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## Morphological cladistic analysis of some bifurcate hairy sections of *Astragalus* (Fabaceae) in Iran

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**Abstract:** The phylogenetic relationships among some bifurcate hairy sections of *Astragalus* L. were reconstructed using 38 vegetative and reproductive morphological characters. A data matrix comprising 36 ingroups and 2 outgroups was analysed using the maximum parsimony method. The present results revealed that sections *Onobrychoidei* DC. and *Ornithopodium* Bunge are interrelated taxa and form a single monophyletic group. The current status of section *Dissitiflori* DC. is a nonmonophyletic group. Its members form several subclades and unresolved branches across the tree. Sections *Erioceras* Bunge and *Cytisodes* Bunge as well as *Corethrum* Bunge are sister taxa and form weakly to highly supported monophyletic groups, respectively. *Astragalus pravitzii* Podlech, which was recently transferred to section *Ornithopodium* from section *Dissitiflori*, has no affinity with that section.

**Key words:** *Astragalus*, cladistic, *Dissitiflori*, *Erioceras*, *Ornithopodium*, *Onobrychoidei*, phylogeny

### Introduction

*Astragalus* L. (Fabaceae) is probably the largest genus of flowering plants on earth and contains an estimated 2500 annual and perennial species and about 250 sections worldwide (Lock & Simpson, 1991; Podlech, 1998). The majority of species are found in the temperate semiarid and arid continental regions of south-western and central Asia, the Sino-Himalayan region, western North America, and along the Andes in South America (Lock & Simpson, 1991; Yakovlev et al., 1996; Maassoumi, 1998). Moreover, many

*Astragalus* species are distributed in Mediterranean climatic regions along the Pacific coasts of North and South America and in southern Europe and northern Africa (Maassoumi, 1998). South-western and central Asia is the centre of diversity for *Astragalus*, and there may be more than 800 species (belonging to more than 60 sections) in Iran, which has a high endemism rate of 65% (Podlech, 1986, 1998, 1999; Maassoumi, 1998, 2003, 2005). The earlier classification of *Astragalus* was carried out by De Candolle (1825) at the sectional level. After him,

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Bunge (1868-69) recognised 10 subgenera for the Old World *Astragalus*, and 9 of these were accepted by Gontscharov et al. (1946) for the flora of the former USSR. Podlech (1982) further reduced the number of subgenera by recognising only 2 groups of perennials, subgenera *Astragalus* and *Cercidothrix* Bunge, solely on the basis of type of pubescence; annual species were placed within subgenus *Trimeniaeus* Bunge irrespective of hair characteristics (Podlech, 1994). Later on, Maassoumi (1998) reduced Bunge's subgenera to 8 by transferring the species of 2 subgenera, *Caprinus* Bunge and *Pogonophace* Bunge, into others. Various molecular studies on the genus showed that none of these subgenera are monophyletic groups (Wojciechowski et al., 1999; Kazempour Osaloo et al., 2003, 2005). As a result, Maassoumi (2003) did not accept any subgenera for the genus while revising *Astragalus* for *Flora of Iran*. The only inclusive molecular phylogenetic analyses of the Old World *Astragalus* using nrDNA ITS and, in part, plastid gene *ndhF* sequences demonstrated 8 large monophyletic groups (so-called A to H; Kazempour Osaloo et al., 2003, 2005), as none of these overlap with those subgeneric classifications. Among the many species-rich sections analysed in these studies, only sections *Ammodendron* Bunge, *Cenanthrum* Koch, *Chronopus* Bunge, *Laxiflori* Agerer-Kirchhoff, *Lotidium* Bunge, and *Incani* DC. are monophyletic. Based on the work of Kazempour Osaloo et al. (2003, 2005), sections with basifixed hairs are basal, and some of these are intermixed with medifixed sections in the upper part of the cladograms. However, with these results, the phylogenetic relationships among many sections remained largely unresolved, requiring complementary molecular and morphological studies using more taxon sampling of each section. On the basis of these molecular analyses (Kazempour Osaloo et al., 2003, 2005), some bifurcate hairy species belonging to sections such as *Dissitiflori* DC., *Erioceras* Bunge, *Onobrychoidei* DC., and *Ornithopodium* Bunge form a large polytomic assemblage (clade F; Kazempour Osaloo et al., 2003, 2005) that shows some affinity; however, relationships among them remained unresolved. Although the above mentioned sections have been studied taxonomically in Iran or adjacent regions by various authors (Gahreman et al., 1996; Maassoumi et al., 2000; Ranjbar & Karamian, 2002; Ranjbar, 2004;

Gahremani-nejad, 2004; Maassoumi, 2005; Ekici et al., 2011), no previous molecular or morphological phylogenetic study has focused on these exclusively.

