.



l.c.

Figure 6.—*L. Cosentinii* Guss.

DISTRIBUTION: Tunisia, Morocco, S.W. Spain, S. Portgual, with isolated occurrences in Corsica, Sardinia, Sicily and neighbouring small islands—Map 6. Naturalized and cultivated in S.W. and to a smaller extent S. Australia and New South Wales. In all areas strictly confined to low altitudes and coastal localities, on light textured ± neutral soils.

SPAIN: Puerto Santa Maria, Bourgeau 150. PORTUGAL: Faro, Bourgeau 1819. SARDINIA: Sinai, Müller. SICILY: Palermo, Lojacono 373; Palermo, Todaro. IS. PANTELLARIA: Monte Grande, Davies. TUNISIA: Hammomet, Cosson. MOROCCO: Trethewy 24. WESTERN AUSTRALIA (naturalized): George 1519.

Much confusion has existed over the taxonomy of *L. cosentinii.* Some collectors have incorrectly labelled it *L. varius* L., a mistake which has been perpetuated in the modern Australian and European literature (see later section on "*L. varius*"). Other botanists regard it as a sub-species of *L. pilosus* Murray, but this cannot be sustained in the light of evidence now available. *L. pilosus* has a chromosome number n = 21, compared with 16 in *L. cosentinii* (Savcenko 1935; Malheiros 1942; Gladstones 1958a). Crosses between the two (Gladstones 1958a; Kazimierski 1964) have yielded only inviable seeds, or, in the case of one of Kazimierski's crosses which did give viable seeds, a completely sterile F1. Moreover the species are morphologically distinct, albeit with similarities, and have widely separate distributions.

Some writers, including myself (1958a, etc.), have previously held *L. cosentinii* to be synonymous with *L. digitatus* Forskål, the latter epithet taking priority because it was the earlier. Further investigation has shown the two almost certainly to be separate species (see further discussion under *L. digitatus*).

One epithet prior to *cosentinii* which could possibly have referred to the same species is *L. semiverticillatus* of Desrousseaux (1791). However, this lacks confirmation and seems too dubious to be accepted.

L. cosentinii is fairly limited in its distribution. Only in Morocco has it been reported to be common, all other occurrences in the Mediterranean region being apparently very small. Italian authors refer to the presence of *L. cosentinii* in Southern Italy at Otranto (Apulia) and Squillace (Calabria), but no specimen has been seen from there and a brief search of both districts by the writer failed to locate any. Significantly, Tenore (1835) recorded the Squillace occurrence as "from the cultivated state". The possibility exists that this and other minor Mediterranean occurrences derive, like those of *L. luteus,* from early attempts at cultivation.

In Western Australia, *L. cosentinii* is extensively naturalized along much of a 400-mile coastal strip, from south of Busselton to 50 miles north of Geraldton. It also occurs to a smaller extent in South Australia and New South Wales. In Australia the species volunteers mainly on littoral or sub-littoral sands of mildly acid, neutral, or mildly alkaline pH, while in Sicily and adjacent islands it grows on the more porous types of volcanic soils of about neutral pH. In Corsica, its occurrence is at the junction of limestone and granite soils (Briquet 1913). North African and Iberian populations (personal observation) are mostly on sub-littoral sands and sandy alluvium ranging from very mildly acid to moderately calcareous, in situations closely analogous to those where the species is naturalized in Australia.

Natural variability in *L. cosentinii* is poorly documented. Italian floras describe the seeds as greyish, but all Iberian and North African specimens seen have brown seeds. Both seed colours occur in Western Australia. Naturalized populations from Perth northwards nearly all have brown seeds, whereas those south of Perth mostly have pale grey seeds with only a tinge of brown and are also a few days later flowering. Presumably these represent two or more independent introductions.

Specimens collected by Bourgeau in Southern Spain and Portugal in the mid-19th century have flowers ranging from irregularly verticillate to subalternate. On the other hand specimens seen from Sicily and Sardinia, together with the naturalized populations in Western Australia, are more or less perfectly verticillate. North African populations have subverticillate to verticillate inflorescences, more commonly the latter. The normal flower colour is blue, but among naturalized and cultivated populations in Western Australia natural mutants with pale blue, pink, and white flowers occur and have been selected.

Seed size is relatively uniform, most lines having seeds about the same size as those of cultivated *L. angustifolius.* However, some smaller-seeded forms occur within the natural range.

No reference has been found to contemporary use of *L. cosentinii* as a cultivated plant except in Western Australia, where it is grown on slightly calcareous to moderately acid sands for summer forage and soil improvement. Current genetic improvement to develop the species as a true crop plant is described briefly by Gladstones (1970).

7. L. digitatus Forskål

Forskål, *Fl. Aegypt.* 131 (1775); *Vis., *Icon. Plant. Aegypt. Nub.* 29, t.5 (1836); Boiss., *Fl. Or.* **2**:27 (1872); Montasir & Hassib, *Man. Fl. Egypt* 231 (1956); Tackholm, *Stud. Fl. Egypt* 276 (1956).

Typification: "In Delta ad pagum Nedjel. Copiose in agris, an spontaneus, nescio." Type not seen.

L. forskahlei Boiss., *Diagn.* Ser. I, 9 p. 10 (1849).

L. tassilicus Maire, *Mém. Soc. Hist. Nat. Afr. Nord* **3**:266 (1933); *Chevalier & Trochain, *Rev. Bot. appl. Ag. trop.* **17**:88, pl 1. (1937).

Typification: "Tassili-n-Ajjer: Djanet, lit de l'Oued Tirririne à Iferouan, avril-mai 1933 (Petit-Lagrange No. 164, comm. A. Chevalier)." (Paris, photo seen.)

L. luthereaui Maire, *Bull. Soc. Hist. Nat. Afr. Nord.* **26**:154 (1935); Hernandez-Pacheco *et. al., Sahara Espagn.* 750 (1949).

Typification: "Dans les oueds de la Guelta du Zemmour Serait abondant (renseignements indigènes) dans les Akmadim, dans le Hank, et dans l'Asbat el Hassian (Adrar)." Type not seen.

L. pilosus ssp. *tassilicus* (Maire) Quezel & Santa, *Nouv. Fl. Algérie* **1**:521 (1962).

L. varius auct. non L., ssp. *orientalis* Franco & Silva, P., *Feddes Repert.* **79**:52 (1968) and in Tutin *et al., Fl. Europ.* **2**:106 (1968) pro parte, excl. *L. pilosus.*

Annual, 15-40 cm or more high, erect, rather sparsely branched. Stems and petioles shortly villous, hairs ± 1 mm long. Stipules linear. Leaflets 9-11, 20-50 x 5-10 mm, oblong-obovate to linear-obovate, lightish green, densely sericeous below, more sparsely sericeous above. Racemes 3-15 cm long on moderately stout peduncles; flowers verticillate to subalternate on pedicels ± ½ the length of the calyx; bracts linear-lanceolate, caducous; bracteoles linear-lanceolate. Upper lip of calyx deeply 2-partite, lower lip slightly longer, ± entire. Corolla about 16 mm long x 18 mm high, blue with a centrobasal white or yellow spot on the standard, not reaching the upper margin; keel pointed, white with a yellowish tip, the style protruding very quickly after anthesis. Pods 30-60 x 9-12 mm, slightly arched and tapering, with somewhat oblique septae and a long curved beak which readily breaks off; softly hirsute, 3-4 seeded. Seeds about 7 x 6 x 3 mm, compressed, with a prominent smooth hump over the hilum; testa otherwise scabrous, reddish brown with darker mottling and an arc around the hilum.

Chromosome number n = 18? (as *L. tassilicus* Maire).

DISTRIBUTION: Egypt, in desert regions and especially as a volunteer among crops of the Nile Delta and some oases; Central Saharan uplands; semi-desert coastal zone of the N.W. Sahara; Senegal Valley—Map 7.

EGYPT: Cairo, Muschler; Medinch el Fayum, Muschler; Senures im Fajum, Schweinfurth; Rad el Kharuf, Shabetai; Giza, Shabetai; Wadi Khareit, Tackholm; prov. Minyet. Tanard.

I have only seen Egyptian specimens of *L. digitatus,* but descriptions and illustrations of *L. tassilicus* Maire from the Central Sahara, N.W. Africa and Senegal agree well and are very probably the same species. The only difference between Chevalier and Trochain's detailed description of *L. tassilicus* and the Egyptian specimens of *L. digitatus* is that the former is held to have sub-alternate flowers (as opposed to ± verticillate) and greyish white rather than reddish brown seeds. However, Maire's original diagnosis of *L. tassilicus* itself gives the flowers as ± verticillate, while Chevalier and Trochain's plants were grown in Paris and failed to ripen; greyish white may merely have been the colour of the immature seeds, as I have observed in the closely related *L. cosentinii.* Quezel and Santa (1962), writing of the flora of Algeria, describe "*L. pilosus* L. ssp. *tassilicus* Maire" as having brown and fawn seeds.

Detailed information on the species' distribution and natural habitat is not available, but it probably grows on sandy soils at the bottoms of occasionally-flooded desert watercourses (wadis), among desert grasses and *Acacia* scrub. *L. digitatus* is a common winter volunteer in cultivated fields of the Nile Valley and Delta and (assuming *L. tassilicus* Maire to be identical) of the Senegal Valley. There it is recorded as providing useful grazing for sheep though disdained by camels (Maire 1935). It is not known to be cultivated.

L. digitatus clearly belongs in the "rough-seeded" lupin group (see later discussion). It has characters in common with *L. princei* and *L. somaliensis* which occur in the East African Highlands to the south, and with *L. pilosus, L. atlanticus* and *L. cosentinii* to the north. The last of these species has at times been confounded with *L. digitatus,* but the two appear distinct, especially in seed characteristics. The recorded chromosome numbers of 32 for *L. cosentinii* compared with 36 for *L. digitatus* (as *L. tassilicus* Maire (Eichorn 1949)) support their separation, although this evidence cannot be regarded as conclusive until Eichorn's chromosome count and the identity of *L. tassilicus* with *L. digitatus* have been confirmed.

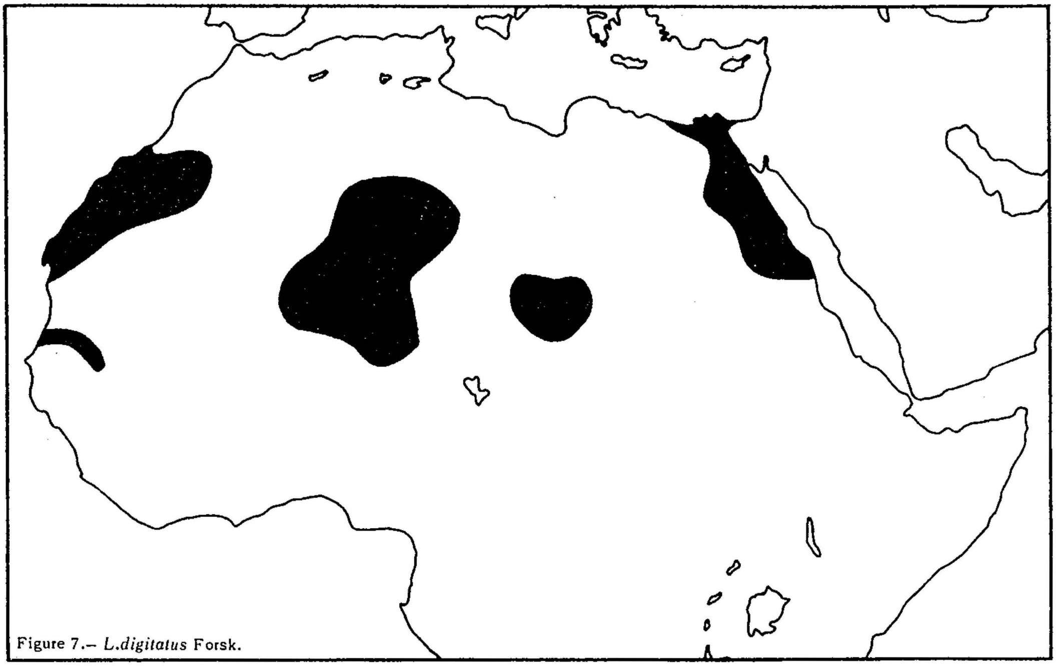


Figure 7.– *L.digitatus* Forsk.

8. L. princei Harms

Harms in Engler, *Bot. Jahrb.* **28**:401 (1901); Baker, *Leg. Trop. Afr.* **1**:60 (1926).
Typification: "Iringa, Savanne (Hauptmann Prince 1898)." Type not seen.

Robust annual, 30-120 cm high, erect, rather sparsely branched. Stems and petioles shortly villous, hairs ± 1 mm long. Stipules linear. Leaflets 9-13, 30-60 x 6-11 mm, linear-oblanceolate, palish green, densely sericeous above and below. Racemes 5-20 cm long on stout peduncles; flowers subverticillate on pedicels ± 1/3 the length of the calyx; bracts lanceolate, caducous; bracteoles lanceolate.

Upper lip of calyx deeply 2-partite, lower lip slightly longer, entire or slightly 3-toothed, ± pointed. Corolla large, 17-18 mm long x 18-20 mm high, bright blue apart from a pale yellowish band tipped pale blue up the centre of the standard; keel upcurved through 80-90°, tip ± blunt, non-pigmented. Pods 50-70 x 16-18 mm, softly hirsute, 3-4 seeded. Seeds 9-10 x 7-8 x 4 mm, quadrangular compressed, with a slight hump over the hilum; testa slightly rough, mottled dark brown on a pale yellow background, with a dark brown arc bordered yellow around the hilum.

DISTRIBUTION: Highlands of Kenya and N. Tanzania (Tanganyika) at 1 700-3 000 metres in open scrub or woodland; Mega district, S. Ethiopia—Map 8.

