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POLLEN MORPHOLOGY OF THE GENUS *TRAGOPOGON* (ASTERACEAE)

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Tragopogon L. (Cichorioideae, Lactuceae, Scorzonerinae) is an Old World genus with 150 species. Pollen morphology has proved useful in the systematics of some genera and species of Asteraceae as well as in that of some of its genera and species. The pollen morphology of 24 taxa of the genus *Tragopogon* was investigated in detail by scanning electron microscopy (SEM). The pollen grain type ranged from suboblate, oblate-spheroidal to prolate-spheroidal in equatorial view and hexagonal, obtuse-hexagonal to hexagonal-angular in polar view. In this study separation of the species of the sections *Majores*, *Profundisulcati*, *Sosnovsky*, *Chromopappus*, *Rubriflori* according to Flora Iranica is presented from the other species of *Tragopogon*. *T. jezdianus*, *T. porphyrocephalus*, *T. rezaiyensis* are suggested to belong to *Rubriflori* section. The results indicate that the palynological characters of the genus *Tragopogon* are valuable for taxonomic applications and are useful for classification.

Key words: Iran, pollen, SEM, taxonomy, *Tragopogon*

INTRODUCTION

Tragopogon L. (Cichorioideae, Lactuceae, Scorzonerinae) is an Old World genus with 150 species that occurs across Eurasia from the Atlantic to the Pacific Ocean, with a centre of distribution in the Mediterranean region, the Middle East, and Eastern Europe. It was divided into 17 sections and 79 species by Shishkin (1961), 10 species of them were shared with flora of Iran. Following Shishkin's concept Rechinger (1977) divided this genus into 13 sections and 37 species in Flora Iranica, 26 species (11 species endemic) of them exist in Iran (Rechinger 1977). Safavi *et al.* (2014) divided it into 26 species without sections in flora of Iran. *Tragopogon* includes biennial and perennial herbs with linear or linear-lanceolate leaves; solitary, simple or sparingly branched stems; one or only a few capitula; and receptacles without scales. Most species are diploid (2n = 12), but some polyploidy species or cytotypes have been reported. The monophyly of the genus was strongly supported in a recent phylogenetic analysis of Scorzonerinae based on internal transcribed spacer (ITS) sequence data (Mavrodiev *et al*. 2004) The pollen characters are useful patterns

in the context of recent molecular hypotheses of relationship, and could be used to support the species relationships, or provide diagnostic characters for groups at a variety of levels particularly in Asteraceae (Wodehouse 1926, 1928, Wortley *et al*. 2007). There are three characteristics of Compositae pollen: (1) a structured tectum, (2) the presence of moderately long spines, and (3) a tripartite apertural system consisting of an outer aperture involving the foot layer and an inner or endoaperture limited to the endexine (Dimon 1971). Wodehouse recognised four pollen morphological forms in the family: simple echinate, sub-echinolophate, echinolophate, and psilolophate together with many intermediates. Wodehouse (1935) showed one morphological form to be present in the genus *Tragopogon* of tribe Lactuceae.

Palynology provides a whole new set of characters for studying the species relationships and taxonomy, compared to the conventional macro morphological study and also provides data which may be considered less affected by ecological specialisation of the taxa, the use of additional pollen characters to possibly avoid such limitations and improve the results (Scotland *et al*. 2003). Pausinger (1951) divided Lactuceae into two main types based on pollen characters, *Leontodon* type was characterised by the possession of poral lacunae, and this *Tragopogon* type of the lack of poral lacunae, the abporal ones communicating to form long lacunae, *Tragopogon* type has six abpolar, three equatorial, and six interapertural lacunae (Blackmore 1982, Nazarova 1997). *Tragopogon* pollen differs from other Lactuceae in the absence of tectum and columellae in the lacunae; this also appears to be the result of differential primexine deposition. The development of once and their extrusion at the apertures have been described (Blackmore and Barnes 1987). To date no comprehensive morphological, palynological and anatomical studies have been done on this genus, the species of which are often difficult to distinguish from each other and whose infrageneric classification is only preliminary. The present paper aims to study general pollen morphological characters and to assess their taxonomic value as well as their application in species delimitation.

