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Cladistic Analysis of the Tribe *Loteae* (Leguminosae) Based on Morphological Characters

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ABSTRACT

The tribe *Loteae* was recently re-defined in wide sense (Lassen, 1989); Polhill, 1994; Sokoloff, 2003) by inclusion of members of the former tribe Coronilleae as well as the S and SW Asian genus *Podolotus* which was formerly often regarded as a synonym of *Astragalus* of the tribe Galegeae. If accepted in this wide sense, the tribe *Loteae* represents quite a natural, monophyletic unit and includes 18 genera and 256 species (Sokoloff, 2003). Main centres of species diversity are Mediterranean Region and California. Molecular phylogenetic analysis of the tribe *Loteae* based on sequences of ITS region of nuclear ribosomal DNA were performed by Allan and Porter (2000), Allan et al. (2003) and Degtjareva et al. (in press). We have conducted cladistic analyses of *Loteae* based on 132 morphological, including anatomical and palynological characters (Sokoloff, 2003). Besides, combined analyses absed on molecular and morphological data were performed (Sokoloff, 2003). All analyses suggest homoplasious nature of many morphological characters. There are some morphological character states, which appear unique for the tribe Loteae (if compared to related legumes tribes). The majority of such character states were probably evolved two or several times in course of *Loteae* evolution (or were lost in some lineages). We suggest that 'homoplastic tendencies' (Sanderson, 1991) are common in morphological evolution of *Loteae* as well as other plant groups.

Keywords: *Loteae*, Leguminosae, Cladistic analysis

INTRODUCTION

The tribe *Loteae* (incl. Coronilleae) is a diverse group of mainly temperate legumes, which includes about 265 species (Sokoloff, 2003a,b). Main centres of species diversity are Mediterranean Region and California.

Taxonomic and phylogenetic relationships between various members of the tribe *Loteae* were extensively discussed in the literature. However, many important questions are still to be clarified. In particular, there is no consensus regarding generic delimitation in the tribe. Recent molecular phylogenetic studies (Allan and Porter, 2000; Allan, 2001; Allan et al., 2002, 2003; Degtjareva et al., 2003) based on sequences of ITS1 2 region of nuclear ribosomal DNA have added much to knowledge of Loteae phylogeny. Cladistic analyses of *Loteae* based on morphological characters (with special emphasis to seed morphology) were conducted by Arambarri (2000a,b). The analyses by Arambarri have covered Old World (2000b) and New World (2000a) members of the genus *Lotus* (which was accepted in wide sense in these publications). These analyses, as well as recent non cladistic studies (e.g., Lassen, 1986; Crompton and Grant, 1993; Díez and Ferguson, 1994; Tikhomirov and Sokoloff, 1997; Kramina and Sokoloff, 1997 2003; Sokoloff, 1998 2000; Kramina, 2001) have demonstrated that traditional classification of *Lotus* should be modified in several important aspects.

As far as we know, a cladistic analysis covering all genera of the tribe *Loteae* was not yet conducted. The purpose of the present publication is to present results of such an analysis based on morphological characters. These results were briefly discussed in a previous paper (Sokoloff, 2003a), where simplified cladorgam showing relationships between *Loteae* genera was published. Neither character list nor full list of terminal groups was published there.

MATERIAL AND METHODS

Taxon sampling. It was not reasonable to include all 265 species of the tribe into the present analysis. Such cryptic characters as fruit anatomy and pollen morphology were not available for some species. Besides, even for well studied *Loteae* species, it is very difficult to find more than 200 morphological characters, which are estimated to be parsimony informative in the final matrix. It is hardly even possible to find enough morphological characters to construct a well resolved phylogenetic tree for all species of *Loteae*. Besides, it seems that hybridization events are not uncommon among closely related Loteae species (e.g., Ottley, 1944; Isely, 1981; Liston et al., 1990; Grant and Small 1996; Kramina, 1999; Sokoloff, 1999). For example, the most known species of the tribe, *Lotus corniculatus*, is possibly of hybrid origin (e.g., Grant and Small, 1996; Gauthier et al., 1997; Kramina, 1999). The cladistic analysis is not designed for study of reticulate evolution, and an attempt of revealing the phylogeny of *Loteae* up to specific level in form of cladistic tree seems to be inadequate. However, we believe that phylogeny of *Loteae* was more or less divergent (rather than reticulate) on higher level. To reveal this pattern of *Loteae* phylogeny, it is reasonable to analyze a set of representative species of each genus.

We have selected 54 *Loteae* species for the present analysis. Among them are all species included in the molecular phylogenetic analysis by Degtjareva et al. (2003), the most comprehensive study with respect to number of counted genera. This choice of species will allow comparing molecular and morphological inferences of phylogeny. To make our analysis more comprehensive, we have added few other species, including members of three monotypic genera (*Antopetitia, Podolotus,* and *Pseudolotus*), which were not yet analyzed by molecular methods.

NOMENCLATURE

There is no universally accepted generic system of the tribe *Loteae*. In this paper, the nomenclature proposed by Sokoloff (2003a,b) is used. Basic information about *Loteae* genera is given in the table 1. Different viewpoints regarding generic position of species used in the present study are summarised in the table 2.

