

A NEW INFRAGENERIC GROUPING OF ASTRAGALUS (FABACEAE)

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This work is an updated phylogenetic study on the huge genus *Astragalus* using nuclear ribosomal DNA internal transcribed spacer (ITS) data. Seven groups, each encompassing several sections, corresponding to the same number of clades appeared, were recognized in the phylogenetic tree. A short description for each group along with the name of appropriate sections as well as a diagnostic key regarding new reliable morphological characters for these groups is provided.

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Key words: Infrageneric classification, phylogenetic analysis, Bayesian inference, *Astragalus*

گروه بندی جدید تحت جنس در گون (*Astragalus*)

علی اصغر معصومی: استاد پژوهش، مؤسسه تحقیقات جنگلها و مراتع کشور

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بر اساس کارهای ملکولی انجام شده با استفاده از ITS هفت گروه از بخش‌های جنس گون تفکیک شده است که هر یک با شماره‌های خود بر روی درخت فیلوژنی مطابقت دارند. برای هر گروه نام بخش‌ها به همراه کلید شناسایی بخش‌ها با استفاده از صفات مورفولوژی برای جدا سازی استفاده شده است.

INTRODUCTION

Since Linnaeus, who established the genus *Astragalus* (Linnaeus 1753), until 1800 only 54 species were described for the genus, without any infrageneric subdivisions like subgenus or section. De Candolle (1825) introduced sections provisionally to sub-divide the genus in a dozen of sections for the first time.

The first conclusive infrageneric classification of the genus in the Old World was done by Bunge (Bunge 1868 & 1869). In his monographic work, Bunge described about 791 species belonging to nine subgenera and 102 sections. Later, Boissier (1872) in *Flora Orientalis* mainly accepted Bunge's classification. At the same time, the North American *Astragalus* species were divided into several sections (Gray 1854, Rydberg 1928, 1929, 1943). In the *Flora of*

USSR, Goncharov (1965) followed Bunge's system in dividing the genus into subgenera and sections. Barneby (1964), in his monumental work on the North American *Astragalus*, used "phalanx" instead of the formal subgenera. Podlech (1982) dramatically reduced Bunge's eight perennial subgenera to two subgenera. *Astragalus* and subgen. *Cercidothrix*, solely based on hair type (simple or bifurcate) and retained all annuals in subgen. *Trimenia*. During the complicated classification history of *Astragalus*, about 57 genera were segregated, but gradually re-merged into the genus again (Maassoumi 1998, Wojciechowski & al. 1999, Kazempour Osaloo & al. 2003).

At present, only two genera *Podlechiella* Maassoumi & Kaz. Osaloo, which was established recently (Kazempour Osaloo & al. 2003), and

Phyllolobium Fisch. (Kang & al. 2003, Wojciechowski 2005, Zhang and Podlech 2006) were segregated from *Astragalus*, based on molecular data. These two genera are now belonging to the Coluteoid clade (tribe Coluteae) of Fabaceae (Wojciechowski 2005, Moghadam & al. unpublished data 2016). On the basis of molecular data, the aneuploid New World *Astragalus* species with chromosome base numbers of $x=11, 12, 13, 14$ and 15 form a clade within the Old World *Astragalus* the so called Neo-*Astragalus* (Wojciechowski & al. 1993, 1999, Wojciechowski 2005, Kazempour Osaloo & al. 2003, 2005).

Kazempour Osaloo & al. (2003), using both nrDNA ITS and plastid *ndhF* sequences, demonstrated that none of the traditionally recognized subgenera (Bunge 1869, Podlech 1982, Maassoumi 1998) are monophyletic. Subsequently, Maassoumi (2003), based on these molecular systematic data, reduced all subgenera to the synonymy of *Astragalus*.

In the new work "Taxonomic Revision of the Genus *Astragalus* in the Old World", Podlech & Zarre (2013), in agreement with molecular phylogenetic findings, arranged the genus and its species into sections only.

In this work, we try (1) to propose new taxonomic groups, encompassing several sections, corresponding to the appropriate clades identified in our previous works and (2) to compile diagnostic characters defining each group.

MATERIALS AND METHODS

A total of 194 species of *Astragalus* was included in the analysis of nrDNA ITS region (Appendix 1). The sequences were either previously determined by us (Kazempour Osaloo & al. 2003, 2005, Javanmardi & al. 2012, Dastpak & al. 2013, Naderi-Safari & al. 2014) or other workers (Wojciechowski & al. 1999, Abdol-Samad & al. 2014) and retrieved from the GenBank nucleotide database. Forty-five Iranian species were newly sequenced for this study. Two species of *Oxytropis* (*O. aucheri*, *O. szovitsii*), two subspecies of *Podlechiella* (*P. vogelii* subsp. *fatmensis*, *P. vogelii* subsp. *vogelii*) and some traditional species of *Astragalus* (*A. leucocephalus*, *A. annularis*, *A. cysticalyx*, *Biserrula pellicina*, *Sphaerophysa salsola*) were chosen as outgroups. Forward and reverse ITS sequences were edited and aligned using Bioedit ver. 5.06 (Hall 2004).

The models of sequence evolution were evaluated using the program Mr. Model test version 2.3 (Nylander 2004) and selected based on the Akaike information criterion (AIC) (Posada and Buckley 2004). On the basis of this analysis, datasets were analyzed using the K2+G model. The program Mr. Bayes version 3.2 (Ronquist & al. 2012) was used for

the Bayesian inference. Posteriors on the model parameters were estimated from the data using the default priors. The analysis was run for 10 million generations with two times four chains starting from different random trees (nruns = 2). Trees were sampled every 100 generations. The first 25% of trees were discarded as burn-in. The remaining trees were then used to build a 50% majority rule consensus tree accompanied with posterior probability (PP) values. The convergence of MCMC chains was visualized with the Tracer program version 1.5 (Rambaut and Drummond 2009). Tree visualization was carried out using Tree View version 1.6.6 (Page 2001). The studied materials, their collecting data and gene bank code is provided in appendix 1 at the end of the manuscript.

RESULTS

The tree resulting from dataset was topologically identical with high resolution and supports with eight major clades (fig. 1: A-I). None of the traditionally recognized subgenera is monophyletic in this tree. We identified important character states for these clades, which were listed in fig. 1.

-**Clade I** containing 41 sections of which 21 sections were examined with molecular data. Some sections with one and some with several species were analyzed. This clade is sister clade of the rest of *Astragalus* in the tree [Kazempour Osaloo & al. 2003, 2005; Riahi & al. 2011; Javanmardi & al. 2012].

-**Clade II** with 6 sections which were all examined. This clade contains species with basifixed and medifixed hairs. [Kazempour Osaloo & al. 2003, 2005].

-**Clade III** with 9 sections, all of them were analyzed with molecular data [Kazempour Osaloo & al. 2003, 2005].