KENYA: dist. Eldoret, Williams 297; Mau summit, Bogdan and Williams 178; Menengai (Nairobi), Tweedie 1277; N.W. Kenya, Battiscombe 928. TANGANYIKA: Pole Evans and Erens 877; Milne-Redhead and Taylor 11127; Tropnell 2165. ETHIOPIA: Mega, Gillett 14199.

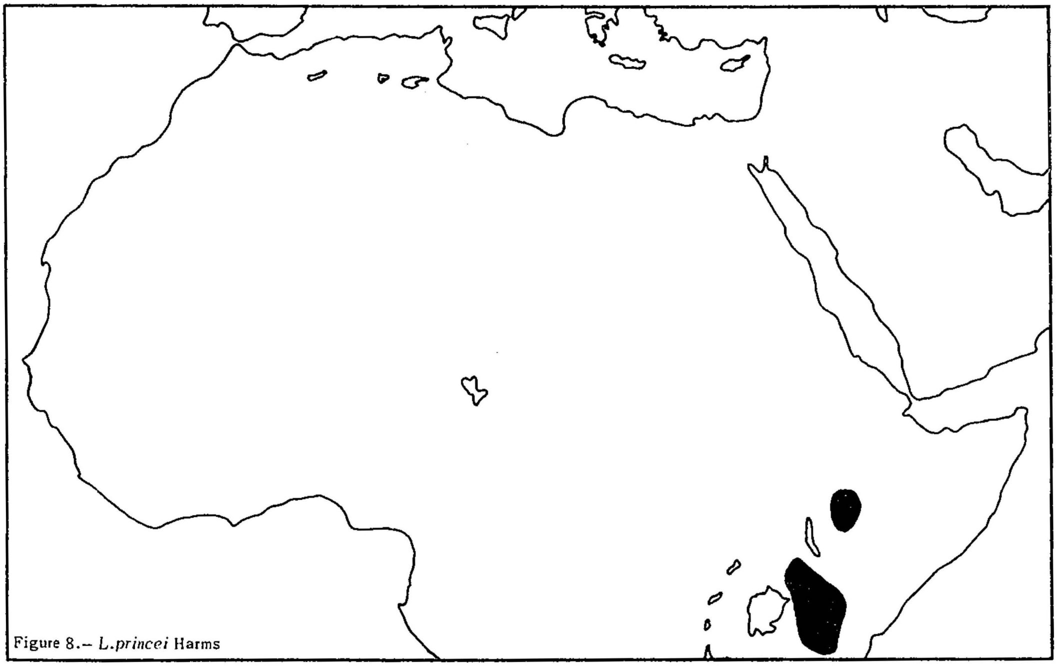


Figure 8.– *L.princei* Harms

All specimens seen but one have been from Kenya or Tanganyika, together with living material from seeds ex Kenya. The extent of distribution in Ethiopia is unknown, but the Gillett specimen from the Mega district of S. Ethiopia, though atypical in having white flowers, appears fully consistent with the species. It was noted as being abundant in the locality but not seen elsewhere. With the likely existence of suitable conditions in other parts of Ethiopia, however, it would not be surprising to find its distribution there more widespread.

L. princei clearly belongs in the "rough-seeded" group of lupins. Its closest apparent affinity is to *L. digitatus.* With very large seeds, exceeded only by *L. pilosus* and *L. albus,* it has some of the attributes of a food crop. However, no reference to its cultivation has been sighted.

9. **L. pilosus** Murray

Murray in L., *Syst. Veg.* ed.13, 545 (1774); Desr. in Lam., *Encycl. Méth. Bot.* 3:623 (1791); Willd., *Sp. Pl.* ed.4, 3:1024 (1803); Ten., *Fl. Nap.* 2:143 (1820); **Sibth. & Sm., *Fl. Graeca* 7:77, t.684 (1830); Agardh, *Syn. Gen. Lup.* 6 (1835); Boiss., *Fl. Or.* 2:27

(1872); Arcangeli, *Fl. Ital.* ed.2, 479 (1894); Post, *Fl. Syr. Pal. Sin.* 212 (1896); *Fiori & Paol., *Fl. Anal. Ital.* **2**:11 (α only), fig. 1865 excl. distr. (1899); *Coste, *Fl. Fr.* **1**:307 (pro parte) (1901); Halácsy, *Consp. Fl. Graec.* **1**:339 (1901); Ascherson & Graebner, *Syn. Mitteleur. Fl.* **6**(2):226 (1907); Fiori, *Nuov. Fl. Anal. Ital.* **1**:805 (α only) (1925); *Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:262 (excl. ssp.), fig. 10 (1929); Bouloumoy, *Fl. Lib. Syr.* 77 (1930); Thiébaut, *Fl. Lib.-Syr.* **2**:7 (1940); *Gladstones, *J. Roy. Soc. W. Aust.* **41**:31, pl. 1, 1 (1958a); *Hanelt, *Lupinen* 89, figs. 32, 34-5 (1960); *Kazimierski & Nowacki, *Genet. polon.* **2**:115 (1961); *Kazimierski & Kazimierska, *Genet. polon.* **11**:208 (1970b).

Typification: non published. The diagnosis clearly indicates a cultivated pink-flowered form of the species. Type not seen.

L. hirsutus L., *Sp. Pl.* 721 (1753) (diagn. inaccurate), non L. *Sp. Pl.* ed.2, 1015 (1763); Reichenb. & Reichenb. fil., *Icon Fl. Germ.* **22**:35, t.7 (1903) pro parte; Hegi, *Ill. Fl. Mitteleur.* **4**:1154 (1923) pro parte; Bailey, *Man. Cult. Pl.* 408 (1924) pro parte.

Typification: Linnaeus gives no indication of type or distribution for *L. hirsutus* in *Sp. Pl.* ed.1, but the references in this edition to Hort. Cliff. and other sources clearly point to the species here called *L. pilosus* Murray. However, no Linnaean specimen so labelled has survived, the two specimens in his collection labelled *L. hirsutus* being clearly of *L. micranthus* Guss., = *hirsutus* L. sensu *Sp. Pl.* ed.2 (1763).

L. varius L., specimen 898.3 (date unknown), but not specimen 898.4 so labelled or diagnosis, typification or references in *Sp. Pl.* eds. 1 or 2; **Kniphof, *Herb. Viv.* t.668 (1761); *Gaertner, *Fruct. Sem. Pl.* **2**:324, t.150 fig. 4 (1791); **St. Hilaire, *Pl. Fr.* **3**, t.16 (1809); D'Urv., *Enum.* no. 633 (1822); Chamberlain in Davis, *Fl. Turkey* **3**:40 (1970).

Typification: the Linnaean specimen 898.3 is a pink-flowered form of *L. pilosus* Murr; 898.4 is of *L. micranthus* Guss., = *hirsutus* L. sensu *Sp. Pl.* ed.2 (1763). Neither specimen agrees with the diagnosis, typification or references for *L. varius* in *Sp. Pl.* eds. 1 or 2.

L. varius ssp. *orientalis* Franco & Silva, P., *Feddes Repert.* **79**:52 (1968) and in Tutin *et al.*, *Fl. Europ.* **2**:106 (1968) pro parte excl. *L. digitatus* Forsk.; *Zohary, *Fl. Palaestina* **2**:41, t.53 (1972).

L. angustifolius auct. non L.: **Kniphof, *Herb. Viv.* t.666 (1761); **Buc'hoz., *Hist. Règne Vég.* **11**, dec.5, t.1 (1776).

L. digitatus auct. non Forskål: Muschler, *Man. Fl. Egypt* 474 (1912) (excl. distr.); *Chevalier & Trochain, *Rev. Bot. appl.* **17**:94, pl. 2 (1937).

Pre-Linnaean Synonyms

Lupinus sativus major, flore è coeruleo purpurascente—*Besl., *Eyst.* **2**, ord.13, 3 (1613).
Lupinus caeruleus major villosus—Bauh., *Prodr.* 148 (1620); Ray, *Hist.* **1**:907 (1686).
Lupinus peregrinus major vel villosus caeruleus major—Bauh., *Pin.* 348 (1623); Herm., *Lugd.* 386 (1687); Magnol, *Hort. Monsp.* 124 (1697); Boerh., *Lugd.* **2**:48 (1720); Miller, *Dict.*, no. 4 (1754).
Lupinus caeruleus maximus—Park., *Paradisus* 335 (1629).
Lupinus major flore caeruleo—*Ger., *Herb.* 1217 (1633).
Lupinus indicus—*Corn., *Canad.* 205, ill. p. 207 (1635).
Lupinus indicus medius coeruleus—Park., *Theat.* 1075 (1640).
Lupinus flore carneo—Park., *Theat.* 1075 (1640).
Lupinus peregrinus coeruleus major villosus—Morison, *Hist.* **2**:88 (1680).
Lupinus peregrinus major, flore incarnatus—Herm., *Lugd.* 386 (1687); Tourn., *Inst.* 392 (1719); Boerh., *Lugd.* **2**:48 (1720); Miller, *Dict.*, no. 5 (1754).
Lupinus flore coeruleo 1. rubro—*Riv., *Tetrap*, t.152 (1691).
Lupinus calycibus verticillatus: labio inferiore integerrimo—Linn., *Hort. Cliff.* 499 (1737); Ferber, *Hort. Ager.* 56 (1739); Roy., *Lugd.* 367 (1740); Linn., *Hort. Ups.* 209 (1748).
Lupinus flore coeruleo minore—**Knorrs, *Thes. Rei Herb.* 2, t.L7 (1772) (diagn. incorrectly from Riv. *Tetrap.).*

Annual 30-80 cm, erect and sparsely branched. Stems and petioles softly hirsute, hairs long (2-4 mm), white. Stipules linear-subulate. Leaflets (7-)9-11, 25-60 x 10-18 mm, oblong-obovate, softly villous on both surfaces. Inflorescences 10-30 cm long, somewhat lax on a slender peduncle; bracts lanceolate, caducous. Flowers large, 15-20 mm long x 16-22 mm high, subverticillate to verticillate on pedicels about $\frac{1}{2}$-$\frac{2}{3}$ as long as the calyx, with a faint spicy scent. Upper lip of calyx deeply 2-partite, lower lip longer, entire. Corolla deep blue apart from a central white spot or band on the standard which extends nearly to the upper margin and becomes purple with age; keel pointed, base white or tinged blue, tip darker blue; or flowers pink or more rarely white in cultivated selections.

Pods 50-80 x 20-25 mm, hirsute, 2-4 seeded. Seeds very large, 10-14 x 9-12 x 6-8 mm, mottled brownish red to purple, with a short, broad, darker crescent around the hilum, surface markedly scabrous.

Chromosome number n = 21.

DISTRIBUTION: Greece, Crete and Aegean Islands, W. and S. Turkey, Syria, Lebanon, Israel and W. Jordan—Map 9.

GREECE: Tybaki, etc., Atchley 1212; Is. Melos, Heldreich and Halácsy; Crete, Vamos-Kelfalas, Goulimy 50; rd. to Kandanos, Barclay 39. TURKEY: Atbükü, Tengwall; prov. Adana, Davis and Hedge; prov. Mersin, Davis and Polunin; prov. Antalya, Davis and Polunin. SYRIA: N. Syria, Osborne; Ain-Halakim, Haradjian 3503; Ghab Marshes, Wyndham. LEBANON: Harissa, Polunin 5316; Ramhala, Maitland 441; Beskinta, Mooney. PALESTINE: Kafar Kana (Lower Galilee), Heyn, Grizi and Baldinger; Lejera (Galilee), Myers and Dinsmore; Hartah, Myers and Dinsmore.

Although the epithet *pilosus* Murray (not L. as sometimes seen) has gained almost universal acceptance, some central European botanists have preferred *hirsutus* L., following the earlier (but inaccurate and later abandoned) diagnosis of Linnaeus in Species Plantarum ed. 1. (Reasons for rejecting the epithet "*hirsutus*" are discussed under *L. micranthus.*) One consequence has been that *L. pilosus* and *L. micranthus* have tended to be confounded, and some later diagnoses incorporate features of both (Reichenbach 1903; Hegi 1923; Bailey 1924).

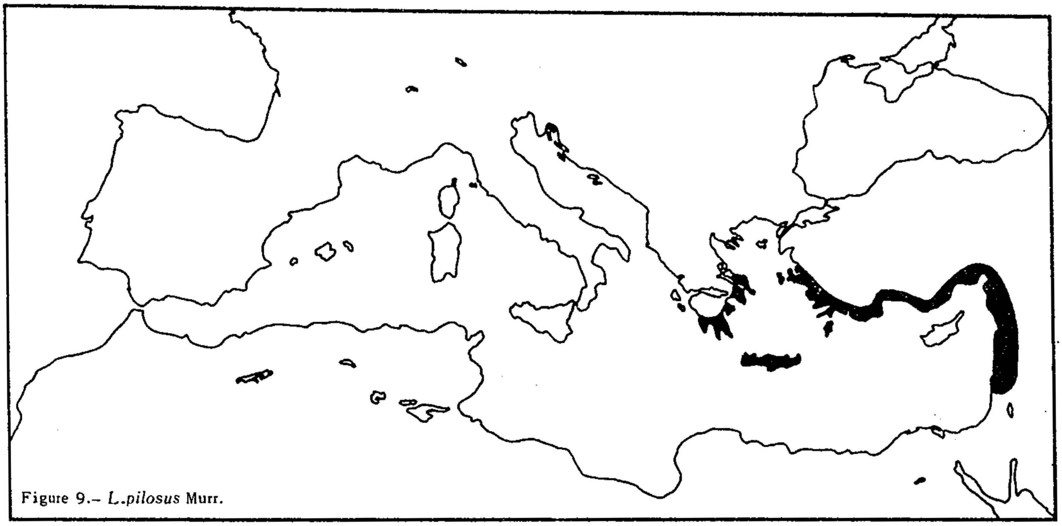


Figure 9.– *L.pilosus* Murr.

