

***Lotus roudairei* Bonnet and taxonomic relationships between African and North American species of the tribe Loteae (Papilionaceae)**

Tatjana E. KRAMINA

Higher Plants Department, Biological Faculty,
Moscow State University, 119899 Moscow, Russia.
tanya@florin.ru

Dmitry D. SOKOLOFF

Higher Plants Department, Biological Faculty,
Moscow State University, 119899 Moscow, Russia.
sokoloff@dds.srcc.msu.su

ABSTRACT

A comparative analysis of morphological features in NW African *Lotus roudairei*, N American *Lotus* sect. *Simpeteria*, and American *Lotus* sect. *Microlotus* (= gen. *Acmispon* s. str.) was carried out. According to the data obtained, these three taxa seemed not to form the distinct genus or subgenus *Acmispon* sensu P. LASSEN (1986). A new section *Pseudosimpeteria* with a single species, *L. roudairei*, is described within the Old World *Lotus* subgen. *Lotus*. The relationships between Old World and New World Loteae are briefly discussed.

KEY WORDS

Lotus roudairei,
Papilionaceae,
Loteae,
Africa,
N America.

RÉSUMÉ

Une analyse morphologique comparative de *Lotus roudairei* nord-ouest-africain, *Lotus* sect. *Simpeteria* nord-américain et *Lotus* sect. *Microlotus* (= gen. *Acmispon* s. str.) américain a été réalisée. En partant des données obtenues, il apparaît que ces 3 taxons ne peuvent pas former un genre (ou sous-genre) particulier, *Acmispon* sensu P. LASSEN (1986). Une section nouvelle *Pseudosimpeteria*, avec une seule espèce *L. roudairei*, est décrite dans le genre *Lotus* subgen. *Lotus*, répandu dans l'Ancien Monde. Les relations entre les Loteae de l'Ancien Monde et ceux du Nouveau Monde sont brièvement discutées.

MOTS CLÉS

Lotus roudairei,
Papilionaceae,
Loteae,
Afrique,
N Amérique.

INTRODUCTION

The taxonomic boundaries of the genus *Lotus* remain one of the most complicated issues in the intergeneric delimitation of the tribe Loteae. In a broad sense, the genus comprises, according to different views, from 100 species (POLHILL 1981) to 176 species (KIRKBRIDE 1994) on all continents except the Antarctic. The majority of species occur in the Mediterranean region, Macaronesia, and in the western part of North America, especially in California. All native North-American species of Loteae belong to the genus *Lotus* in the broadest sense.

A number of authors disagree with the broad concept of the genus *Lotus* and tend to break it up into several separate genera. In particular, the taxonomic position of North-American species has been disputed. The review of the discussion was presented by OTTLEY (1923) and CALLEN (1959). OTTLEY (1923) recognized four main approaches to the taxonomy of N American Loteae.

1. All N American species should be included in the Old World genus *Lotus*.
2. All N American species should be treated as a distinct genus *Hosackia* Dougl. ex Benth.
3. American species should be excluded from *Lotus* of the Old World and segregated into several genera: *Hosackia*, *Acmispon* Raf., *Syrmatium* Vogel, and *Anisolotus* Bernh.
4. The genus *Hosackia* should include the majority of American species, whereas remaining species should be left within the Old World genus *Lotus*.

OTTLEY (1923) accepted a broad concept of the genus *Lotus* and recognized three subgenera in America: subgen. *Hosackia* Ottley (syn. gen. *Hosackia* Dougl. ex Benth. s. str.), subgen. *Acmispon* Ottley (syn. gen. *Acmispon* Raf., gen. *Anisolotus* Bernh.), and subgen. *Syrmatium* Ottley (syn. gen. *Syrmatium* Vogel). Species of the first subgenus have membranaceous or foliaceous stipules, while in the remaining two subgenera they are glandular. Subgen. *Syrmatium* differs from subgen. *Hosackia* and subgen. *Acmispon* by the indehiscent fruits. Later OTTLEY (1944) recognized two sections—*Microlotus* Benth. and *Simpeteria* Ottley—in subgen. *Acmispon*.