The objectives of the present study were to test the phylogenetic status of sections *Dissitiflori*, *Erioceras*, *Onobrychoidei*, *Ornithopodium*, *Corethrurum* Bunge, and *Cytisodes* Bunge in Iran on the basis of morphological features and to explore the position of some debatable and newly introduced species from Iran in relation to these sections.

## Materials and methods

### Taxon sampling

A total of 34 species of *Astragalus* representing some related sections (*Dissitiflori*, *Erioceras*, *Corethrurum*, *Onobrychoidei*, and *Ornithopodium*) plus 2 species belonging to the section *Cytisodes* were included as ingroup taxa in the analyses. Based on previous phylogenetic studies of the various sections of *Astragalus* (Kazempour Osaloo et al., 2003, 2005), 2 species in sections *Incani* DC. and *Caraganelia* Bunge were selected as outgroups.

### Characters and character states

Characters used in the cladistic analyses were obtained through examination of fresh materials in the field and herbarium specimens deposited at the Central Herbarium of Iran (TARI), the herbarium at Shahid Beheshti University (S. Beheshti Univ. Hb.), and the herbarium of Ferdowsi University (FUMH). Voucher specimen information is given in Table 1. The 38 characters and their relevant states used in the present analyses are given in Table 2. The data matrix is given in Table 3. Character state transformations were selected as unordered. The polarity of characters was determined using the outgroup method (Maddison et al., 1984).

### Cladistic analyses

Analyses were performed on the data matrix using maximum parsimony (MP) as implemented in version 4.0b10 of PAUP\* (Swofford, 2002). Multiple tree searches were conducted using heuristic search options that included random addition sequences (1000 replicates) holding 5 trees per replicate, and tree bisection-reconnection (TBR) branch swapping with retention of multiple parsimonious trees (maximum

Table 1. Voucher information for specimens used in present cladistic analysis.