OUTGROUP SELECTION

Traditionally, the tribe *Loteae* was allied with another mainly temperate herbaceous tribe, *Galegeae* (e.g., Polhill, 1981; Yakovlev, 1991). Morphology based higher level cladistic analysis of legumes (Chappill, 1995) suggested that *Loteae* is closely related to mainly temperate herbaceous tribes *Galegeae, Vicieae, Trifolieae,* and *Cicereae*. However, molecular data strongly suggest against these ideas (Lavin et al., 1990; Liston, 1995; Doyle et al., 1997; Hu et al., 2000; Wojciechowski et al., 2000; Kajita et al., 2001; Wojciechowski, 2003). The majority of recent molecular phylogenetic studies revealed that the tribe *Loteae* is closely related to members of mainly neotropical and predominantly woody tribe *Robinieae*. Within *Robinieae*, the genus *Sesbania* appears to be especially close to *Loteae*, forming a putative sister group to *Loteae* (e.g., Wojciechowski et al., 2000; Wojciechowski, 2003). In the present study of *Loteae* phylogeny, members of *Robinia* and *Sesbania* are used as outgroups. It would be logical to include in the analysis also some members of the tribe *Galegeae*. We made an attempt to do this, but the result was not positive, because jackknife and bootstrap support of the majority of clades in the cladogram was low. The tribe *Loteae* was not revealed as a monophyletic unit in the analysis, which included members of *Galegeae*. Representatives of *Galegeae* were nested within *Loteae*. In our opinion, this preliminary result indicates high level of parallelism in morphological evolution of *Galegeae* and *Loteae* (see also Doyle et al., 1997). The maximum parsimony algorithm of analysis probably effects in treating false synapomorphies as true ones. We have decided not to include members of *Galegeae* in the present analysis.

Morphological characters used in the cladistic analysis. 108 morphological characters were selected for the analysis. All characters are parsimony informative. Multistate characters were analysed as ordered. A priori character polarisation was not used, and character state '0' does not necessarily represent a plesiomorphy.

Table 1. Genera of the tribe Loteae (after Sokoloff 2003 a,b).

Genus	Species number	Distribution
Hippocrepis L.	34	Europe and North Africa (incl. Macaronesia), Asia (eastwards to Pakistan)
Scorpiurus L.	2	South Europe, East and North Africa (incl. Madeira and Canary islands), West Asia (incl. the Caucasus)
Coronilla L.	22	Europe, North and East Africa, West Asia (incl. the Caucasus)
Podolotus Benth.	1	Asia (India, Pakistan, Afghanistan, Iran, Oman)
Hosackia Douglas ex Benth.	11	North America
Ottleya D.D. Sokoloff	13	North America
Acmispon Raf.	8	7 spp. in North America, 1 sp. (*A. subpinnatus*) in South America (Chile)
Syrmatium Vogel	14	North America
Kebirita Kramina et D. D. Sokoloff	1	North-West Africa
Pseudolotus Rech. f.	1	Asia (Pakistan, Iran, Oman)
Lotus L.	121	Europe and Africa (incl. Macaronesia), Asia (incl. Japan, Taiwan), Australia (incl. Tasmania), Pacific region (New Caledonia, Vanuatu)
Tripodion Medik.	1	Mediterranean region
Cytisopsis Jaub. et Spach	2	Mediterranean region
Hammatolobium Fenzl	2	Mediterranean region
Antopetitia A. Rich.	1	Mountains of tropical Africa
Ornithopus L.	6	5 spp. in Europe and North Africa (incl. Macaronesia), West Asia (incl. the Caucasus); 1 sp. (O. micranthus) in South America (Argentina, Uruguay, Southern Brazil)
Dorycnopsis Boiss.	2	Western Mediterranean, East Africa, Arabian peninsula
Anthyllis L.	23	Europe, East and North Africa (incl. Madeira), West Asia (incl. the Caucasus)

Table 2: Representative species of the tribe *Loteae* used for the cladistic analysis and their generic position according to various classifications

Species (nomenclature after Sokoloff, 2003a,b)	Generic position according to various classifications					
	Bentham & Hooker (1865)	Polhill (1981)	Lassen (1986-1998)	Polhill (1994)	Sokoloff (1998)	Talavera & Salgueiro (1999)
Acmispon americanus (Nutt.) Rydb.	*Lotus*	*Lotus*	*Acmispon*	*Lotus*	*Acmispon*	*Lotus*
Acmispon maritimus (Nutt.) D.D. Sokoloff	?*Lotus*	*Lotus*	?*Acmispon*	*Lotus*	*Acmispon*	*Lotus*
Acmispon parviflorus (Benth.) D.D. Sokoloff	*Lotus*	*Lotus*	?*Acmspon*	*Lotus*	*Acmispon*	*Lotus*
Acmispon subpinnatus (Lag.) D.D. Sokoloff	*Lotus*	*Lotus*	*Anisolotus*	*Lotus*	*Acmispon*	*Lotus*
Anthyllis barba-jovis L.	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*
Anthyllis circinnata (L.) D.D. Sokoloff	*Hymenocarpos*	*Hymenocarpos*	*Hymenocarpos*	*Hymenocarpos*	*Hymenocarpos*	*Hymenocarpos*
Anthyllis hermanniae L.	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*
Anthyllis lotoides L.	*Anthyllis*	*Anthyllis*	*Hymenocarpos*	*Hymenocarpos*	*Anthyllis*	*Hymenocarpos*
Anthyllis montana L.	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*
Anthyllis onobrychioides Cav.	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*
Anthyllis terniflora (Lag.) Pau	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*
Anthyllis vulneraria L.	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*	*Anthyllis*

Contd....

