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A NUMERICAL ANALYSIS OF *EPHEDRA* L. BASED ON REPRODUCTIVE FEATURES

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Abstract

A numerical analysis of *Ephedra* L. was conducted based on 29 characters of reproductive organs. The results indicate that species are not grouped according to their geographic ranges, sect. *Alatae* is in one group, sect. *Asarca* excluding *E. cutleri* and *E. viridis* consists of a *Eu-asarca* group while sect. *Ephedra* plus *E. cutleri* and *E. viridis* of the traditional sect. *Asarca* make up a third expanded *Ephedra* group. The Old World sect. *Monospermae* including *E. rhytidosperma*, *E. equisetina*, *E. nebrodensis*, *E. monosperma* and *E. procera* was rediscovered in this study while those Himalayan endemic species (e.g. *E. minuta*, *E. likiangensis*, *E. saxatilis*, *E. dawuensis* and *E. gerardiana*) used to be grouped in the Old World sect. *Monospermae* are clustered together with sect. *Scandentes* including *E. foeminea*, *E. ciliata*, *E. altissima* and *E. fragilis*. This study further confirms that the adaptive seed dispersal syndromes of sect. *Asarca* have originated for not only once. Some new features are introduced as related to dispersal, e.g. weight and size of seeds, and nature and thickness of the outer envelope.

Introduction

Phylogeny of *Ephedra* L. has not been well resolved. Traditionally, botanists use one or few morphological characters to subdivide the genus into sections or groups. Meyer (1846) grouped 20 species of *Ephedra* known at that time into two sections, namely *Ephedra* sect. *Discostoma* and *Ephedra* sect. *Plagiostoma*. Subsequent botanists paid no attention to this classification because Meyer's subdivision does not mirror the interspecific relationships. Stapf (1889) classified the genus into 3 sections, *viz.* sect. *Alatae*, sect. *Asarca*, sect. *Pseudobaccatae* (= sect. *Ephedra*), and 7 "Tribus" (= subsection or series), *viz. Tropidolepides*, *Habrolepides*, *Asarca*, *Scandentes*, *Pachycladae*, *Leptocladae* and *Antisyphiliticae* based on both reproductive and vegetative morphology.

Soskov (1968) believed that smooth branchlets are correlated with uniovulate cones while rough branchlets are correlated with biovulate cones, and proposed thereby two new evolutionary lines of *Ephedra* and established two new subsections, namely *Ephedra* subsect. *Glabrae* Soskov (including *Ephedra equisetina* Bunge, *E. procera* C. A. Meyer, *E. monosperma* Gmel. *ex* C. A. Meyer, *E. gerardiana* Wall. *ex* Stapf, and *E. fedtschenkoae* Paulsen) and *Ephedra* subsect. *Scabrae* Soskov (including *E. intermedia* Schrenk *ex* C. A. Meyer, *E. tesquorum* Nikitin, *E. sinica* Stapf, *E. distachya* L., *E. regeliana* Florin, and *E. minuta* Florin). At the same time, Soskov (1968) recombined "Tribus *Scandentes* Stapf" (= *E.* subsect. *Scandentes*) into subsect. *Scandentes* (Stapf) Soskov. Pachomova (1969, 1971) argued that roughness of branchlets is not correlated with the seed number of a female cone, and rejected Soskov's two new subsections (*E.* subsect. *Glabrae* Soskov and *E.* subsect. *Scabrae* Soskov), but those species with scrambling habits within *E.* sect. *Ephedra* were segregated into a new section (*E.* sect. *Scandentes*) and those with frequent uniovulate cones were ascribed into a new section (*E.* sect. *Monospermae*).