-**Clade IV** with two examined sections [Kazempour Osaloo & al. 2003, 2005].

-**Clade V** containing only members of sect. *Incani*. [Kazempour Osaloo & al. 2003, 2005; Amini & al. 2016].

-**Clade VI** containing 26 thorny-cushion forming sections (except sect. *Macrosemium*) having mainly basifixed (rarely medifixed) hairs. [Kazempour Osaloo & al. 2003, 2005; Naderi & al. 2014; Darzi, 2014; Bagheri 2015; Ghalenoyi 2013; Rezaee 2014; Heidari, 2014].

-**Clade VII** with 61 sections of basifixed and medifixed hair, perennials and annuals, mixed with Neo-*Astragalus*. In this clade 32 sections were analyzed using molecular markers [Kazempour Osaloo & al. 2003, 2005; Sheikh Akbari & al. 2012; Ghorbani, 2012; Dastpak & al. 2013].

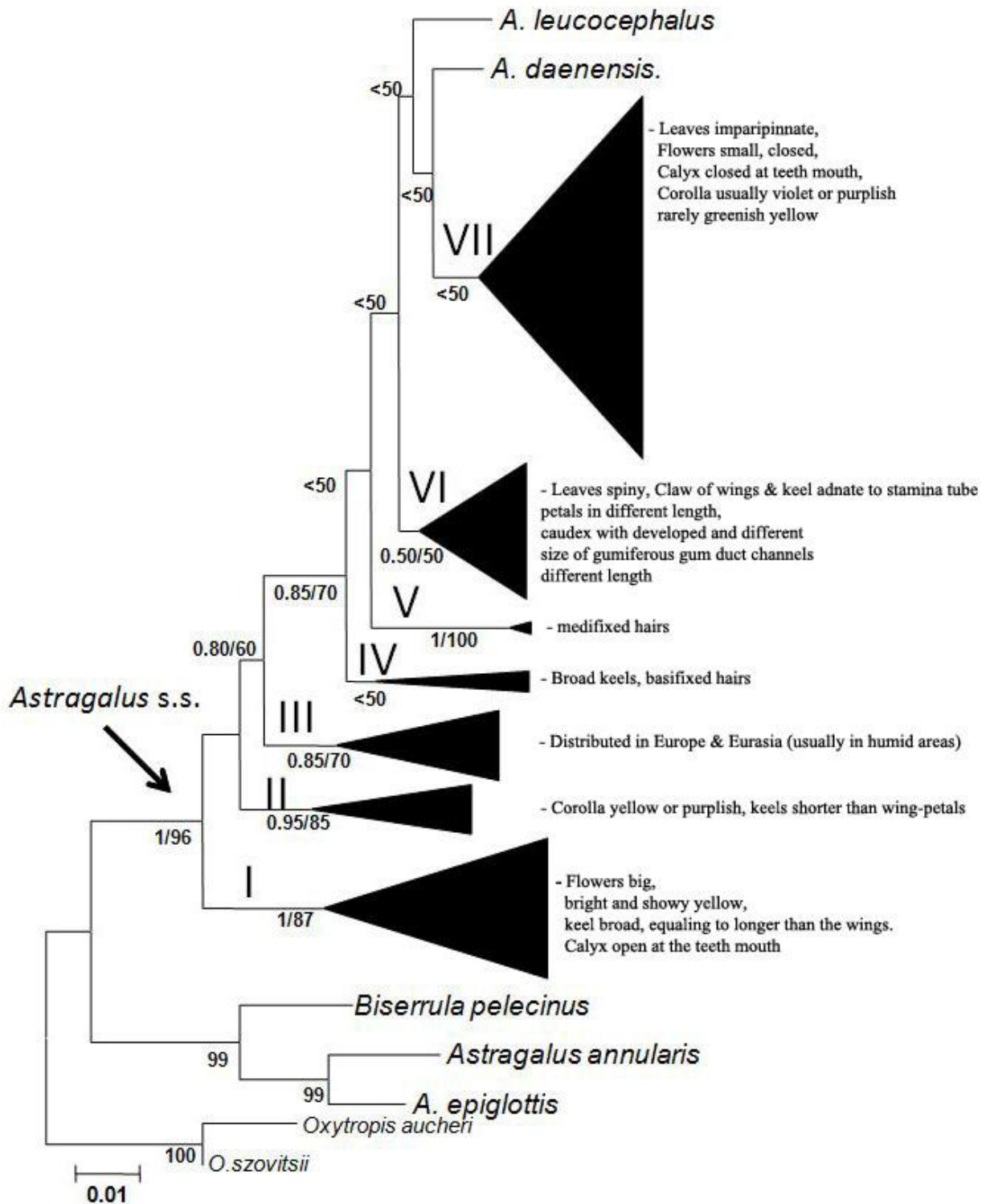


Fig. 1. Phylogenetic tree derived from Bayesian inference of nrDNA ITS sequences of 194 *Astragalus* and 5 outgroup species. Seven major clades (I-VII) within *Astragalus* s. str. are depicted and detailed in the text. [Kazempour Osaloo, Maassoumi, Murakami 2003, 2005; Riahi & al. 2011; Javanmardi & al. 2012; Dastpak & al. 2013; Naderi & al. 2014].

Sect. *Brachylobium*, represented by *A. daenensis*, is sister to all other sections, which are included within clade VII [Kazempour Osaloo & al. 2005].

A. leucocephalus which belong to sect. *Poliothrix* make a single clade, but other species of this group nested to clade VII [Kazempour Osaloo & al. 2005].

Clade V with two taxa (*A. incanus* and *A. laguopsis*) with medifixed hairs, gum duct but no adnation of claw with staminal tube, segregated from other medifixed sections and regrouped as a single clade [Kazempour Osaloo & al. 2005].

Astragalus leucocephalus which belong to sect. *Poliothrix* forms a single clade, while other species of this group are nested in clade VII [Kazempour Osaloo & al. 2005].

a) The phylogenetic position of sections

Based on the present study and our previous works (Kazempour Osaloo & al. 2003, 2005), the great majority of sections analyzed herein are monophyletic and thus are natural groups. This is consistent with the morphological characters (vegetative and reproductive ones), which support the sectional delimitation of them. However, some annual sections are non-monophyletic and their representatives are scattered across the tree within the clades B, C and I, indicating multiple shifts from perennial to annual life history. Bifurcate hairs are occurring in different clades and some are in clade A, partly with spiny leaves but with paripinnate leaves and well-developed gum duct mixed with *tragacanthic* clade (sect. *Leucocercis*,) and imparipinnate leaves (sect. *Macrosemium*) with its special structure of wing and keel claw belong to the *tragacanthic* clade (fig. 1).

The species of some huge sections, which were reduced to the synonymous, are distributed among different clades. For example some *Poliothrix* Bunge = *Polycladus* species nested within different clades.