No Linnaean specimen of *L. pilosus* exists, apart from one of the two labelled *L. varius* (No. 898.3: the other, 898.4, being clearly of *L. micranthus).* This is presumably the basis upon which Franco and da Silva (1968a and b) accepted the Linnaean epithet *varius* as applying to *L. pilosus* Murray. Unfortunately they accepted it as applying also to *L. cosentinii* Guss. and *L. digitatus* Forskål, which are separate species, and confused matters further by nominating *L. cosentinii* Guss. as *L. varius* spp. *varius,* and *L. pilosus* Murray and *L. digitatus* Forskål together as *L. varius* spp. *orientalis* Franco and da Silva. Some argument might perhaps be made for retention of *L. varius* as applying to *L. pilosus* Murray alone; but considering the whole situation (see also the later section on "*L. varius* L."), I have little hesitation in rejecting it as a *nomen confusum* and accepting instead the later but unequivocal epithet *pilosus* Murray.

L. pilosus grows both on coastal sandy soils and inland to altitudes of 1 200 metres or more. In Galilee it is reported to grow abundantly on basalt soils, but most other reports refer to a sandy soil surface, sometimes over limestone but never markedly alkaline.

No direct reference has been found to cultivation of *L. pilosus* in its region of origin. As with other lupin species, collectors have noted it to occur mainly as a volunteer on disturbed or fallow soils, or sometimes as a weed in crops. However, in the first clearly identifiable description in the Western European literature, Besler (1613) refers to it as *Lupinus sativus major, flore è coeruleo purpurascente,* implying that it was already known as a cultivated plant. Undoubtedly *L. pilosus* had been, as it still is, occasionally grown as an ornamental since its reported introduction in Western Europe in the late 16th century (C. Bauhin 1620). On the other hand Cornut (1635), and Morison (1680) both noted (correctly) that the seeds were only semi-bitter in taste, and that they found use for production of meal and flour in the same way as the older-established *L. albus.* Cornut's reference indicates that the species had already been introduced into Canada, presumably deliberately. Specimens in the Kew collection show it also to be present and perhaps cultivated in the E. African Highlands. (The possibility of *L. pilosus* being native in E. Africa and introduced in the E. Mediterranean seems remote, but cannot be discounted entirely.) From these references and the very large seed size of *P. pilosus,* which would seem anomalous in a wild plant, it seems likely that the species has played at least some role as a food crop in Western Europe during the last few hundred years. The presumption is strong that it must have done likewise in the East Mediterranean, perhaps for a very long time.

No breeding of *L. pilosus* has been attempted in modern times, and little is known of its natural variation. Specimens from the Eastern Mediterranean show some variation in flower size and perhaps also seed size. The flowers are normally fully verticillate, but sometimes the verticels are not perfect. Poor specimens are often misleading in respect to flower arrangement. The peduncle of *L. pilosus* is at any time relatively slender, and in poorly-grown specimens very much so. In such cases, instead of reducing the number of verticels per inflorescence like other lupins, *L. pilosus* tends rather to reduce the number of flowers per verticel to only 1 or 2, and to some extent to reduce the intervals between verticels. This can result in an appearance of alternate flower arrangement.

Flower colour in the wild state is always blue. However, horticultural varieties with pink or occasionally white flowers are frequently encountered in botanic gardens and collections. This fact has contributed to the misunderstandings in some of the early taxonomic literature on *L. pilosus* and species resembling it.

Differences are apparent within the species in flower form. Some (cultivated types?) have a slightly larger flower, with the central white area in the form of a band which more or less reaches the tip of the standard. The pedicels are relatively short and thick. Others have a slightly smaller flower, with the white area on the standard more definitely in the form of a spot which does not reach the upper margin. The pedicels are relatively long and slender. These may represent subspecific differences, but I have insufficient information at present to delineate definite taxa.

10. **L. palaestinus** Boiss.

Boiss., *Diagn. Pl. Or. Nov.* 9:9 (1849) and *Fl. Or.* **2**:27 (1872); Post, *Fl. Syr. Pal. Sin.* 212 (1896); *Zhukovsky, *Bull. appl. Bot. Pl. Breed. Leningrad* **21**:265, fig. 11 (1929); Tackholm, *Stud. Fl. Egypt* 276 (1956); *Zohary, *Fl. Palaestina* **2**:42, t.54 (1972).

Typification: "Hab. in cultis regionis Philistaeorum et in Arabiâ Palestinae contermina." Type not seen.

Annual resembling *L. pilosus* but lower growing (10-40 cm); early growth as a rosette, from which are sent up short stems bearing long inflorescences. Stems and petioles softly hirsute, hairs long (2-4 mm). Stipules linear-subulate. Leaflets 7-9, 20-50 x 5-10 mm, linear-obovate, mucronate, sericeous on both surfaces. Inflorescences 5-20 cm, somewhat lax on a slender peduncle; bracts linear, caducous; bracteoles linear; flowers about 17 mm long x 18 mm high, verticillate to subalternate on slender pedicels only slightly shorter than the calyx; upper lip of calyx deeply 2-partite, lower lip longer, narrow, entire; corolla pale yellow to pale pink, tinged with blue; keel pointed, tip pigmented blue or violet. Pods 50-70 x 18-20 mm, coarsely hirsute, 3-4 seeded. Seeds about 10 x 8 x 4-5 mm, compressed, mottled brown to dark brown with a thick dark brown crescent around the hilum; surface scabrous.

DISTRIBUTION: Central and S. Israel on the plains of Sharon and Philistia; Sinai Peninsula in the Jebel El Tîh—Map 10.

ISRAEL: Jaffa, Bornmüller 311; Sharon Plain, Heyn, Grizi, and Baldinger; Anjeh River, Myers and Dinsmore; dist. Ramleh, Fishelsohn; Pirard.

The distribution of *L. palaestinus* is contiguous with that of *L. pilosus,* to which it is probably closely related. Kazimierski (1964b) reported successful crossing between the two species, but that the Fl plants yielded only 50 per cent viable pollen and were completely sterile; which together with morphological and distributional differences seems sufficient ground for retaining the specific distinction.

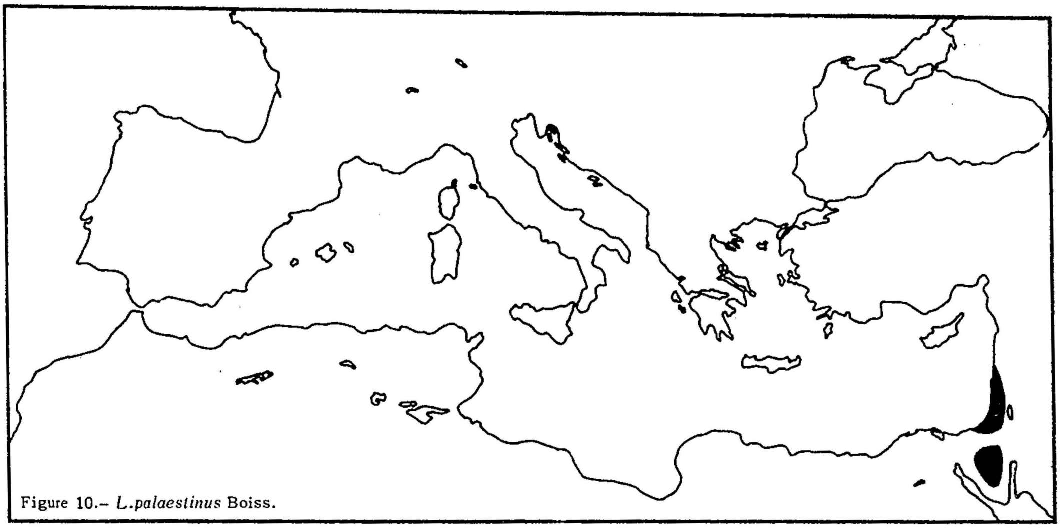


Figure 10.– *L.palaestinus* Boiss.

The natural habitat of *L. palaestinus* extends from the semi-arid sandy soils of the Israeli plains into true semi-desert and desert regions of the Sinai Peninsula. Like *L. digitatus* in N. Africa, it probably grows there as a winter annual or ephemeral on sandy wash soils in the bottoms of wadis, where moisture conditions are occasionally favourable. Little is known of its natural variability.

11. **L. atlanticus** J. S. Gladstones, sp. nov.

Herba annua, robusta. Caules et petioli molliter villoso, pilis albis circa 2 mm longis. Stipulae lineares, 8-18 x 1 mm. Foliola 9-11, oblongo-oblanceolata vel linearo-oblanceolata. Laminae sericeo villosae. Inflorescentia longi-pedunculata, racemosa sub-verticillata vel verticillata. Pedicelli crassissimi calycibus triplo breviores. Flores grandes circa 18 mm longi, 20-22 mm alti. Calycis labium superum profunde bipartitum, labium inferum longior plus minusve integrum. Vexillum cyaneum, ad apicem area grandis lata V-formata alba vel flavida ad marginem superum attingens. Alae cyaneae.

Carina alba, apice obtuso, atro-cyaneo. Legumina hirsuta, 40-70 mm x 15-22 mm, 3-5 seminalis. Semina grandia, oblonga, compressa, 8-11 x 6-8 x 4-5 mm, subrosea vel fusca maculata. Testa aspera, protuberatione laevi super hilo.

Holotypus: Loc. Amizmiz, Morocco, alt. 4 500 feet June 16 1936, E. K. Balls 2846 (K).

Robust annual to 60 cm. Stems and petioles softly villous, hairs white, about 2 mm long. Stipules linear, 8-18 x 1 mm. Leaflets 9-11, oblong-oblanceolate to linear-oblanceolate, light green in colour, both surfaces sericeous. Inflorescence subtended by a long peduncle. Pedicels about ⅓ length of calyx, very thick. Flowers subverticillate to verticillate, large, about 18 mm long x 20-22 mm high. Upper lip of calyx deeply 2-partite, lower lip slightly longer, ± entire. Standard blue with a large white or yellowish central sector which broadens towards the upper margin; wings blue; keel blunt-tipped, white with the tip blue. Pods hairy, 40-70 x 15-22 mm, with 3-5 large seeds. Seeds oblong, compressed, 8-11 x 6-8 x 4-5 mm, mottled brown, or pinkish with a pale arc around the hilum, slightly rough, with a distinct smooth hump over the hilum.

DISTRIBUTION: Anti Atlas, foothills of the High Atlas Mountains, and in the Djebilet, Morocco, at altitudes around 900-1 500 metres—Map 11.

MOROCCO: Ourika, Ball; Ourika, Hooker; Amizmiz, Hooker; Adadès and Cazalaght (dist. Ida Ouchemlal), Cosson; Imi n'Ifri near Demnate, Whiting and Richmond 194.

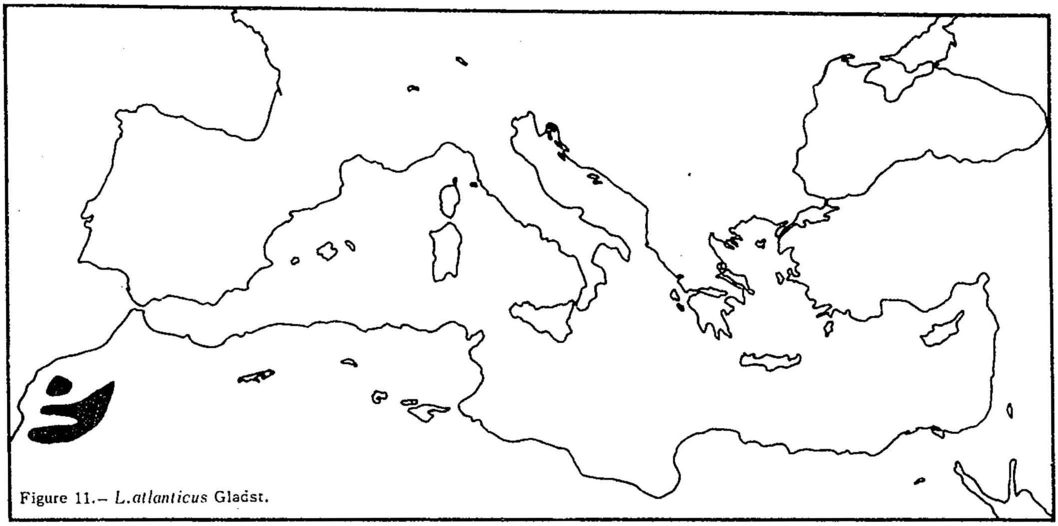


Figure 11.– *L.atlanticus* Gladst.

Hooker and Ball made several collections of this species in their Morocco expedition of 1871, and there are several quite good later specimens in the Kew collection. I have selected that of E. K. Balls as type for the species because it shows the main features well, including nearly mature seeds. All collections were originally determined as either *L. pilosus* or *L. varius.*

L. atlanticus clearly belongs in the rough-seeded group of Mediterranean and African lupins, with fairly close resemblances to *L. pilosus, L. digitatus,* and *L. cosentinir.* It is nevertheless quite distinct from them. The very large flowers resemble those of some *L. pilosus* forms, but the lightish green colour of the leaves more closely resembles that of *L. digitatus.* Seed shape and colour are variable but distinctive.

The full geographical range of *L. atlanticus* is not known. It is here assumed (Map 11) to occur in other parts of the Southern Atlas Mountains with altitudes and rainfall comparable with those of Amizmiz, and could conceivably be present in more easterly parts of the Atlas Range as well. I have recently collected seeds of it in the Anti Atlas near Tafraout and in the Djebilet north of Marrakech. The latter population, at a much lower altitude than the others, is probably an outlier. The main populations appear to occur between 1 200 and 1 500 m, on rubbly schistose and granite soils of about neutral reaction. The habitat of *L. atlanticus* is clearly distinct from those of *L. cosentinii,* which grows at lower altitudes on the Moroccan coastal plain, and *L. digitatus,* which is found in the semi-desert and desert regions to the south.

12. **L. somaliensis** Baker

J. G. Baker, *Bull. Roy. Gard. Kew* **105**:213 (1895); E. G. Baker, *Leg. Trop. Afr.* **1**:60 (1926); Zhukovsky, *Bull. appl. Bot. Pl. Breed.* **21**:273 (1929).