Antopetitia abyssinica A. Rich.	*Ornithopus*	*Antopetitia*	*Antopetitia*	*Antopetitia*	*Antopetitia*	*Antopetitia*
Coronilla coronata L.	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*
Coronilla minima L.	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*
Coronilla orientalis Mill.	*Coronilla*	*Coronilla*	*Securigera*	*Securigera*	*Securigera*	*Securigera*
Coronilla scorpioides (L.) W.D.J. Koch	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*	*Coronilla*
Coronilla varia L.	*Coronilla*	*Coronilla*	*Securigera*	*Securigera*	*Securigera*	*Securigera*
Cytisopsis pseudocytisus (Boiss.) Fertig	*Cytisposis*	*Cytisposis*	*Cytisposis*	*Cytisposis*	*Cytisposis*	*Cytisposis*
Dorycnopsis abyssinica (A. Rich.) V.N. Tikhom. et D.D. Sokoloff	*Helminthocarpon*	*Lotus*	*Vermifrux*	*Vermifrux*	*Dorycnopsis*	?
Hammatolobium kremerianum (Coss.) C. Muell.	*Hammatolobium*	*Hammatolobium*	*Tripodion*	*Hammatolobium*	*Hammatolobium*	*Hammatolobium*
						Hammatolobium
Hammatolobium lotoides Fenzl	*Hammatolobium*	*Hammatolobium*	*Tripodion*	*Hammatolobium*	*Hammatolobium*	*Emerus*
Hippocrepis emerus (L.) Lassen	*Coronilla*	*Coronilla*	*Hippocrepis*	*Hippocrepis*	*Hippocrepis*	*Hippocrepis*
Hippocrepis unisiliquosa L.	*Hippocrepis*	*Hippocrepis*	*Hippocrepis*	*Hippocrepis*	*Hippocrepis*	*Lotus*
Hosackia crassifolia Benth.	*Hosackia*	*Lotus*	*Hosackia*	*Lotus*	*Hosackia*	*Lotus*
	Hosackia	*Lotus*	*Hosackia*	*Lotus*	*Hosackia*	*Lotus*

Contd....

***Hosackia gracilis* Benth.**	***Hosackia***	***Lotus***	***Hosackia***	***Lotus***	***Hosackia***	***Lotus***
Hosackia oblongifolia Benth.	*?*	*Lotus*	*Acmispon*	*Lotus*	*Kebirita*	*Lotus*
Kebirita roudairei (Bonnet) Kramina et D.D. Sokoloff	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus angustissimus L.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus australis Andrews	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus campylocladus Webb et Berth.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus conimbricensis Brot.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus corniculatus L.	*Dorycnium*	*Lotus*	*Dorycnium*	*Dorycnium*	*Dorycnium*	*Dorycnium*
Lotus dorycnium L.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus edulis L.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Lotus*
Lotus ornithopodioides L.	*Dorycnium*	*Lotus*	*Dorycnium*	*Dorycnium*	*Dorycnium*	*Dorycnium*
Lotus rectus L.	*Lotus*	*Lotus*	*Lotus*	*Lotus*	*Tetragonolobus*	*Tetragonolobus*
Lotus tetragonolobus L.	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*
Ornithopus compressus L.	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*
Ornithopus micranthus (Benth.) Arechav.	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*
Ornithopus perpusillus L.	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*

Contd....

Ornithopus pinnatus (Mill.) Druce	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*
Ornithopus sativus Brot.	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*	*Ornithopus*
Ottleya oroboides (Kunth) D.D. Sokoloff	*Hosackia*	*Lotus*	*Acmispon*	*Lotus*	*Ottleya*	*Lotus*
Ottleya rigida (Benth.) D.D. Sokoloff	*Hosackia*	*Lotus*	*Acmispon*	*Lotus*	*Ottleya*	*Lotus*
Ottleya strigosa (Nutt.) D.D. Sokoloff	*Hosackia*	*Lotus*	*Acmispon*	*Lotus*	*Ottleya*	*Lotus*
Podolotus hosackioides Benth.	*Astragalus*	*Lotus*	*Podolotus*	*Podolotus*	*Podolotus*	*Lotus*
Pseudolotus villosus (Blatt. et Hallb.) Ali et D.D. Sokoloff	?	*Lotus*	*Pseudolotus*	*Pseudolotus*	*Pseudolotus*	*Lotus*
Scorpiurus muricatus L.	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*
Scorpiurus vermiculatus L.	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*	*Scorpiurus*
Syrmatium glabrum Vogel	*Hosackia*	*Lotus*	*Syrmatium*	*Lotus*	*Syrmatium*	*Lotus*
Syrmatium prostratum (Nutt.) Greene	*Hosackia*	*Lotus*	*Syrmatium*	*Lotus*	*Syrmatium*	*Lotus*
Syrmatium tomentosum (Hook. et Arn.) Vogel	*Hosackia*	*Lotus*	*Syrmatium*	*Lotus*	*Syrmatium*	*Lotus*
Tripodion tetraphyllum (L.) Fourr.	*Anthyllis*	*Anthyllis*	*Tripodion*	*Tripodion*	*Tripodion*	*Tripodion*

Characters of pollen morphology and chromosome numbers as well as character # 2 are included using literature data (see references below). The rest of the characters were studied in representatives of *Loteae* by the author using herbarium specimens deposited at A, BM, CAS, DS, E, G, GH, H, K, KPABG, LE, LECB, LL, MHA, MW, NSW, NY, P, PCU, POM, RSA, S, TEX, TUS, TUSG, UPS, US, and YALT. Besides, a number of species were studied and/or collected in wild conditions in European Russia, Crimea, the Caucasus, Switzerland, Spain, and California or in culture. Taxonomic literature was also taken into account (especially Ottley 1923, 1944; Tutin et al. 1968; Davis 1970; Schmidt 1979; Jafri 1980; Isely 1981; Rechinger 1984; Lassen 1989; Talavera et al. 2000). The data for *Robinieae* are based on Lavin and Sousa (1995) and partially on personal observations.