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Mussayev (1978) developed Stapf's classification and proposed a detailed classification of the genus including five sections based on female cone characters and biogeographic characters, *viz.* sect. *Alatae*, sect. *Asarca*, sect. *Ephedra*, sect. *Monospermae* and sect. *Scandentes*. Shen (1993), however, maintained Stapf's classification and believed that the two new sections of Pachomova (1969, 1971) are worth two subsections within sect. *Ephedra*. Freitag and Maier-Stolte (1994) divided the Old World species into four groups, the group *Alatae* includes three Old World species bearing membranous bracts of female cones, the group *Sarcocarpae* consists *E. transitoria*, *E. sarcocarpa*, *E. lomatolepis*, the group *Fragilis* comprises members of traditional *Scandentes* of Stapf, the group *Distachyae* was again subdivided into two subgroups, the subgroup *Distachyae* includes *E. distachya*, *E. regeliana*, *E. intermedia* and *E. fedtschenkoae*, the subgroup *Leptocladae* includes *E. pachyclada*, *E. major*, *E. monosperma* and *E. saxatilis*. Yang (2011), and Ickert-Bond and Rydin (2011) recognized three clear-cut morphological groups in *Ephedra* based on cuticular characters of seeds, they are the transverse lamellar type (e.g. *E. rhytidosperma* Pachomova), the papillate type (e.g. *E. equisetina* Bunge), and the smooth-striate-reticulate type (e.g. *E. sinica* Stapf). This makes the controversy of classification of the genus more serious.

Despite limited sampling of species and low resolution of molecular characters, modern molecular systematic studies have consistently suggested that the genus *Ephedra* can be subdivided into three groups according to geographic ranges of species and bract nature of female cones can not be used for classification of the genus because they are adaptive features with high probability of parallel evolution (Huang and Price, 2003; Ickert-Bond and Wojciechowski, 2004; Rydin *et al.*, 2004; Huang *et al.*, 2005; Ickert-Bond *et al*., 2009; Rydin and Korall, 2009). Additional study suggests that *Ephedra* has three distinct seed dispersal syndromes including membranous bracts, coriaceous bracts, and fleshy bracts, and sect. *Asarca* was evolved and diversified perhaps because of presence of a more diverse assemblage of seed-catching rodents in North America than other continents (Hollander & Wall, 2009).

Using one or few morphological characters in classification may bias the results, while using only molecular characters has low resolution and bootstrap supports. A possible solution to current situation of taxonomy of *Ephedra* may integrate a set of morphological characters into phylogenetic analyses. Vegetative organs of *Ephedra* gave rise to few useful characters, and a few species groups can not be clearly clarified due to complicated variation of vegetative characters. On the contrary, reproductive morphology is important to taxonomy of the genus. This study is to reanalyze those "potentially important" morphological characters and to test the traditional classifications and molecular results using a phenetic analysis based on overall resemblance.

Materials and Methods

Plant samples:

Forty six species of *Ephedra* are used in this study (Table 1). Reproductive characters of *Ephedra* in this study are directly from observations of herbarium specimens (MO, PE), but male characters are coded according to herbarium observations and information from literature. Over 2000 specimens were observed.

Characters and character states:

Altogether 29 characters of 46 OTUs (Operational Taxonomic Units) were analyzed, including 23 characters from seeds, four characters from bracts of female cones, and two characters from male cones (Table 2). Among the 29 characters, 13 are quantitative. For measurements of weight (g), Electronic Balance AR2130 (Ohaus Corp., Pine Brook, NJ, USA) was used. For measurements of size, e.g. length, width, and thickness, Vernier Caliper with an accuracy of 0.02 mm was used under normal indoor temperature (around 25 ^{o}C).

Table 1. List of *Ephedra* species employed in the present study.