Species	Voucher	Section
<i>A. argyroides</i> Beck	31795 (TARI); 31777 (TARI); 15323 (TARI)	<i>Dissitiflori</i>
<i>A. eburneus</i> Bornm. & Gauba	44936 (TARI); 43050 (TARI); 42868 (TARI)	<i>Dissitiflori</i>
<i>A. juladakensis</i> Maassoumi	50898 (TARI); 90551 (S. Beheshti Univ. Hb.)	<i>Dissitiflori</i>
<i>A. juratzkanus</i> Freyn & Sint.	72351 (TARI); 39457 (TARI); 92530 (S. Beheshti Univ. Hb.)	<i>Dissitiflori</i>
<i>A. melanocalyx</i> Boiss. & Buhse	5860 (TARI); 15263 (TARI); 17976 (TARI)	<i>Dissitiflori</i>
<i>A. nigrolineatus</i> Sirj. & Rech. f.	29042 (FUMH); 11988 (FUMH); 22773 (FUMH)	<i>Dissitiflori</i>
<i>A. pravitzii</i> Podlech	2118 (TARI); 7362 (TARI); 2607 (TARI)	<i>Dissitiflori</i>
<i>A. saadatabadensis</i> Podlech	15784 (TARI); 92531 (S. Beheshti Univ. Hb.); 92532 (S. Beheshti Univ. Hb.)	<i>Dissitiflori</i>
<i>A. sitiens</i> Bunge	26633 (TARI); 11270 (TARI); 28806 (TARI)	<i>Dissitiflori</i>
<i>A. ruscifolius</i> Boiss.	92535 (S. Beheshti Univ. Hb.); 28640 (TARI); 15798 (TARI)	<i>Dissitiflori</i>
<i>A. xiphidium</i> Bunge	72780 (TARI); 4425 (TARI); 228 (TARI)	<i>Dissitiflori</i>
<i>A. brachyodontus</i> Boiss.	92533 (S. Beheshti Univ. Hb.); 27666 (TARI); 13735 (TARI)	<i>Ornithopodium</i>
<i>A. glochideus</i> Boiss.	56952 (TARI); 55145 (TARI); 82606 (TARI)	<i>Ornithopodium</i>
<i>A. jodostachys</i> Boiss. & Buhse	56871 (TARI); 45496 (TARI); 80113 (TARI)	<i>Ornithopodium</i>
<i>A. lunatus</i> Pall.	12396 (TARI); 82421 (TARI); 75469 (TARI)	<i>Ornithopodium</i>
<i>A. ornithopodioides</i> Lam.	27860 (TARI); 28015 (TARI); 80129 (TARI)	<i>Ornithopodium</i>
<i>A. stevenianus</i> DC.	30128 (TARI); 41104 (TARI); 30067 (TARI)	<i>Ornithopodium</i>
<i>A. goktschaicus</i> Grossh.	68845 (TARI); 70521 (TARI); 13756 (TARI)	<i>Onobrychoidei</i>
<i>A. lilacinus</i> Boiss.	33157 (TARI); 83516 (TARI); 40424 (TARI)	<i>Onobrychoidei</i>
<i>A. tehranicus</i> Boiss.	47890 (TARI); 28824 (TARI); 15814 (TARI)	<i>Onobrychoidei</i>
<i>A. alamliensis</i> Rech. f.	84461 (TARI); 83358 (TARI); 14535 (TARI)	<i>Erioceras</i>
<i>A. anacamptus</i> Bunge	15932 (FUMH); 92532 (S. Beheshti Univ. Hb.); 50423 (TARI)	<i>Erioceras</i>
<i>A. catacamptus</i> Bunge	5328 (TARI); 82720 (TARI); 50423 (TARI)	<i>Erioceras</i>
<i>A. djenarensis</i> Sirj. & Rech. f.	40602 (FUMH); 16786 (TARI); 92555 (S. Beheshti Univ. Hb.)	<i>Erioceras</i>
<i>A. keredjensis</i> Podlech	82404 (TARI); 15449 (TARI); 23515 (TARI)	<i>Erioceras</i>
<i>A. neosytinii</i> Ranjbar	84571 (TARI); 77446 (TARI); 1250 (TARI)	<i>Erioceras</i>
<i>A. nubicola</i> Podlech	11165 (TARI); 2707 (TARI); 92544 (S. Beheshti Univ. Hb.)	<i>Erioceras</i>
<i>A. pakravaniae</i> Podlech & Maassoumi	92563 (S. Beheshti Univ. Hb.); 55534 (TARI); 55472 (TARI)	<i>Erioceras</i>
<i>A. pentanthus</i> Boiss.	1917 (TARI); 82459 (TARI); 16875 (TARI)	<i>Erioceras</i>
<i>A. sympileicarpus</i> Rech. f.	83362 (TARI); 91333 (S. Beheshti Univ. Hb.); 17121 (FUMH)	<i>Erioceras</i>
<i>A. versipilus</i> Rech. f. & Koeie	34272 (FUMH); 84615 (TARI); 25303 (FUMH)	<i>Erioceras</i>
<i>A. zoshkensis</i> Ghahremani-nejad	77059 (TARI); 48819 (TARI)	<i>Cytisodes</i>
<i>A. gigantirostratus</i> Maassoumi	72339 (TARI); 34860 (TARI); 53087 (TARI)	<i>Cytisodes</i>
<i>A. aestimabilis</i> Podlech	38523 (TARI); 1939 (TARI)	<i>Corethron</i>
<i>A. dendroproselius</i> Rech. f.	2832 (TARI); 30231 (TARI); 1152 (TARI)	<i>Corethron</i>
<i>A. viridis</i> Bunge	36132 (TARI); 30231 (TARI); 7329 (TARI)	<i>Corethron</i>
<i>A. supervises</i> (Kuntze) Sheld.	80104 (TARI); 82344 (TARI); 11473 (TARI)	<i>Incani</i>
<i>A. stocksii</i> Benth. ex Bunge	22325 (TARI); 23347 (TARI); 70132 (TARI)	<i>Caraganella</i>

Table 2. Characters and character states used in cladistic analysis.