The description of characters is given below (numbers in parentheses are character states). The full matrix used in the analysis is presented in the Appendix.

A. Vegetative characters

1. Habit: trees (0) shrubs or dwarf shrubs (1) undershrubs (2) perennial or biennial herbs (3) annuals (4).
2. Xylem of the primary root in seedlings: triarch or tetrarch (0) diarch (1). The following sources are used: Compton (1912), Barykina (1958), Jahn (1974), Tsutsupa et al. (2002).
3. Creeping rhizomes: absent (0) present (1).
4. Type of shoot renewal (not applicable to annuals): (almost) always sympodial (0) always monopodial or often monopodial (1).
5. Monocarpic shoots (in case of sympodial renewal): monocyclic (0) dicyclic or polycyclic (1).
6. Rosette part of shoots: absent (0) present (1).
7. Leaf arrangement formula: 1/3 or 2/5, i.e. leaves spirally arranged (0) 1/2, i.e., leaves distichous (1).
8. Lower foliage leaves: leaf base does not (or does not completely) encircle the node (0) leaf base completely encircles the node (1).
9. Subtending leaves of partial inflorescences: leaf base does not (or does not completely) encircle the node (0) leaf base completely encircles the node (1).
10. Pulvinus at the leaf base: present (0) absent (1).
11. Foliage leaves (excluding pseudobracts): all petiolate (0) some leaves within a given plant petiolate, while others sessile (1) all sessile (2).
12. Lower foliage leaves: without of a sheathing base (0) with a sheathing base (1).
13. Stipules: present (0) absent (1).
14. Stipule base of lower foliage leaves: not extending to the abaxial leaf side (0)extending to the abaxial leaf side (1).
15. Stipule base of lower foliage leaves: not extending to leaf petiole or leaf sheathing base (0) extending to petiole base (1) stipule base confined to leaf petiole or leaf sheathing base (2).
16. Stipules of lower leaves: not fused to each other on side opposite to leaf petiole (0) fused to each other on side opposite to leaf petiole (1).

17. **Dark stipule glands:** absent or situated at the base of membranous stipule (0) stipule margin totally black (1) stipule top glandular (2) stipule is represented by gland only (3).
18. **Stipels** present (0) absent (1).
19. **Lower foliage leaves:** compound or strongly dissected (0) simple; entire or slightly dissceted (1).
20. **Leaflet or simple leaf blade venation in lower foliage leaves:** pinnate (0) camptodrome (1).
21. **Upper foliage leaves** compound (0) simple, lobed to strongly dissected (1) simple, entire (2).
22. **Rhachis of upper foliage leaves** (excluding pseudobracts) elongated (0) shortened (1).
23. **Terminal leaflet or leaf lobe (segment):** present (0) absent, i.e., leaves paripinnate (1).
24. **Leaflet number in compound leaves:** 12 and more (0) 6 11 (1) 5 (2) 4 (3) 2 3 (4) 1 (5).
25. **Terminal (middle) leaflet:** almost as long as other leaflets of the same leaf (0) much longer than other leaflets (1).
26. **Two lower leaflets (or the only lower leaflet):** of almost the same shape as the rest of leaflets (0) significantly differ in shape from the rest of leaflets (1).
27. **Heterophylly:** absent or slightly pronounced (0) well pronounced (1).
28. **Multicellular emergences on stems and leaves:** absent (0) present (1).
29. **Indumentum of hairs on stems and/or leaves:** present (0) absent (1).
30. **Straight patent hairs on stems and/or leaves:** absent (0) present (1).

B. Inflorescence characters (see also Akulova et al. 2000; Sokoloff 2003a,b; Degtjareva et al. 2003).

31. **Internodes of main axis between subtending leaves of partial inflorescences:** elongated (0) shortened (1).
32. **Peduncles of axillary partial inflorescences:** elongated (0) shortened (1).
33. **Pseudobract:** absent (0) present (1). Morphologically, the pseudobract is the first developed leaf on the axillary peduncle (Sokoloff 2003a, Degtjareva et al. 2003). In contrast to bracts, the pseudobract never possesses an axillary flower. The pseudobract usually is represented by a foliage leaf, which is quite different from bracts in morphology and size. Sometimes, however, the pseudobract is scale like and as small as true bracts (Sokoloff 2003a, Degtjareva et al. 2003).
34. **Pseudobract morphology:** foliage leaf (0) scale like leaf (1).
35. **Pseudobract morphology:** compound or scale like leaf (0) simple foliage leaf (1).
36. **Pseudobract location:** there is an elongated internode between the pseudobract and the partial inflorescence (0) there is a shortened internode between the pseudobract and the partial inflorescence (1) the pseudobract is situated within the partial inflorescence (2). Although in the latter case the pseudobract is situated within the mature partial inflorescence, it represents here (as well as in other cases) the first developed leaf on the peduncle (see Akulova et al. 2000). This conclusion is supported by developmental studies (Sokoloff 2003b).

37. Flower number per partial inflorescence: 4 and more (0) 2 3 (1) 1 (2).
38. Type of partial inflorescence: raceme (0) head or umbel (1).
39. Floral buds position: not bent backwards (0) strongly bent backwards (1).
40. Floral bract morphology: herbaceous (0) membranous, sometimes with gland(s) (1) totally glandular (2).
41. Floral bract fusion: bracts free (0) fused in a ring (1).
42. Bracteoles: always present (0) always or often absent (1).

