

A taxonomic study of *Lotus australis* complex (Leguminosae), with special emphasis on plants from Pacific Ocean islands

Tatiana KRAMINA
Dmitry SOKOLOFF

Higher Plants Department, Biological Faculty, Moscow State University,
119992 Moscow (Russia)
kramina@herba.msu.ru
sokoloff@dds.srcc.msu.su

ABSTRACT

The genus *Lotus* comprises about 140 species and has major centres of diversity in the Mediterranean Region and in Macaronesia. The *Lotus australis* complex, however, is confined to Australia and some islands of Pacific Ocean. The present morphological study recognises four species of the complex, namely *L. australis* Andrews s.str. (Australia, Tasmania), *L. pacificus* Kramina & D.D. Sokoloff, sp. nov. (Ryukyu Is., Japan; Lanyu Is., Taiwan), *L. anfractuusus* (Bak.f.) Kramina & D.D. Sokoloff, comb. et stat. nov. (Loyalty Is. and Île des Pins, New Caledonia; Aniwa Is., Vanuatu), and *L. cruentus* Court (Australia). Two new varieties are described: *Lotus anfractuusus* var. *vanuatensis* Kramina & D.D. Sokoloff, var. nov. and *Lotus australis* var. *austroglalber* Kramina & D.D. Sokoloff, var. nov. Disjunctive distribution of the *L. australis* complex could be explained by long distance dispersal rather than by vicariance. *L. australis* and *L. cruentus*, if compared to Mediterranean and Macaronesian species, possess many presumably plesiomorphic character states. However, we do not consider this fact as an indication of Australian origin of the genus *Lotus*.

KEY WORDS

Leguminosae,
Lotus,
Australia,
New Caledonia,
Vanuatu,
Japan,
Taiwan,
morphology,
taxonomy,
biogeography.

RÉSUMÉ

Étude taxonomique du complexe Lotus australis (Leguminosae), en particulier dans les îles de l'océan Pacifique.

Le genre *Lotus* inclut presque 140 espèces et a son centre de diversité dans la région méditerranéenne et en Macaronésie. Le complexe *Lotus australis* est cependant restreint à l'Australie et quelques îles de l'océan Pacifique. D'après les résultats de notre recherche morphologique nous distinguons quatre espèces dans le complexe examiné : *L. australis* Andrews s.str. (Australie, Tasmanie), *L. pacificus* Kramina & D.D. Sokoloff, sp. nov. (Île Ryukyu, Japon ; Île Lanyu, Taiwan), *L. anfractuusus* (Bak.f.) Kramina & D.D. Sokoloff, comb.

MOTS CLÉS

Leguminosae,
Lotus,
Australie,
Nouvelle-Calédonie,
Vanuatu,
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et stat. nov. (Îles Loyauté et Île des Pins, Nouvelle-Calédonie ; Île Aniwa, Vanuatu) et *L. cruentus* Court (Australie). Deux nouvelles variétés sont décrites : *Lotus anfractuosus* var. *vanuatensis* Kramina & D.D. Sokoloff, var. nov. et *Lotus australis* var. *austruglaber* Kramina & D.D. Sokoloff, var. nov. L'aire disjointe du complexe *L. australis* pourrait s'expliquer par la dispersion à longue distance plutôt que par la vicariance. *L. australis* et *L. cruentus* possèdent plus de caractères plésiomorphiques en comparaison des espèces méditerranéennes et macaronésiennes, ce qui ne fournit aucune preuve décisive en faveur de l'origine Australienne du genre *Lotus*.

INTRODUCTION

The genus *Lotus* is the largest genus of the tribe Loteae. In the circumscription adopted by the present authors (SOKOLOFF 1999, 2000, 2003; KRAMINA & SOKOLOFF 2001), it comprises about 140 species and has major centres of diversity in the Mediterranean Region and in Macaronesia. However, some natural species groups within the genus are restricted to South, Central and East Africa, SW Asia, Australia and Pacific Ocean islands (KRAMINA & SOKOLOFF 2003). In this work, we analyse the *Lotus australis* species group, whose members are known from Australia, Japan, Taiwan, New Caledonia and Vanuatu. With the exception of Ryukyu islands, along the whole geographical range *Lotus australis* complex does not coexist with other native members of the genus.

To our knowledge, no comparative taxonomic study of the whole complex was previously published although LARSEN & ŽERTOVÁ (1965) presented a detailed revision of Australian material.

BRAND (1898), in a monographic revision of the genus *Lotus*, treated the whole *Lotus australis* complex as a single variable species, *L. australis* Andrews. He reported *L. australis* s.l. from mainland Australia, Tasmania, and "Nova Ierlandia" (Bismarck Archipelago). The report from New Ireland was based on a single specimen from Berlin Herbarium (B), which was destroyed during World War II. No other collections of the genus *Lotus* from Papua New Guinea were made (VERDCOURT 1979; BISBY *et al.* 2001). According to VERDCOURT (1979), there must have been some error of labelling particularly as no collector's

name is given by BRAND. Since BRAND gave quite insufficient data on morphology of the specimen from New Ireland, we are unable to attribute it to one of the four species accepted in the present paper.

DOMIN (1926) studied material of *Lotus* from mainland Australia, Tasmania, and New Caledonia (Île des Pins). He accepted two species, *L. australis* s.str. and *L. coccineus* Schtdl. The latter species is found as relatively monomorphic and restricted to mainland Australia. DOMIN (1926) accepted six varieties of *L. australis*, five from mainland Australia and Tasmania, and one (var. *gillivrayi* Domin) from New Caledonia. LARSEN & ŽERTOVÁ (1965) accepted the same two species, correcting illegitimate name *L. coccineus* to *L. cruentus* Court. They studied more material from New Caledonia and revealed that both *L. australis* and *L. cruentus* occur there. Besides, they have cited a specimen of *L. australis* from the Lord Howe Island (*Saunders 10/74 - K*). However, a re-examination of label of this specimen revealed that it was in fact collected from Île des Pins.

LARSEN & ŽERTOVÁ accepted four informal groups, instead of six varieties, within the polymorphic species *L. australis*. Recent floras also accept two species and no varieties of native Australian *Lotus* (NORRIS & HARDEN 1991; JEANES 1996).

In Northern Hemisphere, the complex was reported from Japan (Ryukyu islands), Taiwan (Lanyu Island), mainland China and Philippines. The material was always attributed to *L. australis* s.str., and no varieties was accepted (CHUANG & HUANG 1965; WALKER 1976; WIERSEMA *et al.*

1990; HUANG & OHASHI 1993; WEI & HUANG 1993; KIRKBRIDE 1999; see also a draft version of "Flora of China" manuscript at http://flora.huh.harvard.edu/china/mss/volume10/Fabaceae-MO-various_edited.htm). We were unable to find any specimen of *Lotus* from Philippines. It is highly possible that all reports of *L. australis* from Philippines are based on work by HUANG & OHASHI (1993). T.C. HUANG (*in litt.*, 26 Feb. 2001) kindly confirmed that the Philippines record in this work was erroneous. We agree with KIRKBRIDE (1999) that there is no evidence of occurrence of native *Lotus* species in Philippines. The record of *L. australis* from mainland China (KIRKBRIDE 1999) is very dubious. It is seemingly based on a Chinese specimen from NY(!), annotated by J.H. KIRKBRIDE JR. However, the specimen is quite poorly preserved and lacks all basic diagnostic features. We were unable to confirm or reject its identification as a member of *Lotus australis* complex. In *Flora of RPS* (WEI & HUANG 1993), *L. australis* is indicated for the Lanyu Is. only. There is no collections of *L. australis* from mainland China in PE Herbarium (M. ZHANG *in litt.*, 19 Mar. 2000), as well as in all Herbaria which material is used for the present work. It is reasonable to conclude that, in the Northern Hemisphere, the *L. australis* complex is definitely known from Ryukyu and Lanyu islands only.

We have studied all available for us material of *L. australis* complex from Australia, Tasmania, New Caledonia (here and below including Île des Pins and Loyalty Islands), Vanuatu, Lanyu and Ryukyu islands. Collections of A, BM, GH, K, LE, MHA, MW, NSW, NY, P, POM, RSA, S, TUS, TUSG, UPS, US have been used.

VARIABILITY OF MORPHOLOGICAL CHARACTERS (TABLE 1)

Leaf morphology

The great majority of *Lotus* species possesses sessile pinnate leaves with five leaflets and very small stipules. The stipules are dark and supposed to be glandular, although there are only few direct observations of a secretion (e.g., HEYN 1976). The two lowermost leaflets often differ in shape from the rest three leaflets of the same leaf. Since true stipules are often inconspicuous, the lowermost leaflets are sometimes described as stipules

(and thus the whole leaf is treated as petiolate and trifoliolate). Such an interpretation is especially widespread in old publications. Some members of *L. australis* complex, along with some other species of *Lotus*, deviate from the typical for the genus (but not necessarily ancestral!) leaf structure.

We found true stipules in all examined specimens of *L. australis* and *L. cruentus* from Australia (here and below, including Tasmania, if not stated otherwise), with the only exception of *Whinray s.n.* (NSW 100535; *L. australis*), which has no stipules (BLACK [1933] described "*Lotus australis* var. *exstipulatus*" from Australia. However, he meant absence of lower leaflet pair [which usually simulates herbaceous stipules in *Lotus*], rather than absence of true stipules). Usually Australian plants have well visible stipules, less often the stipules are very small and can be detected only using a binocular lens. In specimens from Japan and Taiwan, true stipules are either absent or extremely small and scarcely detectable. All examined plants from New Caledonia and Vanuatu have no stipules.

All plants from Japan, Taiwan, New Caledonia and Vanuatu have sessile leaves. Australian plants often have a very short petiole, although specimens with sessile leaves were also found in both *L. australis* and *L. cruentus*.

Plants from New Caledonia have leaves with five leaflets. The only available specimen from Vanuatu has five to probably four leaflets (it is not clear whether the fifth leaflet was broken during botanizing). In plants from Northern Hemisphere, leaves with five to (rarely) seven leaflets were found. Australian plants usually have five leaflets, but specimens with fewer (up to three) or higher (up to seven) leaflets are observed in both *L. australis* and *L. cruentus*. Leaflet number may be variable within a given specimen.

With a bit of experience, it is possible to distinguish *L. cruentus* and *L. australis* in Australian material using leaflet shape and size. *L. cruentus* has usually obovate and obtuse leaflets; rarely they are oblanceolate. In *L. australis* leaflets may be linear, oblanceolate or obovate. If *L. australis* has obovate leaflets, they are generally bigger than in *L. cruentus* and are prominently acute. Plants from Taiwan and Japan have oblanceolate to

TABLE 1. — Morphological characters and geographical distribution of species recognised within the *Lotus australis* complex.

Character	<i>Lotus australis</i>	<i>Lotus pacificus</i>	<i>Lotus anfractuosus</i>	<i>Lotus cruentus</i>
Indumentum of hairs on stem and leaves	Present (var. <i>australis</i>) or absent (var. <i>austroglaber</i>)	Present	Absent	Present
Stipules (dark glands)	Almost always present	Absent or present	Absent	Present
Leaf petiole	Absent or present	Absent	Absent	Absent or present
Rachis length (mm)	1.5-9	4-12	4-11.5	2-7.5
Number of leaflets per leaf	(3-)5(-7)	5(-7)	(?4-)5	(3-)5(-7)
Leaflet shape	Linear, oblanceolate, obovate, with usually acute apex	Oblanceolate to narrow obovate, with acute to almost rounded, mucronate apex	Obovate, with acute or obtuse apex	Usually obovate with obtuse apex, rarely oblanceolate
Upper leaflet length (mm) (i.e. distal leaflets within a leaf)	(5-)13-28	15-22	9-20	6.5-15
Peduncle length, mm	18-135	6-26	(5-)10-35	8-40
Foliage leaf on the peduncle	1-3-foliolate	1-3-foliolate	1-foliolate	1-3-foliolate
Number of flowers per umbel	2-8	(1)2-6	1-5	1-4
Bract	Present, glandular	Present, wholly glandular or rarely with a minute blade and a pair of glands	Inconspicuous or eglandular	Present, glandular
Flower length (mm)	(9-)10-22	(8.5-)10-14.5(-16)	(8.5-)9-11.5(-12.5)	(4-)5-9(-10)
Calyx length (mm)	6-10	7-11	5.5-8	3-6
Calyx teeth, length	≥ tube	≥ tube	≈ tube	≤ tube
Internal side of calyx teeth	Pubescent (var. <i>australis</i>) or glabrous (var. <i>austroglaber</i>)	Pubescent	Pubescent (var. <i>anfractuosus</i>) or glabrous (var. <i>vanuatisensis</i>)	Pubescent
Wing and standard colour	White or pink, rarely red	White	Red (?rarely pink)	Red, rarely pink, very rarely white
Standard claw	Not clearly delimited from the blade	Not clearly delimited from the blade	Clearly delimited from the blade	Not clearly delimited from the blade
Keel shape	Slightly incurved, long rostrate	Incurved by acute angle, shortly rostrate	Slightly incurved, rostrate	Incurved by obtuse (rarely by right) angle
Style length (mm)	(4.2-)4.5-6.5(-8)	(3-)4.5-6.5	(4-)4.5-5.5	2.5-4
Fruit shape	Usually straight	Usually straight	Usually straight	Usually incurved
Fruit width (mm)	2.4-3.5	2.7-4.4	2.8-3.6	2.2-2.7
Distribution	Australia, Tasmania	Ryukyu Is. (Japan), Lanyu Is. (Taiwan)	New Caledonia, Vanuatu	Australia

narrow obovate leaflets similar to those of some Australian *L. australis*. Plants from New Caledonia and Vanuatu have obovate leaflets which are somewhat intermediate between those of Australian *L. australis* and *L. cruentus*.

Plants from New Caledonia and Vanuatu differ from the rest of examined specimens by very fleshy leaflets.