Holotypus: Somaliland: rocks above Dara-as, Golis Range, alt. 5 000 feet; Miss Edith Cole, Mrs. Lort Phillips (K).

Erect, branching annual (or doubtfully perennial). Stems and petioles softly hirsute, hairs about 2 mm long. Stipules linear, 10-18 x 1 mm, setaceous. Leaflets 9-13, 25-50 x 7-12 mm, oblong-oblanceolate, shortly mucronate, upper surface glabrous, lower surface softly hirsute. Flowers about 18 mm long x 16 mm high, subverticillate on stout, slightly upcurving pedicels about half the length of the calyx. Upper lip of calyx deeply 2-partite, lower lip much longer, ± entire. Corolla blue apart from a centrobasal white spot on the standard, reaching to about 3 mm from the upper margin; keel ± pointed, not pigmented. Pods and seeds not seen.

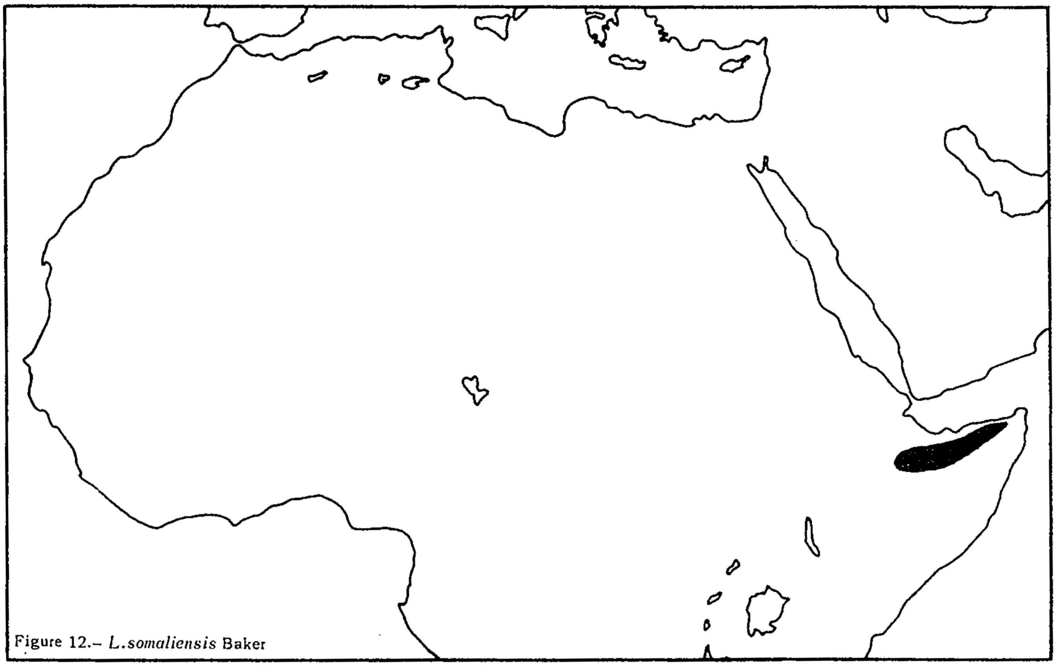


Figure 12.– *L. somaliensis* Baker

DISTRIBUTION: Highlands of Somaliland, perhaps extending westward into Ethiopia—Map 12.

This species is described from the single specimen collected by Miss Edith Cole and Mrs. Lort Phillips in Somaliland. The Battiscombe specimen from Kenya, which E. G. Baker (1926) and Zhukovsky (1929) identify with *L. somaliensis,* belongs in fact to *L. princei.*

L. somaliensis can fairly confidently be placed in the rough-seeded group of lupins, although no description of its seeds or pods is available. The very distinctive feature (within this species group) of a glabrous leaflet upper surface allows the tentative acceptance of species status.

The specimen collected was recorded as being perennial, and has been so described since. Considerable doubt must attach to this description. No other lupin species in the Mediterranean region or Africa is perennial, although a number of specimens have been mistakenly labelled as such, including *L. digitatus* Forskål in its original diagnosis. This is an easy mistake to make because of the bushy habit of most lupins, together with the fact that at least some, e.g., *L. cosentinii* (personal observation) can at times continue vegetative growth after seed maturity.

With only a single specimen, the geographical range of *L. somaliensis* (map 12) is very speculative. Its presence in the highlands of Somaliland suggests that it might possibly extend westwards into Ethiopia, but this has not been demonstrated to my knowledge.

LUPINS IN THE PRE-LINNAEAN LITERATURE

Pre-Linnaean synonyms and references are listed under the different species, insofar as their identities could reasonably be established. Internal evidence, and extensive cross-referencing by the early writers, left little doubt in most cases, although uncritical cataloguing of within-species variants by certain of the later pre-Linnaean writers introduced difficulties which necessitated omissions.

Three *Lupinus* species were fairly clearly distinguished by the end of the 16th century: *L. albus, L. angustifolius,* and *L. luteus.* The latter two were in some cases grouped as forms of *Lupinus sylvestris* (wild lupin), in contrast to the cultivated lupin *Lupinus sativus.*

The first reference to *L. pilosus* appeared in 1619. This species was widely represented in botanic gardens by the end of that century, often in both blue and pink-flowered forms. The latin names *Lupinus peregrinus major* and *Lupinus indicus,* given by 17th and 18th century writers, reflect its known eastern origin; and as pointed out in the commentary on the species, it was from the beginning regarded by at least some botanists as a cultivated plant.

L. micranthus was first described by J. Bauhin in 1651, under the name *Lupinus exoticus hirsutissimus.* Bauhin's description is reasonably clear, but he also appends a description of *L. pilosus* under the same heading. *L. micranthus* was also fairly clearly distinguished by Magnol (1676) in Southern France and by Cupani (1696) in Italy. An interesting point is that *L. micranthus* cannot definitely be identified among any of the Northern European collections of the time. The one possible reference, which may give a clue to the reason, is that of Parkinson (1640), under the name *"Lupinus flore obsoleto"*. Of it he wrote "We have had another sorte of Lupine sent us from Boel by this name, but perishing in an intemperate year, we can describe it no further.". The generally late flowering and maturing of *L. micranthus* could well have militated against its survival in the Northern European botanic gardens. This in turn may partly explain the tendency of later Northern European botanists to confound it (as *"L. hirsutus")* with *L. pilosus.*

Morison (1690) received seeds of *L. perennis* from America a few years before that date. The species was well established in the literature by the time of Linnaeus.

There are only two other species to which possible reference is made in the pre-Linnaean literature. Morison (op. cit.) described a type of lupin very similar to *L. pilosus,* but smaller, with constantly smaller dark brown, rough seeds marked with black lines and dots, which could have been *L. cosentinii.* The likelihood of this is heightened by the fact that it was supposed to have come from Cadiz *("Lupinus minoris caerulei Gadensis"),* a known habitat of *L. cosentinii* from the collections of the 19th century botanist Bourgeou. No further reference to *L. cosentinii* can be found until that of Gussone (1828), apart from the dubious one by Desrousseaux in 1791 as *"L. semiverticillatus"*. Perhaps the frost susceptibility and preference for warm temperatures of *L. cosentinii,* suggested by its natural distribution and confirmed by agricultural experience in Western Australia (Gladstones 1970), prevented its survival under Northern European conditions in the same way as *L. micranthus.*

Lupinus obsoleto colore, lusitanicus, latifolius, listed by Tournefort (1719), was very possibly *L. hispanicus.* This is another generally late-flowering species, which would probably have failed to seed in Northern Europe.

THE PROBLEM OF "LUPINUS VARIUS"

The Linnaean species *L. varius* has been a focal point of controversy throughout the history of lupin taxonomy. Over the last 120 years the epithet has often been applied to *L. cosentinii* Guss., or more rarely to *L. pilosus* Murray. Franco and da Silva (1968a, 1968b) brought together *L. pilosus* and *L. digitatus* Forskål on the one hand, and *L. cosentinii* on the other, as two subspecies of *L. varius,* a conclusion previously reached by Caruel (1894). *"L. varius"* has appeared in some floras with diagnoses that fit no known species.

Australian writers have been similarly divided. The problem is topical in that *L. cosentinii* has assumed some economic importance in Western Australia, where it is naturalized and cultivated under such popular names as "Western Australian blue lupin" and "sandplain lupin". Originally the species was identified in Australia as *L. pilosus* (Gardner and Elliott 1929;

C.S.I.R.O. 1953). Later it was thought to be *L. varius* (Gardner and Bennetts 1956). I initially concluded (Gladstones 1955) that it was identical with *L. cosentinii* Guss., but later (1958a) gave priority to *L. digitatus* Forskål because of the latter's earlier date and supposed synonymy. The two epithets *varius* and *digitatus* subsequently appeared in the Australian literature up to about 1969 with similar frequencies. Since the publications of Gladstones (1969, 1970), the epithet *cosentinii* has gained more or less general acceptance.

The reasons for the misunderstandings surrounding *"L. varius"* go back to Linnaeus and even earlier. The following discussion attempts to reconstruct Linnaeus' thinking, based on his diaries, publications and specimens, and to trace the sequence of events which led to the epithet's modern misapplication.

In the 1st (1753) edition of *Species Plantarum,* Linnaeus gave diagnoses for six *Lupinus* species: *L. perennis, L. albus, L. varius, L. hirsutus, L. angustifolius,* and *L. luteus.* No controversy attaches to the first two or last two of these, and, as previously pointed out, the *"L. hirsutus"* of the 1st edition was probably the species here known as *L. pilosus* Murray.

To what plant, then, did Linnaeus originally give the name *L. varius?* Its diagnosis, synonymy and distribution as cited in both Linnaean editions of *Species Plantarum,* when compared with those in the pre-Linnaean literature including his own earlier publications, show clearly that it must have been a form of *L. angustifolius.* Supporting evidence for this is found in *Mantissa Plantarum* (1771), in which Linnaeus added "foliola linearia" (a characteristic found only in *L. angustifolius)* to the diagnoses of both *L. angustifolius* and *L. varius.* The epithet *varius* itself appears to be derived from the description *"Lupinus sylvestris, flore purpureo, semine rotundo vario"* of J. Bauhin (1651), which Linnaeus cited as a synonym of *L. varius* and which from Bauhin's illustration and extensive description was undoubtedly *L. angustifolius.*

What difference did Linnaeus see between *L. varius* and *L. angustifolius* to justify their separation? According to the diagnoses, he based the distinction on two characters. In *L. varius* the flowers were described as semi-verticillate, and the lower calyx lip as sub-tridentate; in *L. angustifolius,* as verticillate and entire respectively. But these are two characteristics of *L. angustifolius* which show considerable variability. Flowers of the wild types—and less frequently those of the cultivated large-seeded varieties—tend distinctly to become verticillate towards the tops of the inflorescences, and on many specimens could easily be described as semi-verticillate. A sub-tridentate lower calyx lip is normal in many of the small-seeded wild types of *L. angustifolius,* whereas in the large-seeded cultivated types it tends to be entire. It may therefore be suggested that Linnaeus' distinction between *L. varius,* in its original sense, and *L. angustifolius* was merely that between the small-leaved, small-seeded wild type of *L. angustifolius* and the larger cultivated type. This is supported by the following further facts. (a) The Linnaean type specimen of *L. angustifolius* (No. 898.7) is almost certainly of the large-leaved cultivated type. (b) He cited *Lupinus angustifolius caeruleus elatior,* i.e. the larger-growing type distinguished by Ray (1686), as a synonym of *L. angustifolius,* and not the very clear description and illustration given by J. Bauhin (1651), which he referred instead to *L. varius.*

The later authors of *L. linifolius* Roth (1787) and *L. reticulatus* Desv. (1835) attempted to make a similar specific distinction from cultivated *L. angustifolius.* Subsequent research has shown, however, that the cultivated and wild forms are very closely related and there is little to suggest the occurrence even of sub-speciation processes within the species (see commentary on *L. angustifolius).*

The two surviving Linnaean specimens labelled *L. varius* do not at first sight support the above argument. They agree neither with Linnaeus' published diagnosis of *L. varius* (in ed. 1 of *Species Plantarum* or any subsequent edition), nor with each other. Specimen 898.3 is clearly a pink-flowered form of *L. pilosus* Murray, while 898.4 is equally clearly *L. micranthus* Guss.

No date can be found for specimen 898.3, but Kniphof's illustration of 1761 shows a pink-flowered form of *L. pilosus* under the binomial *L. varius,* indicating that it or a similar specimen existed by then. Specimen 898.4 was one of a series of specimens sent by L. Gérard, who corresponded with Linnaeus between 1755 and 1757, and may reasonably be assigned to that period. Two other specimens of *L. micranthus,* nos.

898.5 and 898.6, appear identical but are labelled *L. hirsutus,* consonant with the diagnosis for *L. hirsutus* in *Species Plantarum* ed. 2. It would seem that Linnaeus changed his mind some time after the publication of *Species Plantarum* ed. 1 and before publication of ed. 2, perhaps following receipt of the *L. micranthus* specimens.