Based on previous molecular investigations some sections such as sects. *Lamprocarpa*, *Koelziana* and *Davisiana* have distinct differences with clear delimitation [Ghalenoyi, 2013, Bagheri, 2015, unpublished, Kazempour Osaloo, 2016, unpublished data].

In clade VII, several basifixed hair and medifixed are mixed together.

The Neo-*Astragalus* sections of the New World are, according to previous and our investigation during the last 15 years, nested within clade VII, which is a very young group and mixed with basifixed and medifixed hairs sections, including also some annual sections. This feature can be the result of rapid radiation and fast speciation phenomena. In this group beside the basifixed hairs there are some sections, which show different types of hair bifurcation, from extremely asymmetric to symmetric bifurcate hairs.

b) Description of groups based on new useful morphological characters

The following characters are considered as new important morphological characters for defining groups: 1-Corolla big, dense yellow, keel broad (Colutea type), ca. 3-10 mm wide, if narrow then corolla purplish, violet or greenish yellow.

2-Claw of the wings and keels in different length adnate to the staminal tube. Inflorescences terminal or lateral or synflorescences

3-Stems in cross section showing different size of gum duct. Leaves paripinnate.

1. Group I

This group is defined by the first split within the tree of *Astragalus* s. str. The taxa are characterized by the distinct trait of very wide keeled petals (fig. 2)

Perennial herbs or shrublets with a woody base, stemless or with well-developed stem. Stipules usually foliaceous. Corolla bright showy yellow; keel broad (limb of keels ca. 3–10 mm wide), wing-petals equaling or minutely shorter, very rarely longer than keels, if keels less than 3 mm wide then wing longer than keels. Standard orbicular or elliptic. Calyx gibbose at the base (fig. 2 C), at the teeth mouth open. Plants covered with basifixed hairs or rarely covered with medifixed hairs (section *Caraganella*).

Sections: *Alopecuroidei*, *Laxiflori*, *Christaniophysa*, *Astragalus*, *Caraganella*, *Eremophysa*, *Cenantrum*, *Chlorostachys*, *Christianopsis*, *Chronopus*, *Eremophysopsis*, *Pseudosesbanella*, *Coluteocarpus*, *Mesocarpon*, *Skytropos*, *Lithoon*, *Alopeciodes*, *Galegiformis*, *Macropodium*, *Nuculiella*, *Thaumasiophaca*, *Rechingeriana*, *Stipitella*, *Christianophysa*, *Pendulina*, *Erionotus*, *Aegacantha*, *Caprini*, *Rhabdotud*, *Hololeios*, *Leptophysa*, *Chrysopterus*, *Ebracteolati*, *Lithophilus*, *Hookeriana*, *Scheremeteviana*, *Pelta*, *Pendulina*, *Gontscharoviella*, *Bungeastrum*, *Pogonotropis*

Type: Section *Astragalus*

2. Group II

This is the second lineage that split from the remaining taxa within *Astragalus*.

Annuals or perennials, herbaceous, caulescent or with developed stem, rarely caespitose. Plant covered only with basifixed hairs. Calyx closed at the teeth mouth. Corolla yellow or purplish. Keels narrow, usually shorter than the wing-petals. Standard elliptic or oblong, rarely orbicular. Vegetative parts covered with basifixed hairs.

Sections: *Hemiphragmium*, *Annulares*, *Oroboidei*, *Oxyglottis*, *Sesamei*, *Theiochorus*, *Thlaspidium*, *Heterodontus*, *Melilotopsis*.

3. Group III

Annuals or perennials, herbaceous, caulescent; stem rarely fistulate. Plant covered with basifixed or rarely medifixed hairs. Corolla yellow or purplish. Keels narrow, usually shorter than the wing-petals. This

group is usually growing in humid habitats or meadows. Pods ovoid, cylindric straight or arcuat.

Sections: *Glycyphyllus*, *Tapinodes*, *Bucerates*, *Cyamodes*, *Synochreati*, *Uliginosi*

4. Group IV

Annual or perennial, covered with only basifixed hairs. Corolla yellow. Keel equaling or longer than wing petals. Keels ca. 6–9 mm wide, limb longer than claw. Growing in China, Taiwan, Japan and Central Asia.

Example section: *Lotidium*, *Komaroviella*

5. Group V

Herbaceous, acaulescent, covered with medifixed hairs, symmetric or asymmetric. Leaves imparipinnate, usually with dark violet punctat. Corolla always violet to purplish, rarely yellowish; keels narrow, shorter than the wing-petals. With clear gum duct in some species. Claw of the keels and wings free from staminal tube. Calyx covered with black and white medifixed, mixed

with basifixed hairs or very rarely, extremely asymmetric medifixed hairs. Pods bilocular, usually maculate.

Example section: *Incani*, *Laguropsis*.

6. Group VI

Perennials, thorny cushion-form or shrublets, rarely non-thorny herbs, with gum duct. Inflorescence pedunculate or synflorescence. Vegetative parts covered with basifixed hairs rarely covered with medifixed hairs (section *Leucocercis*). Leaves paripinnate, rachis ending in a spine, very rarely imparipinnate with a terminal leaflet. Corolla yellow or purplish. Keels narrow, c 2. 5–3 mm wide, always shorter than the wing-petals, claw of the wing-petals and keels in different length, adnate to the staminal tube. Pods unilocular or bilocular, few seeds.



Fig. 2. (Clade I). A, open calyx, teeth mouth of calyx - *A. litwinowii*; B, *A. Caragana*; C, calyx, gibbose at the base - *A. caragana*; claw shorter than blade - *A. ponticus*, *A. alopecuroides*; H, keel - *A. macrocephalus*; I, if keel narrow, then claw longer than blade - *A. remotijugus*.