Indumentum

Plants from Japan and Taiwan always have distinct indumentum on stems, leaves and calyces. Australian plants are considerably variable in degree of pubescence. However, with the exception of four specimens of *L. australis*, which are totally glabrous, all Australian plants have at least some hairs on young leaves, in the upper parts of peduncles, and on the calyx. Plants from New Caledonia have glabrous stems, leaves, and calyx tube. They have hairs on internal side of calyx teeth only. The specimen from Vanuatu is totally glabrous.

Inflorescence

The genus *Lotus* is characterised by axillary umbels. Each peduncle usually has a foliage leaf inserted near the umbel or rarely below it. Although this leaf is often treated as a bract, there is no flower in its axis.

Australian *L. australis* generally has peduncles much longer than subtending leaves. The rest of examined specimens generally possess peduncles of about the same length as subtending leaves. However, this is a tendency, rather than a strong regularity.

All plants from Australia have distinct true bracts (i.e. subtending leaves of flowers), which are represented by dark glands. In plants from Japan and Taiwan, true bracts are represented by either dark glands or (rarely) by a herbaceous blade plus a pair of basal glands. In plants from New Caledonia and Vanuatu, true bracts are wanting or scarcely visible, or, contrary, relatively large (1-2 mm long), linear, herbaceous, eglandular.

Flower size

In Australia, *L. cruentus* usually has flowers 5-9 mm long, while *L. australis* 10-20 mm long.

However, if ample material is analysed, overlapping in flower size variation between the two species is evident. Plants from New Caledonia and Vanuatu have flowers (8.5-)9-11.5(-12.5) mm long, plants from the Northern Hemisphere are similar to Australian *L. australis* in pattern of variation of flower size.

Calyx shape

In Australia, *L. cruentus* has calyx teeth equalling to, or shorter than the tube, while *L. australis* has teeth equalling to, or longer than the calyx tube. In plants from Japan and Taiwan teeth are usually longer than the tube. Specimens from New Caledonia and Vanuatu have teeth of almost the same length as the tube.

Petal colour

Petal colour frequently is lost on a herbarium material. We have used few specimens that retain presumably native petal colour, as well as label and literature information. Petal colour varies within the *L. australis* complex from white to deep red. Within a flower, keel tip is the most dark coloured part. In Australia, *L. cruentus* has usually red, sometimes pink and only rarely white flowers; *L. australis*, in contrast, often has white (with the exception of the keel tip) or pink, rarely red flowers. Plants from New Caledonia have red flowers. In plants from Japan and Taiwan, petals are always white (with the exception of the keel tip).

Standard shape

Plants from New Caledonia and Vanuatu have standard claw clearly delimited from the blade (Fig. 9). In the rest of examined specimens, the claw is gradually widening upwards and not clearly delimited from the blade (Figs 1; 5).

Keel shape

Plants from the Northern Hemisphere (Fig. 6) clearly differ from those of the Southern Hemisphere (Fig. 2) in a peculiar keel shape: the keel is strongly incurved and only shortly rostrate.

Style length

Australian *L. cruentus* differs from the rest of the material examined in the shorter style (2.5-4 vs >

(4.2-)4.5 mm). The only exception found is *Miyagi 6784* (TUSG) from Japan, which has style of 3 mm long.

Fruit morphology

Australian *L. cruentus* has usually incurved upwards and relatively narrow fruits. In the rest of material examined, fruits are usually straight and thicker. However, these are tendencies only.

TAXONOMIC CONCLUSIONS

Our study confirms the traditional viewpoint that two species should be recognized in Australia, viz. *L. australis* and *L. cruentus*. Flower size is often used as one of key distinctions between them (e.g., LARSEN & ŽERTOŮVÁ 1965; Jeanes 1996). However, there is overlapping in floral size between *L. australis* and *L. cruentus* (see also NORRIS & HARDEN 1991). We found that style length may be used as a more stable distinction (besides, it is useful also for fruiting plants). Utility of style length as a diagnostic character was demonstrated for *Lotus arabicus* group (GILLETT 1959; SOKOLOFF 2001), which is related to *L. australis* complex.

Our data clearly shows that the New Caledonian material is homogeneous and represents a single taxon. We disagree with LARSEN & ŽERTOŮVÁ (1965), who attributed some of the New Caledonian plants to *L. australis* while others to *L. cruentus*. Although the New Caledonian plants are closer to *L. australis* (DOMIN 1926), they also resemble *L. cruentus* in some respects (e.g., flower size and colour, leaflet shape, peduncle length). Thus it is not surprising that LARSEN & ŽERTOŮVÁ (1965) had difficulties with attribution of the New Caledonian material (they noticed atypically thick fruits in New Caledonian *L. cruentus*). We have found several characters, in which the New Caledonian plants differs from Australian ones, viz. very fleshy leaflets, standard claw clearly delimited from the blade, bract structure, and wanting stipules (utility of stipules presence/absence as a diagnostic character was demonstrated for *L. arabicus* group [SOKOLOFF 2001]) (a single Australian specimen also has no stipules, but it fits Australian *L. australis* in all other important features). We think it logical to recognize the New

Caledonian plants as a separate species, *L. anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff, comb. nov.

The only available specimen from Vanuatu is similar to the New Caledonian plants in all above-mentioned characters and should be also treated as *L. anfractuosus*. However, it differs from the New Caledonian specimens in glabrous calyx teeth. It has also a distinctive habit. We think it reasonable to describe a separate variety for this plant (var. *vanuatuensis*). In our experience, presence of hairs on internal side of calyx teeth is a conservative character in the genus *Lotus*.

Plants from Taiwan and Japan are similar to Australian *L. australis*. However, they clearly differ from the Australian material in the keel shape. There are also such distinctive tendencies as usually short peduncles and often wanting stipules. Bearing in mind a great geographic disjunction between Australian and North Hemisphere plants, it is reasonable, in our opinion, to recognise plants from Taiwan and Japan as a separate species, *L. pacificus* Kramina & D.D. Sokoloff, sp. nov.

Thus we treat *L. australis* as a species endemic to Australia (including Tasmania). Even accepted in such a narrow sense, *L. australis* remains to be the most variable species in the group. While classifying *L. australis* into varieties, DOMIN (1926) and LARSEN & ŽERTOŮVÁ (1965) focused in distinction between: 1) almost glabrous; and 2) considerable pubescent plants. We confirm the opinion of LARSEN & ŽERTOŮVÁ (1965) that there are transitions between more and less pubescent plants. We found, however, that another distinction, between *completely* glabrous and *more or less* pubescent plants is rather stable. We suggest that it should be used as a taxonomic character. We are describing completely glabrous plants as a new variety, var. *austroglaber*. It is reasonable to unite all other plants of *L. australis* within a polymorphic type variety (var. *australis*). DOMIN (1926) and LARSEN & ŽERTOŮVÁ (1965) used leaflet shape as another important feature in their infraspecific classifications of *L. australis*. However, it is not easy to segregate plants with linear, oblanceolate and obovate leaflets due to presence of intermediate forms, which is mentioned also by LARSEN & ŽERTOŮVÁ (1965). It is

not surprising that LARSEN & ŽERTOVÁ themselves did not accept these groups as formal taxa.

Indumentum characters, in our opinion, are most suitable for delimitation of varieties in the group under discussion. The presence/absence of indumentum on vegetative organs and calyx teeth is constant within each plant studied. This allows attributing each plant to a certain variety. Indumentum characters are also important, as tendencies, in distinguishing species. More or less pubescent leaves and shoots, as a general tendency, is a very important feature of *L. australis* (as compared to *L. anfractuosus*). However, analysing many hundreds of specimens, we found few glabrous plants of *L. australis* (i.e. var. *austroroglaber*). Var. *austroroglaber* is similar in this respect to *L. anfractuosus*, but, interestingly, it has no hairs on calyx teeth, while New Caledonian *L. anfractuosus* does have pubescent calyx teeth. In this context, it is important that the specimen of *L. anfractuosus* from Vanuatu has glabrous calyx teeth. This was the reason to distinguish it as var. *vanuatensis*. In general, these data demonstrate that *L. australis* and *L. anfractuosus* possess different patterns of indumentum variation. We think that this fact supports specific rank of *L. australis* and *L. anfractuosus*.

PHYTOGEOGRAPHIC AND EVOLUTIONARY CONCLUSIONS

The *Lotus australis* complex is distributed far away from the main centres of *Lotus* diversity, i.e. Mediterranean Region and Macaronesia. Parsimonious optimisation of geographical distribution data onto phylogenetic trees inferred from a study of ITS1-2 region of nuclear ribosomal DNA suggested that single migration of *Lotus* from Asia to Australia taken place (Allan *et al.* 2003, this study covered only two species of *L. australis* complex [*L. australis* s.str. and *L. cruentus*]). In this context it is interesting that the *L. australis* complex is characterised by many putatively plesiomorphic character states in the genus *Lotus*, i.e. plants usually perennial, leaf rachis usually elongated, leaflets of the basal pair never strongly differ in shape from other leaflets of the same leaf (in many species of *Lotus* [but not in the *L. australis* complex], the basal leaflets have maximum width in the lower part [e.g.,

ovate]), whereas terminal leaflets of the same leaf have maximum width in the upper part [e.g., obovate]), peduncles elongated, calyx not pronouncedly bilabiate, wing petals free from each other, style without of a teeth or an outgrowth, fruit dehiscent, not winged, base chromosome number $x = 7$ (not 6) (studied for *L. australis* and *L. cruentus* only; these species are tetraploids [LARSEN & ŽERTOVÁ 1965; GRANT 1995], which is the only known to us serious apomorphic character state of *L. australis* complex). Besides, we found *L. australis* and *L. cruentus* to be surprisingly variable in presence/absence of a short petiole and in the leaflet number. As indicated above, sessile leaf with five leaflets is one of key features of the genus *Lotus* (but likely not a synapomorphy of the genus). All Mediterranean species have always sessile leaves, and variability in leaflet number is extremely rare (found only in *L. tetraphyllus* L.f. and *L. benoistii* (Maire) Lassen, which are derived in many other respects). We think it reasonable to treat the leaf variability in *L. australis* and *L. cruentus* as a *primitive polymorphism*. A similar (although less pronounced) variability in leaf structure was found in the *Lotus arabicus* group (ALI & SOKOLOFF 2001; SOKOLOFF 2001), whose members have a centre of distribution around the Red Sea and do not penetrate into the Mediterranean floristic region. *Kebirita* and *Pseudolotus*, two closely related to *Lotus* monotypic genera with primitive leaf structure also do not occur in the Mediterranean floristic region (ALI & SOKOLOFF 2001; KRAMINA & SOKOLOFF, 2001). These data are congruent with an "ousted relics" concept of A. WALLACE (cf. ESKOV 1992, 2002). Regarding data on *Lotus*, this implies that many primitive taxa are survived away from the region of intensive diversification of the genus. Surviving of primitive species in Australia, of course, does not indicate Australian origin of *Lotus*.

The disjunctive distribution of the *Lotus australis* complex around the Pacific Region should be explained by long distance dispersal rather than by vicariance. Indeed, *L. pacificus* and *L. anfractuosus* do occur on many islands of coral and volcanic origin. Interestingly, we are unable to indicate any peculiar adaptation to long distance seed dispersal in these plants (they have also

no vegetative propagation). Seeds are of normal size for *Lotus*, not floating, smooth, and dry. It may be possible that long distance dispersals are very rare events, which should explain absence of these species in many close islands (why, for example, *L. pacificus* is seemingly absent from the Huoshaodao Is., although it was many times collected from Lanyu?).

It seems that distribution of *L. pacificus* and *L. anfractuosus* is limited also by ecological factors. Both species occur on close latitudes in Northern and Southern hemispheres, respectively. Both species are restricted to seashore, where they grow on rocky and sandy places, with the substrate often of coral origin. Interestingly, southern boundary of *L. anfractuosus* distribution coincides with southern boundary of coral reef formation in that region of Pacific Ocean. The northern boundary of *L. pacificus* area is close to northern limit of coral reef formation.

In New Caledonia archipelago, calcareous substrates of coral reef origin are abundant in the Loyalty Islands and Île des Pins, but are relatively rare in the main island (MORAT *et al.* 2001). All available New Caledonian herbarium specimens of *L. anfractuosus* with precise labels were collected from the Loyalty Islands and Île des Pins. The species seemingly has not been collected from the New Caledonia main island (Fig. 11).

Although the flora of New Caledonia is extremely rich in endemic species, the endemism

level is relatively low among species of calcareous habitats (MORAT *et al.* 2001). It is important in this respect that *L. anfractuosus* cannot be treated as a true New Caledonian endemic species (present in Vanuatu, probably absent from New Caledonia main island).

It should be noticed that geographical range of *L. pacificus* is not completely congruent to floristic delimitation of E Asia region (Fig. 7). According to TAKHTAJAN (1978, 1986), the Lanyu Island, as well as southernmost part of Taiwan Island, belong to Palaeotropis, whereas the Ryukyu Islands belong to Holarctis (another delimitation of floristic regions was proposed by WU & WU [1996], who extended Palaeotropis northwards). *Lotus pacificus* represents an example of plant species common to Ryukyu and Lanyu. In contrast, south-eastern boundary of distribution of *L. corniculatus* complex (represented here by *L. japonicus* (Regel) Larsen) fits well to SE boundary of Holarctis, as accepted by TAKHTAJAN (1978, 1986). Namely, the *L. corniculatus* complex occurs in the northern part of the Taiwan Island, in the Ryukyu islands, and in main Japanese islands.

The morphological gap between *L. anfractuosus* and *L. australis* s.str. is more significant than distinctions between *L. pacificus* and *L. australis*. This is in contrast with the fact that New Caledonia is geographically much closer to Australia than Taiwan and Japan.