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1- Habit: spiny lignified (0); nonspiny lignified (1); herbaceous (2).
2- Plant height: $\leq 10$ cm (0); 10-50 cm (1); $> 50$ cm (2).
3- Shoot branching: low (0); high (1).
4- Stem: absent (0); stem with long internodes (1); stem with short internodes (2).
5- Stem status: standing (0); prostrate (1).
6- Stem hair compression: dispersed (0); dense (1).
7- Stem hair status: appressed (0); standing (1).
8- Black hair on stem: absent (0); present (1).
9- Stipule length: $\leq 2$ mm (0); $> 2$ mm (1).
10- Stipule colour: greenish (0); membranous white (1).
11- Stipule hair compression: dispersed (0); dense (1).
12- Stipule hair colour: only white (0); white mixed with black (1).
13- Leaf type: paripinnate (0); imparipinnate (1); single leaflet (2).
14- Leaf length: $\leq 2$ cm (0); 2-7 cm (1); $> 7$ cm (2).
15- Leaflet pairs number: $\leq 3$ (0); 3-10 (1); $> 10$ (2).
16- Leaflet L/W ratio: $\leq 1.5$ (0); $> 1.5$ (1).
17- Leaflet shape: linear (0); oblong elliptic (1); elliptic (2); obovate (3).
18- Leaflet hair type: both sides densely covered (0); both sides dispersedly covered (1); one side densely and other dispersedly covered (2).
19- Black hair on peduncle: absent (0); present (1).
20- Inflorescence: sparse raceme (0); dense raceme (1).
21- Calyx type: campanulate (0); tubular (1); gibbose tubular (2).
22- Calyx hair status: appressed hair (0); standing hair (1).
23- Calyx hair symmetry: symmetrical (0); asymmetrical (1).
24- Calyx length: $\leq 5$ mm (0); 5-15 mm (1); $> 15$ mm (2).
25- Calyx teeth type: equal (0); unequal (1).
26- Calyx teeth internal surface hair: absent (0); present (1).
27- Corolla colour: yellow (0); purple (1); blue (2).
28- Standard L/W ratio: $\leq 2.5$ (0); $> 2.5$ (1).
29- Standard shape: elliptic (0); obovate (1); rhomboid (2).
30- Standard tip: obtuse (0); acute (1); emarginated (2).
31- Ovary stalk: absent (0); present (1).
32- Style hair: absent (0); present (1).
33- Pod shape: linear (0); oblong elliptic (1); beaded linear (2).
34- Pod cross section: orbicular (0); triangular (1).
35- Pod hair: absent (0); present (1).
36- Pod hair type: long and asymmetrical (0); short and symmetrical (1).
37- Hair compression on pod: dispersed (0); dense (1).
38- Black hair on pod: absent (0); present (1).

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Table 3. Data matrix of morphological characters used in cladistic analyses. ?: character states were unavailable.