Further light is thrown by a series of annotations in Linnaeus' hand in his personal copies of *Species Plantarum,* now in the possession of the Linnaean Society of London. In one copy of ed. 1 he removed the previous synonyms (which refer clearly to *L. angustifolius)* from *L. varius* and placed them opposite *L. angustifolius.* He also moved distribution data from *L. varius* to *L. angustifolius.* From this it may be deduced that Linnaeus himself decided, sometime before publication of ed. 2, that the original *L. varius* and *L. angustifolius* were synonymous and should be merged under *L. angustifolius.*

In the same copy of ed. 1, Linnaeus crossed out the first three lines (diagnosis and some synonyms) of *L. hirsutus* and added, opposite, what appears to be *"L. varius flore rubro",* together with a dubiously identifiable synonym of Tournefort, which may have been *L. micranthus,* and the synonym *"Lupinus peregrinus major, flore incarnata"* of Boerhaave, which clearly refers to the pink-flowered form of *L. pilosus.* Other synonyms not deleted from the original *L. hirsutus* could refer to either *L. micranthus* or *L. pilosus.* The evidence is not entirely clear, but seems to indicate an intended merging of *L. micranthus* and *L. pilosus* under the now-discarded epithet *varius.* This agrees with the specimen of *L. micranthus,* probably dated 1755-7, and the one of pink-flowered *L. pilosus* presumed to date to before 1761, both of which are labelled *L. varius.*

In a second copy of ed. 1, perhaps used later, Linnaeus made alterations and additions to *L. hirsutus* which bring it fully in line with *L. micranthus,* and these appear in ed. 2 (1763) of *Species Plantarum.* The additional diagnostic point *"foliola spatulata"* is noted in Linnaeus' hand in a personal copy of ed. 2, and appears in *Mantissa Plantarum* (1771) and later editions of *Species Plantarum.* The evidence thus points to a final decision to separate *L. micranthus* from *L. pilosus,* placing the former under *L. hirsutus* (with suitably amended diagnosis) and presumably leaving *L. pilosus* under the epithet *varius.*

If such were the intended changes, they were never fully carried through. While two specimens of *L. micranthus* in the Linnaean collection were labelled *L. hirsutus,* the third and apparently identical specimen (perhaps separated at the time?) remained labelled *L. varius,* together with the specimen of *L. pilosus.* Nor was any amendment made to the diagnosis of *L. varius,* apart from addition of *"Florum vexilli medio rubri"* in ed. 2, which brought it partly into line with *L. pilosus.*

Some evidence that Linnaeus remained undecided, and possibly confused, is that in *Mantissa Plantarum* the characters *"Flores rubri"* (presumably from the *L. pilosus* specimen) and *"Foliola linearia"* (incompatible with *L. pilosus* but fitting *L. angustifolius)* were both added to the *"L. varius"* diagnosis. That "linear leaflets" was used in the same sense as for *L. angustifolius* is suggested by the fact that he simultaneously added it to the description of *L. angustifolius.* Perhaps, consciously or otherwise, Linnaeus was again thinking of *L. varius* in the same light as in the 1st edition of *Species Plantarum,* i.e. as a form of *L. angustifolius.*

Most early post-Linnaean writers used *L. varius* in this original sense, the contexts leaving little doubt, in the light of subsequent knowledge of species distributions, that wild types of *L. angustifolius* were meant. The appropriate references are listed under synonyms of *L. angustifolius.* Following introduction of the less equivocal synonyms *L. linifolius* Roth (1787) and *L. reticulatus* Desv. (1835), use of *"L. varius"* in this sense was largely abandoned.

A few later botanists, including recently Franco and da Silva (1968) have attempted to reinstate *"L. varius"* as a prior synonym of *L. pilosus,* which in the post-Linnaean literature was first clearly diagnosed as a separate species by Murray in the 13th (1774) edition of Linnaeus' *Systema Vegetabilium.* This argument presumably rests on the Linnaean specimen 898.3. It ignores the second Linnaean specimen (898.4, of *L. micranthus)* which is also labelled *L. varius,* together with the inapplicability to *L. pilosus* of any of Linnaeus' *L. varius* diagnoses (particularly that of *Species Plantarum* ed. 1), and the almost general acceptance of Murray's epithet by later botanists.

Soon after Linnaeus the first possible reference to *L. cosentinii* appeared. Desrousseaux' description of *"L. semiverticillatus"* (1791) strongly suggests *L. cosentinii,* but no outside corroboration can be found and their identity must be regarded as dubious. This may have been the starting point from which the epithet *"varius"* came to be misapplied to *L. cosentinii.* De Candolle (1825) followed Willdenow (1803) in listing *L. semiverticillatus* Desr. as a synonym of *L. varius* L. His diagnosis for *"L. varius"* differed from that of Linnaeus in giving the leaflets as oblong, not linear. He also rejected as applying to *L. varius* the illustration of Bauhin (1651, p. 291), listed by Linnaeus under *"L. varius"* and clearly of *L. angustifolius;* but accepted as a synonym *"L. sylvestris* ∝*"* of Lamarck (1778), which is equally clearly *L. angustifolius.* De Candolle's cited distribution for *"L. varius"* fits *L. angustifolius* rather than *L. cosentinii,* as does his description of the leaflets as villous on the underside only. Thus the only difference from *L. angustifolius* lay in the leaflet shape. De Candolle's intention remains decidedly obscure, as he recognized both *L. angustifolius* and *L. linifolius,* and *L. pilosus* as well.

Whatever De Candolle's intention, his diagnosis of *"L. varius"* fitted *L. cosentinii* quite well, except in giving the leaflets as villous on the underside only. The latter point was overlooked by later botanists. Perhaps their readiness to apply the epithet to *L. cosentinii* was influenced by the lack of any other species fitting the literature description of *"L. varius".* Also, the diagnostic character originally supposed by Linnaeus to distinguish *"L. varius"* from the cultivated forms of *L. angustifolius* proved by accident equally to distinguish *L. cosentinii* from *L. pilosus.*

Specimens of *L. cosentinii* labelled *L. varius* were extant in or soon after De Candolle's time. Agardh (1835) gave a confused diagnosis and references for *L. varius,* but noted that the specimens seen by him and so labelled seemed indistinguishable from *L. cosentinii* Guss., whose diagnosis had meantime (1828) been published and which Agardh considered hardly distinct from *L. pilosus.*

The earliest specimens I have sighted of *L. cosentinii* labelled *L. varius* were those of Bourgeau, who collected in Southern Spain and Portugal in 1849 and 1853. (These specimens, interestingly, are rather anomolous for the species in showing the flowers as approaching sub-alternate rather than the more usual verticillate arrangement, which would add apparent weight to their identification with the Linnaean *L. varius.)* Bourgeau's specimens were distributed widely as *L. varius,* and one of them, N 1819, was cited by Reichenbach (1903) as the source of his accurate description and rather less than accurate illustration of *"L. varius".* The later descriptions and illustrations of *"L. varius"* by Gardner and Bennetts (1956) and Hanelt (1960) followed Reichenbach, but were based directly on living material of *L. cosentinii.*

Meanwhile, a number of other diagnoses of *L. varius* have persisted in the literature. These appear at least in part to have descended directly from De Candolle, because they have continued to describe the upper surface of the leaflets as glabrous (Willkomm and Lange 1880; Merino 1905; Coutinho 1913; Hegi 1923; Chevalier and Trochain 1937; Foury 1950). The distributions cited for *L. varius* in the first three references, which are from Iberia (the supposed main habitat of *L. varius)* are of interest. Specimens cited by Willkomm and Lange date mainly from the time when the epithet *varius* was generally applied to *L. angustifolius.* Merino cited "a single example" from Galicia. Coutinho, who was the only one to describe *L. cosentinii* as well as *L. varius,* indicated that no Portuguese specimen of the latter had been seen.

Continued use of the epithet *varius* is hard to justify in view of this history, whether in application to *L. pilosus* or to *L. cosentinii,* or as a synonym for *L. angustifolius.* A barely tenable argument based on the Linnaean specimen 898.3 might be made for retention of *varius* if *L. pilosus* and *L. cosentinii* could be proved con-specific. This course is attempted by Franco and da Silva (1968a, 1968b), who regard the two as sub-species of *L. varius.* But the evidence of consistently differing morphology and distribution, different chromosome numbers, and genetic incompatibility on crossing (Gladstones 1958a; Kazimierski 1964b) shows conclusively that these are separate species. No alternative is left but to reject the epithet *varius* entirely, as a *nomen confusum.*

PHYLOGENY OF THE MEDITERRANEAN AND AFRICAN LUPINS

In contrast to the North and Central American lupins, in which species boundaries are often ill-defined and inter-species crossing is common, the Mediterranean and African lupins are mostly separated by profound genetic barriers. Chromosome numbers vary widely (Appendix 1), with no readily apparent overall pattern of species relationships. Recent cytological studies by Kazimierski and Kazimierska (1970a) of haploids in *L. luteus,* whose somatic chromosome number of 52 is the highest recorded for any European or African species of *Lupinus,* revealed typically diploid behaviour. This could be reconciled with at the most a very ancient origin through polyploidy. Mutation studies with several lupin species (for review see Gustafsson and Gadd 1965) have likewise shown typically diploid behaviour. Attempted inter-species crosses have in most combinations been entirely unsuccessful (Gollmick 1937; Gladstones 1955, 1958a; Kazimierski 1961, 1964b; Jaranowski 1962), while fairly basic species differences are apparent in chemical composition and alkaloid patterns (Hackbarth and Troll 1957; Nowacki 1960). It therefore seems clear that the main processes of speciation are well advanced.

Certain species groups, totalling 4 or possibly 5, can tentatively be recognized. *L. luteus,* together with *L. hispanicus/L. rothmaleri,* form a distinct group with its centre of origin in the Iberian Peninsula. Their differentiation *inter se* is incomplete and probably quite recent. *L. angustifolius* constitutes a group on its own, with a pan-(though mainly northern) Mediterranean distribution and no obviously localized centre of origin. *L. albus,* with its centre of origin in the Balkan Peninsula, is also isolated, although both crossing behaviour (Gladstones 1955) and alkaloid composition (Nowacki 1960) suggest a very faint affinity to the more southerly rough-seeded group (below).

The position of *L. micranthus* is uncertain. Hackbarth and Troll (1957) and Nowacki (1960) place *"L. hirsutus"* in the rough-seeded group, but this is almost certainly due to nomenclatural confusion. Certainly the smooth-seeded *L. micranthus* does not fall naturally into that group, although there are some similarities in other respects. The single recorded chromosome count attributed to *L. micranthus* as such (this being a binomical which, as far as I know, has not been misapplied to any other species) is that of Tuschnjakowa (1935). She found a probable diploid number of 50, i.e. the same as *L. albus.* No attempt to cross *L. micranthus* with any other lupin species has been recorded.

A relationship between *L. micranthus* and *L. albus* seems not impossible. Morphologically, there is some resemblance to the wild forms of *L. albus* (var. *graecus).* The greatest variability in the *L. micranthus* specimens seen was among those from the Balkan Peninsula, suggesting the possibility of a common centre of origin with *L. albus.* However serological evidence (Nowacki and Prus-Glowacki 1971) indicates *L. micranthus* to be distinctly separated and in a group of its own.

The remaining 7 species, *L. pilosus, L. palaestinus, L. digitatus, L. cosentinii, L. atlanticus, L. somaliensis,* and *L. princei* form the rough-seeded group, so named on account of the distinctively rough-surfaced seeds of all its members. Apart from similarities of morphology, the species studied further *(L. pilosus, L. palaestinus,* and *L. cosentinii)* have shown a common alkaloid pattern (Nowacki 1960) and a genetic relationship in their ability, in at least some combinations, to form viable seeds on crossing (Kazimierski 1964b). However, in no case yet has a fertile F1 been obtained. This and the differences in chromosome numbers suggest that speciation is well established for at least most members of the group. *L. palaestinus* could perhaps be very close to *L. pilosus,* with which it is contiguous in distribution. Examination of lesser-known members of the group may reveal other relationships.

The rough-seeded lupins show a well-defined pattern of distribution around the periphery of the Saharan and Arabian Desert regions. Most of the species have quite limited distributions. Possibly they are relics of what was once a more continuous population, spread over the northern half of the African Continent when its climate was less arid than now.

The position of *Lupinus* in the tribe *Genisteae,* together with its presence on both sides of the Atlantic, likewise bespeak a relatively ancient origin, from a group whose distribution is predominantly tropical and sub-tropical (for general discussion of evolution within the sub-order *Papilionateae,* see Norris (1956) and Nowacki (1960)). The nearest other genera, on morphological and biochemical grounds respectively, appear to be *Crotalaria* and *Cytisus* (Zhukovsky 1929; Nowacki 1960). Nevertheless, most *Lupinus* species have fairly rigid requirements for moderate temperatures. Occasional species have become adapted to very low temperatures, e.g. the North American species *L. arcticus;* but adaptation to tropical temperatures is rare. One atypical group of species is found in the tropical forests of Brazil, but Zhukovsky (1929) considered they should perhaps be transferred to the genus *Crotalaria.*

An origin or main development of the genus under warm temperate conditions, and if in the tropics under highland rather than lowland conditions, therefore seems probable. At least in the case of the rough-seeded group, present-day species distributions and the known range of soil preferences point to the crystalline, pre-Cambrian massif of the Central Sahara and its associated deposits as a likely centre of early distribution. If this is so, only *L. digitatus* and to some extent *L. palaestinus* have maintained their existence *in situ* under conditions of increasing aridity. The remaining members of the group occupy peripheral pockets where conditions have remained more favourable, or to which they have been able to escape.

The origins of the other Mediterranean species groups are more obscure. Few morphological or cytological relationships are apparent amongst them or with the rough-seeded group (Appendix 1 and above). The major species groups are therefore presumably the products of early differentiation within the genus. Paucity of species within the groups suggests further that they may be the survivors of drastic species elimination.

Several factors suggest that the northern Mediterranean species may have evolved more recently than the rough-seeded lupins occurring only in Africa. This applies particularly to the *L. luteus* group, which is still actively evolving.

(1) The northern species, especially *L. luteus,* have moved furthest away from the primitive shrubby habit of most of the *Genisteae* and the related alkaloid-containing tribes the *Podalyrieae* and *Sophoreae,* towards a herbaceous habit approaching that in more recently (Norris 1956) developed Mediterranean tribes such as the *Vicieae.*

(2) Nowacki (1960) finds evidence of advanced evolution, relative to other lupins, in the alkaloid constitution of the *L. luteus* group.

(3) Chromosome numbers, insofar as they are known, tend to increase from south to north, reaching maxima of 50 in *L. albus* and (?) *L. micranthus,* and 52 in *L. luteus.* This represents a progressive increase away from the 16-18 chromosomes characterizing most of the *Podalyrieae* and *Sophoreae* and the tropical and sub-tropical *Genisteae* (Darlington and Wylie 1955).