Generally, the native N American species of *Lotus* s.l. are distributed from Mexico to S Canada and from the Atlantic to Pacific coasts; the only native S American species occurs in Chile. The section *Simpeteria* contains 2-3 annual and 10 perennial species in the SW part of U.S.A. (Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah), and in Mexico, south to Veracruz and Puebla. The species tend to be geographically separated from each other, e.g. two endemic species occur in Mexico, one in Nevada, and one in Arizona. The center of diversity of sect. *Simpeteria* is located in Mexico and Arizona. The section *Microlotus* contains about 8 annual species primarily in Western N America (British Columbia, Washington, Oregon, California, Arizona, New Mexico, and Mexico). One species, *L. subpinnatus* Lag., is however, restricted to Chile, and one species, *L. unifoliolatus* (Hook.) Benth. has a wide area of distribution, extending from Mexico, Texas and Arkansas to British Columbia and Manitoba, and from the Pacific coast to North and South Carolina. In contrast with sect. *Simpeteria*, sect. *Microlotus* has a center of diversity in California, and all the species reported for United States occur also in California. Even the Chilean *L. subpinnatus* is very close to *L. wrangelianus* Fisch. & Mey. from California, and sometimes the two species are merged. The members of subgenera *Hosackia* and *Syrmatium*, which are not the subject of this paper, occur in Western N America, from British Columbia and Idaho to Mexico.

According to GILLET (1958), only one insignificant trait separates Old World *Lotus* species from American Loteae, viz. leaf morphology. Old World species have five leaflets, with the lower pair (of which one leaflet is occasionally absent) situated at the base of the rachis, simulating foliaceous stipules, very close to the true stipules which, if present, are reduced to glands. Less often, they have three leaflets, with petiolules but without petiole or rachis. American species have three leaflets with a definite petiole or rachis, or 4-19 leaflets, pinnately arranged, often alternate, the lowest one situated above the base of the rachis and well separated from the glandular or

membranaceous stipules. GILLETT (1958) noted that "even this definition fails for *L. roudairei* Bonnet from Morocco which has up to 6 alternately pinnate leaflets, the lowest well above the base of the rachis and separated from the glandular stipules just as in *Hosackia*" (p. 363). COSSON named this species "*L. hosackioides*" (in herb.) thus implying a similarity to American species. BONNET (1893), describing *L. roudairei* in accordance with the rules of botanical nomenclature, also compared it with North American *Hosackia*. The species is distributed in the W of N Africa (Morocco, Algeria, and Tunisia), and in adjacent parts of Tropical Africa.

MAIRE et al. (1935) described a new species, *L. simonae* Maire, Weiller & Wilczek from the SE foothills of the Anti-Atlas mountains in Morocco and included it, along with *L. roudairei*, in the proposed new section *Stipulati* Maire, Weiller & Wilczek. Recognition of sect. *Stipulati* was based on a single feature, the presence of true stipules reduced to small dark glands. MONOD (1980) justly noted that not only *L. simonae* and *L. roudairei*, but a number of Old World *Lotus* species, demonstrated glandular stipules, and therefore rejected the sect. *Stipulati*. According to LASSEN (1986), *L. simonae* and *L. roudairei* have nothing in common except the structure of the stipules; in floral and vegetative characters *L. simonae* is a true *Lotus*. LASSEN (1986, 1989) accepted at least two genera of N American Loteae, namely *Hosackia* and *Acmispon*. He recognized sect. *Simpeteria* within the genus *Acmispon* in accordance with OTTLEY's classification, where the section was included in subgen. *Acmispon*. LASSEN (1986) transferred *L. roudairei* to *Acmispon* sect. *Simpeteria* (Ottley) Lassen making a new combination, *Acmispon roudairei* (Bonnet) Lassen. Since sect. *Stipulati* had been described earlier than sect. *Simpeteria*, he selected *L. simonae* as lectotype of sect. *Stipulati* so that the latter name would not interfere with OTTLEY's epithet¹.

1. LASSEN also reported, that he had studied the lectotype of *L. simonae* in MPU. Lectotypification is, however, not needed, because the type specimen exists ("Morocco, prov. Tatta. In alveo lapidoso amnis Bouzezza ad septentr. oasis Tatta ad radices meridionales Anti Atlantis. 730 m. 3 apr. 1934. Maire et Wilczek.", P!).

The name "*Acmispon roudairei*" is accepted by LOCK (1989) and by GREUTER et al. (1989). On the other hand, LEBRUN & STORK (1992) and KIRKBRIDE (1994) again place the species in the genus *Lotus*; it is not clear however whether these authors include *L. roudairei* in sect. *Simpeteria*.