Key to species and varieties of the *Lotus australis* complex

1. Stems and leaves completely glabrous 2
- 1'. Stems and leaves with more or less conspicuous indumentum; in less pubescent plants hairs are well detectable at least on axillary buds and upper parts of peduncles 4
2. True stipules wanting (a pair of basal leaflets should not be mistaken to stipules). Leaflets obovate. True bracts are wanting or scarcely visible, or, contrary, relatively large (1-2 mm long), linear, herbaceous, always eglandular (a foliage leaf situated at the umbel base should not be mistaken to a bract). Standard blade clearly delimited from the narrow claw. Internal side of calyx teeth glabrous or pubescent 3
- 2'. True stipules are represented by small dark glands situated just between stem node and place of insertion of basal leaflets. Leaflets linear to oblanceolate. True bracts are small, but always well detectable, with dark glandular margins. Standard claw gradually widening upwards and not clearly delimited from the blade. Internal side of calyx teeth is glabrous 1.2. *Lotus australis* var. *austroglaber*
3. Internal side of calyx teeth pubescent (the only pubescent plant part) 3.1. *Lotus anfractuosus* var. *anfractuosus*
- 3'. Internal side of calyx teeth glabrous (plant is totally glabrous) 3.2. *Lotus anfractuosus* var. *vanuatensis*

4. Style 2.5-4 mm long. Flowers (4)5-9(10) mm long. Calyx teeth as long as the tube or shorter. Umbels 1-4 flowered. Fruits usually incurved, less often straight. Leaflets usually obovate, rarely oblanceolate 4. **Lotus cruentus**
- 4'. Style (4.2)4.5-6.5(8) mm long. Flowers (8.5)10-20(22) mm long. Calyx teeth as long as the tube or longer. Umbels 2-8-flowered. Fruits usually straight. Leaflets obovate, oblanceolate or linear 5
5. Keel strongly incurved, shortly rostrate. True stipules wanting, less often present and very small. Peduncles often as long as subtending leaves. Wings and standard white 2. **Lotus pacificus**
- 5'. Keel moderately incurved, long rostrate. True stipules usually small, but well detectable, less often scarcely detectable, extremely rare absent. Peduncles often much longer than the subtending leaves. Wings and standard white, pink or purple 1.1 **Lotus australis** var. **australis**

1. *Lotus australis* Andrews

Bot. Repos. 10: t. 624 (1811). — *Lotus australis* Andrews var. *normalis* Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 737 (1926), nom. illeg. — Lectotype (designated here): [Icon] t. 624 in Bot. Repos. 10 (1811).

Lotus australis Andrews var. *angustifoliolus* DC., Prodr. 2: 212 (1825). — *Lotus candolleanus* Sweet, Hort. Brit.: 477 (1826) (not seen). — Type: "Nov. Holl. in Lambert. 1816" (G-DC).

Lotus australis Andrews var. *pubescens* Benth. in T.L.Mitch., Journ. Exped. Inter. Trop. Austral.: 348 (1848). — Type: *Mitchell 419*, "Sub-Tropical New Holland", 10 Oct. 1846 (lecto-, K!, designated here).

Lotus australis Andrews var. *longifolius* Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 737 (1926). — Type: *Cunningham 47*, [Australia, Queensland], Moreton Bay, Sep. 1824 (lecto-, K!, designated here).

Lotus australis Andrews var. *maritimus* Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 737 (1926). — Type: *Gunn 439*, Tasmania (lecto-, K!, designated here; isolecto-, NSW 1029!).

Lotus australis Andrews var. *venustus* Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 737 (1926). — Type: *McGillivray 66*, [Australia, Queensland], Port Curtis, Nov. 1847 (lecto-, K!, designated here).

Lotus laevigatus Benth., in Mitchell, Journ. Exped. Inter. Trop. Austral.: 62 (1848). — *Lotus australis* var. *laevigatus* (Benth.) Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 736 (1926). — Type: *Mitchell 80*, [Australia, New South Wales], Macquarie River, marshy among reeds, 16 Feb. 1846 (lecto-, K!, designated here).

Perennial herbs with thick taproot, rarely annuals. Stems straight or slightly flexuose, sparsely to densely pubescent by ± appressed or patent hairs, rarely glabrous. Leaves sessile to shortly petiolate (petiole up to 0.7 mm long), (3)5(7)-foliolate, sparsely to densely pubescent by

± appressed or patent hairs, rarely glabrous. Stipules small (0.1-0.5 mm) but usually conspicuous, rarely inconspicuous, in extremely rare cases absent. Rachis 1.5-9 mm long. Leaflets soft to slightly fleshy, linear, oblanceolate, or obovate, with usually acute apex, those of the lower pair (4-)10-25 mm long, 1.5-6.5 mm wide, upper leaflets (5-)13-28 mm long, 1.5-6.5 mm wide. Peduncles 18-135 mm long, usually longer than subtending leaves. Foliage leaf on the peduncle 1-3-foliolate. Umbels 2-8-flowered. Bracts present, glandular, 0.1-0.5 mm long and 0.3-0.8 mm wide. Flowers (9-)10-22 mm long. Calyx 6-10 mm long, tube pubescent outside, teeth longer than, or equalling the tube, with both sides pubescent; rarely calyx totally glabrous. Wings and standard white or pink, rarely red, keel white with pink tip or pink with red tip, or red. Standard claw gradually widening upwards and not clearly delimited from the blade. Keel slightly incurved, long rostrate. Style (4.2-)4.5-6.5(-8) mm long. Fruits usually straight, 2.4-3.5 mm wide, 15-45 mm long. — Figs 1; 2.

1.1. *Lotus australis* Andrews var. **australis**

Stems, leaves and calyces more or less pubescent, in less pubescent plants hairs are well detectable at least on axillary buds, upper parts of peduncles and on internal side of calyx teeth.

HABITAT. — Grasslands, open forests, seashores, roadsides and other disturbed places.

DISTRIBUTION. — Australia: all states, including Tasmania. Absent from extreme north of the continent, rare in central Australia.

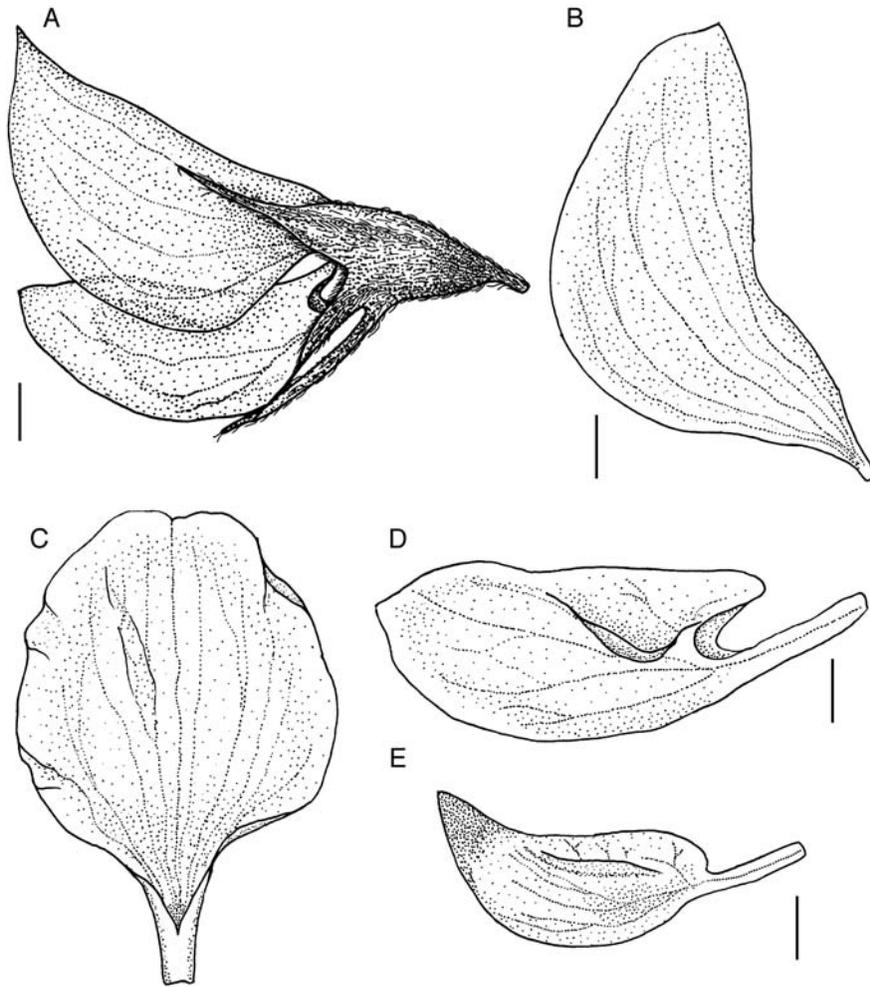


FIG. 1. — Floral morphology of *Lotus australis* Andrews var. *australis*, Koch 831, South Australia, Mt Lofty Ranges, NSW 1042: **A**, flower; **B**, standard, side view; **C**, standard, view from inside; **D**, wing; **E**, keel. Scale bars: 2 mm. Drawing by M.V. REMIZOVA and T.E. KRAMINA.

SELECTED MATERIAL EXAMINED. — AUSTRALIA: Australian Capital Territory: *Crisp* 7732, 8 km S of Canberra City, Mt. Mugga Mugga, alt. 740 m, 24 Feb. 1986 (NSW 512815); *Darbyshire* 127, 1.5 miles S of Gudgenby Ford, alt. 3600 ft, 25 Jan. 1961 (K, NSW 512715); *Evans* 2582, Kowen Forest, 8 miles E of Canberra, 8 Dec. 1966 (K); *Hardy s.n.*, near Canberra, Nov. 1967 (NSW 98235); *MacKee* 8823, Kowen, Dec. 1961 (K); *Slater* 204, Kowen, 22 Jan. 1962 (NSW 513170).

New South Wales: *Anonymous*, Herb. Al. de Bunge, Sydney (P00202646); *Armstrong* 546, Wollomombi Gorge, 22 Nov. 1973 (NSW 298098); *Baker s.n.*, Camboon, Oct. 1893 (NSW 512834);

Betche s.n., Wellington, 30 Oct. 1886 (NSW 1384); *Boorman s.n.*, Georges Plains, Nov. 1906 (NSW 1381); *Boorman s.n.*, Howell, Dec. 1914 (NSW 1008); *Boorman s.n.*, Nundle, June 1904 (LE, NSW 1020); *Boorman s.n.*, Wallangarra, Nov. 1904 (NSW 1003); *Boorman s.n.*, Warialda, Oct. 1914 (NSW 1018, 1005); *Booth & Rhodes s.n.*, Marra Downs, via Brewarrina, Oct. 1979 (NSW 443808); *Boyd s.n.*, 10 miles N of Cootamundra, Nov. 1963 (NSW 512811); *Cambage* 3460, Queanbeyan, 16 Jan. 1912 (NSW 997); *Cardell* 1388, Gulargambone, Sep. 1888 (NSW 1388); *Carre s.n.*, Bombala, Jan. 1906 (NSW 1000); *Consett-Davis s.n.*, 5 miles NW of Armidale, 22 Dec. 1940 (NSW 513109); *Constable* 24337,

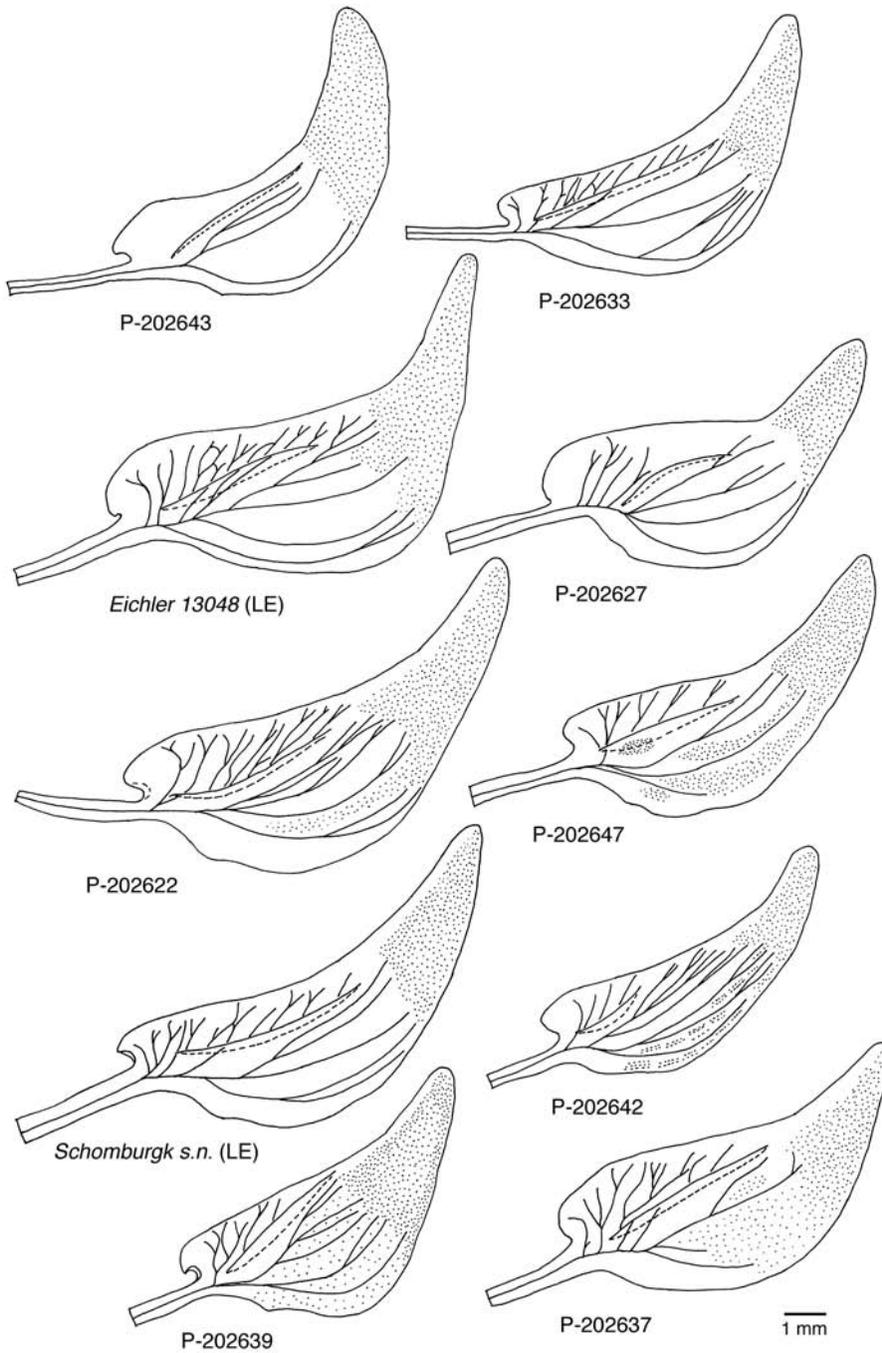


FIG. 2. — Variability of keel shape in *Lotus australis* Andrews var. *australis* (Australia). Dotted areas correspond to red or pink colour. Drawing by D.D. SOKOLOFF.