No.	Species	Specimens and storage
1	*Ephedra alata* Decaisne	E. Cosson s.n., Apr 8th, 1958 (MO)
2	*E. altissima* Desf.	Reading Univ/BM Exped. 428 (MO)
3	*E. americana* Humb. & Bonpl. *ex* Willd.	Benkt Sparre 13640 (MO)
4	*E. antisyphilitica* Berl. *ex* C.A. Meyer	DS Correll 29249 (MO)
5	*E. aspera* Engelmann *ex* S. Watson	S. B. & W. F. Parish s.n., June 1882 (MO)
6	*E. breana* Phil.	E. Werdermann 1031 (MO)
7	*E. californica* S. Watson	James Henrickson 5559 (MO)
8	*E. chilensis* K. Presl	E. Werdermann 1250 (MO)
9	*E. ciliata* C.A. Meyer	N. Androssov 448 (Herb. no. 00017451, PE)
10	*E. clockeyi* Cutler	Marcus E. Jones s.n., Mar 17th, 1932 (MO)
11	*E. compacta* Rose	Z.S. Debreczy, G.Y. Biro, I. Racz & Y.H. Zhao 39069a (PE)
12	*E. cutleri* Peebles	H. C. Cutler 2169 (MO)
13	*E. dawuensis* Y. Yang	W. K. Hu 13049 (PE)
14	*E. distachya* L.	Qinghai-Xizang Exped. 1111 (PE)
15	*E. equisetina* Bunge	Y. Yang NM06070502 (PE); Y.Yang 99016 (PE)
16	*E. fasciculata* A. Nelson	LM Shultz & JS Shultz 8330 (MO)
17	*E. foeminea* Forssk.	1526: 1983 (PE-seed bank)
18	*E. fragilis* Desf.	1633: 1990 (PE-seed bank); 3708: 1989 (PE-seed bank); 5290: 1990 (PE-seed bank); 1080: 1989 (PE-seed bank)
19	*E. frustillata* Miers	J. Krach 7433 (Institut fuer Systematische Botanik Muenchen); A. Donat 42 (MO)
20	*E. funerea* Coville & Morton	RF Thorne, B. Prigge et al. 51414 (MO); SB & WF Parish 1385 (MO)
21	*E. gerardiana* Wall. *ex* C.A. Meyer	Qinghai-Xizang Exped. 76-8734 (PE); C. Y. Wu 75341 (PE)
22	*E. glauca* Regel	Xinjiang Exped. 666 (PE)
23	*E. gracilis* Phil. *ex* Stapf	L. R. Landrum, and S. S. Landrum 7554 (MO)
24	*E. intermedia* Schrenk & C.A. Meyer	Taohe Exped. 3741 (PE); PC Kuo & WY Wang 11729 (PE); Qinghai-Xizang Exped. 12981 (PE)
25	*E. likiangensis* Florin	Nanshuibeidiao Exped. 6335 (PE); Tsui Yu-Wen, 4329c (PE)
26	*E. major* Host	J. Lewalle 9642 (MO)
27	*E. minuta* Florin	Smith H 11822 (PE); X. Li 71811 (PE); C. S. Liu 1347 (PE); Sichuan Exped. 1492 (PE); H.L. Tsiang 11002 (PE); K.C. Kuan & W.T. Wang 787 (PE); C.W. Wang 69441 (PE)
28	*E. monosperma* Gmel. *ex* C.A. Meyer	Q. Q. Wang 7636 (PE); A. J. Li & J. N. Zhu 6427 (PE).
29	*E. nevadensis* S. Watson	B.F. Harrison & E. Larson 7747 (MO); W.P. Cottam 12823; S.D. McKelvey 2253(Arizona, PE)
30	*E. nebrodensis* Tineo	Unknown collector s.n. (K); B. F. Harrison & E. Larson 7747 (MO)
31	*E. ochreata* Miers	Isla delJabali, Rincon del Banco, 13235 (MO)
32	*E. pedunculata* Engelmann *ex* S. Watson	HB Parks 3199 (MO)

Table 1 contd.