MATERIAL AND METHODS

The work is based on the study of herbarium specimens from herbaria LE, MHA, and P. The following American species were studied: sect. *Simpeteria*: *L. argyraeus* (Greene) Greene, *L. grandiflorus* (Benth.) Greene, *L. greenii* Ottley, *L. mearnsii* (Britton) Greene, *L. oroboides* (Humboldt, Bonpland & Kunth) Ottley, *L. rigidus* (Benth.) Greene, *L. strigosus* (Nuttall ex Torrey & A. Gray) Greene, *L. tomentellus* Greene, *L. utahensis* Ottley, *L. wrightii* (A. Gray) Greene; sect. *Microlotus*: *L. denticulatus* (Drew) Greene, *L. humistratus* Greene, *L. micranthus* Benth., *L. salsuginosus* Greene, *L. subpinnatus* Lag., *L. unifoliolatus* (Hook.) Benth. [*L. purshianus* (Benth.) Clements & Clements], *L. wrangelianus* Fisch. & Mey.

For the study of floral morphology flowers were placed for two days into a mixture of equal parts of glycerin, ethyl alcohol and water, and then dissected. For the study of ovule arrangement and orientation additional material was used, namely the herbarium specimens from MW, and flowers of *L. corniculatus* L., *L. krylovii* Schischk. & Serg., *L. ucrainicus* Klok., fixed in 70% ethyl alcohol in the field from several locations in European Russia, Ukraine, and Kazakhstan.

RESULTS AND DISCUSSION

A comparative morphological study of *Lotus roudairei* and New World Loteae does not support the conclusion of LASSEN (1986), that *L. roudairei* belongs to the N American sect. *Simpeteria*.

OTTLEY (1944) gave a short and clear diagnosis of sect. *Simpeteria*: "Herbae vel suffrutices; carina obtusa, quam alis brevior; vexillo sine ungue; stilo sub stigmatate circumcirca barbato". Accord-

TABLE 1.—The main differences between *Lotus roudairei* Bonnet, *Lotus* sect. *Microlotus* Benth., and *Lotus* sect. *Simpeteria* Ottley.

Characters	<i>Microlotus</i>	<i>Simpeteria</i>	<i>L. roudairei</i>
Can be annuals	Yes	Yes	No
Can be perennials	No	Yes	Yes
Corolla asymmetrical: wings and keel turned to the one side and obliquely oriented in relation to standard	No	Yes	No
Standard blade abruptly clawed	Yes	No	Yes
Wings conspicuously longer than the keel	No	Yes	No
Ovules*: micropylae...	inferae	alternantes	alternantes
Stylodium with a collar of spreading hairs below the stigma	No	Yes	No
Pollen grains: number of apertures**	4	4-7	3
Geographical distribution	America	America	Africa

* Micropyle infera means that the ovule has the micropyle oriented towards the proximal end of the ovary; micropyle supera means that micropyle is oriented towards the distal end of the ovary. Micropylae alternantes means that the ovules are alternately oriented in the ovary, i.e. the micropylae of two nearest ovules are oriented in the opposite directions (see TIKHOMIROV & SOKOLOFF 1997). This important character was first used in the taxonomy of Loteae by LASSEN (1989). He demonstrated that the genus *Hippocrepis* differed in this feature from *Coronilla* and *Securigera*. All Old World *Lotus* species seemed to have micropylae alternantes (TIKHOMIROV & SOKOLOFF 1997).

** According to CROMPTON & GRANT (1993) and DIEZ & FERGUSON (1994).

ing to our data, *Lotus roudairei* has neither an obtuse keel, nor long wings, nor a standard blade with indistinct claw, nor a stylodium with a collar of spreading hairs below the stigma. *L. roudairei* is indeed a perennial herb but this fact alone does not seem to be a sufficient reason to transfer this species to sect. *Simpeteria*, because this section, as well as the Old World *Lotus* species, comprises both annual and perennial plants.

The main differences between sect. *Simpeteria*, sect. *Microlotus* and *L. roudairei* are summarized in Table 1. *Lotus roudairei* differs as much from both sect. *Simpeteria* and sect. *Microlotus* as these sections differ from each other, therefore, we believe that *L. roudairei* should be accepted as a member of a monotypic new section, *Pseudosimpeteria*. The name "*Stipulati*" cannot be used, because *Lotus* sect. *Stipulati* is lectotypified by *L. simonae* (see above).