Character no. Species	1111111112222222223333333333 12345678901234567890123456789012345678
<i>A. supervisus</i>	1110?100100022003011200101001210001110
<i>A. stoksii</i>	021101010000010030100?0010001010200100
<i>A. argyroides</i>	11010100101011013010200111011200001010
<i>A. eburneus</i>	11110101110011110000200101011200001001
<i>A. juratzkanus</i>	11110101110011111010200101010110001001
<i>A. melanocalyx</i>	11110100100011113010200101111210001000
<i>A. nigrolineatus</i>	11010100111011110000200211011000001010
<i>A. pravitzii</i>	11011100111011113000200100000210001000
<i>A. ruscifolius</i>	11110101101011003010200101011200001000
<i>A. saadatabadensis</i>	11011100010011013000200100001210001000
<i>A. sitiens</i>	11010100110011010000200101001000001011
<i>A. xiphidium</i>	11110100110011110010200101010201001010
<i>A. aestimabilis</i>	21110001111011110011211101201000101111
<i>A. dendroproselius</i>	21110101110011111111211101210100101111
<i>A. viridis</i>	21110101111012111101211101211000101111
<i>A. zoshkensis</i>	11120101110012111210211101000101101111
<i>A. gigantirostratus</i>	11120111010011111010111101000000101110
<i>A. juladakensis</i>	12110101110012110010201101?11001101111
<i>A. alamliensis</i>	10021100100111111011211101011200111110
<i>A. anacamptus</i>	10021110100010111011111101001000111110
<i>A. catacamptus</i>	11021100110111112001211111001200111110
<i>A. djenarensis</i>	11021100100011111011211101011200111110
<i>A. keredjensis</i>	11021100110011112011211101111200110???
<i>A. neosytini</i>	11021100100111111011211101012000111110
<i>A. nubicola</i>	1012110011001011101111101002001?????
<i>A. pakravaniae</i>	1102111010001011211121201012200111010
<i>A. pentanthus</i>	1002110011011111201111101112200111110
<i>A. sympileicarpus</i>	10021110100111111011111201010000111110
<i>A. versipilus</i>	10021110100111112011211101111200111110
<i>A. brachyodontus</i>	11110001111011111010100111202200201000
<i>A. glochideus</i>	11110100111111211110100111201100201011
<i>A. ornithopodioides</i>	11110100101011213011000101202200201010
<i>A. jodostachys</i>	11010100101012211110100110201100201011
<i>A. lunatus</i>	11110100111011211100100101110100201001
<i>A. stevenianus</i>	11110100111111111011100111211110201001
<i>A. goktschaicus</i>	11110100101011213011000101202200201010
<i>A. lilacinus</i>	11110000101011110011100111202100201010
<i>A. tehranicus</i>	1111010011111111011100111211110201001

trees = 15,000). Analyses were then conducted using a successive reweighting strategy (Farris, 1989) in order to improve the tree indices and decrease the effect of characters showing high homoplasy on tree topologies. Weights were assigned to characters using the “reweight characters” option based on the rescaled consistency (RC) index (Farris, 1989) with a base weight of 1. After 4 rounds of reweighting, no change in tree indices was observed, and a strict consensus tree of this analysis was computed. Supports for clades were evaluated by bootstrapping (Felsenstein, 1985) using 1000 replicates with the heuristic search option, random addition sequence, and TBR branch swapping.

## Results

The phylogenetic analysis based upon equally weighted characters yielded 327 most-parsimonious trees of 39 steps in length, with a consistency index (CI) of 0.464 and retention index (RI) of 0.821 (Figure 1). All characters used in the analyses were parsimony-informative. Parsimony analysis of equally weighted characters resulted in a phylogenetic tree comprising 2 major clades (Figure 1): 1 clade is composed of 3 species of section *Onobrychoidei* plus 6 species of *Ornithopodium*, and the second is a larger assemblage that comprises members of the remaining sections analysed here. Within this assemblage, 1 subclade is solely composed of section *Erioceras*, weakly supported (bootstrap percentage (BP) = 51%), and the second subclade contains the species of section *Corethrum* (BP = 70%). The relationships within these sections were not properly resolved. All members of section *Dissitiflori* did not form a clade.

Successive reweighting analyses generated 90 most-parsimonious trees of 26.85 steps in length, CI = 0.654, and RI = 0.870. The strict consensus tree of these trees is shown in Figure 2. The general topology of the tree was the same as in Figure 1, except that species relationships were resolved and statistically improved. Within the larger clade, *A. xiphidium* Bunge and *A. juladakensis* Maassoumi were sister taxa (BP = 64%), as were *A. saadatabadensis* Podlech and *A. pravitzii* Podlech. In addition, section *Corethrum* (Maassoumi, 2005) was sister to the sections *Cytisodes* and *Erioceras* (Figure 2). Again, all members of section *Dissitiflori* did not form a clade.

## Discussion

In previous phylogenetic studies based on nrDNA ITS sequences, Kazempour Osaloo et al. (2003, 2005) demonstrated that many sections of *Astragalus* did not form a monophyletic group, as currently circumscribed, and should be revised following additional molecular and morphological studies.

Cladistic analysis of the morphological data revealed that members of sections *Onobrychoidei* and *Ornithopodium* are intermixed and nested in the moderately supported single clade (Figures 1 and 2).