- Dalmorton, 28 Oct. 1952 (K); *Constable 4246*, 7.5 miles E of Bathurst, 25 June 1963 (LE); *Constable s.n.*, Bugaldie, 10 Mar. 1951 (NSW 15920); *Constable s.n.*, Wollar-Sandy Hollow Road, 16 Sep. 1948 (NSW 512699); *Costin s.n.*, Cooma, 14 Nov. 1948 (NSW 512759); *Coveny s.n.*, Marayong, 3 July 1966 (NSW 248091); *Coveny 12374 et al.*, Glen Innes, 13 Dec. 1986 (NSW 278068); *D'Aubert 438 et al.*, Denman, 6 Dec. 1988 (NSW 211699); *Dalby 86/136*, Killarney Gap near top, Mt. Kaputar NP, c. 35 km from Narrabri, 720 m, 2 Oct. 1986 (NSW 214177); *Errington 71*, Central Coast, 33°50'00"S, 150°52'40"E, 27 Jan. 1993 (NSW 264568); *Frazer s.n.*, Mt. Kaputar, 7 Sep. 1964 (NSW 512702); *Frazer s.n.*, Warrumbungle National Park, 9 Oct. 1964 (NSW 512703); *Gilmour 8079*, Guy Fawkes River National Park, c. 3 km NE of Spion Kopje, alt. 830 m, 3 Mar. 1998 (NSW 439783); *Glenfield Veterinary Research Station s.n.*, Tamworth, 10 Feb. 1936 (NSW 1086); *Grantham s.n.*, Armidale Distr., 28 Nov. 1951 (NSW 512827); *Greuter 21221*, Liverpool Range, N of the pass of the road from Willow Tree to Merriwa, 7 Oct. 1988 (NSW 513107); *Hosking 251*, Oxley Park, Tamworth, alt. 770 m, 16 Nov. 1985 (NSW 512705); *Kennedy & Galgon 239*, near Campbelltown, 20 Nov. 1991 (NSW 246894); *Lee 66*, S Nandewar Ra., 21 Mar. 1968 (NSW 100186); *Lee 77*, c. 14 miles NE of Inverell, 22 Mar. 1968 (NSW 100187); *Leigh 5375*, Denilquin, 1 July 1965 (NSW 76121); *Maiden & Boorman s.n.*, Jennings, Dec. 1903 (NSW 1013); *Maiden s.n.*, Jindabyne, Jan. 1899 (NSW 1011); *Maiden s.n.*, St Marys, Oct. 1886 (NSW 512809); *Maiden s.n.*, Tantawanglo Mts., Dec. 1886 (NSW 998); *McBarron 11426*, Narellan, 24 Oct. 1965 (NSW 89613); *McBarron 14547*, Camden, 3 Nov. 1967 (K); *McBarron 2790bis*, Gerogery, 16 Dec. 1948 (NSW 513113); *McBarron 5670*, Near Culcairn, 6 Nov. 1951 (NSW 513111); *McBarron 592*, Badgerys Creek, Oct. 1941 (NSW 512530); *McIntyre 42-11*, Dumaresq, 20 Nov. 1990 (NSW 415150); *McReaddie 68/16*, 2 miles from Sandy Hollow on road to Muswellbrook, 7 Nov. 1967 (NSW 99952); *McReadie s.n.*, Sawpit Creek, Kosciusko, Jan. 1963 (NSW 512813); *McReadie s.n.*, Warrumbungle National Park, Nov. 1960 (NSW 52669); *Meecham s.n.*, Tumut, Nov. 1894 (NSW 512814); *Mitchell A. s.n.*, Kiakatoe c. 30 km W of Condobolin, Oct. 1973 (NSW 512818); *Mitchell T.L. 80*, Macquarie River, 16 Feb. 1846 (K); *Paterson 316/17*, Young, Dec. 1916 (NSW 999); *Rodd & Coveny 2710*, Ravine, c. 7 miles NW of Kiandra, 14 Dec. 1969 (NSW 120445); *Rodway s.n.*, Barraba, Oct. 1924 (NSW 512701 and 512749); *Rowe s.n.*, Kosciusko National Park, The Pinch (Moyangul) River, 21 Dec. 1991 (NSW 249048); *Ryan G.E. & Ryan M.K. MCB18848*, Goulburn River, 35 miles NW of Rylstone, 7 Dec. 1969 (NSW 512709); *Salasoo 2021*, SE of Nimmitabel, 30 Dec. 1960 (NSW 53132); *Salasoo 2326*, 3-4 miles SSE of Coonabarabran, 7 Jan. 1962 (NSW 512706); *Solling 956*, River Lett Hill [between Lithgow and Mt. Victoria], 16 Mar. 1972 (NSW 248089); *Taylor s.n.*, Armidale/Uralla district, Mar. 1977 (NSW 513105); *Whaite 3363*, Holbrook, Sep. 1969 (NSW 513114); *Wilson s.n.*, Severn Vale via Inverell, 28 Nov. 1969 (NSW 512700).
- Queensland: *Batianoff & Dillewaard 9086*, North End, North Keppel Is., 7 Oct. 1987 (NSW 512817); *Brown s.n.*, Keppel (?Keppel) Bay (P00202635); *Clemens 44534*, Darling Downs Distr., 9 Nov. 1944 (K); *Cambage 3977*, Bogantungan, 220 miles W Rockhampton, 5 Sep. 1913 (NSW 1026); *Constable s.n.*, Bald Mt., 4 miles N of Wallangarra, 9 May 1961 (NSW 513104); *Cunningham 47*, Moreton Bay, Sep. 1824 (K); *Everist 7936*, Maranoa Distr., near Hodson, about 14 miles W of Roma, 14 Sep. 1966 (K); *Everist & Webb 1360*, Darling Downs Distr., just W of Glen Aplin, 23 Feb. 1946 (K); *Hubbard 5040*, S of Wandoan 17-18 Nov. 1930 (K); *Hubbard 5346*, between Laidley and Forest Hill, 28 Nov. 1930 (K); *Hubbard 5725*, Stanthorpe, 11 Mar. 1931 (K); *Johnson 1333*, Leichhardt Distr., Seymour, N of Capella, 23 Feb. 1960 (K); *Johnson 2235*, Maranoa Distr., Mitchell-Roma road about 39 miles E of Mitchell, 23 Apr. 1961 (K); *McGillivray 66*, Port Curtis, Nov. 1847 (K); *Melvaine s.n.*, Biloela, 6 June 1941 (NSW 1089); *Mitchell 419*, "Sub-Tropical New Holland", 10 Oct. 1846 (K); *Mueller s.n.*, Rockhampton (P00202636); *Pedley 4532*, 25 km NE of Dalby, 2 Nov. 1978 (NSW 512816); *Rodd 1092*, 25°03'S, 148°12'E, 11 Aug. 1970 (NSW 401563); *Smith 03563*, Biloela, 26 Oct. 1947 (K); *Tate 6*, Peak Vale Station, near Clermont, Oct. 1917 (NSW 1028); *White 12658*, Darling Downs, between Cambooga and Clifton, 19 Oct. 1944 (K).
- South Australia: *Behr s.n.*, Port Adelaide (P00202647 and 00202622); *Benham s.n.*, Belaevis Nat. Park, 26. Oct. 1907 (K); *Eichler 13048*, Adelaide, 13 Oct. 1956 (LE); *Haegi 3450 & Moore*, Flinders Ranges, 32°28'S, 137°58'E (RSA 618243; LE); *Hind 5837*, 1 km W of Tea Tree Crossing on Younghusband Peninsula, 1 Feb. 1989 (NSW 215640); *Koch 831*, Mt. Lofty Ranges, Sep. 1902 (P00202637; NSW 1041 and 1042); *Kraehenbuehl 514*, Adelaide Plans, c. 18 km NW of Adelaide, Oct. 1961 (RSA 169657); *Mauritzon s.n.*, near Adelaide, Sep. 1936 (UPS 224683; S); *Mueller s.n.*, Port Lincoln (LE); *Pickard 2435*, 1.5 km NW Yatina, 20 km NW Peterborough, 5 Dec. 1973 (NSW 512538); *Rogers s.n.*, Kangaroo Is., Jan. 1907 (NSW 1041); *Rogers s.n.*, Port Elliston, Sep. 1907 (NSW 1038); *Rogers 8146/15*, between Beltana and Blinman, Oct. 1915 (NSW 512537).
- Tasmania: *Adams L.G. & Adams C.J. 3412*, c. 3 km ESE of Port Latta, 40°52'S, 145°25'E, 9 Dec. 1977 (K); *Anonymous*, ex herb. Hook.f. (UPS 224682); *Archer s.n.*, ex herb. Hook.f. (P00202627);

Gamber 2080, W Coast, 16 Feb. 1930 (K); *Gunn 20*, ex herb. Hook.f. (P00202623); *Gunn 439*, 1837 (NSW 1029); *Gunn s.n.*, "Van-Diemen (Gunn-M. Lindley 1839)" (P00202624); *Gunn s.n.* (LE); *Rodway 2058*, NW Coast, Feb. 1917 (NSW 513102); *Whinray s.n.*, Flinders Is., about 500 yards on the W side of the W end of Killiecrankie Bay, 23 Nov. 1968 (NSW 100535). Victoria: *Lucas s.n.*, Myrtleford, Nov. 1883 (NSW 1023); *Morrison 1576*, Werribee, 26 Dec. 1891 (K); *Mueller s.n.*, Little River, 7 May (MW); *Vroland s.n.*, Strathbogie, Nov. 1902 (NSW 1021); *Whan 102*, Hamilton, 1861 (NSW 1022).

Western Australia: *Froggat s.n.*, Kings Sound, 1888 (NSW 1035); *Helms s.n.*, Dongarra, Oct. 1898 (NSW 1031); *Helms s.n.*, Geraldton, Oct. 1898 (NSW 1033); *Johnson 15/73*, North West Cape, 12 June 1973 (NSW 512820); *Morat 8146*, Shark Bay, Doore Is., 15 July 1988 (P00202634); *Morat 8318*, Shark Bay, Steep Point et environs, 24 July 1988 (P00202633); *Phillips s.n.*, Murchison River mouth, 27 Sep. 1962 (NSW 512712); *Wilson 1123 & Rowe*, Carnarvon, 16 Sep. 1991 (NSW 249869).

Unknown state: *Brown s.n.*, Iter Australiense, 1802-1805 (LE).

1.2. *Lotus australis* Andrews var. *austroglaber* Kramina & D.D. Sokoloff, var. nov.

Tota planta perfecte glabra.

TYPUS. — *Wilson & Lapinpuro LL40*, Australia, New South Wales, 13 km S of Graman on Delungra road, 29°34'S, 150°54'E, roadside, grassland, on grey red soil, 27 Nov. 1982 (holo-, NSW 512828!). — Fig. 3.

Plants are totally glabrous.

HABITAT. — Roadside, grassland.

DISTRIBUTION. — Australia: New South Wales, rare. It is possible that the variety is present, although rare, in other states. We have studied more *Lotus* material from NSW than from any other state.

PARATYPES. — AUSTRALIA: New South Wales: *Faby s.n.*, Inverell [29°47'S, 151°07'E], 18 Dec. 1959 (NSW 512708!); *Forsyth s.n.*, Upper Richmond River [about 28°25'S, 152°46'E], Oct. 1900 (NSW 1019!); *McCaffrey s.n.*, Inverell, Soil Conservation Research Station, brown chernozemic soil, 7 Jan. 1955 (NSW 512707!).

2. *Lotus pacificus* Kramina & D.D. Sokoloff, sp. nov.

A species proxima L. australis Andrews *carina valde incurva rostro conspicuo, brevi, lato et obtuso (nec leviter incurva rostro longo et angusto vel male definito), plicis carinae vix evolutis vel nullis (nec plerumque conspicuis), alis vexilloque semper albis (nec albis, roseis vel rubris), pedunculis plerumque brevioribus, stipulis veris nullis vel inconspicuis (nec plerumque parvis, sed conspicuis) differt.*

TYPUS. — *Furuse 2385*, Japan, Ryukyu, Pref. Okinawa, Ishigaki Is., Ohono, by sea side (sandy sea shore), 10 Feb. 1973 (holo-, MHA!; iso-, K!). — Fig. 4.

Perennial herbs with thick taproot. Stems straight or slightly flexuose, sparsely to moderately pubescent by ± appressed hairs. Leaves sessile, 5(-7)-foliolate, sparsely to moderately pubescent by ± appressed hairs. Stipules wanting, less often present and then very small, inconspicuous. Rachis 4-12 mm long. Leaflets slightly fleshy, oblanceolate to narrow obovate, with acute to almost rounded, mucronate apex, those of the lower pair 10-18 mm long, 3-6 mm wide, upper leaflets 15-22 mm long, 4.5-8 mm wide. Peduncles 6-26 mm long, usually not longer or slightly longer than subtending leaves. Foliage leaf on the peduncle 1-3-foliolate. Umbels (1-)2-6-flowered. Bracts present, 0.5-1 mm wide and 0.1-0.4 mm long, glandular or, rarely, with a minute herbaceous blade plus a pair of basal glands. Flowers (8.5-)10-14.5(-16) mm long. Calyx 7-11 mm long, tube pubescent outside, teeth usually longer than, rarely equalling to the tube, with both sides pubescent. Wings and standard white, keel white with pink tip. Standard claw gradually widening upwards and not clearly delimited from the blade. Keel incurved by acute angle, shortly rostrate. Style (3-)4.5-6.5 mm long. Fruits usually straight, 2.7-4.4 mm wide, 24-60 mm long. — Figs 4-7.