No.	Species	Specimens and storage
33	*E. procera* Fisch. & C.A. Meyer	Stutz 626; PE Herb. no. 1341644 (PE)
34	*E. przewalskii* Stapf	Y. Z. Zhao s. n., Sept. 18th, 2000 (PE)
35	*E. regeliana* Florin	K. C. Kuan 1067 (PE)
36	*E. rhytidosperma* Pachom.	Y. C. Hou 2985 (PE); Y. Yang 20060606, 2004002, 20060620 (PE)
37	*E. rituensis* Y. Yang	Qinghai-Xizang Exped. 12981 (PE)
38	*E. rupestris* Benth.	H. Balslev, G. Pazymino and SS Renner 69131 (MO)
39	*E. saxatilis* (Stapf) Royle *ex* Florin	Mt. Zhumulangma Exped. 592 (PE); Qinghai-Xizang Exped. 750775 (PE); G. Forrest 5564 (PE); Nanshuibeidiao 6335 (PE); R.C. Ching 31011 (PE)
40	*E. sinica* Stapf	Y. Yang 9977-1 (PE); H. H. Zeng 238 (PE)
41	*E. strobilacea* Bunge	0679: 1961 (PE-seed bank); A. Michelson s.n., 15. June, 1912, (PE); W.H. Lipsky 4181 (PE); PE Herb. no. 200087(PE)
42	*E. torreyana* S. Watson	E. Payson 353 (MO)
43	*E. triandra* Tul.	J. West 8297 (MO)
44	*E. trifurca* Torrey. *ex* S. Watson	W. Hess, S. Vuono, K. Bolger 8006 (MO); A.E. Skjot-Pedersen s.n. 31 March, 1928 (PE)
45	*E. tweediana* Fisch. *ex* C.A. Meyer	G. Herter 1010 (MO)
46	*E. viridis* Coville	M. S. Taylor 2048 (MO)

Table 2. Characters and their scoring employed in the present study.

No.	Characters	Character states
1	Seed protective layer	thin (0), thick with many layers of fibre (1)
2	Seed sculpture character	smooth (0), papillate (1), transverse lamellar (2)
3	Seed number per cone	3 seeds (0), usually 2 seeds (1), usually 1 seed (2)
4	Seed glossy	yes (0), no (1)
5	Seed color	purplish black (0), yellowish brown (1), greyish (2)
6	Seed shape	ovoid to narrow ovoid (0), ellipsoid (1), lanceolate (2)
7	Seed dorsal ridge	present (0), absent (1)
8	Seed cross section	triangular (0), circular or nearly so (1), four angled or three angled with an adaxial ridge (2)
9	Seed dorsal lateral furrows	present (0), absent (1)
10	Seed micropylar tube	short and straight as that in *E. minuta* (0), longer and/or slightly curved as that in *E. sinica* (1), contorted or coiled as that in *E. intermedia* (2), unknown (3)
11	Female cone: bract insertion	bracts decussate and opposite (0), ternately whorled (1)
12	Female cone: bracts nature	membranous (0), coriaceous (1), fleshy (2)
13	Female cone: bracts whorl	3 whorls or less (0), 4-5 pairs/whorls (1), 6 or more (2)
14	Female cone: connation of the uppermost whorl of bracts in mature female cone	free (0), lower than 1/3 (1), 1/3-2/3 (2), 2/3 or more (3)
15	Male cone: bract whorls	lower than 3 (0), 4-6 (1), more than 6 (2), unknown (3)
16	Male cone: synangia number	less than 4 (0), 5 or more (1), unknown (2)

Table 2 contd.

No.	Characters	Character states
17	Seed average weight (g). (For each species, mature seeds were sampled as many as possible and weighed together. The seed average weight is the value of the weight of these seeds divided by number of seeds).	This is a numeric character which was used directly in the analysis.
18	Seed length minimum (mm)	This is a numeric character which was used directly in the analysis.
19	Seed length maximum (mm)	This is a numeric character which was used directly in the analysis.
20	Seed length mean (mm). The mid-point between minimum and maximum length	This is a numeric character which was used directly in the analysis.
21	Seed width minimum (mm)	This is a numeric character which was used directly in the analysis.
22	Seed width maximum (mm)	This is a numeric character which was used directly in the analysis.
23	Seed width mean (mm). The mid-point between minimum and maximum width.	This is a numeric character which was used directly in the analysis.
24	Seed thickness minimum (mm)	This is a numeric character which was used directly in the analysis.
25	Seed thickness maximum (mm)	This is a numeric character which was used directly in the analysis.
26	Seed thickness mean (mm). The mid-point between minimum and maximum thickness	This is a numeric character which was used directly in the analysis.
27	Seed length/width	This is a numeric character which was used directly in the analysis.
28	Seed length/thickness	This is a numeric character which was used directly in the analysis.
29	Seed width/thickness	This is a numeric character which was used directly in the analysis.