It is difficult to include all 3 sections under discussion (*Simpeteria*, *Microlotus*, and *Pseudosimpeteria*) in the genus, or subgenus, *Acmispon*. Moreover, we are unable to indicate any diagnos-

tic character of a group formed by these 3 sections. In particular, leaf morphology cannot be used as such a diagnostic feature. The definition by GILLETT (1958, see above) appears deficient not only for *L. roudairei* but also for some other species. There are several species in sect. *Simpeteria* with sessile palmately compound leaves (*L. utahensis* Ottley, *L. wrightii* (A. Gray) Greene). Their leaves do not display any significant difference from those of some species of *Lotus* and *Dorycnium* (such as *Dorycnium pentaphyllum* Scop. or *Lotus polyphyllum* Clarke) (see OTTLEY 1924, 1944). On the other hand, LASSEN (1986) himself transferred the N African species *Benedictiella benoistii* Maire with 7-9-pinnately compound leaves into the genus *Lotus* and considered it a member of sect. *Heinekenia* Webb. & Berth., which comprises several species with leaves typical for Old World *Lotus* species.

We believe that *L. roudairei* demonstrates the characters of Old World *Lotus* subgen. *Lotus* (= subgen. *Edentolotus* Brand). When BRAND (1898) recognized sections in this subgenus he attached a significant importance to leaf structu-

re to distinguish sect. *Ononidium* Boiss. (leaves sessile, 3-foliolate) and sect. *Quadrifolium* Brand (leaves sessile, of 4 leaflets, 3 of them attached to the top of rachis) from sect. *Xantholotus* Brand and sect. *Erythrolotus* Brand (leaves sessile, 5-foliolate with distinct rachis). Thus, we include the section *Pseudosimpetaria* with leaves pinnately compound and distinct petiole, in *Lotus* subgen. *Lotus*.

In addition to unusual leaf structure, *L. roudairei* differs from the majority of species of subgen. *Lotus* (including *L. simonae*) by the arrangement of flowers.

Lotus roudairei has very short peduncles in the axils of foliage leaves (i.e. leaves with distinct blades). Each peduncle bears two dark glands, each close by other, and a single flower. These dark glands are very similar to the stipules of foliage leaves. The subtending leaves of flowers² represented in *Lotus* (as well as in a number of other Loteae³) by the leaves without a blade, corresponding in morphology to the stipules of foliage leaves. Sometimes subtending leaves of flowers consisting of two almost free stipules may be observed. The structure of the inflorescence in *L. roudairei* may be treated in 3 different ways according to the discussed data.

1. The foliage leaf has in the axil a shoot with two aggregated (subopposite) leaves, each reduced to one dark gland. One of the leaves (reduced to glands) subtends a flower (Fig. 1A). This structure can arise from the typical case for the genus *Lotus* where an axillary head occurs possessing at the base a foliage leaf without any flower in the axil. The number of flowers then becomes reduced to 1, and the blade of the foliage leaf is lost.

2. The foliage leaf has in the axil a shoot with a single leaf, namely that subtending the flower. This subtending leaf of the flower is represented by two free stipules (Fig. 1B). This structure can arise from the case typical for the genus *Coronilla* and its closest allies where an axillary head occurs without any foliage leaf on the peduncle. The number of flowers then becomes reduced to 1.

3. The flower with two bracteoles is situated in the axil of a foliage leaf (Fig. 1C). Bracteoles are found in a few Loteae species unrelated to each other (e.g. *Hammatolobium lotoides* Fenzl.-Tikhomirov, SOKOLOFF 1996, *Lotus strictus* Fisch. & Mey.). Flowers situated in the axils of foliage leaves were found in tribe Loteae only in *Dorycnium sanguineum* (VURAL & KIT TAN 1983).

The listed types of flower arrangement may be distinguished through the study of relative orientation of organs (see Fig. 1). A detailed study shows the inflorescence of *L. roudairei* to be in accordance with the first of the 3 types listed above. Therefore, the inflorescence of *L. roudairei*, being strongly reduced, possesses a typical flower arrangement for the genus *Lotus*. The unusual structure of the inflorescence does not prevent the inclusion of sect. *Pseudosimpetaria* into the subgen. *Lotus*, because the SW Asian and NE African sect. *Ononidium* is characterized by similar (and even more reduced) 1-flowered heads.