MATERIAL AND METHODS

Pollen morphology was studied by scanning electron microscopy (SEM) in 24 *Tragopogon* species growing in Iran (Table 1). The voucher specimens are deposited in the Shahid Beheshti University herbarium (HSBU) and herbarium of Research Institute of Forests and Rangeland. The pollen samples were obtained mostly from freshly collected specimens and also from dry herbarium materials. Fully mature anthers were removed from specimens. For scanning electron microscopy, the pollen grains were attached to aluminium stubs with double-sided cellophane tape, air-dried at room temperature and coated with gold. The specimens were examined and photographed with a

scanning electron microscope (SU3500; Hitachi, Japan) at an accelerating voltage of 20 kV. The terminology follows mainly Erdtman (1952). Image Tool ver. 3 software was used for pollen measurements, and then data obtained were scored. For multivariate analyses 18 pollen grain characteristics including 3 qualitative and 7 quantitative characters were used (Tables 2–3). For multivariate analyses the mean of quantitative characters were used, while qualitative characters were coded as binary/multistate characters. Standardised data (mean = 0, variance = 1) were used for multivariate statistical analyses. The average taxonomic distance and squared Euclidean distance were used as dissimilarity coefficient in cluster analysis of data (Podani 2000). Principal Components Analysis (PCA) was performed among the species studied to determine palynological characteristics useful for separating the species. In order to group the species, cluster analysis using UPGMA (Un-weighted Paired Group with Arithmetic Average) and NJ (Neighbour-joining) methods and PCA ordination plot were used performed using Euclidean and taxonomic distances calculated among the species (Podani 2000). Clustering and ordination plot analyses using NTSYS ver. 2 (1998) and PAST ver. 2.17 software.

RESULTS

In the present study, the pollen grains of 24 species from 9 sections belong to the genus *Tragopogon* were investigated and SEM micrographs of all species were taken (Figs 1–3). The pollen grain type ranged from suboblate, oblate-spheroidal to prolate-spheroidal in equatorial view and hexagonal, obtuse-hexagonal to hexagonal-angular in polar view. Polar diameters of the pollen grains ranged from 31.02 μm (*T. graminifolius*) to 49.90 μm (*T. buphthalmoides* var. *latifolius*) and the equatorial diameters ranged from 31.05 μm (*T. pterocarpus*) to 47.38 μm (*T. buphthalmoides* var. *latifolius*) (Table 2). According to the 24 analysed species, the P/E ratio varied from 0.85 (*T. collinus*) to 1.13 (*T. pterocarpus*). The main features of the investigated pollen grains are summarised in Table 2–3.

PCA analysis revealed that the first two components comprised about 89% of the total morphological variability. Palynological characters like exine surface in polar view, spinule on the opercule, opercule position and polar diameter/equatorial diameter showed the highest positive correlation with the first PCA component, while opercule surface and spine type in polar view showed the second PCA component these characters may be used in the taxonomy of the genus and the delimitation of *Tragopogon* species. The results of dendrogram NJ, UPGMA and WARD are consistent with PCA and PCO plots. The boundary between the sections accordance with the sections in the Flora Iranica. Based on NJ dendrogram *T. buphthalmoides* var. *buphthalmoides*, *T. buphthalmoides* var. *latifolius*, *T. bornmuelleri* var. *bornmuelleri*, *T. bornmuelleri* var. *latifolius*, *T. acanthocarpus*, *T. rechingeri* were placed in the first cluster and

Table 1
List of studied taxa of *Tragopogon* (Asteraceae) with localities and voucher numbers