In the phylogenetic tree based on nrDNA ITS sequences, sections *Onobrychoidei* and *Ornithopodium*, plus a few members of *Malacothrix* Bunge, are sister taxa and formed their own subclade within clade F. Within this subclade, *A. ornithopodioides* (sect. *Ornithopodium*) united with *A. tehranicus* Boiss. & Hohen. (sect. *Onobrychoidei*), suggesting that these 2 sections are closely related phylogenetically (Kazempour Osaloo et al., 2003). On the other hand, Ghahremani-nejad (2004) postulated that these 2 sections are gross morphologically interrelated. Our results are also in agreement with the findings of a recent work in which the members of the 2 sections were intermixed on the basis of seed morphology and micromorphology (Vural et al., 2008).

Recently, *Astragalus pravitzii*, endemic to Iran, was separated from section *Dissitiflori* and placed in section *Ornithopodium* by Podlech and Sytin (2010). Our results verified, however, the position of *A. pravitzii* within the section *Dissitiflori*, and it is allied with another member of the section, *A. saadatabadensis* (Figures 1 and 2).

As noted above in Results, members of sections *Cytisodes*, *Corethrum*, *Dissitiflori*, and *Erioceras* were well nested within a single clade (Figure 1).

Section *Cytisodes* is distinguished among bifurcate hairy sections with a stem of short internodes, a calyx with standing and asymmetrical hairs, and long pods (Bunge, 1868-1869). This section was introduced for *Flora of Iran* after the discovery of a remarkable new species (*A. gigantirostratus* Maassoumi, Ghahr., Ghahremani & Matin) from the eastern Elburz Mountains by Maassoumi et al. (1999). Later on, Maassoumi (2005) moved the newly established species, *A. zoshkensis* F.Ghahremani. (Ghahremani-nejad, 2003), from section *Dissitiflori* to *Cytisodes* based on calyx hairs and pod features (see Podlech,