The only character distinguishing *L. roudairei* from all Old World species of *Lotus* s.l. [except for Himalayan *Podolotus hosackioides* Benth. = *Lotus hosackioides* (Benth.) Ali] is revealed by DÍEZ & FERGUSON (1994). *Lotus roudairei* has pollen grains with endoapertures 5-9 × 10-14 μm, while in remaining species they are 1-5 × 3-10 μm. We believe however, that this character is insufficient evidence for recognizing *L. roudairei* as a member of a separate monotypic subgenus. On the other hand, an important difference was found between *L. roudairei* and the American species of sections *Simpetaria* and *Microlotus* in the number of apertures (Table 1). *Lotus roudairei*, as well as all Old World *Lotus* species, has 3 apertures (DÍEZ & FERGUSON 1994), while in sect. *Microlotus* and sect. *Simpetaria* pollen grains are tetra- or stephanocolporate (CROMPTON & GRANT 1993; DÍEZ & FERGUSON 1994).

2. i.e. the leaves bearing flowers in their axils. We do not use the term "bract" because the foliage leaf on the peduncle of *Lotus* and *Anthyllis* is often incorrectly regarded as a bract. Really, the foliage leaf on the peduncle bears no flower in the axil and cannot be treated as a bract.

3. The exceptions are *Cytisopsis pseudocytisus* (Boiss.) Fertig and *Dorycnium sanguineum* Vural. In both species the distinct stipules are absent. The subtending leaves of flowers are broad scales in *C. pseudocytisus*, and leaves with entire green blade in *D. sanguineum* (VURAL & KIT TAN 1983; SOKOLOFF 1997).

Lotus sect. **Pseudosimpeteria** Kramina & D.D.
Sokoloff, **sect. nov.** (subgen. *Lotus*)

Lotus sect. *Eulotus* auct. non Ser., p.p.: Bonnet, J. Bot. (Morot) 7: 232 (1893).

Lotus sect. *Stipulati* Maire, Weiller & Wilczek, Bull. Soc. Hist. Nat. Afrique N. 26: 121 (1935), p.p., excl. lectotypo.

Acmispon Raf. sect. *Simpeteria* (Ottley) Lassen, Willdenowia 16: 107 (1986), p. min. p., excl. typo, non *Lotus* sect. *Simpeteria* Ottley, Brittonia 5: 81 (1944).

Acmispon auct. non Raf.: Greuter, Burdet & Long, Med-Checklist, 4: 4 (1989); Lock, Legumes of Africa. A Check-list: 339 (1989).

Plantae perennes rhizomatis repentibus nullis, foliis breviter petiolatis 3-6-foliolatis. Rachis distincta foliolis plus minusve alternatim affixis. Stipulae parvae, sed bene conspicuae, carnosae, nigrae. Capitula uniflora pedunculis quam folia laminas ferentes multo brevioribus. Pedunculus apice par foliorum suboppositorum squamuliformium, carnosorum, nigrorum habens, quorum unum in axilla sua florem ferens. Bracteolae nullae. Calyx campanulatus. Petala lutea, vexillum glabrum unguiculatum, carina rotundato-curvata, acuta, vix brevior quam alae. Stylodium sub stigmate glabrum. Ovula micropylis alternantibus. Fructus polyspermi, dehiscentes, glabri. Semina levia. Pollina 3-colporata.

A sect. Ononidium Boiss. *rachidi distincta, a sect. Loto*, *Quadrifolium* Brand, *Lotea* (Medik.) Ser., *Stipulatis* Maire, Weiller & Wilczek, *Krokeria* (Moench) Ser. *et Erythroloto* Brand *pedunculo folio laminam habente semper nullo, sed par foliorum squamuliformium floremque unicum ferente atque structura foliorum reliquorum, a L. benoistii* (Maire) Lassen *fructu dehiscente differt. A sect. Microloto* Benth. *ovulis micropylis alternantibus, pollinibus 3-colporatis habituque perenni, a sect. Simpeteria* Ottley *stylodium sub stigmate glabro, nec circumcirca barbato, carinae structura atque pollinibus 3-colporatis bene differt.*