(4) Of the species for which observations on natural cross-pollination are available (author, unpublished), *L. luteus* has the highest level of crossing, followed by *L. albus* and then *L. angustifolius,* with *L. cosentii* the lowest of the four and almost exclusively self-pollinating. A high level of cross-pollination is taken to imply a greater probability of active current evolution.

(5) The species around the north of the Mediterranean have wider and more varied habitats than the solely or predominantly African species. *L. digitatus* in the Sahara region is a possible exception to this. Other rough-seeded lupin species in Africa have very limited known distributions, consistent with their being relicts.

In summary, a plausible hypothesis is that the genus is a fairly ancient one, having evolved out of the tropical-subtropical *Genisteae* to occupy the acid crystalline and associated soils of warm temperate North Africa and the central American highlands. The American group is currently in a state of active evolution. By contrast, the sedentary African species have contracted with recent increased aridity, and may in the past have been subject to drastic species elimination. The most active recent evolution in this region would appear to have been at the northern fringe of the distribution, perhaps in response to the same climatic fluctuations and other factors as underlay the post-Tertiary Mediterranean evolution of the herbaceous *Vicieae* and *Trifolieae* (see Norris 1956).

It is worth noting that the Mediterranean lupins have retained the adaptation to soils low in bases which, according to Norris (op. cit.), is characteristic of most tropical legumes. They occupy the scattered and in most regions limited areas of non-calcareous soils, in contrast to the more typically calciphile tribes of the Mediterranean. Similarly, they are nodulated by the "slow growing" root nodule bacterium *Phytomyxa* (Graham 1963, 1964), which is characteristic of most tropical and subtropical legumes and of non-calcareous soils, rather than by the "fast growing" *Rhizobium* of the *Phaseoleae, Vicieae* and *Trifolieae*. *Phytomyxa* is able to withstand high temperatures and to colonize and persist in acid and sandy soils low in bases better than *Rhizobium* (Parker 1962; Marshall, Mulcahy and Chowdhury 1963; Chatel and Parker 1973a, 1973b). This parallel adaptation of host and symbiont could have considerable importance for the development of lupins as agricultural plants for poor soils.

RECENT EVOLUTIONARY DEVELOPMENTS

Modification of the environment by clearing and cultivation since neolithic times, together with possibly deliberate sowing and conscious or unconscious selection by man, has undoubtedly done much to determine the present distribution of *Lupinus* in the Mediterranean region and Africa, and helped to create new variability. Lupins in their natural, undisturbed state appear to have quite limited habitats. According to my observations in the Western Mediterranean, these comprise two main types. The first is littoral sands and small areas further inland of similar lightly vegetated, loose, sandy soils formed mainly on granite, especially where there has been soil disturbance by foraging or burrowing animals. Bitterness of lupins protects them from grazing in such situations, while the ready leaching to which these soils are subject ensures that nitrogen levels and consequent competition from non-legumes remain minimal. The second situation, mainly in hilly inland districts, is on steep detrital slopes formed from schist, slate, or volcanic or similar rocks. Mainly neutral in reaction, these "soils" form a medium into which the rather large lupin seeds roll and become covered, and where the deep and rapidly penetrating root system of lupins is clearly advantageous.

Clearing, cultivation and the depletion of soil nitrogen by cropping must have opened up vastly enhanced ecological opportunities. Lupins became efficient weeds of cultivated fields and roadsides where suitable soils existed. Scattering of seeds at maturity over considerable distances allowed them to exploit changes in habitat quickly, and to overrun fallow land. At the same time occasional seeds harvested with crops assist in their spread to new cultivated habitats. Modern road building and the frequent formation of steep rocky embankments has further enhanced the ecological opportunities for lupins.

In addition to these opportunities, several lupin species appear at some time to have been either cultivated or tolerated as marginally useful. *L. albus* has long been a plant of peasant cultivation, both for its seeds and for its favourable effect on soil fertility, which has been known at least since classical Greek and Roman times. Selection under cultivation has directly resulted in the white flowers and seeds, permeable seed coats, non-shattering pods, larger seeds, and earlier maturity which distinguish var. *albus* from var. *graecus*. Cultivation has almost certainly been entirely responsible for the subsequent spread of the species beyond its original Balkan habitat, though not, it may be noted, in most cases as a truly naturalized plant. Var. *albus* sometimes volunteers for one or more generations after cropping, but loss of its wild characteristics has deprived it of the ability to compete successfully under more natural conditions.

Although early botanists generally referred to *L. angustifolius* as a wild lupin, its seeds have been variously used for a long time. Writing of the manifold pharmaceutical uses of *L. albus* seeds in Roman times, Parkinson (1640) stated that those of wild lupins (i.e. *L. angustifolius)* are "stronger and more effectuall to all purposes". *L. angustifolius* seeds are widely recorded as having been used as a coffee substitute or adulterant, while common names such as "lupino salvatico" (Bauhin *et al.* 1651; Savi 1798) in Italy bespeak a wider use in times of need.

Larger and smaller-seeded types have been known in *L. angustifolius* for at least several hundred years (see species commentary), and at least two authors (Miller 1754; Tourlet 1908) clearly specify the large-seeded varieties as being cultivated, in contrast with the small-seeded wild types. There can be little doubt, therefore, that cultivation has been instrumental in spreading the large-seeded varieties. Whether these were deliberately selected in the first place cannot be ascertained. Were large seeds to be of selective advantage on particular soil types, they might conceivably have arisen naturally as edaphic ecotypes. Equally, establishment of lupins as weeds among sown crops, by putting a premium on rapid seeding growth, could have created new natural selection pressures favouring larger seeds.

The undoubted part played by cultivation and naturalization in the spread of *L. luteus* has already been mentioned in the commentary on that species. Populations outside the Iberian Peninsula conform generally to the cultivated type in having relatively large seeds and early flowering. Human selection would similarly account for some of the variability in Iberian populations. Whether the attractive golden flowers and strong, sweet scent, which among other characters distinguish *L. luteus* from its close relative *L. hispanicus,* could also have arisen through human selection is more doubtful. The presence of a sterility barrier between them, fairly consistent morphological differences, and at least partial differences in distribution and soil preferences point to the action of normal speciation processes. Natural evolution of the *L. luteus* group, which as pointed out in the previous section has evolved furthest among the Mediterranean-African lupins from the ancestral shrubby habit of the *Genisteae,* would appear to be fairly recent and is probably still proceeding.

With the exceptions of *L. pilosus* and possibly *L. micranthus,* none of the other species *(L. cosentinii, L. digitatus, L. palaestinus, L. atlanticus, L. princei,* and *L. somaliensis)* is known to have been cultivated in the Mediterranean region or Africa. Yet they have in varying degrees some of the characteristics of cultivated plants, most notably erect growth and very large seeds. The seeds of *L. pilosus* are amongst the largest known in any annual legumes, and those of *L. princei* and *L. atlanticus* are not much smaller. Might they also have at some time been cultivated, and perhaps selected for seed size and yield?

Certainly, lupins have attributes which would have fitted them for primitive agricultural systems. They tolerate rough cultivation, and once the soil has been broken they will often volunteer for several years with little or no further attention. Their fertility requirements are modest. They are adapted to the lighter and more sparsely vegetated soil types on which, through limitations of clearing and cultivation techniques, much of the earliest agriculture must have been attempted (Cole 1967).

Looking back further, might lupins have been a source of food in still earlier times? Their distribution and characteristics would have fitted them for that role, too. All the annual lupins tend to grow as thickets, whence seed is readily collected. They volunteer in disturbed places, and because of their bitterness when green, escape the worst depredations of wild and domestic animals. Such plants would have grown readily in the vicinity of palaeolithic or early neolithic encampments, in fact anywhere the soil is slightly disturbed. The technology of nurturing and utilizing such plants—cracking and soaking the seeds to leach out the bitter alkaloids—would have been within the capabilities of very primitive men, and could well have antedated the true neolithic revolution by a very long period. It is worth noting that the large-seeded lupins of Africa and the Mediterranean occur in regions populated very early by humans. Especially in the case of the rough-seeded lupin species of Africa and the Middle East, at least some of whose seeds are naturally low in alkaloid and marginally edible without treatment, use by man and his ancestors could conceivably have extended back millions of years. Selection and propagation over such a time scale, whether deliberate or unconscious, would have provided a seemingly adequate basis for modification of the now large-seeded species into their present forms.

The possibility cannot be dismissed that other lupin species besides *L. albus* may at some time have been developed into true crop plants having non-shattering pods, permeable seeds, and even alkaloid freedom. The genetic potential for these characteristics appears to exist in all lupin species (see Gladstones 1970), but by their nature they tend to be lost rapidly when selection pressure is removed. According to this hypothesis the present forms could be either the result of direct reversion of old cultivars, or the weedy products of crossing with wild relatives followed by "disruptive selection" in a primitive agricultural situation (cf. Hutchinson 1971). On balance, however, I prefer the first idea: that large-seeded lupins evolved directly to their present state through many millenia of selection under pre-agricultural conditions of seed collecting, volunteering, and perhaps finally deliberate sowing on disturbed soils around human habitations.

Whatever their early importance, lupins became relegated to a minor and subsidiary role in modern agriculture. Only *L. albus* (together with *L. mutabilis* in South America) remained a significant agricultural plant prior to the start of the 20th century lupin breeding. Other species were at most peripheral to agriculture, perhaps with incidental use from volunteer stands in times of need.

One reason for the neglect of lupins could be that with the coming of the neolithic revolution, with the domestication of cereals and settlement of the fertile river valleys, they were no longer adapted to the conditions under which cultivation was practised. Other pulses such as the *Pisum* and *Vicia* species were better adapted to the predominantly heavy, calcareous farming soils of the Mediterranean basin and Middle East which had the fertility levels necessary for growing cereals and other non-leguminous crops. These genera also gave a more acceptable and easily utilized product, and may have been more amenable to domestication. Even if improved cultivars of lupins had been selected, admixture or crossing with wild relatives in many areas would have set up disruptive selection pressures and almost certainly resulted in reversion to the natural weedy habits of the wild species.

THE FUTURE OF LUPINS AS CROP PLANTS

Hutchinson (1970) has already pointed out that the well-established crop legumes belong exclusively to the *Vicieae* and *Phaseoleae,* with the sole addition of *Arachis* (peanuts) from the *Hedysareae.* All these are plants adapted predominantly to neutral or calcareous soils of moderate to high fertility, and are nodulated by "fast-growing" bacteria *(Rhizobium)* which are themselves adapted to the same soil types.

But legumes theoretically have their greatest ecological advantage on soils low in nitrogen. Here the legume-bacteria symbiosis, provided that both plant and bacterium are individually adapted to the soil type in other respects, enables the legume to thrive and surpass its non-leguminous competitors. Usually such soils have in the past been deficient also in phosphorus or other mineral elements, and this has limited their use for legumes. Increasing knowledge of plant nutrition is now making it possible to overcome these deficiencies economically. At the same time it is becoming realized that some of the hitherto neglected legume groups and their associated "slow growing" nodule bacteria *(Phytomyxa)* are less demanding of mineral nutrients than traditional crop and pasture types, as well as tolerating coarse soil textures and often low pH. Typically they are tropical or subtropical, but they also include a few temperate genera such as *Lupinus.* Such plants, if appropriately domesticated, should not only be able to exploit soil types which hitherto have been marginal or too poor for agriculture. They should also have enhanced agronomic value compared with traditional legume crops because they grow on soils where biological nitrogen fixation confers its greatest ecological and economic advantage.

Several *Lupinus* species appear to have agronomic possibilities in addition to the five *(L. albus, L. luteus, L. angustifolius, L. cosentinii* and *L. mutabilis)* currently being bred. *L. pilosus, L. princei, L. atlanticus* and *L. digitatus* have the erect, vigorous growth and large seeds which mark them out potentially as high-yielding grain legumes. There is little doubt that genes for alkaloid-freedom, non-shedding, and soft-seededness homologous with those in existing improved species could be found in all of them, while their recombination within species into agriculturally valuable genotypes poses no known genetic problems. Separate selection and breeding would be needed for each species because of the profound cyto-genetic barriers among them. So far the ecological characteristics of these species are largely unknown. Assuming their soil requirements to resemble those of the better known lupin species, and natural distributions to reflect their temperature requirements, all these species could be regarded as potential grain legumes, which would complement and perhaps extend the environmental range of cultivated lupins.

Taken as a group, the Mediterranean and African *Lupinus* species, together with *L. mutabilis* from South Africa, hold promise of furnishing a valuable new type of crop plant for the light-textured soils of the world's temperate and cooler subtropical regions. Having a high seed protein content and high yield potential, they could make a significant contribution towards meeting the world's growing protein need.

ACKNOWLEDGMENTS

I wish to record my sincere thanks to the Director and to the herbarium and library staff of the Royal Botanic Gardens, Kew, England, for their ready assistance and for access to specimens and facilities. Mr. R. D. Meikle (Kew) and Mr. P. G. Wilson (Western Australian Herbarium) kindly read the manuscript and gave valuable help in many ways. I am indebted to Dr. N. H. Brittan (University of Western Australia) for assistance with the diagnosis of *L. atlanticus*. The study was undertaken during tenure of a Nuffield Foundation Dominion Travelling Fellowship, which is gratefully acknowledged.

REFERENCES

Abbe, E. (1965)—The Plants of Virgil's Georgics. (Cornell University Press: Ithaca.)

Agardh, J. G. (1835)—Synopsis Generis Lupini. (Lund.)

Allioni, C. (1785)—Flora Pedemontana. (Turin.)

Aniol, A., Kazimierski, T., and Nowacki, E. (1968)—Further studies on a species hybrid *Lupinus albus* x *L. jugoslavicus* Kazim. et. Now. *Zeitschrift für Pflanzenzüchtung* **59**: 317-26.