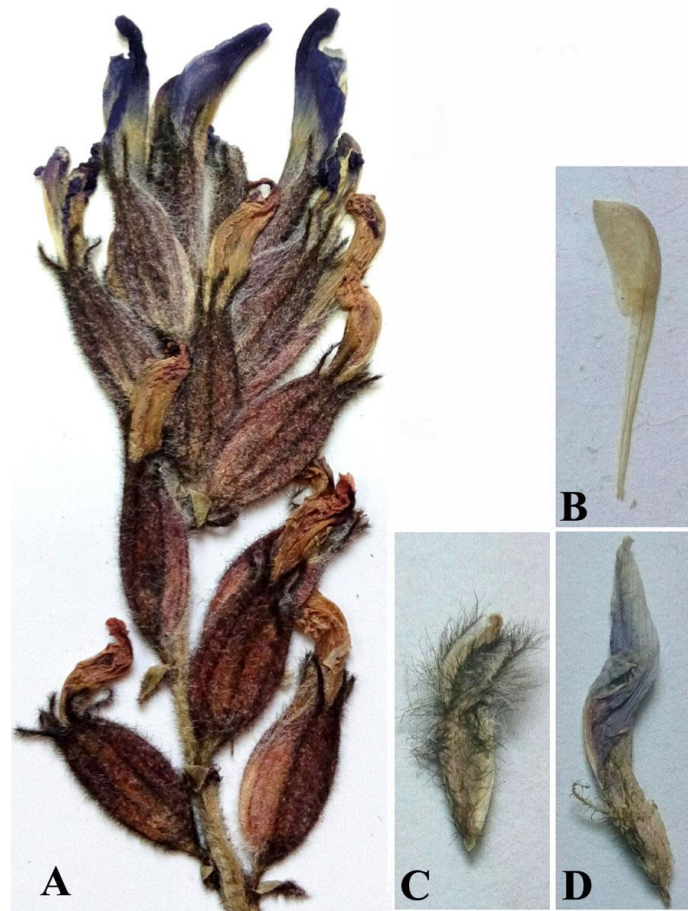


Fig. 3. (Clade VII): A, *A. beckii*; B, claw longer than keel blade – *A. senilis*; C, closed calyx – *A. atricapilus*; D, calyx closed at mouth - *A. vegetus*.

Example section: *Acanthophaea*, *Macrophyllum*, *Rhacophorus*, *Pterophorus*, *Platonychium*, *Polystegis*, *Hystrix*, *Microphysa*, *Campylanthus*, *Leucocercis*, *Poterion*, *Anthylloidei*, *Davisiana*, *Eriostoma*, *Semnanenses*, *Adiaspastus*, *Acidodes*, *Diacme*, *Halicacabus*, *Hymenocloeus*, *Hymenostegis*, *Tricholobus*, *Lamprocarpa*, *Argaeus*, *Macrosemium*, *Lamprocarpa*.

Geographical Distribution: Europe, European Asia, S. W. Asia, Central Asia

7. Group VII

Herbaceous, perennial, very rarely annual, caulescent or acaulescent, woody base. Covered with basifixed or medifixed hairs; symmetric or asymmetric. Leaves imparipinnate, if in young age paripinnate then flowers pink or purplish. Flowers small, closed. Corolla always violet to purplish, rarely yellowish; keels narrow, shorter than the wing-petals. Without gum duct. Claw of the keels and wing free from staminal tube. Calyx covered with medifixed hairs mixed with basifixed

hairs or only basifixed hairs or very rarely extremely asymmetric medifixed hairs. Pods bilocular.

Example sections: *Malcothrix*, *Stereothrix*, *Koelziana*, *Hypoglottidei*, *Brachylobium*, *Pseudotapinodes*, *Brachycephalae*, *Picrophaca*, *Ammodendron*, *Dissitiflori*, *Corethron*, *Erioceras*, *Acantherioceras*, *Trachycercis*, *Ornithopodium*, *Onobrychoidei*, *Craccina*, *Uliginosi*, *Chaetodon*, *Ammotrophus*, *Pseudoammotrophus*, *Baldaccia*, *Sisyrophorus*, *Ammodytes*, *Tropidolobus*, *Cremoceras*, *Helmia*, *Tanythrix*, *Cytisodes*, *Paracystium*, *Cysticalyx*, *Macrocystis*, *Macrocystodes*, *Leucophysa*, *Eustales*, *Vulneraria*, *Hypsophilus*, *Holophyllum*, *Bulimioides*, *Tragacantha* and *Hololeuce*+ some annuals: *Sesamei*, *Hispiduli*, *Dipelta*, *Mirae*, *Platyglottis*, *Heterodontus*, *Ankylotus*, *Pentaglottis*, *Ophiocarpus*, *Brachycarpus*, *Grammocalyx*, *Plagiophaca*, *Poliothrix*, *Dasyphyllum*, *Mikrophyton*, *Drepanodes*, *Irina*, *Woronowia*, *Aberrantes*, *Leptophysa* + *Neo-Astragalus* (New world Aneuploid)

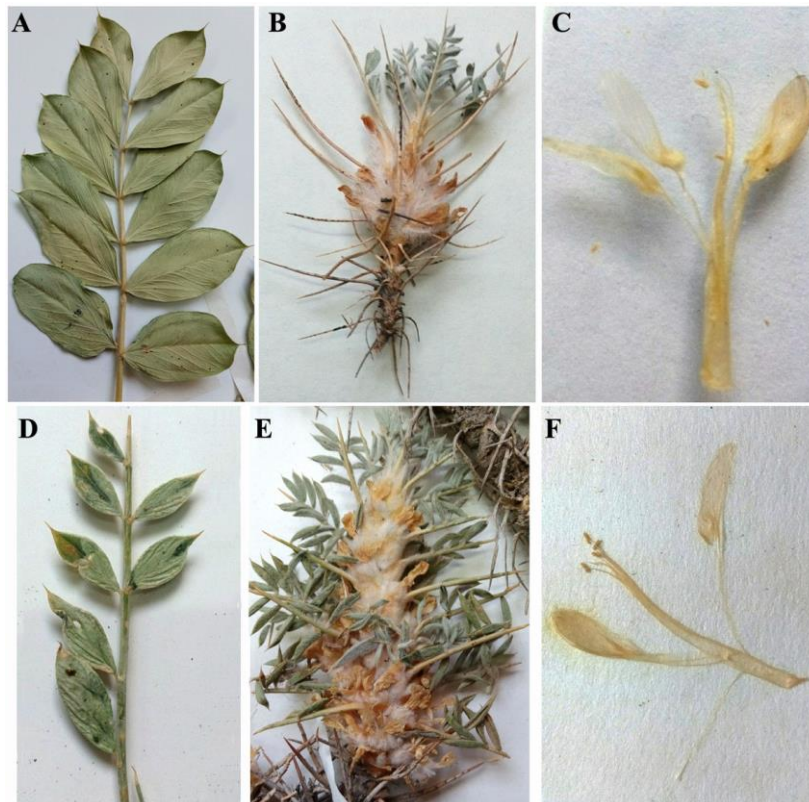


Fig. 4. (Clade VI): A, paripinnate - *A. oleaefolius*; B, paripinnate leaves and synflorescens - *A. verus*; C, claw of wing and keel adnate to staminal tube - *A. psilostylus*; D, paripinnate leaves - *A. muschianus*; E, *A. verus*; F, claw of wing and keel adnate to staminal tube - *A. globiflorus*.

Conclusions

The ITS region provided significant resolution for *Astragalus* species and even with some limitation, the basic evolutionary history of this genus has become clearer. Therefore, the small percentage of nucleotide sequence variations along with some morphological characteristics, which have been not used previously in any other studies or floras, could provide appropriate criteria in setting the taxon boundaries in new groups.