Perennial herbs without creeping rhizome. Leaves shortly petiolate, with 3-6 leaflets. Rachis well developed, with more or less alternately attached leaflets. Stipules small, but conspicuous, fleshy, dark. Heads 1-flowered, with peduncles much shorter than foliage leaves. Peduncle bearing two small subopposite fleshy dark leaves, one of which subtends the flower. Bracteoles absent. Calyx campanulate. Petals yellow; standard glabrous, abruptly clawed; keel roundly curved, acute, slightly shorter than the wings. Stylodium below the stigma glabrous. Ovules with alternate micropylae. Fruit many-seeded, dehiscent, glabrous. Seeds smooth. Pollen grains with 3 apertures.

Sect. *Pseudosimpeteria* differs from sect. *Ononidium* Boiss. by the well developed rachis and from sections *Lotus*, *Quadrifolium* Brand, *Lotea* (Medik.) Ser., *Stipulati* Maire, Weiller & Wilczek, *Krokeria* (Moench) Ser. and *Erythrolotus* Brand by the foliage leaf morphology and by the single flowered peduncle always without a foliage leaf, but with two small fleshy subopposite leaves lacking a blade. Sect. *Pseudosimpeteria* can also be distinguished from *L. benoistii* (Maire) Lassen by the dehiscent fruit; from sect. *Microlotus* Benth. by alternate micropylae, pollen grains with 3 apertures, and the perennial habit; and from sect. *Simpeteria* Ottley by the stylodium without a collar of hairs below the stigma, the structure of the keel, wings, and standard, and pollen grains with 3 apertures.

TYPUS (et species unica).—*Lotus roudairei* Bonnet.



Fig. 1.—Diagrams of possible types of flower arrangement in *Lotus roudairei*. Each diagram demonstrates structures situated in the axil of a single foliage leaf. A detailed study shows the inflorescence of *L. roudairei* to be in accordance with the diagram A. See also explanation in the text.

Lotus roudairei Bonnet

J. Bot. (Morot) 7: 232 (1893).—*Acmispon roudairei* (Bonnet) Lassen, Willdenowia 16: 108 (1986).—Lectotype (hic designatus): *Letourneux s.n.* [Regnum Tunetanus] "In lapidosis inter Ain Kebirita et oued Chaba. 10 Junio 1884" (P!).

Lotus fruticulosus Coss., Bull. Soc. Bot. France 22: 57 (1875), nom. nud., non Desf.

Lotus hosackioides Coss., nom. in sched.

GEOGRAPHICAL DISTRIBUTION.—North Africa (Tunisia, Algeria, Morocco) and North-Western part of Tropical Africa (Sahara).

Thus *L. roudairei* seems to be a true Old World *Lotus* and should not be considered as a "connecting link" between the N American and African Loteae. There is a second African species often thought to be closely related to N American species of *Lotus*. OTTLEY (1944) reported that "if it should be desirable to segregate the American species [of *Lotus*] that have indehiscent from those with dehiscent fruits, the logical procedure would be to unite them with the genus *Helminthocarpon*, and not to set them off in a genus by themselves". The correct name for *Helminthocarpon* A. Rich. is *Vermifruux* Gillett. The single species of *Vermifruux*, *V. abyssinica* (A. Rich.) Gillett, is restricted to E Africa and Yemen. *Vermifruux* is often considered as closely related to *Lotus* s.l. and is sometimes included in this genus (see for example POLHILL 1981). Detailed studies showed that the genus *Vermifruux* could neither be treated as being related to American *Lotus* species, nor to any other species of *Lotus* and should be merged with the monotypic W Mediterranean genus *Dorycnopsis* (TIKHOMIROV & SOKOLOFF 1997). Thus, we would conclude, that close relatives of N American taxa of Loteae are absent in African flora; they are absent also in Europe. We suggest, that neither subgenera nor sections comprising both native American and Mediterranean species can be distinguished within the genus *Lotus*. The New World *Lotus* species form several distinct groups that strongly differ from each other. They could be joined only within a very broad concept of the genus *Lotus* as POLHILL does (1981). In this case, it would perhaps be necessary to also

include in *Lotus* a number of taxa that are now accepted as distinct, e.g. *Hammatolobium* Fenzl. and *Tripodion* Medik.

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