VERNACULAR NAME. — Shiro-bana-Miyakogusa (Japanese) (Walker 1976); Yambaru-ebosigusa (Japanese) (Chuang & Huang 1965).

HABITAT. — Sandy or rocky (limestone, coral rock) places at sea shore.



FIG. 3. — Holotype of *Lotus australis* Andrews var. *austroglaber* Kramina & D.D. Sokoloff, *Wilson & Lapinpuro* LL40, Australia, New South Wales, 13 km S of Graman on Delungra road, 27 Nov. 1982 (NSW 512828).

DISTRIBUTION. — Ryukyu Is. (Japan), Lanyu Is. (Taiwan) (Fig. 7).

PARATYPES. — JAPAN: Pref. Kagoshima: *Mimoro, Shimada & Ozaki* 2634, Tekutsuku, Kikaicho, Ooshimagun Kikaizima, on the sea side, 1 Apr. 1981

(A – two sheets!, MHA!, NY!, OOM 23609); *Tashiro* 28, Osumi, ex(?) Yowanmura, 1881 (LE!). Pref. Okinawa: Hateruma: *Miyagi* 6784, 9–15 July 1975 (TUSG!); Iriomote: *Amano* 7310, Haemi, 23 Feb. 1954 (US 2156293!); *Atsuko Hosokawa s.n.*, Komi-Yuhu, 24 Mar. 1965 (TUSG!); *Hisao Migo*

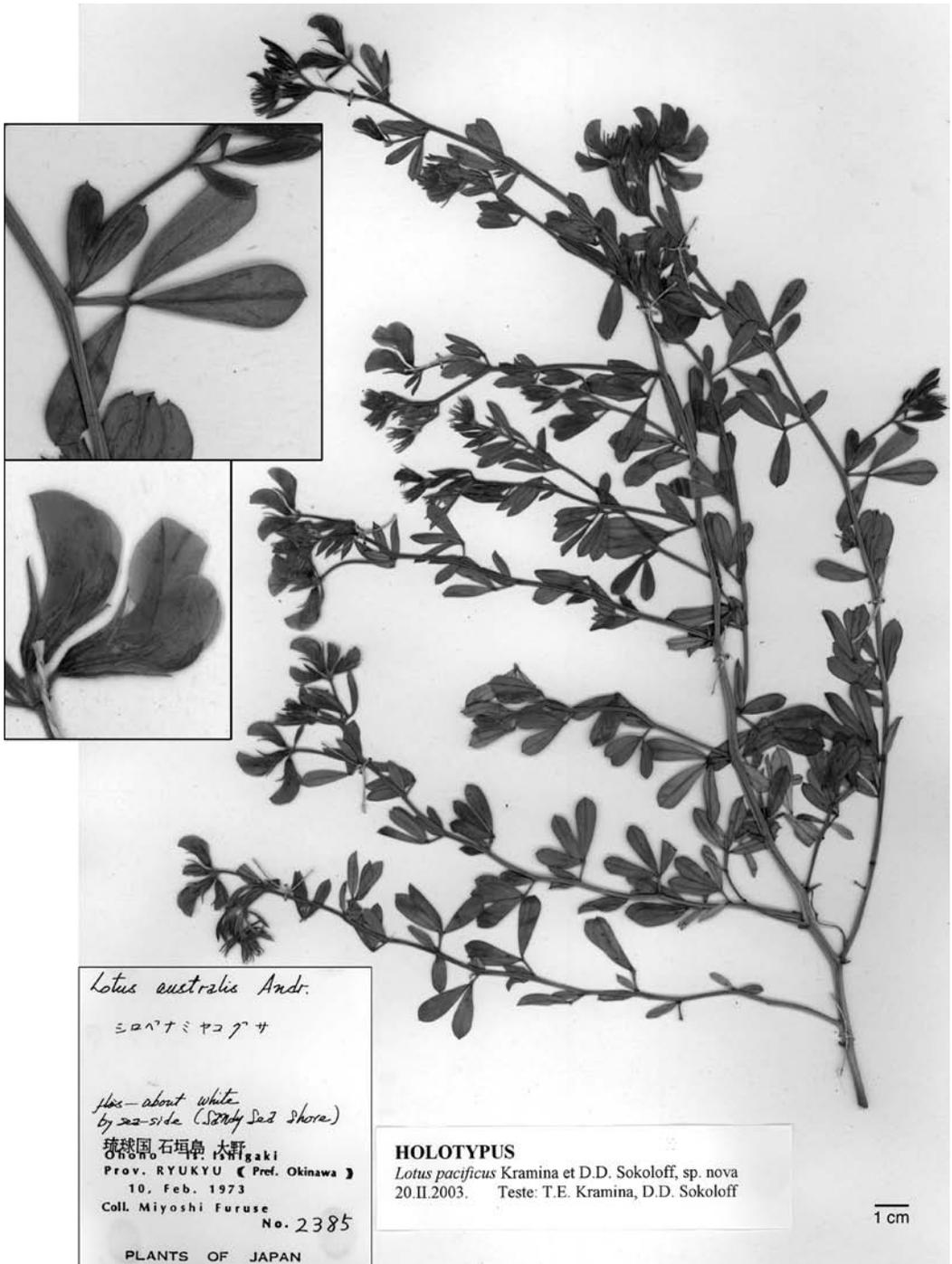


FIG. 4. — Holotype of *Lotus pacificus* Kramina & D.D. Sokoloff, Furuse 2385, Japan, Ryukyu, Pref. Okinawa, Ishigaki Is., Ohono, 10 Feb. 1973 (MHA).

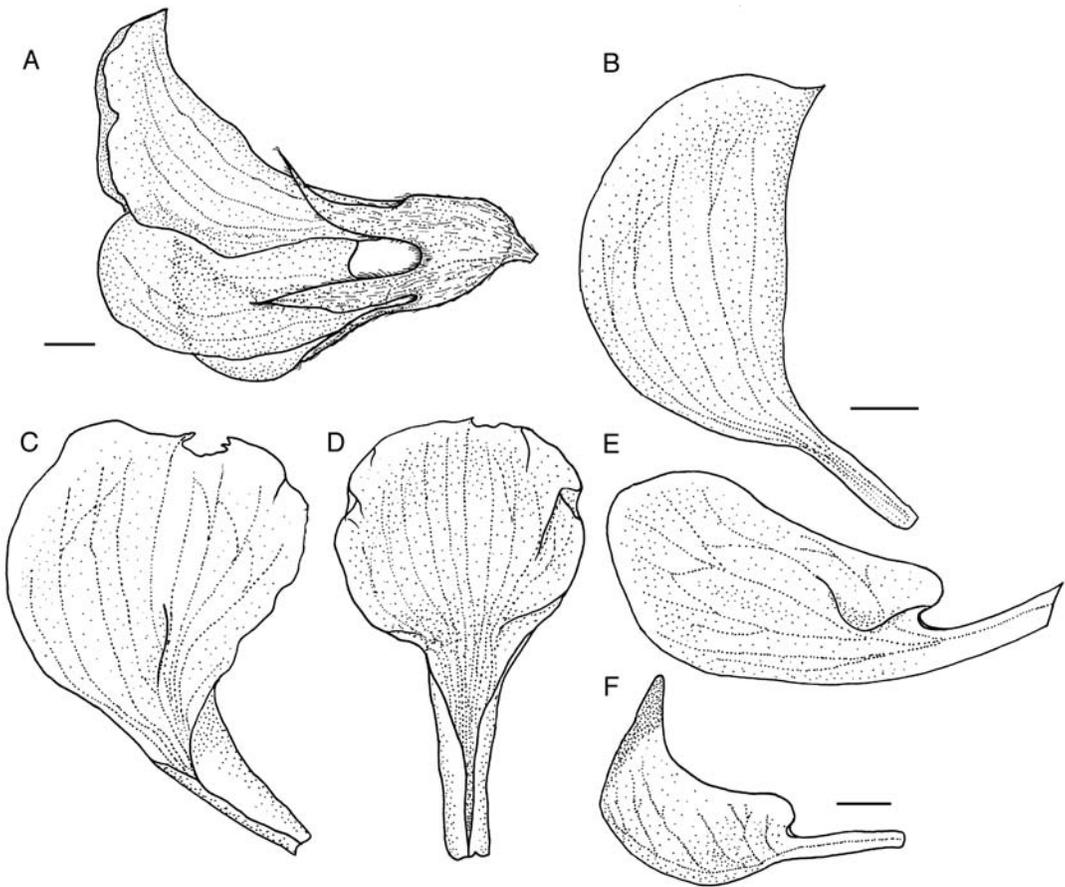


FIG. 5. — Floral morphology of *Lotus pacificus* Kramina & D.D. Sokoloff, *Tateishi & Murata 4794*, Japan, Okinawa, Iriomote, Toyohara, TUS 56572: **A**, flower; **B**, **C**, standard, side view; **D**, standard, view from inside; **E**, wing; **F**, keel. Scale bars: 2 mm. Drawing by M.V. REMIZOVA and T.E. KRAMINA.

s.n., W of Toyohara, seashore (TUS 41667/18461!); *Tateishi & Murata 4794*, Toyohara, seaside, 4 Feb. 1980 (TUS 56571!, TUS 56572!); Ishigaki: *Fosberg 37493*, 1 km NW of Ohama, on Miyara-Wan, near Isobe, on sandy beach, alt. 1 m, 15 June 1956 (US 2459795!); *Fosberg 37517*, Tada Hama, on coast SSE of Hiare, on rough limestone, alt. 1-3 m, 15 June 1956 (US 2459783!, POM 340712!); *Fosberg 37597*, Taketomi Is., near Aibaru Saki, east point of island, at top of sandy beach, alt. 1-2 m, 18 June 1956 (US 2459784!); *Furuse 118*, Tamatorimisaki, by sea shore, 29 June 1972 (SI!); *Furuse 2782*, Oohama, by sandy beach, 5 Apr. 1973 (K!); *Furuse 2807*, Shiraho, at sea shore, sandy beach, 5 Apr. 1973 (K!); *Furuse 440*, Ohno, by sea shore, 29 June 1972 (SI!); *Furuse 5455*, Oohama, by sandy beach, 28 Mar. 1974 (K!); *Hisao Migo s.n.*, Shiraho (TUS

41666/18462!); *Tateishi 4092*, Hirae, seaside, 15 Mar. 1978 (TUS 61839!); Izena: *Takahiro Shimizu 84-62*, Ruins of Izena Castle-Nakada, sandy seashore, 19 Apr. 1984 (TUS 115052!, TUS 115667!); Okinawa: *Hatusima 17495*, Shimajiri, Nakagusuku, on the sandy beach, 30 Apr. 1955 (KAG, US 2243252!); *Miyagi 10205*, Ohgimi-son, Shioya, sandy coast, 14 May 1984 (NY!, TUS 94660!); *Nakamine 373*, Kyan-ku, Miwa-son, seashore, 24 Feb. 1955 (URO; US 2594312!); *Tawada, Nakamine & Moran 4920*, Kiyan, sand, just above tide, 24 Feb. 1955 (GH!, UC, US 2186446!); *Yamashita 11102*, Shimajiri, Chinen, sandy sea-coast, 23 Mar. 1968 (A!, TI, TUSG!); Yonaguni: *Hisao Migo s.n.*, Hikawa (TUS 41665/18463!); without precise island location: *Tashiro 110.5* "Archip. Yoyama inter Lickiu et Formosa", 1886 (LE!).

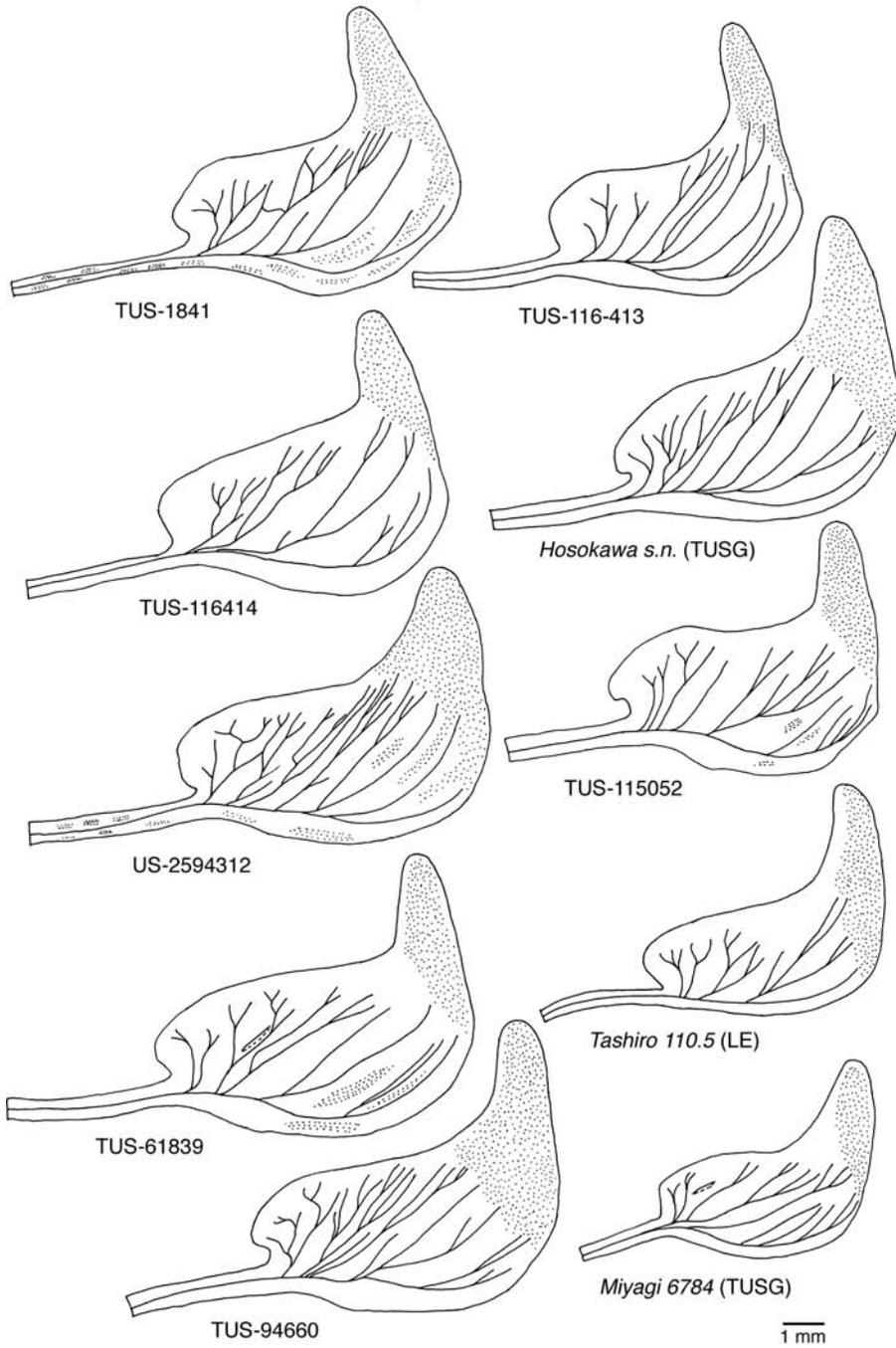


FIG. 6. — Variability of keel shape in *Lotus pacificus* Kramina & D.D. Sokoloff from Ryukyu, Japan and Lanyu, Taiwan. Dotted areas correspond to red or pink colour. Drawing by D.D. SOKOLOFF.