Data analysis:

For analyses, analytic tools integrated in MVSP ver. 3.1.3 were applied. In cluster analysis, data transformation using *Log e* was done before conducting unified analysis of both qualitative and quantitative characters. Dendogram was constructed using UPGMA (unweighted pair grouped method with arithmetic mean). PCO (Principal Coordinates analysis) analysis was done to show overall resemblance of species of three sections. Scatter plots were dotted after all axes were extracted. For correlation analysis of quantitative characters, graphic function of scatter plots was applied.

Results

Cluster analysis using UPGMA:

A numerical analysis of reproductive characters including 16 qualitative and 13 quantitative characters generated one dendrogram using UPGMA (Fig. 1). Three major groups and eight subgroups are recognized. The first major group consists of all five species of sect. *Alatae* involved in this study. The North American *E. trifurca* and *E. torreyana* are closely related and sister to an Old World group including *E. strobilacea* and *E. alata*. *Ephedra przewalskii* is basal within this *Alatae* group.

The second major group includes five species of sect. *Asarca* with *Ephedra cutleri* and *E. viridis* excluded from this group, which forms *Eu-Asarca* group. *Ephedra clockeyi* and *E. funerea* are clustered together which sister to *E. aspera* and *E. fasciculata*, *E. californica* is basal within this major group. The third major group is an expanded sect. *Ephedra* with *Ephedra cutleri* and *E. viridis* of traditional sect. *Asarca* included. Within this major group, eight subgroups are recognized, they are numbered as groups from 4-11. In the fourth group, *Ephedra cutleri* and *E. viridis* are clustered together with two South American species, *viz. E. tweediana* and *E. triandra*. The fifth group includes *E. ciliata* and *E. altissima* of traditional sect. *Scandentes*. The sixth group is a mixed group of traditional sect. *Monospermae* from Himalaya, *viz. E. dawuensis*, *E. minuta*, *E. saxatilis*, *E. gerardiana*, *E. likiangensis*, and sect. *Scandentes*, *viz. E. foeminea* and *E. fragilis*. The seventh group consists of American species, *E. americana* and *E. chilensis* from South America and *E. pedunculata* from North America. The eighth group includes two species from North America, *viz. E. nevadensis* and *E. antisyphilitica*.

The ninth group rediscovered partial of the Old World sect. *Monospermae* that includes *E. rhytidosperma*, *E. monosperma*, *E. nebrodensis*, *E. procera* and *E. equisetina*. *Ephedra monosperma*, *E. nebrodensis*, *E. procera* and *E. equisetina* bear 1-seeded cone, but *E. rhytidosperma* bears biovulate cones in which one ovulate organ frequently aborted forming 1-seeded cones. In the tenth group, species bearing 2-seeded cones from both the Old World and New World are clustered together, with species related to each according to their geographic ranges, e.g. *E. glauca* is close to *E. regeliana*, *E. sinica* is close to *E. distachya*, *E. rupestris* is near to *E. frustillata*, and *E. compacta* is close to *E. gracilis*. The eleventh group includes species frequently bearing 3-seeded cones, e.g. *E. ochreata*, *E. intermedia* and *E. rituensis*, the South American *E. ochreata* sisters to the Old World *E. intermedia* and *E. rituensis*.

PCO analysis:

The overall resemblance of reproductive organs of *Ephedra* does not show three clear-cut groups, but suggests that species in one section are inclined to cluster together (Fig. 2). *Ephedra funerea* is closer to sect. *Alatae* than to sect. *Asarca*. Sect. *Asarca* is intermediate between sect. *Alatae* and sect. *Ephedra*.

Discussion

Systematic evaluation:

The dendrogram shows only branching hierarchy and the level of similarity but is not rooted, as a result, this study does not intend to analyze character evolution in *Ephedra* or to give a convincing conclusion on phylogeny of *Ephedra*, but tries to give an overview of phenetic relationships of the genus based on overall resemblance of 29 reproductive characters.