Synopsis key to new groups

1. Keels broad, *Colutea* type, ca. 3–10 mm wide, equaling to minutely longer or rarely minutely shorter than the wing-petals 2
 - Keels narrow, plants spiny or herbaceous, claw less than 3 mm wide, if wider, then corolla violet or purplish, shorter than the wing-petals. Covered with basifixed or medifixed hairs 3
 2. Plants perennial, usually herbaceous, rarely shrublet or woody base, usually covered with basifixed hairs on vegetative parts, very rarely with medifixed hairs. Claw of keel shorter or equaling the blade **1. Group I**

-Plants perennial, subcaulescent or caespitose. Vegetative part always covered with basifixed hairs. Claw of keel longer than the blade. Growing in Far-East **2. Group IV**
 3. Leaves always paripinnate, but very rarely imparipinnate, in this case plant covered with basifixed hairs. Claw of the wings and keels in different length adnate to the staminal tube. Inflorescens or synflorescens dense beside subtending leaves. In cross section of the stems there are different size of gum duct. If raceme in terminal or paraclad then calyx inflated **4. Group VI**
 -Leaves imparipinnate. Wings and keel free from staminal tube. Corolla purplish, rarely yellowish. Calyx covered with basifixed or mixed with medifixed hairs 4
 4. Plant absolutely acaulescent, with single leaf or with many pairs of leaflets, only covered with medifixed hairs **6. Group V**
 -Plants covered with basifixed or medifixed hairs, annuals or perennials, erect or prostrate 5

5. Calyx covered with basifixed hairs, inner side of the teeth glabrous. Stem and leaflets covered with basifixed hairs 6
 -Annual or perennial, erect or prostrate **2. Group II**
 6. Annual or perennial. Calyx campanulate. Vegetative parts covered with basifixed or very symmetric medifixed hairs. Plant usually growing in the humid or meadow habitat **3. Group III**
 -Calyx at the teeth mouth closed. Vegetative parts covered with basifixed or medifixed hairs and in some

sections mixed with two kinds hairs, inner side of teeth with basifixed or very asymmetric medifixed hairs. Stem and leaves covered with symmetric, very asymmetric medifixed or clearly basifixed hairs. Inflorescence dense or lax raceme. Corolla usually violet, purple or rarely yellowish **7. Group IV**

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Appendix 1. Taxa included in nrDNA ITS phylogenetic analyses.

Species	Section	Subgenus/ Phalanx	Origin, Voucher accession and herbarium	Gene bank accession no.
<i>Astragalus epiglottis</i> L.	<i>Epiglottis</i>	<i>Epiglottis</i>	Morocco; Podlech 45851 (TARI)	AB051910
<i>A. echinatus</i> Murray			Morocco; Podlech 46718 (TARI)	AB051938
<i>A. vogelii</i> (Webb.) Bornm.	<i>Herpocaulos</i>	<i>Epiglottis</i>	Iran; Mozaffarian & al. 39103 (TARI)	AB051911
<i>A. commixtus</i> Bunge	<i>Ankylotus</i>	<i>Trimeniaeus</i>	Iran; Assadi & Maassoumi 55701 (TARI)	AB051925
<i>A. annularis</i> Forsskal	<i>Annulares</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 51921 (TARI)	AB051912
<i>A. arpilobus</i> Kar. & Kir.	<i>Annulares</i>	<i>Trimeniaeus</i>	Iran; Freitag & Mozaffarian 28435 (TARI)	AB051913
<i>A. campylorrhynchus</i> Fischer	<i>Annulares</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 47561 (TARI)	AB051914
<i>A. crenatus</i> Schultes	<i>Annulares</i>	<i>Trimeniaeus</i>	Iran; Foroughi 55 (TARI)	AB051915
<i>A. eremophilus</i> Boiss.	<i>Annulares</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 52028 (TARI)	AB051916
<i>A. edulis</i> Dur. ex Bunge	<i>Edodimus</i>	<i>Trimeniaeus</i>	Israel; USDA 244273	AF121677
<i>A. hamosus</i> L.	<i>Bucerates</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 47586 (TARI)	AB051936
<i>A. boeticus</i> L.	<i>Cyamodes</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 51949 (TARI)	AB051937
<i>A. dipelta</i> Bunge (syn. <i>Didymopeltaturkestanica</i> Regel & Schmalh.)	<i>Dipelta</i>	<i>Trimeniaeus</i>	Iran; Assadi & Maassoumi 50172 (TARI)	AB051926
<i>A. guttatus</i> Banks & Soland	<i>Heterodontus</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 56984 (TARI)	AB051935
<i>A. bakaliensis</i> Bunge	<i>Hispiduli</i>	<i>Trimeniaeus</i>	Iran; Bonvan 9922 (TARI)	AB051924
<i>A. duplostrigosus</i> Post & Beauverd	<i>Hispiduli</i>	<i>Trimeniaeus</i>	Iran; Bokhari & Wendelbo 113 (TARI)	AB051923
<i>A. biserrula</i> Bunge	<i>Oxyglottis</i>	<i>Trimeniaeus</i>	Iran; Wendelbo & Assadi 28021 (TARI)	AB051931
<i>A. oxyglottis</i> Bieb.	<i>Oxyglottis</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 52079 (TARI)	AB051932
<i>A. schmalhauseni</i> Bunge (syn. <i>Sewerzowiaturkestanica</i> Regel & Schmalh.)	<i>Oxyglottis</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 55146 (TARI)	AB051933
<i>A. vicarius</i> Lipsky (syn. <i>Sewerzowiacaria</i> (Lipsky) Rassulova)	<i>Oxyglottis</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 47570 (TARI)	AB051934
<i>A. echinatus</i> Murray	<i>Pentaglottis</i>	<i>Trimeniaeus</i>	Morocco; Podlech 46718 (TARI)	AB051938
<i>A. bombycinus</i> Boiss.	<i>Platyglottis</i>	<i>Trimeniaeus</i>	Iran; Babakhanlou & Amin 15422 (TARI)	AB051929
<i>A. asterias</i> Hohen.	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Runemark & Mozaffarian 30957 (TARI)	AB051917
<i>A. camptoceras</i> Bunge	<i>Platyglottis</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 47576 (TARI)	AB051930
<i>A. coronilla</i> Bunge	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Assadi & Maassoumi 55895 (TARI)	AB051918
<i>A. filicaulis</i> Kar. & Kir.	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Assadi & Maassoumi 50762 (TARI)	AB051919
<i>A. persepolitianus</i> Boiss.	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Foroughi & Assadi 17897 (TARI)	AB051920

Appendix 1. Continued.