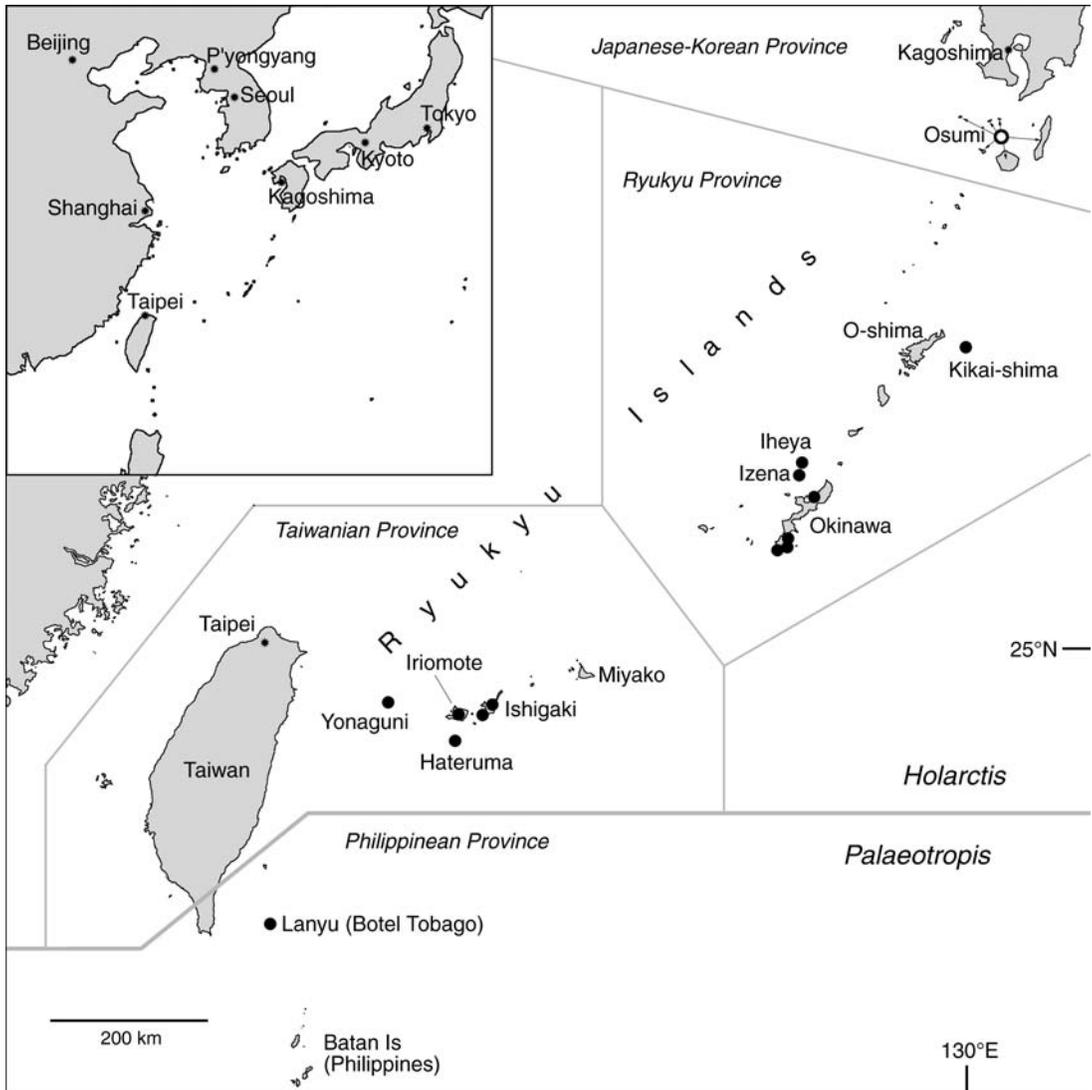


FIG. 7. — Distribution of *Lotus pacificus* Kramina & D.D. Sokoloff, based on studied specimens, the Iheya record is after Walker (1976). The Osumi record is given as an open circle to show that it is linked with a group of islands. Names of floristic provinces and kingdoms (Holarctis and Palaeotropis) are italicised. Grey lines indicate boundaries of floristic provinces and kingdoms, which are accepted according to TAKHTAJAN (1978, 1986).

TAIWAN, Taitung Co., Lanyu Isl. (Botel Tobago): *Chang* 14695, 6 Feb. 1980 (TAI, TUS 56791!); *Chang* 14782, 3 Apr. 1980 (TAI, TUS 52901!, TUS 80455!); *Chang* 16894, 5 Apr. 1985 (TAI, TUS 114345!); *Huang S.F.* 2756, Shuanshuyen, on seaside coral rock, alt. 0-5 m, 4 Feb. 1985 (TAI, TUS 116258!, TUS 116442!, TUS 121468!); *Huang T.C.*, *Huang S.F.*,

Yang & Jeng 10640, Swasy-rock, in thicket, 19 Feb. 1986 (AI, TAI, TUS 116413!, TUS 116414!); *Tadashi Kajita* 830, Tungching-tsun, seaside, on sunny rocky ground, 19 Mar. 1987 (AI, TAI, TUS 141323!).

Besides, a specimen from Japan, Ryukyu, Iheya (*Sakaguchi* 14 – TAI), cited by Walker (1976) under *L. australis*, also seemingly belongs to *L. pacificus*.

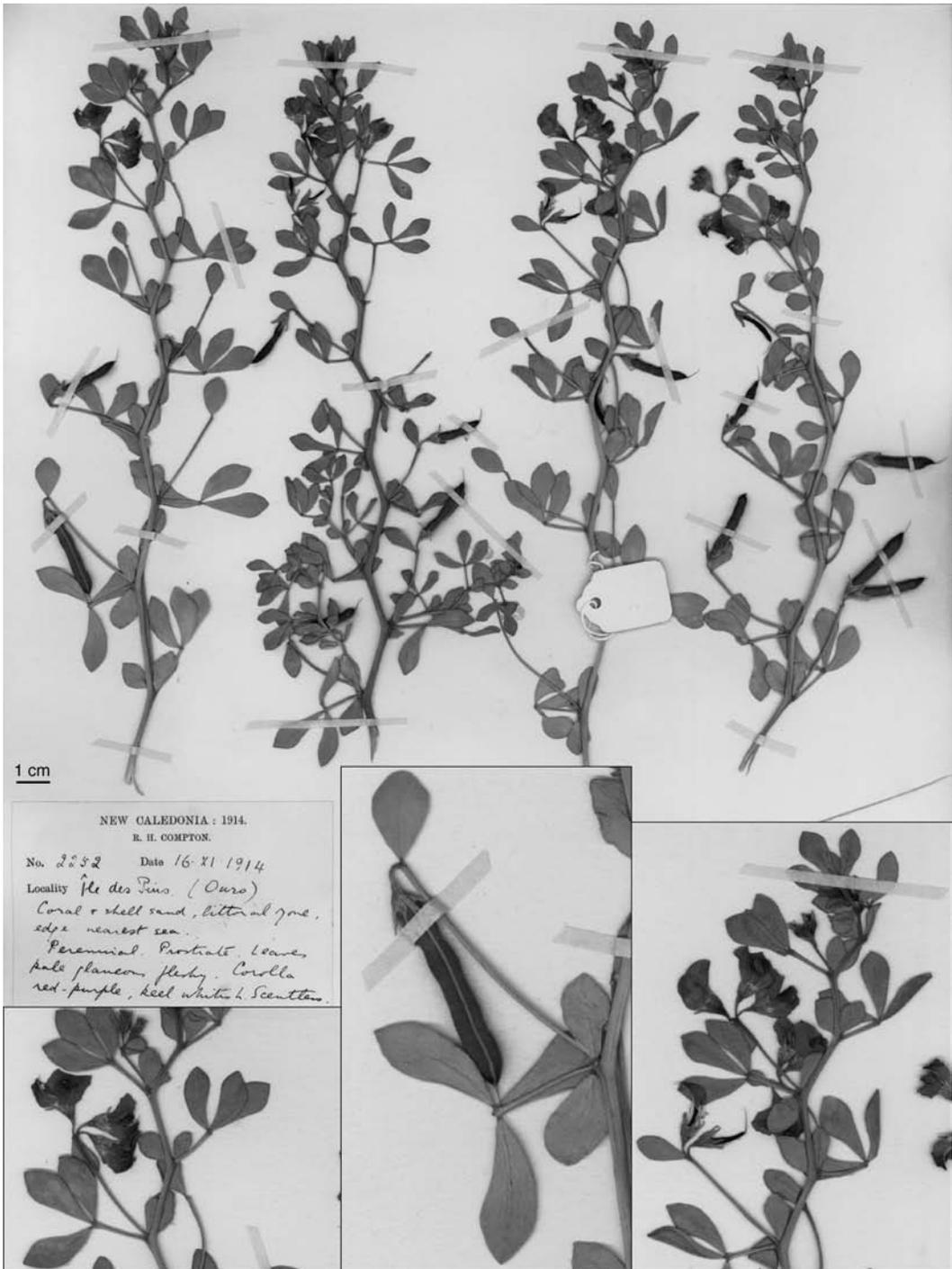


FIG. 8. — Lectotype of *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff, R.H. Compton 2252, New Caledonia, Île des Pins (Ouro), 16. Nov. 1914 (BM). By courtesy of The Natural History Museum, London.

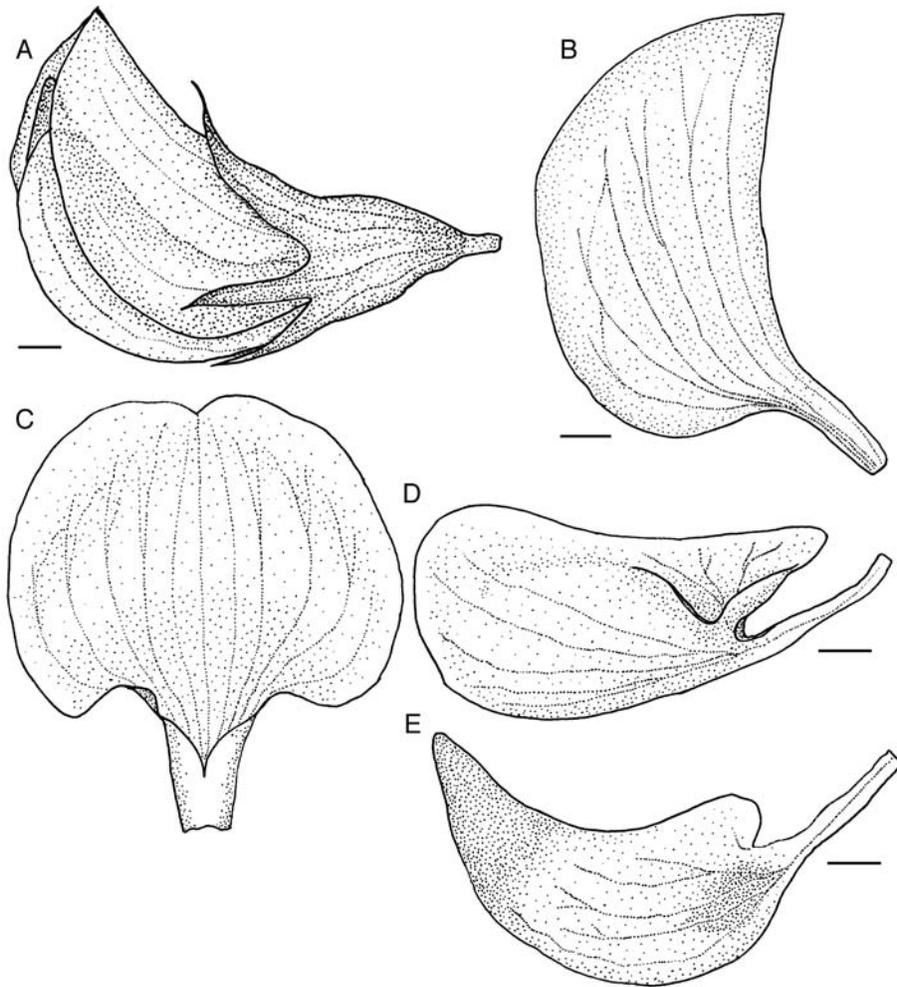


FIG. 9. — Floral morphology of *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff var. *anfractuosus*, Veillon 3089, New Caledonia, Île Beautemps-Beaupré, P00106383: **A**, flower; **B**, standard, side view; **C**, standard, view from inside; **D**, wing; **E**, keel. Scale bars: 1 mm. Drawing by M.V. REMIZOVA and T.E. KRAMINA.