Different hypotheses of classification of the genus *Ephedra* were proposed. Traditionally the genus was classified into morphological groups, e.g. Stapf (1889), Mussayev (1978), and Freitag and Maier-Stolte (1994), but modern molecular studies suggests that living species of *Ephedra* are grouped basically according to their geographic ranges (Ickert-Bond and Wojciechowski, 2004; Rydin *et al.*, 2004; Huang *et al.*, 2005). Phylogeny of the genus *Ephedra* has not been well resolved because traditional classifications were mainly based on one single or few characters on the one hand, and recent molecular studies did not have high bootstrap supports on the other. This

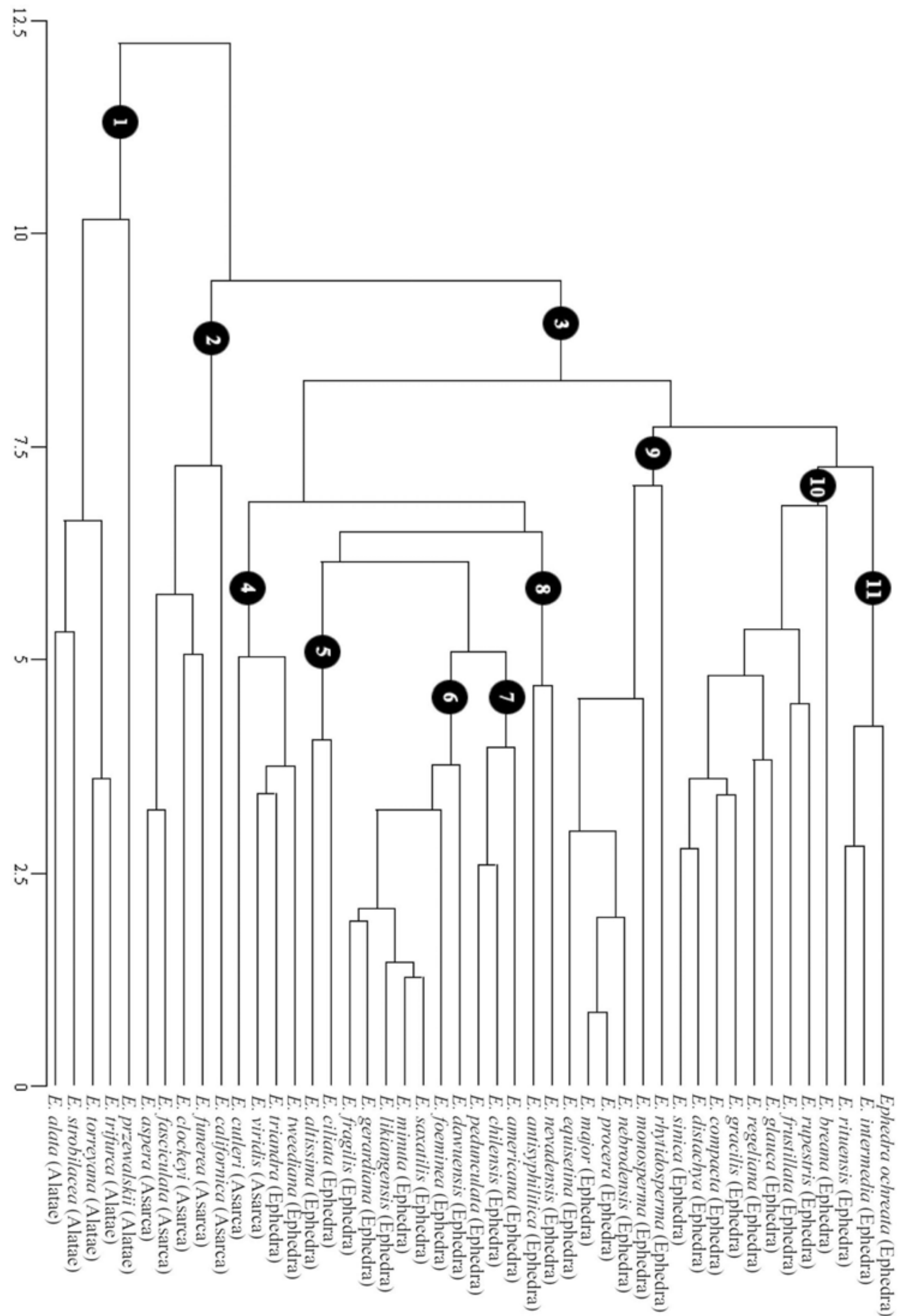

Fig. 1. UPGMA dendrogram showing resemblance of *Ephedra* species based on 29 reproductive characters.