Arcangeli, G. (1882)—Flora Italiana. (Ermanno Loescher: Turin.)

Arcangeli, G. (1894)—Flora Italiana. Ed. 2 (Ermanno Loescher: Turin.)

Ascherson, P., and Graebner, P. (1907)—Synopsis der Mitteleuropaischen Flora. (Wilhelm Engelmann: Leipzig.)

Atabiekova, A. I., and Maissurjan, N. A. (1962)—(A new lupin species, *Lupinus vavilovi* Atab. et Maiss.) *Isv. Timirjazev. sel'skohozjajstv. Akad.* **44** (1): 239-40.

Atabiekova, A. I., and Maissurjan, N. A. (1968)—(New species of lupin from different seed-producing centres.) *Bjull. glav. bot. Sad. Akad. Nauk. SSSR* 1968, 75-7.

Bailey, L. H. (1924)—Manual of Cultivated Plants. (Macmillan: New York.)

Baker, E. G. (1926)—The Leguminosae of Tropical Africa. (Erasmus: Ghent.)

Baker, J. G. (1895)—Bulletin no. 105, Royal Gardens, Kew.

Balbis, J. B. (1827)—Flore Lyonnaise. (C. Coque: Lyon.)

Bauhin, C. (1598)—Matthioli: Opera. (Basle.)

Bauhin, C. (1620)—Prodromus Theatri Botanici. (Frankfurt-on-Main.)

Bauhin, C. (1623)—Pinax Theatri Botanici. (Basle.)

Bauhin, J., Cherlero, J. H., Chabraeus, D., and Agraffenried, Fr. L. (1651)—Historiae Plantarum Universalis. (Ebroduni.)

Bertolini, A. (1847)—Flora Italica. (Richardi Masii: Bologna.)

Besler, B. (1613)—Hortus Eystettensis.

Black, J. M. (1924)—Flora of South Australia. (Adelaide.)

Blackwell, Elizabeth (1757)—Herbarium Blackwellianum. (Eisenberger: Nuremberg.)

Boerhaave, H. (1720)—Index Alter Plantarum Quae in Horto Academico Lugduno-Batavo Aluntur. (Leyden.)

Boissier, E. (1843)—Diagnoses Plantarum Orientalium Novarum, no. 2. (F. Ramboz: Geneva.)

Boissier, E. (1849)—Diagnoses Plantarum Orientalium Novarum, no. 9. (M. Ducloux: Paris.)

Boissier, E. (1872)—Flora Orientalis. (H. Georg: Geneva and Basle.)

Boissier, E. and Reuter, G. (1842)—Diagnoses Plantarum Novarum Hispanicarum. (F. Ramboz: Geneva.)

Bonnet, E., and Barratt, G. (1896)—Catalogue des Plantes Vasculaires de la Tunisie. (Imprimerie Nationale: Paris.)

Bonnier, G. (1914)—Flore Complete de France, Suisse, et Belgique. (Paris.)

Boreau, A. (1849)—Flore du Centre de la France. Ed. 2. (Paris.)

Bouloumoy, L. (1930)—Flore du Liban et de la Syrie. (Vigot Frères: Paris.)

Briquet, J. (1913)—Prodrome de la Flore Corse. (Georg & Co.: Geneva.)

Brotero, F. A. (1804)—Flora Lusitanica. (Olisspone: Lisbon.)

Buc'hoz, P. J. (1776)—Histoire Universelle du Règne Végétal. (Brunet: Paris.)

Caballero, A. (1945)—Dos excursiones botanicas en 1944. *Anales del Jardin Botanico de Madrid* **5**: 505-8.

Cadevall, Joan (1915)—Flora de Catalunya. (Institut d'Estudias Catalans: Barcelona.)

Camerarius, J. (1611)—Kreutterbuch. (Frankfurt-on-Main.)

Cesati, V., Passerini, G., and Gibelli, E. G. (1867)—Compendio della Flora Italiana. (F. Vallardi: Milan.)

Chamberlain, D. F. (1968)—In Davis, Flora of Turkey.

Chatel, D. L., and Parker, C. A. (1973a)—Survival of field-grown rhizobia over the dry summer period in Western Australia. *Soil Biology and Biochemistry* **5**: 415-23.

Chatel, D. L., and Parker, C. A. (1973b)—The colonization of host-root and soil by rhizobia—1. Species and strain differences in the field. *Soil Biology and Biochemistry* **5**: 425-32.

Chevalier, A., and Trochain, J. (1937)—Histoire de trois lupins. *Revue de Botanique Appliquée et d'Agriculture Tropicale* **17**: 85-97.

Clusius, C. (1601)—Rariorum Plantarum Historia. (Antwerp.)

Cole, Sonia (1967)—The Neolithic Revolution. Ed. 4. (British Museum (Natural History): London.)

Colmeiro, D. M. (1886)—Las Plantas de la Peninsula Hispano-Lusitana é Islas Balaeres. (Madrid.)

Columella, Lucius Junicus Moderatus (1st century A.D.)—De Re Rustica. Tr. H. B. Ash. (Heinemann: London, 1948.)

Cornut, J. (1635)—Canadensium Plantarum Historia. (Simonem le Moyne: Paris.)

Coste, H. (1901)—Flore de la France. (Paul Klinksieck: Paris.)

Coutinho, A. X. P. (1913)—Flora de Portugal. (Aillaud, Alves & Co.: Paris.)

C.S.I.R.O., Australia (1953)—Standardized Plant Names. Bulletin No. 272.

Cupani, F. (1696)—Hortus Catholicus. (Franciscum Benzi: Naples.)

Curtis, W. (1791)—*The Botanical Magazine* **4** t. 140.

Cusin, M. L., and Ansberque, M. E. (1870)—Flore Francaise. (Lyon.)

Darlington, C. D., and Wylie, A. P. (1955)—Chromosome Atlas of Flowering Plants. Ed. 2. (Allen & Unwin: London.)

Davis, P. H. (1970)—Flora of Turkey. Vol. 3. (University Press: Edinburgh.)

De Candolle, A. P. (1825)—Prodromus Systematis Naturalis Regni Vegetabilis. (Treuttel & Würtz: Paris.)

Desrousseaux, M. (1791)—*in* Lam. Encycl. Méth. Bot.

Desvaux, A. N. (1827)—Flore de l'Anjou. (Fourier-Mame: Anjers.)

Desvaux, A. N. (1835)—Sur un lupin nouveau. *Annales des Sciences Naturelles,* Series II, **3**: 100.

Dodon, R. (1583)—Stirpium Historiae. (Christoff Plantyn: Antwerp.)

Eichorn, A. (1949)—A propos de la caryologie du *Lupinus tassilicus* Maire. *Revue de Cytologie et de Biologie Végétales* **11**: 333-50.

Eichwald, C. E. (1833)—Plantarum novarum vel minus cognitarum quas in itinere caspio-caucasico observavit.

Engler, A. (1901)—*Botanische Jahrbücher* **28**: 401.

Ferber, J. E. (1739)—Hortus Agerumensis. (Stockholm.)

Fiori, A. (1925)—Nouva Flora Analytica d'Italia. (Florence.)

Fiori, A., and Paoletti, G. (1899)—Flora Analytica d'Italia. (Padua.)

Forbes, I., and Well, H. D. (1966)—Breeding blue lupine forage varieties for the south-eastern United States. Proceedings, X International Grassland Congress, Helsinki, 708-11.

Forskål, P. (1775)—Flora Aegyptico-Arabica. Ed. C. Niebuhr.

Foury, A. (1950)—Les legumineuses fourragères au Maroc (1re partie). *Les Cahiers de la Recherche Agronomique, Rabat* **3**: 25-317.

Franco, J. do A., and Silva, A. R. Pinto da (1968a)—*In* Tutin, T. G. *et al.* (eds.): Flora Europaea.

Franco, J. do A., and Silva, A. R. Pinto da (1968b)—*In* Heywood, V. H. (ed.): Flora Europaea notulae systematicae ad Floram Europaean spectantes. *Feddes Repertorium* **79**: 52.

Gaertner, J. (1791)—De Fructibus et Seminibus Plantarum. (Henricus Schramm: Tubingen.)

Gardner, C. A., and Bennetts, H. W. (1956)—The Toxic Plants of Western Australia. (West Australian Newspapers Ltd.: Perth.)

Gardner, C. A., and Elliott, H. G. (1929)—The common blue lupin. *Journal of Agriculture, Western Australia* (2) **6**: 414-20.

Gasparrini, G. (1851)—*Atti della Real Accademia delle Scienze di Napoli* **6**: 229, t. 10.

Gaterau (1789)—Description des plantes qui croissent aux environs de Montauban. (Montauban.)

Gerarde, J. (1633)—The Herball. Enlarged and Amended by Thomas Johnson. (London.)

Gladstones, J. S. (1955)—A Study of Five *Lupinus* Species. Honours Thesis, University of Western Australia.

Gladstones, J. S. (1958a)—The naturalized and cultivated species of *Lupinus* (Leguminosae) recorded in Western Australia. *Journal of the Royal Society of Western Australia* **41**: 29-33.

Gladstones, J. S. (1958b)—Einige neu selektierte stämme der schmalblättrigen blauen Lupine *(Lupinus angustifolius* L.) *Zeitschrift für Pflanzenzüchtung* **39**: 1-10.

Gladstones, J. S. (1969)—Lupins in Western Australia. 1. Species and varieties. *Journal of Agriculture, Western Australia* (4) **10**: 318-24.

Gladstones, J. S. (1970)—Lupins as crop plants. *I.A.B. Field Crop Abstracts* **23**: 123-48.

Gladstones, J. S. (1972)—Lupins in Westren Australia. Department of Agriculture, Western Australia, Bulletin No. 3834.

Gollmick, F. (1937)—Über Artkreuzungen bei Lupinen. *Züchter* **9**: 65-8.

Goüan, A. (1762)—Hortus Regius Monspeliensis. (Leyden.)

Goüan, A. (1765)—Flora Monspeliaca. (Benedicti Duplain: Leyden.)

Graham, P. H. (1963)—Antigenic affinities of the root-nodule bacteria of legumes. *Antonie van Leeuwenhoek* **29**: 281-91.

Graham, P. H. (1964)—The application of computer techniques to the taxonomy of the root-nodule bacteria of legumes. *Journal of General Microbiology* **35**: 511-7.

Grenier, J. C. M., and Godron, D. A. (1848)—Flore de France. (F. Savy: Paris.)

Gussone, Joanne (1828)—Flora Siculae Prodromus. (Naples.)

Gustafsson, A., and Gadd, I. (1965)—Mutations and crop improvement II. The genus *Lupinus* (Leguminosae). *Hereditas, Lund* **53**: 15-39.

Hackbarth, J. (1938)—Cytologie und Vererbung bei den Lupinenarten. *Züchter* **10**: 34-40.

Hackbarth, J. (1957)—Die Gene der Lupinenarten II. Schmalblättrige Lupine *(Lupinus angustifolius* L.). *Zeitschrift für Pflanzenzüchtung* **37**: 81-95.

Hackbarth, J., and Troll, H.-J. (1957)—Lupinen als Körnerleguminosen und Rudorf, W. (eds.) Handbuch der

Halácsy, E. de (1901)—Conspectus Florae Graecae. (Guilelmiengelmann: Leipzig.)

Hallqvist, C. (1921)—The inheritance of the flower colour and the seed colour in *Lupinus angustifolius. Hereditas, Lund* **2**: 299-363.

Hanelt, P. (1960)—Die Lupinen. (A. Ziemsen: Wittenberg.)

Hegi, G. (1923)—Illustrierte Flora von Mittel-Europa. (J. F. Lehmann: Munich.)

Hermann, P. (1687)—Horti Academici Lugduno-Batavi Catalogus. (Leyden.)

Hernandez-Pacheco, E., Hernandez-Pacheco, F., Medina, M. A., Box, C. V.,
Futterpflanzen. *In* Kappert, H., and
(Paul Parey: Berlin.)
Pflanzenzüchtung. Ed. 2, **4**: 1-51.
Espagnol. (Consejo Superior de In-
and Lopez, E. G. (1949)—El Sahara
vestigaciones Cientificas, Institute de Estudios Africanos: Madrid.)

Hutchinson, J. B. (1970)—The evolutionary diversity of the pulses. *Proceedings of the Nutrition Society* **29**: 49-55.

Hutchinson, J. B. (1971)—Changing concepts of crop plant evolution. *Experimental Agriculture* **7**: 273-80.

Jahandiez, E., and Maire, R. (1932)—Catalogue des Plantes du Maroc. (Minerva: Algiers.)

Jaranowski, J. (1962)—Fertilization and embryo development in the genus *Lupinus* Tourn. 2. Fertilization and embryo development following reciprocal species hybridization. *Genetica Polonica* **3**: 333-68.

Kazimierski, T. (1960)—An interspecific hybrid in the genus *Lupinus (Lupinus albus* L. x *Lupinus jugoslavicus* Kazim. et Now.). *Genetica Polonica* **1**: 3-60.

Kazimierski, T. (1961)—Interspecific hybridization of *Lupinus. Genetica Polonica* **2**: 97-102.

Kazimierski, T. (1963)—Studies on the hybrid *Lupinus graecus* Boiss. x *Lupinus jugoslavicus* Kazim. et Now. *Genetica Polonica* **4**: 269-75,

Kazimierski, T. (1964a)—Inheritance of certain characters in the *Lupinus albus* L. x *L. graecus* Boiss. hybrid. *Genetica Polonica* **5**: 309-25.

Kazimierski, T. (1964b)—Interspecific crossing in the Mediterranean and

American lupin species. *Wissenschaftliche Zeitschrift der Karl-Marx-Universität Leipzig: Mathematisch-Naturwissenschlaftliche Reihe* **13**: 697-8.

Kazimierski, T., and Kazimierska, E. M. (1965)—Studies on a species hybrid *Lupinus rothmaleri* Klink. x *Lupinus luteus* L. *Genetica Polonica* **6**: 125-40.