Species	Section	Subgenus/ Phalanx	Origin, Voucher accession and herbarium	ITS accession No.
<i>A. sesamoides</i> Boiss.	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Assadi & Maassoumi 50670 (TARI)	AB051921
<i>A. tribuloides</i> Delile	<i>Sesamei</i>	<i>Trimeniaeus</i>	Iran; Maassoumi & Abouhamzeh 52003 (TARI)	AB051922
<i>A. brachypetalus</i> Trautv.	<i>Hypoglottidei</i>	<i>Hypoglottis</i>	Iran; Wendelbo & Foroughi 12655 (TARI)	AB051999
<i>A. perpexus</i> Maassoumi	<i>Hypoglottidei</i>	<i>Hypoglottis</i>	Iran; Mozaffarian 59969 (TARI)	AB051998
<i>A. pishchakensis</i> Maassoumi	<i>Hypoglottidei</i>	<i>Hypoglottis</i>	Iran; Mozaffarian 27388 (TARI)	AB052000
<i>A. deickianus</i> Bornm.	<i>Malacothrix</i>	<i>Hypoglottis</i>	Iran; Maassoumi & Mirhosseini 59381 (TARI)	AB051992
<i>A. heterodoxus</i> Bunge	<i>Malacothrix</i>	<i>Hypoglottis</i>	Iran; Assadi & Bazgosha 56102 (TARI)	AB051991
<i>A. holopsilus</i> Bunge	<i>Malacothrix</i>	<i>Hypoglottis</i>	Iran; Mozaffarian 54347 (TARI)	AB051989
<i>A. macrostachys</i> DC.	<i>Malacothrix</i>	<i>Hypoglottis</i>	Iran; Maassoumi & Abouhamzeh 56992 (TARI)	AB051990
<i>A. coelicolor</i> Sirj. & Rech. f.	<i>Plagiophaca</i>	<i>Hypoglottis</i>	Iran; Wendelbo & Assadi 29725 (TARI)	AB051995
<i>A. capito</i> Boiss.	<i>Stereothix</i>	<i>Hypoglottis</i>	Iran; Foroughi 2913 (TARI)	AB051996
<i>A. ledinghamii</i> Barneby	<i>Stereothix</i>	<i>Hypoglottis</i>	Iran; Mozaffarian 44676 (TARI)	AB051997
<i>A. hemsleyi</i> Aitch. & Baker	<i>Acanthophace</i>	<i>Phaca</i>	Iran; Zarre 69578 (TARI)	AB052003
<i>A. horridus</i> Boiss.	<i>Acanthophace</i>	<i>Phaca</i>	Iran; Mozaffarian 54874 (TARI)	AB052002
<i>A. schistocalyx</i> Bunge	<i>Acanthophace</i>	<i>Phaca</i>	Iran; Assadi & Maassoumi 21256 (TARI)	AB052004
<i>A. basineri</i> Trautv.	<i>Astragalus</i>	<i>Phaca</i>	Iran; Assadi & Maassoumi 50259 (TARI)	AB051943
<i>A. caraganae</i> Fisch. & Mey.	<i>Astragalus</i>	<i>Phaca</i>	Iran; Mozaffarian & Maassoumi 48076 (TARI)	AB051942
<i>A. retamocarpus</i> Boiss. & Hohen.	<i>Astragalus</i>	<i>Phaca</i>	Iran; Maassoumi 55136 (TARI)	AB051944
<i>A. aegobromus</i> Boiss. & Hohen.	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 55116 (TARI)	AB051953
<i>A. citrinus</i> Bunge	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 47586 (TARI)	AB051954
<i>A. curvipes</i> Trautv.	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 47553 (TARI)	AB051955
<i>A. multijugus</i> DC.	<i>Caprini</i>	<i>Phaca</i>	Iran; Mozaffarian & Maassoumi 47957 (TARI)	AB051956
<i>A. nephtonensis</i> Freyn	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 55006 (TARI)	AB051957
<i>A. urmiensis</i> Bunge	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 55137 (TARI)	AB051958
<i>A. vereskensis</i> Maassoumi & Podl.	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 55016 (TARI)	AB051959
<i>A. vulcanicus</i> Bornm.	<i>Caprini</i>	<i>Phaca</i>	Iran; Maassoumi 55134 (TARI)	AB051960
<i>A. membranaceus</i> Bunge	<i>Cenanthrum</i>	<i>Phaca</i>	China; Hu 1131	AF121675c
<i>A. umbellatus</i> Bunge	<i>Cenanthrum</i>	<i>Phaca</i>	USA; Parker 88-78	AF121683c
<i>A. atropilosulus</i> (Hochst.) Bunge	<i>Chlorostachys</i>	<i>Phaca</i>	Ethiopia; Yamashita & al. 1068 (KYO)	AB051939
<i>A. dactylocarpus</i> Boiss.	<i>Chronopus</i>	<i>Phaca</i>	Iran; Freitag & Mozaffarian 28506 (TARI)	AB051945
<i>A. jesdianus</i> Boiss. & Buhse	<i>Chronopus</i>	<i>Phaca</i>	Iran; Assadi 23236 (TARI)	AB051946
<i>A. glycyphyllus</i> L.	<i>Glycyphyllus</i>	<i>Phaca</i>	Iran; Assadi & Sardabi 24090 (TARI)	AB051941
<i>A. daenensis</i> Boiss.	<i>Hemiphaca</i>	<i>Phaca</i>	Iran; Foroughi & Assadi 18019 (TARI)	AB051963
<i>A. zerdanus</i> Boiss.	<i>Hemiphaca</i>	<i>Phaca</i>	Iran; Assadi & Abouhamzeh 46167 (TARI)	AB051964
<i>A. williamsii</i> Rydb.	<i>Hemiphaca</i>	<i>Phaca</i>	Canada; Calder & Gillett 25825	AF121685c
<i>A. australis</i> (L.) Lam.	<i>Hemiphragmium</i>	<i>Phaca</i>	USA; Tiehm & Williams 11985	AF121686c
<i>A. lamprocarpus</i> Maassoumi	<i>Lamprocarpa</i>	<i>Phaca</i>	Iran; Runemark & Lazari 26506 (TARI)	AB052015
<i>A. sinicus</i> L.	<i>Lotidium</i>	<i>Phaca</i>	Japan; Kazempour Osaloo 1999-01 (TARI)	AB051965
<i>A. nankotaizanensis</i> Sasaki	<i>Lotidium</i>	<i>Phaca</i>	Taiwan; Hu 1062	AF121680c
<i>A. paradoxus</i> Bunge	<i>Macrosemium</i>	<i>Phaca</i>	Iran; Wendelbo & Assadi 19281 (TARI)	AB052001
<i>A. chinensis</i> L.	<i>Nuculiella</i>	<i>Phaca</i>	Switzerland; USDA 415802	AF121681c
<i>A. peltatus</i> Podl. & Deml	<i>Pelta</i>	<i>Phaca</i>	Afghanistan; Rechinger 37517 (TARI)	AB052034

Appendix 1. Continued.