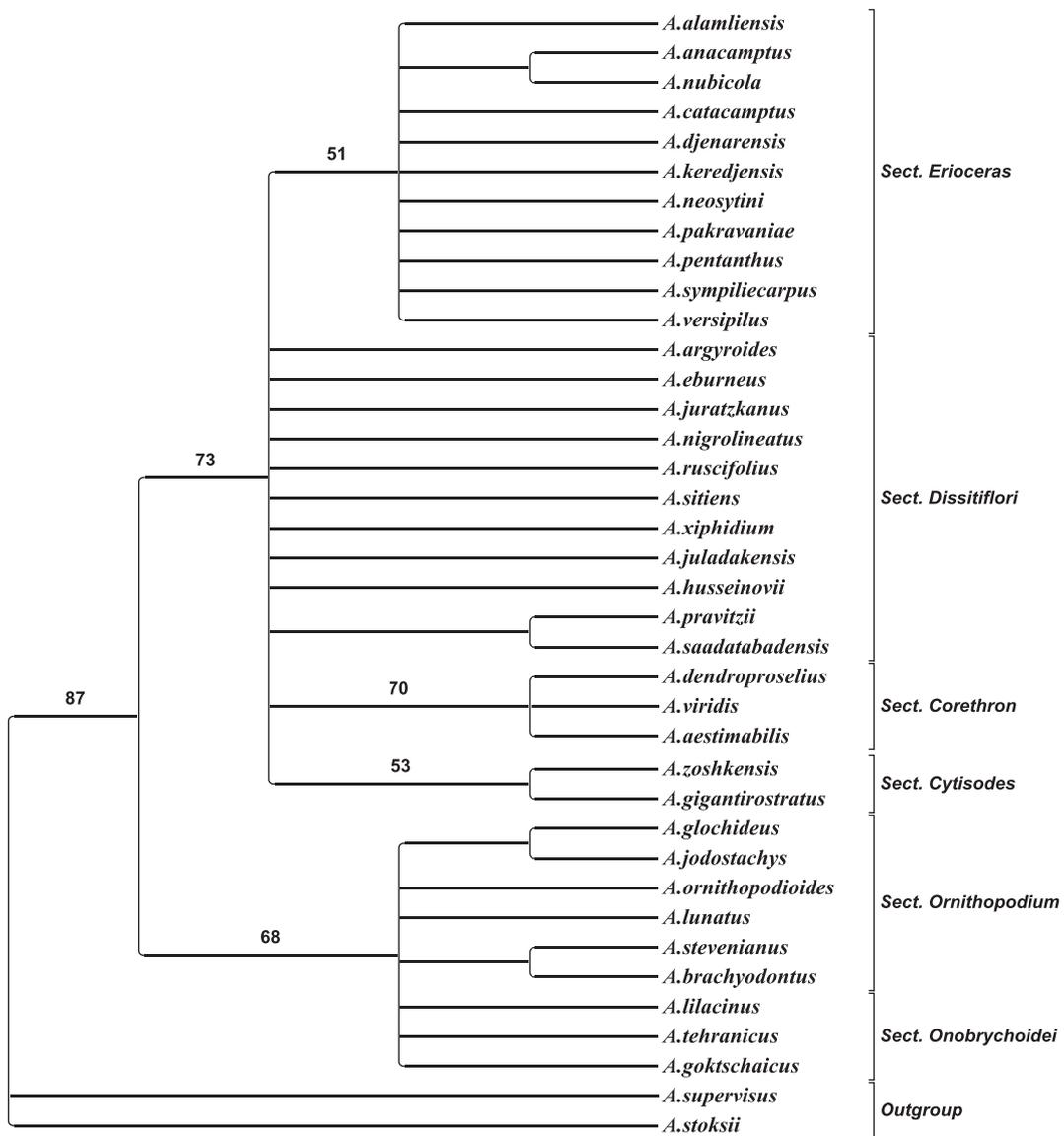


Figure 1. Strict consensus tree of 327 most-parsimonious trees obtained from an equally weighted morphological cladistic analysis. Bootstrap values greater than 50% are shown above the branches.

2010). On the basis of our results, *A. zoshkensis* and *A. gigantirostratus* are sister taxa and allied with the members of *Erioceras* (Figure 1). This result is in agreement with a recent molecular study in which the only sampled species from *Cytisodes* (*A. gigantirostratus*) was nested in a subclade along with members of *Erioceras* (Kazempour Osaloo et al., 2003, 2005).

A recent taxonomic work assumed that *A. viridis* Bunge and *A. dendroproselius* Rech. f. (plus *A. kharvanensis* Ranjbar, not analysed here) are closely

related to each other, in the so-called viridis group, within section *Dissitiflori* (Ranjbar, 2004). This is consistent with our morphology-based cladistic analysis, which found that the first 2 species plus *A. aestimabilis* Podlech are closely related (Figures 1 and 2). On the other hand, these 3 species were separated from section *Dissitiflori* and moved to section *Corethrum* based on their elliptic pods and asymmetrical standing indumentum on the calyx (Maassoumi, 2005). However, the present study revealed that these taxa are related to section