C. Floral characters

43. Hypanthium: shorter than the calyx tube (0) as long as the calyx tube or longer than the calyx tube (1).
44. Calyx tube at fruit maturation: not inflated (0) strongly inflated (1).
45. Calyx tooth apex: always acute (0) obtuse, at least in some teeth of the calyx (1).
46. Lower calyx teeth: shorter than the tube (plus hypanthium) or as long as the tube (0) longer than the tube (1).
47. Lower calyx teeth: 2.5 times and more shorter than the tube (0) longer than the tube, as long as the tube, or less than 2.5 times shorter than the tube (1).
48. Upper calyx teeth: not deeply fused to each other (0) deeply fused to each other, forming an upper calyx lip (1).
49. Calyx teeth width (within a given calyx): almost equal or slightly unequal (0) conspicuously unequal (1).
50. Corolla symmetry: monosymmetric (0) asymmetric (1).
51. Wing and standard colour: yellow or greenish yellow (0) red, pink, white etc., but not completely yellow (1).
52. Petal claws: not or slightly exceeding calyx tube (0) considerably exceeding calyx tube (1).
53. Paired outgrowths or thickenings on the inner surface of the standard claw: present (0) absent (1).
54. Standard claw: well delimited from the blade (0) scarcely delimited from the blade (1).
55. Standard indumentum of hairs: always absent (0) present, at least in some specimens (1).
56. Distal tips of wing blades: not adhering together (0) adhering together (1).
57. Keel shape: pronouncedly rostrate (0) obtuse or obscurely rostrate (1).
58. Stamen filaments: not dilated (0) distally dilated (1).
59. Gynophore: absent or very short (0) present and longer than the hypanthium (1).
60. Ovule number per ovary: 3 and more (0) 2, very rarely 3 (1).
61. Ovule orientation pattern (terminology after Tikhomirov, Sokoloff, 1997): micropylae superae (0) micropylae alternantes (1) micropylae inferae (2).
62. Stylodium shape: not gradually thickened in the middle part (but sometimes with a verntal tooth or dorsal outgrowth) (0) gradually thickened in the middle part (1).
63. Stylodium surface (in the middle part): smooth (0) papillose (1).
64. Distal part of the stylodium: not or almost not dilated (0) spoon shaped (1).
65. Long papillae or hairs on stylodium below the stigma: absent (0) present (1).

D. Carpological characters (most important studies of fruit anatomy in Loteae are Vassilczenko 1931; Kaniewski and Wa¿yñska 1968; Sokoloff 1997, 1998, 2003b; Tikhomirov and Sokoloff 1997; Degtjareva et al. 2003; general publications with important data on fruit anatomy in Loteae are Fucskó 1914; Zazhurilo 1936; Fahn and Zohary 1955; Roth 1977; Arambarri 1993; Loseva and Lotova 1996).

66. Carpophore: absent or not exceeding the calyx tube (0) longer than the calyx tube (1).
67. Fruit length (without carpophore): at least 2 times longer than the fruit width (0) not exceeding the fruit width or less than 2 times longer than the fruit width (1).
68. Fruit shape: (almost) straight or incurved to dorsal side (i.e., towards the keel) (0) considerably incurved to ventral side (i.e., towards the standard) (1).
69. Fruit shape: (almost) straight or incurved to ventral side (i.e., towards the standard) (0) considerably incurved to dorsal side (i.e., towards the keel) (1).
70. Fruit shape in transverse section: not or slightly compressed (0) pronouncedly compressed (1).
71. Longitudinal ribs on fruit surface: absent (0) present (1).
72. Deep longitudinal furrow on ventral side of the fruit: absent (0) present (1).
73. Dorsal wing on the fruit: absent (0) present (1).
74. Fruit surface: with hairs or long papillae (0) glabrous (1).
75. Seed number per fruit: three and more (0) two (1) single (2).
76. Fruit dehiscence along the midrib (i.e., dorsal dehiscence): present (0) absent (1).
77. Ventral fruit dehiscence: present (0) absent (1).
78. Transversal fruit breaking: absent (0) irregular (1) regular, i.e., fruits lomentaceous (2).
79. Distal seedless loment of the fruit: absent (0) present (1).
80. Sclerenchymatous fibres of the pericarp parchment layer:present (0) absent (1).
81. Crystal bearing cells adjacent to external side of pericarp parchment layer: present (0) absent (1).
82. Brown cells adjacent to external side of pericarp parchment layer: absent (0) present (1).
83. Outer surface of isolated parchment layer: (almost) smooth (0) pitted (1).
84. Sclerenchymatous fibres of the pericarp parchment layer: absent at the dorsal region of the pericarp (i.e., along the fruit midrib) (0) present at the dorsal region of the pericarp, so that parchment layers of left and right valves are joining there (1).
85. Number of strata of parchment layer in each valve of the pericarp: one (0) two, i.e. outer and inner fibres of the parchment layer differ from each other in orientation (1). Characters # 86 and 87 are not applicable to taxa with two strata of parchment layer.
86. Pattern of parchment layer fibres orientation: all fibres of single stratum have the same orientation within the valve OR fibres are almost transversally oriented in the midrib region and almost longitudinally oriented in the ventral region, showing gradual transition from transversal to longitudinal orientation along the valve (0) fibres of single stratum are transversally oriented near the midrib and in the ventral region as well as in the greater part of the valves, while in the middle part of each valve the

fibres are longitudinal, and transition zones from longitudinal to transversal fibres are very narrow (1).