Species	Section	Subgenus/ Phalanx	Origin, Voucher accession and herbarium	ITS accession No.
<i>A. dieterlei</i> Podl.	<i>Pendulina</i>	<i>Phaca</i>	Iran; Mirtajaddini 19500b (TARI)	AB051961
<i>A. polycladus</i> Bureau & Franchet	<i>Polycladus</i>	<i>Phaca</i>	China; Donoghue 094 (1996)	AF121676
<i>A. siliquosus</i> Boiss.	<i>Theiochrus</i>	<i>Phaca</i>	Iran; Assadi & Maassoumi 50465 (TARI)	AB051940
<i>A. macrosemius</i> Boiss & Hohen.	<i>Acidodes</i>	<i>Calycophysa</i>	Iran; Wendelbo & Cobham 14495 (TARI)	AB052030
<i>A. saheni</i> Buhse	<i>Acidodes</i>	<i>Calycophysa</i>	Iran; Mozaffarian 69854 (TARI)	AB052029
<i>A. alopecias</i> Pallas	<i>Alopecuroidei</i>	<i>Calycophysa</i>	Iran; Assadi & Mozaffarian 35930 (TARI)	AB051949
<i>A. jessenii</i> Bunge	<i>Alopecuroidei</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Maassoumi 48062 (TARI)	AB051950
<i>A. kirrindicus</i> Boiss.	<i>Alopecuroidei</i>	<i>Calycophysa</i>	Iran; Maassoumi 55130 (TARI)	AB051951
<i>A. obtusifolius</i> DC.	<i>Alopecuroidei</i>	<i>Calycophysa</i>	Iran; Maassoumi & Abouhamzeh 52015 (TARI)	AB051952
<i>A. eriostomus</i> Bornm.	<i>Anthylloidei</i>	<i>Calycophysa</i>	Iran; Mozaffarian 63794 (TARI)	AB052007
<i>A. khoshjailensis</i> Sirj. & Rech. f.	<i>Anthylloidei</i>	<i>Calycophysa</i>	Iran; Maassoumi 47580 (TARI)	AB052010
<i>A. murinus</i> Boiss.	<i>Anthylloidei</i>	<i>Calycophysa</i>	Iran; Assadi & Abouhamzeh 46094 (TARI)	AB052008
<i>A. submits</i> Boiss. & Hohen.	<i>Anthylloidei</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Maassoumi 47960 (TARI)	AB052009
<i>A. campylanthus</i> Boiss.	<i>Campylanthus</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Maassoumi 47790 (TARI)	AB052028
<i>A. chiwensis</i> Bunge	<i>Eremophysa</i>	<i>Calycophysa</i>	Iran; Freitag & Jadidi 29007 (TARI)	AB051962
<i>A. grammocalyx</i> Boiss & Hohen.	<i>Grammocalyx</i>	<i>Calycophysa</i>	Iran; Maassoumi 55123 (TARI)	AB051994
<i>A. chrysostachys</i> Boiss.	<i>Hymenostegis</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Nowruzi 34108 (TARI)	AB052011
<i>A. lagopoides</i> Lam.	<i>Hymenostegis</i>	<i>Calycophysa</i>	Iran; Assadi & Olfat 68825 (TARI)	AB052013
<i>A. straussii</i> Bornm.	<i>Hymenostegis</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Maassoumi 47793 (TARI)	AB052012
<i>A. cephalanthus</i> DC.	<i>Microphysa</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Maassoumi 47788 (TARI)	AB052027
<i>A. fasciculifolius</i> Boiss.	<i>Poterion</i>	<i>Calycophysa</i>	Iran; Mozaffarian 49867 (TARI)	AB052016
<i>A. tawilicus</i> Townsend	<i>Laxiflori</i>	<i>Calycophysa</i>	Iran; Maassoumi 59351 (TARI)	AB051948
<i>A. dictyolobus</i> Bunge	<i>Laxiflori</i>	<i>Calycophysa</i>	Iran; Mozaffarian 69963 (TARI)	AB051947
<i>A. glaucacanthos</i> Fischer	<i>Poterion</i>	<i>Calycophysa</i>	Iran; Assadi & al. 33356 (TARI)	AB052017
<i>A. magistratus</i> Maassoumi & al.	<i>Tricholobus</i>	<i>Calycophysa</i>	Iran; Assadi & Mozaffarian 35244 (TARI)	AB052032
<i>A. tricholobus</i> ssp. <i>tricholobus</i> emend. Tietz	<i>Tricholobus</i>	<i>Calycophysa</i>	Iran; Mozaffarian & Nowroozi 34005 (TARI)	AB052031
<i>A. cerasocrenus</i> Bunge (syn. <i>Astracantha cerasocrena</i> (Bge.) Podl.)	<i>Adiaspastus</i>	<i>Tragacantha</i>	Iran; Assadi & Maassoumi 50846 (TARI)	AB052022
<i>A. brachycalyx</i> Fischer (syn. <i>Astracantha brachycalyx</i> (Fisch.) Podl.)	<i>Brachycalyx</i>	<i>Tragacantha</i>	Iran; Assadi & Mozaffarian 37096 (TARI)	AB052026
<i>A. caspius</i> Bieb. (syn. <i>Astracantha Caspica</i> (Bieb.) Podl.)	<i>Brachycalyx</i>	<i>Tragacantha</i>	Iran; Mozaffarian & Maassoumi 48081 (TARI)	AB052025
<i>A. hystrix</i> Bunge	<i>Hystrix</i>	<i>Tragacantha</i>	Iran; Maassoumi & Mozaffarian 78604 (TARI)	AB052014
<i>A. oleifolius</i> DC. (syn. <i>Astracantha oleifolia</i> (DC.) Podl.)	<i>Macrophyllum</i>	<i>Tragacantha</i>	Iran; Maassoumi & Mozaffarian 79612 (TARI)	AB052019
<i>A. verus</i> Olivier	<i>Platonychium</i>	<i>Tragacantha</i>	Iran; Mozaffarian & Maassoumi 47797 (TARI)	AB052023

Appendix 1. Continued.