Kazimierski, T. and Kazimierska, E. M. (1970a)—Twin and haploid forms in yellow lupins. *Genetica Polonica* **11**: 63-81.

Kazimierski, T., and Kazimierska, E. M. (1970b)—Further studies on the hybrid *Lupinus rothmaleri* Klink. x *Lupinus luteus* L. *Genetica Polonica* **11**: 187-205.

Kazimierski, T., and Nowacki, E. (1961)—Lupins of the old world. *Genetica Polonica* **2**: 113-8.

Klinkowski, M. (1938)—Das iberisch-nordafrikanische Heimatgebiet von *Lupinus luteus* L., *Lupinus angustifolius* L., *Lupinus hirsutus* L., *Lupinus hispanicus* Boiss. et Reut. und *Lupinus rothmaleri* Klink. *Züchter* **10**: 113-26.

Kniphof, J. H. (1761)—Botanica in Originale sev Herbarium Vivum. (J. G. Trampe: Magdeburg.)

Knoche, H. (1922)—Flora Balaerica. (Montpellier.)

Knorrs, G. W. (1772)—Thesaurus Rei Herbariae Hortensisque Universalis. (Knorrs: Haeredes.)

Koch, D. G. D. J. (1837)—Florae Germanicae et Helveticae. (Frederici Wilmans: Frankfurt-on-Main.)

Lamarck, J. (1778)—Flore Francaise. (Paris.)

Lamarck, J. (1791)—Encyclopédie Méthodique. (Paris.)

Lamarck, J., and De Candolle, A. P. (1805)—Flore Francaise. Ed. 3. (H. Agasse: Paris.)

Lamberts, H. (1958)—Ein neuer Typus mit nicht abbrechenden Hülsen und ein neuer Artbastard bei Lupinen. *Züchter* **28**: 15-17.

Laterrade, J.-F. (1811)—Flore Bordelaise. Ed. 1. (de Moreau: Bordeaux.)

Laterrade, J.-F. (1821)—Flore Bordelaise. Ed. 2. (André Brossier: Bordeaux.)

Laterrade, J.-F. (1846)—Flore Bordelaise. Ed. 4. (T. Lafargue: Bordeaux.)

Linnaeus, C. (1737)—Hortus Cliffortianus. (Amsterdam.)

Linnaeus, C. (1748)—Hortus Upsaliensis. (Stockholm.)

Linnaeus, C. (1753)—Species Plantarum. Ed. 1. (Laurentii Salvii: Stockholm.)

Linnaeus, C. (1763)—Species Plantarum. Ed. 2. (Laurentii Salvii: Stockholm.)

Linnaeus, C. (1771)—Mantissa Plantarum (Altera Generum VI et Specierum II). (Laurentii Salvii: Stockholm.)

Linnaeus, C. (1774)—Systema Vegetabilum. Ed. 13 (ed. J. A. Murray). (G. C. Dieterich: Göttingen.)

Linnaeus, C. (1803)—Species Plantarum. Ed. 4 (ed. C. L. Willdenow). (G. C. Nauk: Berlin.)

Lobel, M. de (1576)—Plantarum seu Stirpium Historia: Observationes & Stirpium Adversaria Nova. (Antwerp.)

Lobel, M. de (1581)—Kruydtboeck. (Christoff Plantyn: Antwerp.)

Lojacono Pojero, M. (1891)—Flora Sicula. (Statuto: Palermo.)

Loret, H., and Barrandon, A. (1876)—Flore de Montpellier. (C. Coulet: Montpellier.)

Lowe, R. T. (1868)—A Manual Flora of Madiera. (John van Voorst: London.)

Ludwig, C. G. (1760)—Egypta Vegetabilium. (Halle in Magdeburg.)

Magnol, P. (1676)—Botanicum Monspeliense. (Leyden.)

Magnol, P. (1686)—Botanicum Monspeliense. (Montpellier.)

Magnol, P. (1697)—Hortus Regius Monspeliensis. (Montpellier.)

Maire, R. (1933)—Études sur la flore et la végétation du Sahara Central. *Mémoire de la Société d'Histoire Naturelle de l'Afrique du Nord,* no. 3.

Maire, R. (1935)—Contributions à l'étude de la flore du Sahara Occidentale. *Bulletin de la Société d'Histoire Naturelle de l'Afrique du Nord* **26**: 148-62.

Malheiros, Nydia (1942)—Elementos para o estudo citologico do género *Lupinus. Agronomia Lusitana* **4**: 231-6.

Maratti, J. F. (1822)—Flora Romana. (Joseph Salviucci: Rome.)

Marshall, K. C., Mulcahy, M. J., and Chowdhury, M. S. (1963)—Second year clover mortality in Western Australia—a microbiological problem. *Journal of the Australian Institute of Agricultural Science* **29**: 160-4.

Merino, R. P. B. (1905)—Flora de Galicia. (Tipografia Galaica: Santiago.)

Mikolajczyk, J. (1963)—Inheritance of the growth pattern in *Lupinus angustifolius* L. and species hybrids *L. angustifolius* x *L. linifolius*. *Genetica Polonica* **4**: 139-60.

Mikolajczyk, J. (1966a)—Genetic studies in *Lupinus angustifolius* L. Part II. Inheritance of some morphological characters in blue lupine. *Genetica Polonica* **7**: 153-80.

Mikolajczyk, J. (1966b)—Genetic studies in *Lupinus angustifolius* L. Part III. Inheritance of the alkaloid content, seed hardness, and length of the growing season in blue lupine. *Genetica Polonica* **7**: 181-96.

Miller, P. (1754)—The Gardeners Dictionary. Ed. 4. (J. & J. Rivington: London.)

Montasir, A. H., and Hassib, M. (1956)—Manual Flora of Egypt. (Misr: Cairo.)

Moris, J. H. (1837)—Flora Sardoa. (Turin.)

Morison, R. (1680)—Plantarum Historiae Universalis Oxonensis. (Sheldon: Oxford.)

Muschler, R. (1912)—Manual Flora of Egypt. (Berlin.)

Mutel, A. (1834)—Flore Francaise. (F. G. Levrault: Paris.)

Norris, D. O. (1956)—Legumes and the Rhizobium symbiosis. *Empire Journal of Experimental Agriculture* **24**: 247-70.

Noulet, M. J.-B. (1837)—Flore du Bassin Sous-Pyrenéen. (J.-B. Paya: Toulouse.)

Nowacki, E. (1960)—Systematics of *Genisteae* in the light of chemical analyses. *Genetica Polonica* **1**: 119-43.

Nowacki, E., and Prus-Glowacki, W. (1971)—Differentiation of protein fractions in species and varieties of the genus *Lupinus* with the use of serological methods. *Genetica Polonica* **12**: 245-60.

Oliver, D. (1871)—Flora of Tropical Africa. (Reeve & Co.: London.)

Parker, C. A. (1962)—Light lands in Western Australia. 3. Microbiological problems in the establishment of legumes on light land. *Journal of Agriculture, Western Australia* (4) **3**: 713-6.

Parkinson, J. (1629)—Paradisus Terrestris. (London.)

Parkinson, J. (1640)—Theatricum Botanicum, or An Universall and Compleate Herball. (Tho. Cotes: London.)

Parlatore, P. (1894)—Flora Italiana. (Vol. 10: T. Caruel.) (Florence.)

Plitmann, U. (1966)—Studies in the taxonomy of the Leguminosae of Israel. *Israel Journal of Botany* **15**: 25-30.

Polunin, O., and Huxley, A. (1965)—Flowers of the Mediterranean. (Chatto and Windus: London.)

Post, G. E. (1896)—Flora of Syria, Palestine, and Sinai. (Beirut.)

Pouzolz, P. C. (1856)—Flore du Gard. (Dumas: Montpellier.)

Presl, C. B. (1826)—Flora Sicula. (A. Borrosch: Prague.)

Quer, D. J. (1784)—Flora Espanola. (D. J. Ibarra: Madrid.)

Quezel, P., and Santa, S. (1962)—Nouvelle Flore de l'Algérie. (Centre National de la Recherche Scientifique: Paris.)

Ray, J. (1686)—Historia Plantarum. (Mariae Clark: London.)

Reichenbach, H. G. (1903)—Icones Florae Germanicae et Helveticae. (Leipzig.)

Reichenbach, L. (1832)—Flora Germanica Excursoria. (Dresden.)

Rivinus, A. Q. (1691)—Ordo Plantarium Quae Sunt Flore Irregulari Tetrapetalo. (Christoph Fleischer: Leipzig.)

Roth, A. W. (1787)—Botanische Abhandlungen und Beobrachtungen. (J. J. Winterschmidt: Nuremberg.)

Rothmaler, W. (1935)—Plantae novae vel criticae Peninsulae Ibericae. *Cavanillesia* **7**: 111-21.

Rouy, G. (1897)—Flore de France. (Paris.)

Royen, A. van (1740)—Florae Leydensis Prodromus. (Leyden.)

Saint-Hilaire, J. (1809)—Plantes de la France. (Saint-Hilaire: Paris.)

Saint-Lager (1880)—Réforme de la nomenclature botanique. *Annales de la Société Botanique de Lyon* **7**: 1-154.

Savcenko, P. F. (1935)—(Karyology of some species of the genus *Lupinus.) Bulletin of Applied Botany, of Genetics and Plant-Breeding, Leningrad* (2) **8**: 105-11.

Savi, G. (1798)—Flora Pisana. (P. Giacomelli: Pisa.)

Shaw, T. (1738)—Catalogus Plantarum Quas in Variis Africae & Asiae Partibus. (Oxford.)

Sibthorp, J., and Smith, J. E. (1830)—Flora Graeca. (Richard Taylor: London.)

Silva, A. R. Pinto da (1971)—De flora Lusitana commentarii, fasc. XVIII. *Agronomia Lusitana* **33**: 10-13.

Sypniewski, J. (1925)—(The inheritance of flower colour in *Lupinus angustifolius.) Pamietnik Pulawski* **6**: 220-52. (Cited by Hackbarth 1957b.)

Sypniewski, J. (1930)—Les variétés et les races de *Lupinus angustifolius. Mém. Inst. Nat. Polon. Ec. Rur. Pulawy,* 496-552. (Cited by Hackbarth 1957b.)

Tabernaemontani, J. T. (1591)—Neuw Kreuterbuch. (Nicolaum Bassaeum: Frankfurt-on-Main.)

Tackholm, V. (1956)—Students' Flora of Egypt. (Anglo-Egyptian Bookshop: Cairo.)

Tenore, M. (1820)—Flora Napolitana **2**: 141-3. (Stamperia Reale: Naples.) Also **4** emend XI (1830) and **5**: 99 (1835).

Thellung, A. (1912)—La Flore Adventice de Montpellier. (Le Maout: Cherbourg.)

Thiébaut, J. (1940)—Flore Libano-Syrienne. (L'Institut Francais d'Archéologie Orientale: Cairo.)

Theophrastus (d. 287 B.C.)—(Enquiry into Plants.) Tr. A. Hort. (Heinemann: London, 1948.)

Thompson, H. S. (1914)—Flowering Plants of the Riviera. (Longmans, Green & Co.: London.)

Tornabene, F. (1890)—Flora Aetnea. (Catania.)

Tourlet, E.-H. (1908)—Catalogue des Plantes Vasculaires du Département d'Indre-et-Loire. (Paul Klinksieck: Paris.)

Tournefort, J. P. (1719)—Institutiones Rei Herbariae. (Typographia Regia: Paris.)

Tuschnakowa, M. (1935)—Über die Chromosomen einiger *Lupinus*-Arten. *Züchter* **7**: 169-74.

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M., and Webb, D. A. (eds.) (1968)—Flora Europaea. (Cambridge University Press.)

Urville, J. D. d' (1822)—Enumeratio Plantarum quas in Insulis Archipelagi aut Littoribus Ponti-Euxini, Annis 1819 et 1820. *Mémoires de la Société Linnéenne de Paris* **1**: 255-387.

Varro, Marcus Terentius (116-27 B.C.)—Rerum Rusticarum. Tr. L. Storrs-Best. (G. Bell & Sons: London, 1912.)

Visiani, R. de (1836)—Icones Plantarum quarundum Aegypti ac Nubiae. (Minerva: Patavii.)

Visiani, R. de (1842)—Flora Dalmatica. (F. Hofmeister: Leipzig.)

Willdenow, C. L. (1803)—See Linnaeus (1803).

Willkomm, M., and Lange, Joanne (1880)—Prodromus Florae Hispanicae. (E. Schweizerbart: Stuttgart.)

Zhukovsky, P. M. (1929)—(The genus *Lupinus* Tourn.) *Bulletin of Applied Botany, of Genetics and Plant-Breeding, Leningrad* (1) **21**: 241-92. (Russian; C.S.I.R.O., Australia, Translation no. 2839.)

Zohary, M. (1972)—Flora Palaestina. Part 2. (Israel Academy of Sciences and Humanities: Jerusalem.)

APPENDIX I

Recorded Diploid Chromosome Numbers for Mediterranean and African Species of Lupinus

Some early, and probably inaccurate, counts are omitted. For accounts of these see Hackbarth (1938) and Malheiros (1942).

	Savcenko 1935	Tuschnakowa 1935	Malheiros 1942	Eichorn 1949	Gladstones 1955, 1958a	Kazimierski 1960; Kazimierski and Kazimierska 1965
L. albus	48	50	50	....	50	50[1]
L. angustifolius	40	40	40	....	40	....
L. micranthus	....	50	....	....	....	....
L. luteus	52	52	52	....	52	52
L. hispanicus	....	....	52[2]	....	....	52[2]
L. cosentinii	....	....	32	....	32	....
L. digitatus	....	....	....	36[3]	....	....
L. pilosus	40	42	....	....	42	....

[1] both var. *albus* and var. *graecus* (the latter as *L. jugoslavicus* Kazimierski and Nowacki).

[2] as *L. rothmaleri* Klink.

[3] as *L. tassilicus* Maire.

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