87. **Pattern of parchment layer fibres orientation:** fibres of single parchment layer stratum are obliquely oriented at least in the middle part of each valve (0) fibres of single parchment layer stratum are longitudinally oriented in the middle part of each valve (1).
88. **Pattern of parchment layer fibres orientation:** parchment layer with single stratum of fibres in each valve OR with two strata of fibres and fibres of the inner stratum are oblique or transversal (0) parchment layer with two strata of fibres and fibres of the inner stratum are longitudinally oriented (1).
89. **Pattern of parchment layer fibres orientation:** parchment layer with single stratum of fibres in each valve OR with two strata of fibres and fibres of the inner stratum are longitudinally oriented (0) parchment layer with two strata of fibres and at least some fibres of the inner stratum are transversally oriented (1).
90. **Inner parenchyma of the endocarp:** without brown cells (0) with brown cells (1).
91. **Seed shape:** rounded or slightly elongated (0) considerably elongated or linear (1).
92. **Seed surface** (when studied with binocular lens): smooth or almost smooth (0) with large regular papillae (1).
93. **Cotyledons** (in seed): more or less flattened (0) rounded or ellipsoidal in cross section, at least in the middle part (1). See also Smith (1983).

E. Palynological characters The pollen morphology is described mainly according to Díez and Ferguson (1990, 1994, 1996). The following publications are also used: Burkart et al. (1972); Pire (1974); Ferguson and Skvarla (1981), Crompton and Grant (1993); Lavin and Sousa (1995); Degtjareva et al. (2003).

94. **Mean polar axis length of pollen grains:** less than 34 μm (0) 34 to 40 μm (1) more than 40 ìm (2). Díez and Ferguson (1990, 1994, 1996) reported mean polar length and variation range for each studied species. Mean length is used here as a cladistic character.
95. **Mean equatorial axis length of pollen grains:** less than 19 μm (0) 19 to 23 μm (1) more than 23 μm (2).
96. **Pollen grain shape:** mean polar to equatorial length ratio not exceeding 1.1 (0) more than 1.1 (1).
97. **Aperture number:** 3 (0) 4 5 (1) 6 7 (2).
98. **Endoaperture size:** less than 5 μm (0) more than 5 μm (1).
99. **Exine:** thin (0) thick, 2 3 μm at mesocolpia (1).
100. **Foot layer:** well developed (0) reduced or absent (1).
101. **Exine perforations:** absent (0) exine perforate (1) exine microreticulate (2).
102. **Exine sculpture at mesocolpia:** exine conspicuously sculptured (0) smooth or almost smooth (1).

03. **Exine sculpture at mesocolpia:** neither granulate verrucate nor verrucate (0) granulate verrucate or verrucate (1).

4. **Exine sculpture at mesocolpia:** not fossulate (rugulate fossulate) (0) fossulate (rugulate fossulate) (1).

5. **Exine sculpture at mesocolpia:** not striate (striate rugulate) (0) striate (striate rugulate)(1)

106. **Pattern of exine sculpturing at apocolpia:** does not differ from that at mesocolpia (0) differs from that at mesocolpia (1).
107. **Granules on colpus margin or colpus membrane:** absent (0) present (1).

F. Chromosome number

108. **Base chromosome number:** x=10 and more (0) x=8, 9 (1) x=7 (2) x=6 (3). Literature data are used (summarized in Fedorov, 1969; Goldblatt 1981a 1988; Grant, 1995, 1997; Goldblatt, Johnson, 1996, 1998).

PHYLOGNETIC ANALYSIS

Parsimony cladistic analysis was conducted using Winclada (Nixon, 2002). All characters were treated as equally weighted. The ratchet algorithm of parsimony analysis was used to find initial set of most parsimonious trees. The ratchet algorithm (Nixon 1999) allows effectively finding of trees belonging to different 'tree islands' (see Forey et al., 1992). After generating the first tree, the ratchet algorithm is conducting reweighing of some characters in the data set. In our case, 10% of characters were reweighed. In each ratchet iteration, the list of characters to be reweighed is randomly determined. After reweighing, a simplified (and fast) procedure of branch swapping is carrying out. Then initial weight of each character is restoring (in our case, equal weight of all characters). Then simplified branch swapping is repeated. The shortest tree found during swapping is using as start tree for the next iteration of the ratchet algorithm. At the final stage of the ratchet analysis, the shortest trees are selected among results of all iterations. We have conducted analyses with 200, 500, and 1500 iterations of ratchet. Trees obtained from the ratchet analyses were submitted to tree bisection reconnection (TBR) branch swapping with the maximum number of trees saved set to 10,000. Jackknife analyses (Farris et al., 1996) were performed to assess the degree of support for particular clades. 100 jackknife replicates were conducted.

RESULTS

Number of shortest trees found in parsimony ratchet analysis depends from the number of ratchet iterations. In analyses with 200 iterations, 60 70 shortest trees were found, analyses with 500 iterations resulted in 150 160 shortest trees, and analyses with 1500 iterations yielded more than 400 shortest trees. Exact number of shortest trees found slightly varies from run to run due to random selection of characters to be reweighed in ratchet iterations. All analyses yielded threes of the same length (439 steps), consistency (0.3) and retention index (0.68). Interestingly, in the majority of analyses, the first generated tree was containing a clade comprising New World species of *Ottleya, Syrmatium* and *Acmispon* (Fig. 1). This grouping has very low jackknife support in the present morphological analysis (7%), but it has received high support in molecular analyses (Allan et al., 2003; Degtjareva et al., 2003).