3. *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff, comb. et stat. nov.

Lotus australis Andrews var. *anfractuosus* Bak.f., Journ. Linn. Soc. Bot. 45: 293 (1921). — Type: R.H. Compton 2252, New Caledonia, Île des Pins (Ouro), coral and shell sand, littoral zone edge nearest sea, 16. Nov. 1914 (lecto-, BM!, designated here).

Lotus australis Andrews var. *gillivrayi* Domin, Beitr. Fl. u. Pflanzengeogr. Austral. 1, 3, 1 (Bibl. Bot. 89): 737 (1926). — Type: McGillivray, Voyage of

H.M.S. Herald, Botany 794, Île des Pins, by the sea shore, Oct. 1853 (holo-, K!; iso-, BM!).

Perennial herbs. Stems slightly to pronouncedly flexuose, completely glabrous. Leaves sessile, (?4-)5-foliolate, completely glabrous. Stipules wanting. Rachis 4-11.5 mm long. Leaflets very fleshy, obovate, with acute or obtuse apex, those of the lower pair 6-16 mm long, 4-9 mm wide, upper leaflets 9-20 mm long, 6-10.5 mm wide. Peduncles (5-)10-

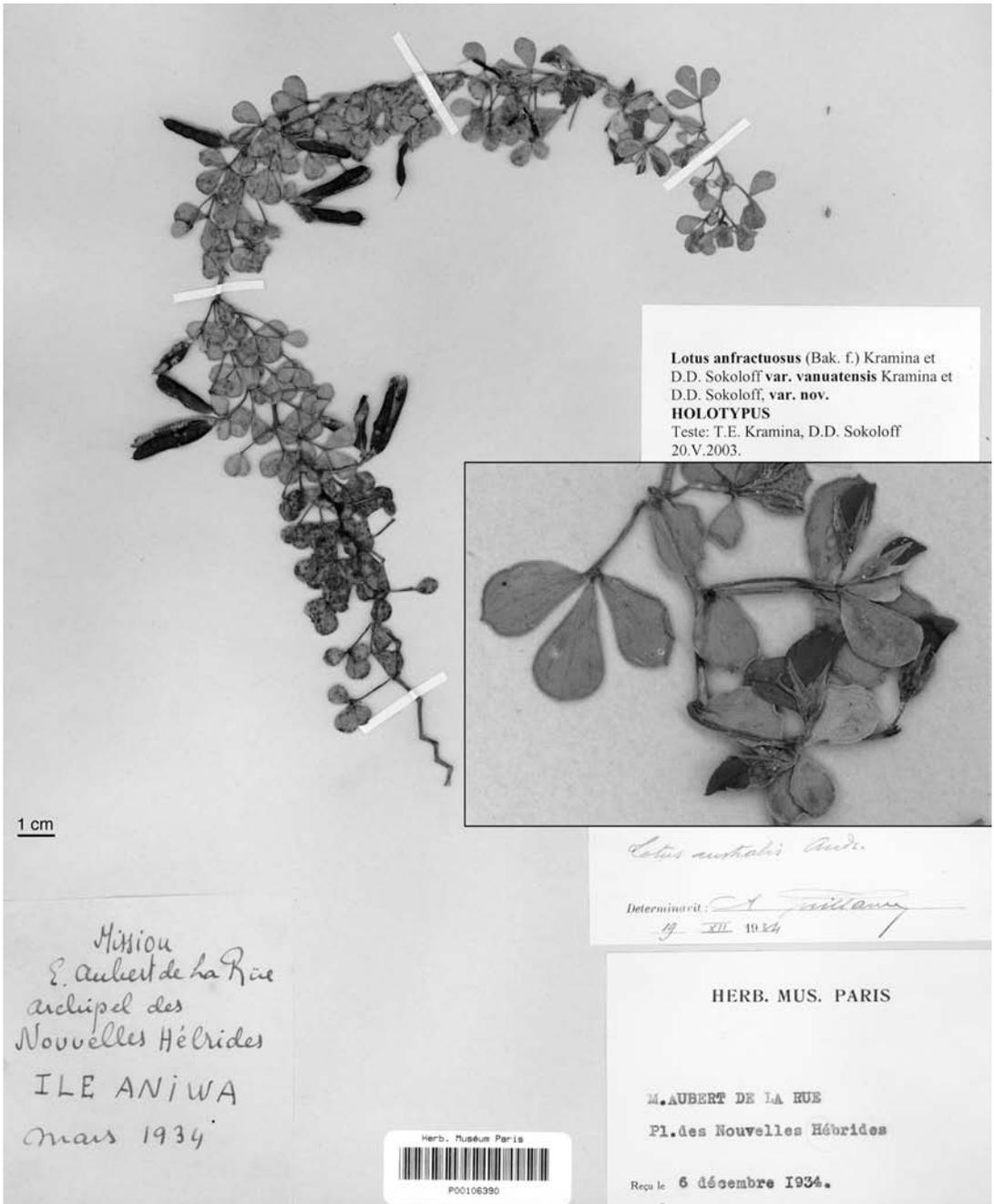


FIG. 10. — Holotype of *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff var. *vanuatuensis* Kramina & D.D. Sokoloff, *Aubert de la Rue* s.n. [Vanuatu], New Hebrides, Île Aniwa, Mar. 1934 (P00106390).

35 mm long, usually of almost the same length as subtending leaves. Foliage leaf on the peduncle 1-foliolate. Umbels 1-5-flowered. Bracts inconspicuous, or very small, or relatively long, 1-2 mm, herbaceous, eglandular. Flowers (8.5-)-9-11.5(-12.5) mm long. Calyx 5.5-8 mm long, tube completely glabrous, teeth almost equalling to the tube, with external side always glabrous, internal side pubescent or rarely glabrous. Petals (?pink or) red. Standard blade clearly delimited from the narrow claw. Keel slightly incurved, pronouncedly rostrate. Style (4-)-4.5-5.5 mm long. Fruits usually straight, 2.8-3.6 mm wide, 13-55 mm long. — Figs 8-11.

NOMENCLATORIAL NOTE. — The Kew specimen cited above as a holotype of *L. australis* var. *gillivrayi*, has a label, which is almost equivalent to the protologue. However, in the protologue (DOMIN, l.c.) the collection date is indicated as September, 1853 (not October, 1853). It is reasonable to suppose a misprint, because DOMIN cited a single specimen and stated (page 736) that he studied *Lotus* material at Kew Herbarium. We found no other MCGILLIVRAY's collections from this locality at Kew. We think that the BM specimen with a label "Isle of Pines. MGillivray (1854)" could represent a duplicate of the Kew specimen and thus an isotype. According to DAVID (1995), H.M.S. *Herald* visited Lord Howe Island, Isle of Pines and Aneityum between 19 February 1853 and 1 January 1854. Thus it is likely that the BM specimen was collected in 1853. Interestingly, this specimen belongs also to original material of *Lotus australis* var. *anfractuosus* Bak.f., because BAKER (l.c.) stated "agrees with a specimen collected by Macgillivray at the Isle of Pines".

According to the Australian Plant Name Index (APNI) (<http://www.anbg.gov.au/cgi-bin/apni>, accessed on 13 December 2002), *L. australis* var. *gillivrayi* is a base name for *Lotus gillivrayi* (Domin) Maiden. However, the name "*Lotus gillivrayi* (Domin) Maiden" is not included into the International Plant Names Index (IPNI) (<http://www.ipni.org/>, accessed on 13 December 2002). We have discussed the question with D.H. NICOLSON (US) and K. CHALLIS (Index

Kewensis). They were unable to find a relevant MAIDEN's publication and were dubious about the name "*Lotus gillivrayi*" because MAIDEN died in 1925 and the basionym was published in 1926 (according to APNI, it was published even later, in 1928).

3.1. *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff var. *anfractuosus*

Internal side of calyx teeth pubescent.

HABITAT. — Coral and shell sand or coral rocks at sea shore.

DISTRIBUTION. — New Caledonia: Loyalty Islands and Île des Pins (Fig. 11).

MATERIAL EXAMINED. — NEW CALEDONIA: Loyalty Islands: *Balansa* 2460, Lifou, July 1869 (K, P00106386); *MacKee* 5268, Lifou, Lucila, 11 Sep. 1956 (K, P00106381); *Veillon* 3089, Île Beautemps-Beaupré, 19 June 1974 (P00106383); *Viro* 1580, Plage de Co (Tcho) La Roche, Maré, 28 Jan. 1946 (P00106378); *Whitmee* 53, Loyalty Islands, Lifou (BM).

Île des Pins: *Baumann-Bodenheim* 13437, Île des Pins, Île Kouibandouï [22°39'30"S, 167°33'E], 25 May 1951 (MW); *Baumann-Bodenheim* 13440, Île des Pins, Île Kouibandouï, 25 May 1951 (P00106379); *Compton* 2252, New Caledonia, Île des Pins (Ouro), 16 Nov. 1914 (BM); *Debray* 2739, Île des Pins, presqu'île Kuto [22°40'S, 167°26'E], 26 Jan. 1978 (P00106382); *Germain s.n.*, Île des Pins, 1874-1876 (BM, US 1123972); *MacKee* 13058, Île des Pins, presqu'île d'Oro (Baie d'Obouai) [22°36'20"S, 167°32'30"E], 17 July 1965 (P00106380); *McGillivray s.n.*, Île des Pins, "1854" (BM); *McGillivray, Voyage of H.M.S. Herald, Botany* 794, Isle of Pines, Oct. 1853 (K); *Saunders* 10/74, Isle of Pines (K); *Vieillard* 360, Île des Pins, 1855-1860 (P00106385).

Unknown island: *Franc* 1067 in *Bonati et Lure*, Nouvelle-Calédonie (BM, K), *Pancher* 806, Caled[onia] (P00106384).

3.2. *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff var. *vanuatensis* Kramina & D.D. Sokoloff, var. *nov.*

Tota planta perfecte glabra (nec dentes calycini intrinsicus hirsuti). *A. L. australis* var. *austroglabro* Kramina

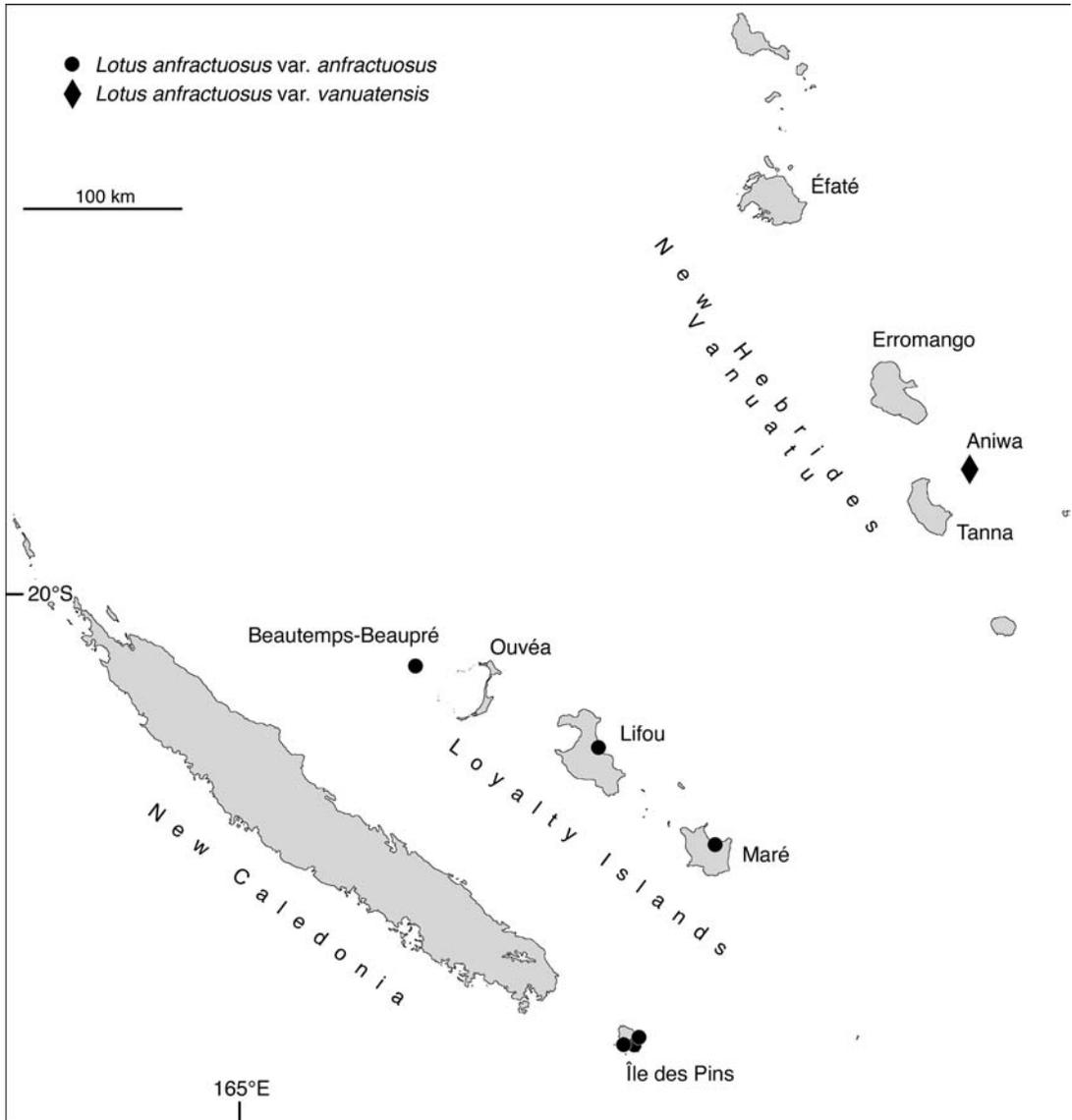


FIG. 11. — Distribution of *Lotus anfractuosus* (Bak.f.) Kramina & D.D. Sokoloff (based on studied specimens with precise locality information).