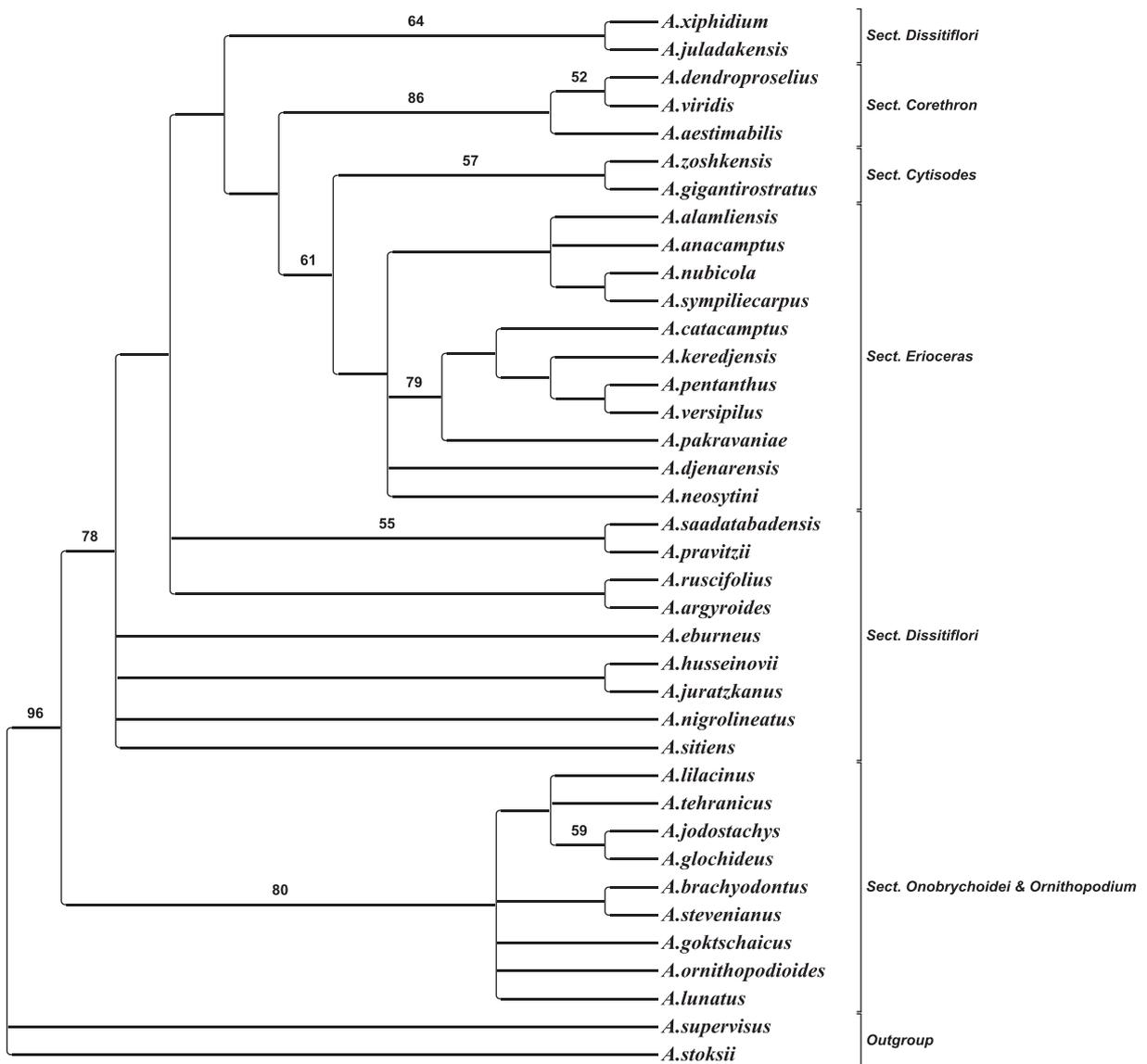


Figure 2. Strict consensus tree of 90 most-parsimonious trees obtained from morphological cladistic analysis after successive reweighting. Bootstrap values greater than 50% are shown above the branches.

*Dissitiflora*, nesting together in a subclade beside members of *Dissitiflora* and *Erioceras* (Figures 1 and 2). According to Kazempour Osaloo et al., using nrDNA ITS data, *A. viridis* (as a representative of section *Corethrum* in Iran) nested with other species of section *Dissitiflora*. It seems that the *viridis* group, as circumscribed in section *Corethrum* (Maassoumi, 2005), should be returned to section *Dissitiflora*. Indeed, the group was treated within section *Dissitiflora* in a recent work by Podlech (2010). With this in mind, the section *Dissitiflora*

is still not monophyletic. Its members form several subclades and unresolved branches across the larger clade (Figures 1 and 2). It is distinguished from the section *Erioceras*, based on symmetrical short hairs on the calyx and pod (vs. asymmetrical long hairs) and a crescent, linear pod (vs. oblong elliptical linear) (Maassoumi, 2005; Podlech et al., 2010). *Erioceras* formed a weakly supported subclade allied with *Cytisodes*, and at least 2 subclades of 4 and 5 species can be found within it (Figure 2). The sister group relationships among these sections are consistent

with the molecular phylogenetic work of Kazempour Osaloo et al. (2003, 2005).

In short, more taxon sampling from these sections, especially from the huge section *Dissitiflori*,

and DNA sequences (nuclear and chloroplast DNAs) are definitely needed to evaluate the phylogenetic status of these sections explicitly. Indeed, our studies of these sections are ongoing.

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