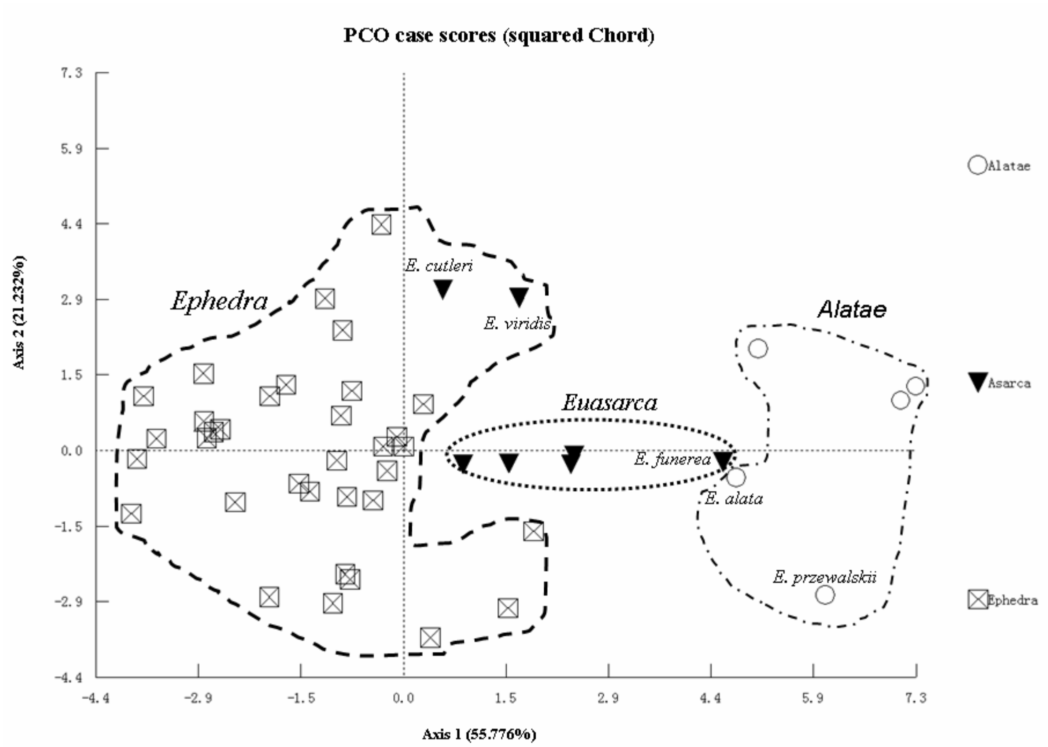

Fig. 2. Scatter plots showing phenetic relationships of species of *Ephedra* based on PCO analysis, dot line circle showing the three major groups of UPGMA dendrogram different from the traditional three sections.

study based on 29 reproductive characters does not agree well with all these classifications, but shows certain similarities to those traditional classifications. Both UPGMA (Fig. 1) and PCO (Fig. 2) analyses support the group sect. *Alatae*. Sect. *Asarca* is not a monophyletic group according to this study. Altogether seven species of sect. *Asarca* are involved in this study, but they were subdivided into two parts. Five species including *E. californica*, *E. funerea*, *E. clockeyi*, *E. aspera*, *E. fasciculata* form the second major group, which is named here as *Eu-Asarca* because this is a rediscovered group of the section. The other two species *Ephedra cutleri* and *E. viridis* are excluded from this major group but show close resemblance with two South American species *E. tweediana* and *E. triandra*.