Regardless of differences in the number of yielded shortest trees, their strict consensus as of almost the same topology in analyses with 200, 500, and 1500 ratchet iterations. The rict consensus tree is presented in Fig. 2. The tribe *Loteae* is revealed as a monophyletic nit. Each genus of the tribe (according to the classification by Sokoloff, 2003a,b) forms its wn clade on the strict consensus tree. Submitting of trees obtained from the ratchet analyes to TBR branch swapping allowed to find much more shortest trees. In total, 6240 trees f 439 steps were found. Strict consensus of 6240 trees differs from the topology presented Fig. 2 only by collapsing of a clade, which comprises *Syrmatium* species. *Cytisopsis* is und as a sister to the rest of the analysed *Loteae* species. The ingroup species (except for *ytisopsis*) are divided into two main clades (Clade A and Clade B, Fig. 2). The Clade A ontains genera *Podolotus, Hosackia, Scorpiurus, Hippocrepis,* and *Coronilla*. These genera are, in particular, leaves with membranous or herbaceous stipules and fruits with single ratum of fibres (or sclereids) in the pericarp parchment layer. The Clade B contains gena *Dorycnopsis, Kebirita, Pseudolotus, Tripodion, Hammatolobium, Ottleya, Syrmatium, cmispon, Antopetitia, Ornithopus, Anthyllis,* and *Lotus*. These genera (excepting *rnithopus*) possess leaves with stipules reduced to dark glands. *Ornithopus* has membraous stipules (as in members of the Clade A), but the pericarp parchment layer of *Ornithopus* with two strata of fibres, as in some other members of the Clade B (*Antopetitia, orycnopsis*, the majority of *Anthyllis* species).

Relationships between the genera in the Clade B are almost unresolved on strict conensus tree (Fig. 2). In the Clade A, *Podolotus* and *Hosackia* occupy basal position. These enera are characterised by dehiscent and not lomentaceous fruits (plesiomorphic character tates). The genera *Scorpiurus, Hippocrepis,* and *Coronilla* with indehiscent lomentaceous fruits form a single subclade within the clade A.

Jackknife analysis demonstrated that all clades present in the strict consensus tree have moderate to high jackknife support (Fig. 2) (terms 'weak', 'moderate', and 'high' jackknife support are defined according to Soltis et al., 2000). Some clades that are absent in the strict consensus tree have received jackknife support more than 50% and thus have appeared in the 50% majority rule consensus tree derived from jackknife analysis (Fig. 3). One of these clades includes genera *Pseudolotus* and *Lotus*; it has received moderate jackknife support (76%). Other such clades are only weakly supported, for example a clade comprising *Tripodion* and *Hammatolobium* and a clade comprising *Dorycnopsis, Antopetitia, Ornithopus,* and *Anthyllis*.

To allow effective comparison between morphological and molecular phylogenetic analyes, we have analysed the same set of *Loteae* species that was previously included in olecular analyses by Degtjareva et al. (2003). In other words, we excluded from the data atrix *Podolotus hosackioides, Pseudolotus villosus, Antopetitia abyssinica, Anthyllis ontana, A. barba jovis, A. hermanniae, Acmispon parviflorus,* and *Scorpiurus uricatus*. Ratchet analysis (1500 iterations) allowed finding only 54 shortest trees (417 teps, CI=0.31, RI=0.64). After TBR branch swapping of them, total number of shortest ees was increased up to 85. Strict consensus of the 54 trees is identical to strict consensus