& D.D. Sokoloff *stipulis veris nullis, foliolis obovatis (nec linearibus vel oblanceolatis) et bracteis veris eglandulosis vel nullis bene differt.*

TYPUS. — *Aubert de la Rüe s.n.* [Vanuatu], New Hebrides, Île Aniwa, Mar. 1934 (holo-, P00106390; iso-, P00354111). — Fig. 10.

Internal side of calyx teeth glabrous (i.e. plant totally glabrous).

HABITAT. — Unknown. Probably sea shore.

DISTRIBUTION. — Vanuatu. The variety is known by type material only (Fig. 11).

4. *Lotus cruentus* Court

Victorian Natur. 73: 174 (1957). — *Lotus coccineus* Schldtl., *Linnaea* 21: 452 (1848), nom. illeg., non Vell. 1825. — Type: *Herb. Schlechtendal* (holo-, HAL 069717, photo seen).

Lotus australis Andrews var. *parviflorus* Benth., *Fl. Austral.* 2: 189 (1864). — Type: *Drummond 31*, 6th Coll., W. Australia, 1854 (lecto-, BM, designated here; isolecto-, P00202641!).

Lotus australis Andrews var. *behrianus* Tate, *Handb. Fl. Extratrop. South Australia*: 69 (1890). — Neotype (the specimen is annotated by J.Z. Weber as a “?Type”, but we see no direct evidence from the label that it was used by Tate to describe var. *behrianus*) (designated here): *Herb. Schomburgk*, [Australia, Northern Territory], Mt Olga, [25°18'S, 130°44'E] (AD 98306152, photo seen).

Lotus australis Andrews var. *behrii* C.Moore & Betche, *Handb. Fl. New South Wales*: 146 (1893). — Type: not designated (no specimen is cited in the protologue).

?*Lotus australis* Andrews var. *exstipulatus* J.M.Black, *Trans. and Proc. Roy. Soc. South Australia* 57: 153 (1933). — Type: *Ising s.n.* [Australia, Northern Territory], Horseshoe Bend [Finke River, 25°13'S, 134°14'E], 22 Aug. 1931 (holo-, AD 96046073, low resolution image seen).

Lotus fraseri Benth. ex A.Gray, *U.S. Explor. Exped.* 15 (Botany, 1): 400 (1854), nom. seminud. — Type: *Herbarium of the U.S. South Pacific Exploring Expedition under the command of Capt. Wilkes, U.S.N. s.n.*, New South Wales, 1838-1842 (holo-, GH 65699!).

Perennial herbs, rarely annuals. Stems straight or slightly flexuose, sparsely to densely pubescent by appressed to semi-spreading, incurved, rarely straight hairs. Leaves sessile to shortly petiolate (petiole up to 0.4-1.6 mm long), (3-)5(-7)-foliolate, sparsely to densely pubescent by appressed, to semi-spreading hairs. Stipules small (0.1-0.4 mm) but always conspicuous. Rachis 2-7.5 mm long. Leaflets soft to slightly fleshy, usually obovate, with obtuse apex, rarely acute and/or oblanceolate, those of the lower pair 5-11.5 mm long, 2.3-5.3 mm wide, upper leaflets 6.5-15 mm long, 2.3-7 mm wide. Peduncles 8-40 mm long, usually of almost the same length as subtending leaves. Foliage leaf on the peduncle 1-3-foliolate. Umbels 1-4-flowered. Bracts present, glandular, 0.2-0.6 mm wide, 0.1-0.5 mm long. Flowers (4-)5-9(-10) mm long. Calyx 3-6 mm long, tube pubescent outside, teeth shorter

than, or equalling to the tube, with both sides pubescent. Petals red, rarely pink and in very rare cases white. Standard claw gradually widening upwards and not clearly delimited from the blade. Keel incurved by obtuse (rarely by right) angle. Style 2.5-4 mm long. Fruits incurved upwards, less often straight, 2.2-2.7 mm wide, 20-48 mm long.

HABITAT. — Common in various types of plant communities, often on sandy soil and in disturbed places.

DISTRIBUTION. — Australia: all mainland states; absent from extreme north of the continent. Generally, *L. cruentus* tends to grow in more arid places than *L. australis*. In SE part of Australia, *L. cruentus* is rare in the coastal region.

SELECTED MATERIAL EXAMINED. — AUSTRALIA: New South Wales: *Abrahams 519*, Louth, Sep. 1910 (NSW 1079); *Alchin 301*, Chibnalwood, Wentworth, 27 Oct. 1975 (NSW 512567); *Andrews s.n.*, Broken Hill, Sep. 1918 (NSW 1396); *Betche s.n.*, Darling River (P00202626); *Betche s.n.*, Dubbo, Sep. 1885 (NSW 1077); *Boorman s.n.*, Tarcoon, Nov. 1903 (NSW 1390); *Bray s.n.*, Hay, May 1937 (NSW 1072); *Barker 356*, Bulloo overflow, 1 May 1977 (NSW 512669); *Caskey 14*, Byrnedale, c. 30 miles N of Menindee, Oct. 1969 (NSW 512559); *Constable 4560*, Mulgowen Station, 35 miles by road south of Bourke, 17 Oct. 1963 (NSW 63855); *Constable 4651A*, Donald's Plain, 75 miles W of Cobar, 27 Oct. 1963 (NSW 85030, RSA 205366); *Couch s.n.*, Urana, Feb. 1917 (NSW 1073); *Coveny 13421 et al.*, NNW of Tibooburra in Sturt National Park, 2 Sep. 1989 (NSW 238852); *Crawford s.n.*, Moulamein, Aug. 1950 (NSW 512623); *Crochett s.n.*, Lake Cargelligo, June 1936 (NSW 1053); *Cunningham & Milthorpe 1193*, Cootawundi, 20 Sep. 1973 (NSW 512782); *Cunningham & Milthorpe 1437*, West Menindee, 28 Aug. 1973 (NSW 512557); *Cunningham & Milthorpe 4185*, 5 km S of Canbeligo on Nymagee Rd, 23 Mar. 1976 (NSW 513224); *Cunningham & Milthorpe 925*, Mt. Grenfell, 13 Aug. 1973 (NSW 513215); *Cunningham & Milthorpe 928*, 83 km on Tilpa Road, N of Cobar-Wilcannia road, 12 Aug. 1973 (NSW 512569); *Fletcher s.n.*, Wagga (NSW 1402); *Ford s.n.*, between Broken Hill and Menindee, 31 Aug. 1946 (NSW 512558); *Glenfield Veterinary Research Station 66/5439*, 6 miles SE of Mungindi, Yarrawa, 19 Oct. 1966 (NSW 94849); *Glenfield Veterinary Research*

Station, Walgett, 21 Apr. 1937 (NSW 1059); *Hartley s.n.*, Cobar-Wilcannia area, 3 Nov. 1974 (NSW 517646); *Honner s.n.*, "Moorna", via Wentworth, 24 May 1969 (NSW 512562); *Irons & Fogarty s.n.*, Enngonia, 17 Sep. 1985 (NSW 512773); *Jacobs 2316*, Fowlers Gap, N of Broken Hill, 9 Oct. 1975 (NSW 512555); *Lee 243*, c. 19 km NW of Milparinka, 27 Sep. 1971 (NSW 512666); *Lee 251*, 45 km SSE of Milparinka, 28 Sep. 1971 (NSW 512553); *Lee 256*, 50 km SSE of Milparinka, 28 Sep. 1972 (NSW 512784); *Lee 261*, Near foot of Koonenberry Mt., 28 Sep. 1971 (NSW 512780); *Lowe s.n.*, Combara, 30 Sep. 1971 (NSW 517647); *Maiden 1399*, Bogan Gate to Condobolin, Aug. 1897 (NSW); *Maiden s.n.*, Narromine, Sep. 1898 (NSW 1080); *Maiden s.n.*, near Wilcannia, June 1896 (NSW 1391); *Mauritson s.n.*, Near Broken Hill, 22 Sep. 1936 (UPS 224679, 224680); *McBarron 15942*, Brewarrina, 16 Oct. 1968 (NSW 489855, 81469); *McBarron 16053*, Goodooga, 17 Oct. 1968 (NSW 87467); *McBarron 18642*, 2 miles N of Bourke, 14 Nov. 1969 (NSW 517648); *McBarron 20833*, 20 km E of Goolgowi, 23 Sep. 1913 (NSW 512613); *McBarron s.n.*, Balranald township, 24 Sep. 1973 (NSW 512561); *Mueller s.n.*, Barrier range, 16 June 1889 (LE, MW); *Noble & Bawden s.n.*, Birdwood Station, Pooncarie, June 1979 (NSW 512560); *Paddison s.n.*, New Angledool, Oct. 1889 (NSW 512833); *Perry 5748*, near Tibbooburra, 8 Sep. 1971 (NSW 512605); *Pickard 3046*, 11 km SW "Moalie Park", 29 Oct. 1976 (NSW 486739); *Pile s.n.*, Wongarbon, SE of Dubbo, Jan. 1920 (NSW 1065); *Reilly s.n.*, White Cliffs, July 1906 (NSW 1068); *Rodd 5786 et al.*, Depot Glen., 30 Oct. 1986 (NSW 196398); *Ryan & Everley 33*, Kinchega National Park, Menindee, 2-5 June 1969 (NSW 512564); *Schulefield 1100/20*, Cryon, Mar. 1920 (NSW 1067); *Semple s.n.*, 90 km N of Balranald, 21 Sep. 1983 (NSW 512568); *Shelley s.n.*, Near Hay, Oct. 1921 (NSW 1054); *Simon 7186/15*, Gilgandra, Sep. 1915 (NSW 1079); *Vickery s.n.*, Barham, 13 Oct. 1949 (NSW 10253); *Whaite 762*, Foot of Barrier Range, 12 Aug. 1950 (NSW 512783); *White et al. s.n.*, near Mt. Wright, Mootwingee Nat. Park, 19 Sep. 1990 (NSW 512611); *White s.n.*, Old Mootwingee Gorge, Mootwingee Nat. Park, 18 Sep. 1990 (NSW 512609); *Wiecek 204 et al.*, Jump Up, c. 3.5 km S of "Olive Downs" homestead on Jump Up loop Rd, Sturt National Park, 2 Sep. 1989 (NSW 250358); *Wiecek 353*, Dead Horse Gully, 6 Sep. 1989 (NSW 228924); *Wilson & Murray 5890*, 10 km NW of "Lachlan Downs" homestead on "Belford" road, 23 Mar. 1984 (NSW 512616); *Wilson & Murray 5899*, 5 km WNW of Roto, 24 Mar. 1984 (NSW 512766).

Northern Territory: *Chippendale s.n.*, Illara Creek, 11 miles NW Temple Downs Homestead, 19 Oct. 1960 (K); *Henry 1013*, Ringwood Station, 23°54'S, 134°39'E (NSW 512822); *Perry 5405*, Palm Valley,

12 miles SW of Hermannsburg Mission, 5 Sep. 1955 (NSW 512757); *Vickery s.n.*, Finke River, near Palm Valley, Aug. 1960 (NSW 529666); *Wilson 708 & Rowe*, Ormiston Gorge, 23°38'S, 132°45'E, 16 Sep. 1990 (NSW 233349).

Queensland: *Drummond s.n.* (P00202621); *Mueller s.n.*, Rockhampton (MW).

South Australia: *Agricult. Bureau SA s.n.*, Lyndhurst, Jan. 1897 (NSW 1412); *Chapman s.n.*, Goyder Channel Shore, Lake Eyre, 2 Sep. 1976 (NSW 513229 and 513228); *Eichler 12567*, Flinders Range, Chambers Gorge near Mt. Chambers, c. 60 km ENE of Blinman, 12 Sep. 1956 (K); *Gill s.n.*, Dalhousie Springs, June 1916 (NSW 1411); *Johnson 73/148*, Road from Marree 1 mile N of old town Farina, 6 Sep. 1973 (NSW 513233); *Kuchel 2670*, c. 170 km ENE of Leigh Creek, Moolawatana Bore, 22 Aug. 1968 (K); *Lee s.n.*, Wilpena Pound near "Cooinda Camp", Flinders Ranges, 10 Oct. 1971 (NSW 513232); *Little 11*, Arkaroola, 30°24'S, 139°23'E, Aug. 1968 (NSW 513093); *Norris 225*, Western Edge of Flinders Ranges, 31°19'S, 138°31'E, 30 Aug. 1984 (NSW 512772); *Rogers 8146/15*, Between Beltana and Blinman, Oct. 1915 (NSW 513230); *Rogers s.n.*, Coward Spring, Sep. 1910 (NSW 1040); *Smyth 128*, Lake Eyre, 29°20'56"S, 138°19'04"E, 8 Apr. 1997 (RSA 627811); *Spencer s.n.*, Lake Eyre, Sep. 1903 (NSW 1039); *Turvey 12900*, Ernabella, 31 July 1966 (NSW 512762); *Turvey MCB14279*, Musgrave Ranges, 4 June 1967 (NSW 512539); *Whibley 272*, Refuge Rock Holes, c. 75 km WSW of Whyalla on Whyalla-Kimba road, 2 Oct. 1958 (K); *Wilson s.n.*, Frame Downs, Dec. 1962 (NSW 513231).

Victoria: *D'Alton 16*, Lake Albacutya, Jan. 1902 (NSW 1024); *Melville s.n.*, Lower Deddich River, about 1.5 m from Snowy River Bridge (K).

Western Australia: *Beard 6618*, Berringarra Station in flood channels of Murchison River, 22 Sep. 1973 (NSW 512824); *Drummond 31*, 6th collection (P00202641); *Fitzgerald s.n.*, Lower Greenough, S of Geraldton (NSW 512823); *McMahon s.n.*, Wittenoom, 1952 (NSW 512710); *Speck 1126*, 1.5 miles S of Koonmarra, Ereman Province, 2 July 1958 (NSW 512825); *Vetch 6-12*, Wanna Station, 23°56'S, 116°33'21"E, Aug. 1970 (NSW 512711).

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