Traditionally, *E. fragilis*, *E. foeminea*, *E. ciliata* and *E. altissima* were ascribed into sect. *Scandentes* (Stapf, 1889; Mussayev, 1978). This, however, is not confirmed in this study. *Ephedra ciliata* and *E. altissima* are clustered together, but *E. fragilis* and *E. foeminea* are related to the Himalayan group used to be classified into sect. *Monospermae*, e.g. *E. saxatilis*, *E. dawuensis*, *E. likiangensis*, *E. gerardiana* and *E. minuta* (group 6 in this study). Sect. *Scandentes* has long been believed to be primitive in the genus *Ephedra* because of their longer leaves and scrambling habits (Soskov, 1968; Mussayev, 1978; Shen, 1995). It is highly impossible because all species of sect. *Scandentes* bear quite reduced female cones with 2-3 pairs of bracts and the innermost pair connate for 2/3 or more. This study indicates that sect. *Scandentes* is quite close to the Himalayan species used to be ascribed into subsect. *Monospermae* in reproductive morphology. The mixed group of sect. *Scandentes* and sect. *Monospermae* shows resemblance to some New World species that belongs to the seventh and the eighth group in this study.

Though those Himalayan species of subsect. *Monospermae* are demonstrated to be mixed with sect. *Scandentes*, this study does rediscover a group including the Old World subsect. *Monospermae*, e.g. *E. rhytidosperma*, *E. monosperma*, *E. nebrodensis*, *E. major* and *E. equisetina*. Grouping of these species is also corroborated by molecular studies (Rydin *et al.*, 2004; Wang *et al.*, 2005).

Despite the resolution and the bootstrap supports were low, recent molecular studies suggested that species of *Ephedra* were not grouped according to bract nature of ripe female cones or other reproductive characters but according to their geographic ranges, *viz.* the Old World clade, the North American clade, and the South American clade (Ickert-Bond and Wojciechowski, 2004; Rydin *et al.*, 2004; Huang *et al.*, 2005). Though our study is based on reproductive morphology, and the tree dendrogram is fundamentally different from those based on molecular, some groups in our study do show geographic pattern, e.g. all species of the second major group, the eighth group, and the fourth group in this study belong to the New World; the fifth, sixth, ninth group comprises species all from the Old World.

Seed dispersal syndromes and their multiple origin:

Morphological differences of reproductive organs can account for adaptive differences in the type of pollinators or seed dispersers that interact with plants (Thomoson and Wilson, 2008). Three morphological types of female cones are present in *Ephedra* which may conform to three different seed dispersal syndromes. Sect. *Alatae* has large membranous wings and light seeds, and is dispersed by wind; sect. *Asarca* has dry coriaceous bracts but heavy seeds, and is dispersed by rodents and sect. *Ephedra* has fleshy bracts and variable sized seeds and is assumed to be dispersed by birds (Hollander and Wall, 2009). Recent molecular studies suggested that bract nature of female cones at maturity in *Ephedra* is a kind of adaptive feature and may have originated for multiple times (Ickert-Bond and Wojciechowski, 2004; Rydin *et al.*, 2004; Huang *et al.*, 2005). Our study shows that seven species of sect. *Asarca* fall within two groups, one constituting the *Eu-Asarca* while the other clustered with species of sect. *Ephedra* from South America. This observation confirms the conclusion from molecular systematics that origin of the adaptive seed dispersal syndromes of sect. *Asarca* might be multiple. Predation of rodents maybe the active selection pressure that push the derivation of seed cone type of sect. *Asarca*.

Other features of seeds of *Ephedra* may also be dispersal syndromes that interact with dispersers. According to our analyses, seed weight of *Ephedra* is positively related to seed length, width and thickness in general. Compared with sect. *Ephedra* and sect. *Asarca*, sect. *Alatae* usually has lighter and longer seeds, the only exception is *E. przewalskii* which have smaller and lighter seeds. Sect. *Ephedra* and sect. *Asarca* have no obvious deviation in seed weight and length. This might also be an adaptive feature. Sect. *Alatae* is dispersed by wind, which is clearly different from the zoochorous seed dispersal syndromes in sect. *Ephedra* and sect. *Asarca*. In addition, seeds of sect. *Alatae* usually have thin and fragile protection (*viz.* the outer envelope) while seeds of sect. *Ephedra* and sect. *Asarca* have thick protection with many layers of fibres.

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