Species	Section	Subgenus/ Phalanx	Origin, Voucher accession and herbarium	ITS accession No.
<i>A. piptocephalus</i> Boiss.	<i>Polystegis</i>	<i>Tragacantha</i>	Iran; Maassoumi & Mozaffarian 76763 (TARI)	AB052018
<i>A. stenolepis</i> Fischer	<i>Rhacophorus</i>	<i>Tragacantha</i>	Iran; Maassoumi 55128 (TARI)	AB052021
<i>A. trachyacanthos</i> Fischer	<i>Rhacophorus</i>	<i>Tragacantha</i>	Iran; Mozaffarian & Maassoumi 47962 (TARI)	AB052024
<i>A. rhodosemius</i> Boiss. & Hausskn.	<i>Rhacophorus</i>	<i>Tragacantha</i>	Iran; Maassoumi & Mozaffarian 78702 (TARI)	AB052020
<i>A. acantherioceras</i> Rech. f. & Koie	<i>Acantherioceras</i>	<i>Cercidothrix</i>	Iran; Mozaffarian 48627 (TARI)	AB051977
<i>A. fragrans</i> Willd.	<i>Acmothrix</i>	<i>Cercidothrix</i>	Iran; Maassoumi & Abouhamzeh 56916 (TARI)	AB051967
<i>A. macrobotrys</i> Bunge	<i>Ammodendron</i>	<i>Cercidothrix</i>	Iran; Assadi & Mozaffarian 35654 (TARI)	AB051986
<i>A. squarrosus</i> Bunge	<i>Ammodendron</i>	<i>Cercidothrix</i>	Iran; Maassoumi & Abouhamzeh 52026 (TARI)	AB051987
<i>A. stocksii</i> Benth. ex Bunge	<i>Caraganella</i>	<i>Cercidothrix</i>	Iran; Foroughi 10802 (TARI)	AB051966
<i>A. ochreatus</i> Bunge	<i>Cremoceras</i>	<i>Cercidothrix</i>	Iran; Assadi & Maassoumi 55568 (TARI)	AB051981
<i>A. masanderanus</i> Bunge	<i>Cystium</i>	<i>Cercidothrix</i>	Iran; Maassoumi 55127 (TARI)	AB051969
<i>A. gigantirostratus</i> Maassoumi & al.	<i>Cytisodes</i>	<i>Cercidothrix</i>	Iran; Maass. & al. 72339 (TARI)	AB052033
<i>A. anacamptus</i> Bunge	<i>Erioceras</i>	<i>Cercidothrix</i>	Iran; Assadi & Mozaffarian 35835 (TARI)	AB051978
<i>A. alyssoides</i> Lam.	<i>Hololeuce</i>	<i>Cercidothrix</i>	Iran; Maassoumi 64819 (TARI)	AB051970
<i>A. campylosema</i> Boiss.	<i>Incani</i>	<i>Cercidothrix</i>	Iran; Mozaffarian & Nowroozi 34384 (TARI)	AB051984
<i>A. latifolius</i> Lam.	<i>Incani</i>	<i>Cercidothrix</i>	Iran; Assadi & Mozaffarian 30428 (TARI)	AB051982
<i>A. robustus</i> Bunge	<i>Incani</i>	<i>Cercidothrix</i>	Iran; Maassoumi 64906 (TARI)	AB051983
<i>A. curviflorus</i> Boiss.	<i>Leucocercis</i>	<i>Cercidothrix</i>	Iran; Zehzad & al. 66937 (TARI)	AB052005
<i>A. mucronifolius</i> Boiss.	<i>Leucocercis</i>	<i>Cercidothrix</i>	Iran; Riazi 5905 (TARI)	AB052006
<i>A. cancellatus</i> Bunge	<i>Onobrychoidei</i>	<i>Cercidothrix</i>	Iran; Foroughi 6259 (TARI)	AB051972
<i>A. teheranicus</i> Boiss.	<i>Onobrychoidei</i>	<i>Cercidothrix</i>	Iran; Emami 31838 (TARI)	AB051973
<i>A. ornithopodioides</i> Lam.	<i>Ornithopodium</i>	<i>Cercidothrix</i>	Iran; Mozaffarian & Nowroozi 34629 (TARI)	AB051975
<i>A. shelkovnikovii</i> Grossh.	<i>Ornithopodium</i>	<i>Cercidothrix</i>	Iran; Foroughi 6032 (TARI)	AB051971
<i>A. dolichophyllus</i> Pallas	<i>Trachycercis</i>	<i>Cercidothrix</i>	Iran; Assadi & Maassoumi 20244 (TARI)	AB051980
<i>A. scaberrimus</i> Bunge	<i>Trachycercis</i>	<i>Cercidothrix</i>	China; Wang & al. 17 (KYO)	AB051988
<i>A. falcatus</i> Lam.	<i>Uliginosi</i>	<i>Cercidothrix</i>	USA; Weber 15359	U50488-9c
<i>A. odoratus</i> Lam.	<i>Uliginosi</i>	<i>Cercidothrix</i>	Iran; Mozaffarian 64537 (TARI)	AB051968
<i>A. oreganus</i> Nutt. ex T. & G.	<i>Uliginosi</i>	<i>Cercidothrix</i>	USA; McCarthy 107	AF121687
<i>A. xiphidioides</i> Freyn & Sint.	<i>Xiphidium</i>	<i>Cercidothrix</i>	Iran; Mozaffarian 67591 (TARI)	AB051976
<i>A. ascicalyx</i> Bunge	<i>Asciocalyx</i>	<i>Calycocystis</i>	Iran; Assadi & Maassoumi 50328 (TARI)	AB051974
<i>A. subsecundus</i> Boiss.	<i>Laguropsis</i>	<i>Calycocystis</i>	Iran; Maassoumi 55105 (TARI)	AB051985
<i>A. pseudorhacodes</i> Gontsch.	<i>Macrocystodes</i>	<i>Calycocystis</i>	Iran; Assadi & Mozaffarian 35472 (TARI)	AB051979
<i>A. arizonicus</i> A. Gray	<i>Leptocarpi</i>	<i>Piptolobi</i>	USA; Sanderson 968	AF121690
<i>A. oophorus</i> Wats.	<i>Megacarpis</i>	<i>Piptolobi</i>	USA; Tiehm 12045 (KYO)	AB051993
<i>Barnebyella calycina</i> (Stocks) Podl. (syn. <i>Astragalus migpo</i> R. Kam.)	<i>Mirae</i>	<i>Trimeniaeus</i>	Iran; Reching 51029 (TARI)	AB051928
<i>Biserrulla pelecimus</i> L. (syn. <i>Astragalus pelecimus</i> (L.) Barneby)	<i>Biserrula</i>	<i>Trimeniaeus</i>	Australia (adventive); USDA186284	U50518-9

Appendix 1. Continued.

Species	Section	Subgenus/ Phalanx	Origin, Voucher accession and herbarium	ITS accession No.
<i>Ophiocarpus aitchisonii</i> (Baker) Podl. (syn. <i>Astragalus ophiocarpus</i> Bunge)	<i>Ophiocarpus</i>	<i>Trimeniaeus</i>	Iran; Maassoumi 55143 (TARI)	AB051927
<i>Caragana grandiflora</i> (M. B.) DC.			Iran; Assadi & Shahsavari 65834 (TARI)	AB051905
<i>Chesneya astragalina</i> Jaub. & Spach.			Iran; Assadi & Maassoumi 55503 (TARI)	AB051906
<i>Colutea persica</i> Boiss.			Iran; Foroughi 17434 (TARI)	AB051907
<i>Oxytropis aucheri</i> Boiss.			Iran; Maassoumi 55104 (TARI)	AB051908
<i>O. szovitsii</i> Boiss. & Buhse			Iran; Maassoumi 55090 (TARI)	AB051909

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