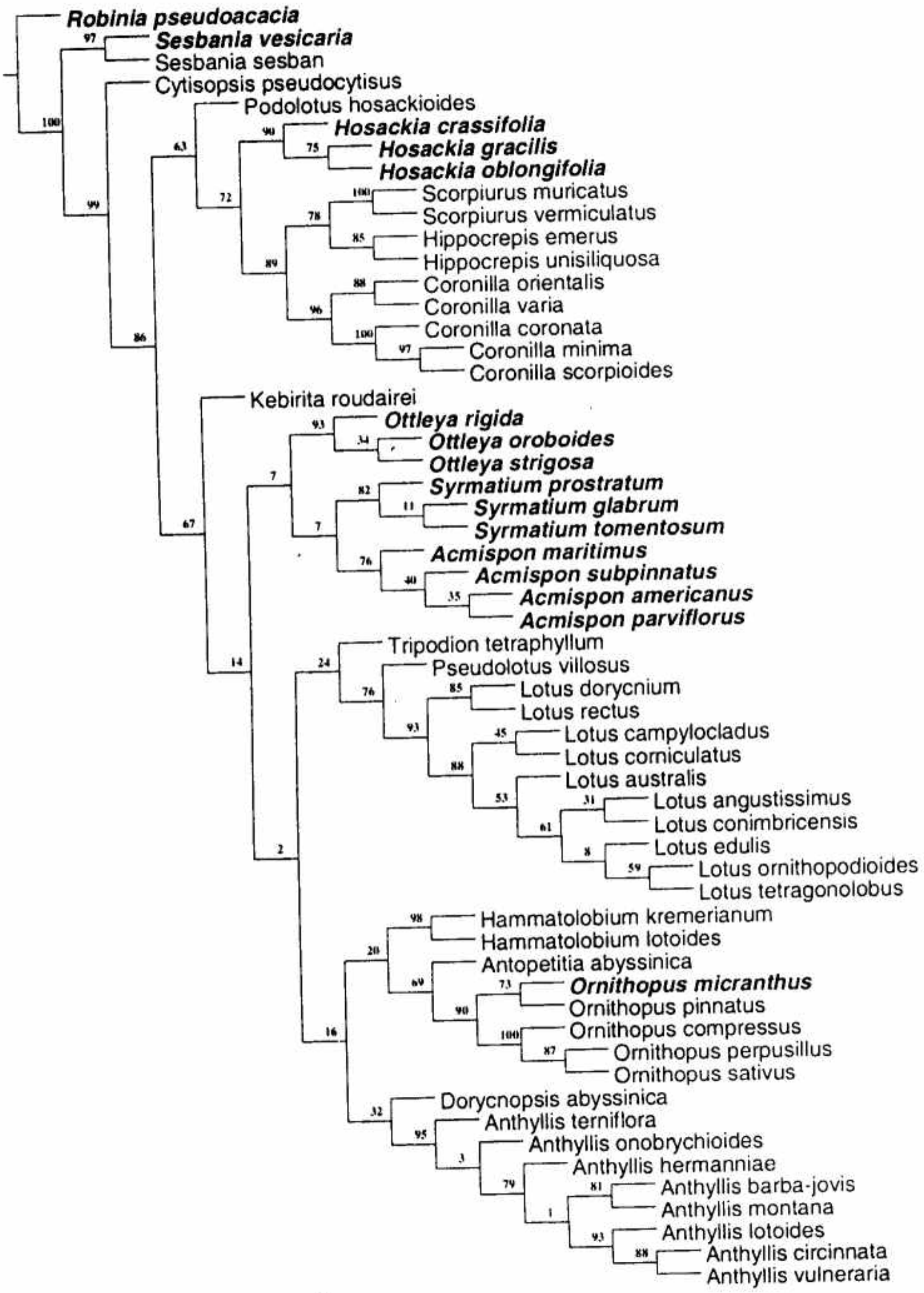
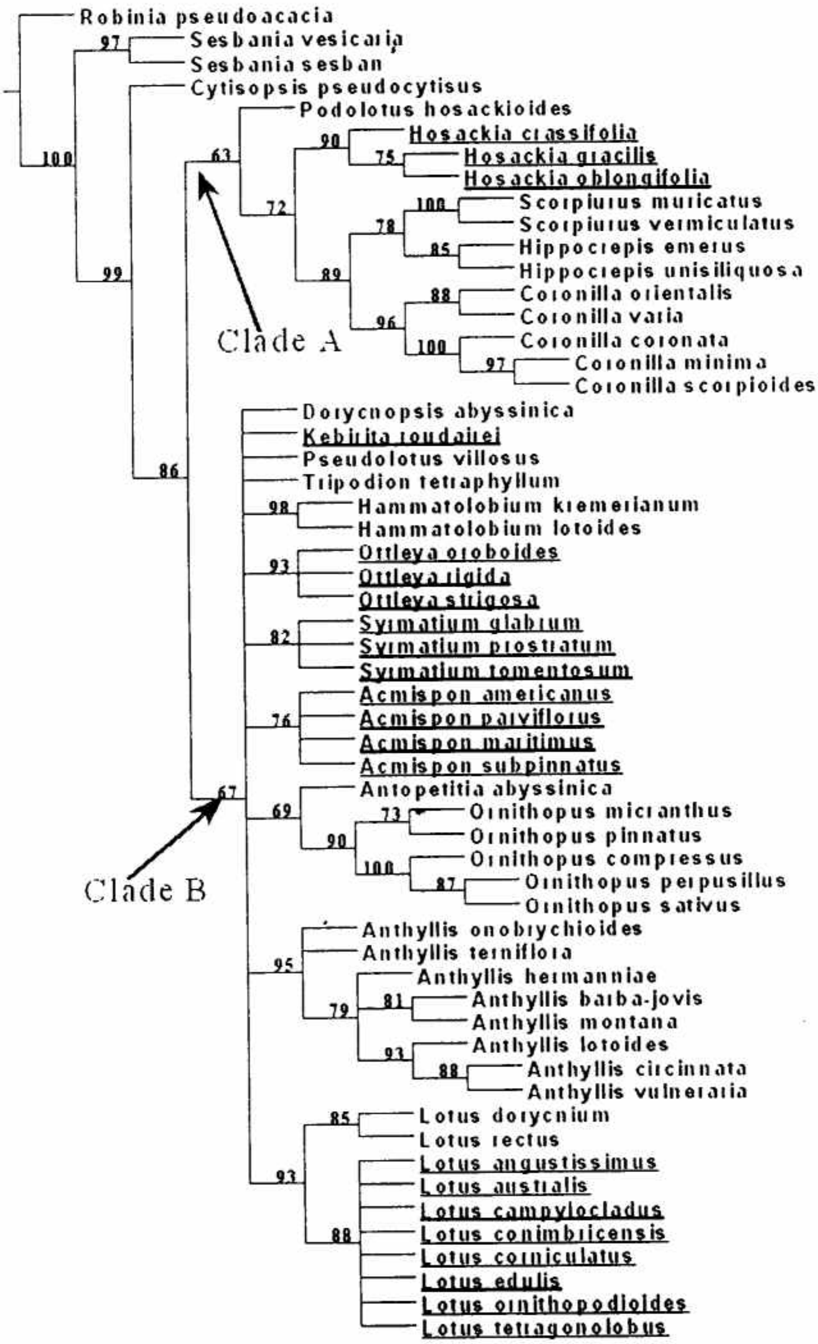


Fig. 1: One (first generated by the program) of 160 shortest trees found in 500 iterations of parsimony ratchet analysis of morphological data set for the tribe *Loteae*. Jackknife support indices are indicated above the branches. New World species are given in bold italics.



2: Strict consensus of 160 shortest trees found in 500 iterations of parsimony ratchet lysis of morphological data set for the tribe *Loteae*. Jackknife support indices are indi- ted above the branches. Species included by Polhill (1994) in the genus *Lotus* are under- ed.