Species	Section	Voucher no.	Locality
T. vaginatus	*Majores*	TARI-7748	West Azarbaijan: between Piranshahr and Sardasht
T. vvedenskyi	*Angustissimi*	HSBU-2018800	Mazandaran: Plur toward Rineh
T. longirostris	*Kraschenninikovia*	HSBU-2018801	Alborez: Karaj–Chalus road, Amir Kabir dam
T. gongylorrhizus	*Tuberosi*	TARI-5123	Gorgan
T. buphthalmoides var. *buphthalmoides*	*Profundisulcati*	HSBU-4007	West Azarbaijan: Sardasht, Tangeh Gerzhal
T. buphthalmoides var. *latifolius*	*Profundisulcati*	HSBU-4015	Kurdestan: Saghez toward Marivan, Haji Mamadan village
T. rechingeri	*Profundisulcati*	TARI-3392	Hamadan: Agh blagh, Agh agh mountain
T. bornmuelleri var. *bornmuelleri*	*Profundisulcati*	TARI-60592	Kurdestan: 36 km sanandaj to Kamiaran, Nshur valley
T. bornmuelleri var. *latifolius*	*Profundisulcati*	TARI-87735	Kermanshah: Kermanshah to Kamiaran, Mahmud abad village
T. acanthocarpus	*Profundisulcati*	TARI-84034	East Azarbaijan: Marand to Jolfa, Zenoz, 22 km zenzogh to koh kamar
T. graminifolius	*Brevirostres*	HSBU-2018807	Tehran: Chitgar
T. reticulatus	*Sosnovskya*	TARI-2081	Kurdestan: Baneh, Boien
T. kotschyi	*Sosnovskya*	HSBU-2018813	Lorestan: Khoram Abad
T. marginatus	*Sosnovskya*	TARI-4374	Alborez: Karaj, Kondure
T. coloratus	*Chromopappus*	TARI-55598	Gorgan: Maraveh tapeh to Ash khaneh
T. pterocarpus	*Chromopappus*	HSBU-2018815	Tehran: Chalus road, Morod
T. collinus	*Rubriflori*	TARI-27662	Gilan: Ghazvin to Rudbar, Kuhin
T. caricifolius	*Rubriflori*	TARI-49230	Tehran: Darban sar
T. bakhtiaricus	*Rubriflori*	TARI-54377	Chahar mahal Bakhtiari: Brojen

Table 1 (continued)

Species	Section	Voucher no.	Locality
T. gaudanicus	*Rubriflori*	TARI-9145	Fars: Kazerun, Ketel Pirezan
T. montanus	*Rubriflori*	TARI-1342	Tehran: Firuz koh to veresk
T. jezdianus	indeterminate	TARI-77777	Yazd: Nedoshan between Sadr abad and Hemat abad
T. porphyrocephalus	indeterminate	TARI-62060	Charmahale Bakhtiari: Shahre kurd, Ben harchegan
T. rezaiyensis	indeterminate	HSBU-2018818	Tehran: Piste Abali

Table 2

Pollen quantitative characters in studied taxa (P = polar diameter, E = equatorial diameter, P/E = polar diameter/ equatorial diameter)

Species	P	E	P/E
T. vaginatus	35.29±0.30	40.83±0.47	0.86
T. vvedenskyi	33.90±0.47	36.57±0.29	0.92
T. longirostris	35.36±0.39	34.90±1.46	1.01
T. gongylorrhizus	34.78±0.45	32.85±0.15	1.05
T. buphthalmoides var. *buphthalmoides*	42.35±2.72	44.22±1.96	0.95
T. buphthalmoides var. *latifolius*	49.90±1.00	47.38±0.71	1.05
T. rechingeri	39.49±2.53	42.59±0.39	0.92
T. bornmuelleri var. *bornmuelleri*	37.19±1.23	39.60±0.45	0.93
T. bornmuelleri var. *latifolius*	37.75±0.39	40.28±0.59	0.93
T. acanthocarpus	33.84±1.29	36.53±0.64	0.92
T. graminifolius	31.02±0.39	34.60±0.98	0.89
T. reticulatus	38.45±2.35	34.84±1.57	1.10
T. kotschyi	37.67±0.74	35.82±0.75	1.05
T. marginatus	35.88±0.09	38.96±1.04	0.92
T. coloratus	34.25±1.31	34.59±0.92	0.99
T. pterocarpus	35.12±0.71	31.05±1.99	1.13
T. collinus	31.63±0.93	36.93±0.38	0.85
T. caricifolius	37.88±0.89	40.93±1.13	0.92
T. bakhtiaricus	39.69±2.02	42.33±0.27	0.93
T. gaudanicus	38.04±1.02	41.13±0.95	0.92
T. montanus	41.17±4.10	43.31±0.22	0.95
T. jezdianus	36.14±0.86	37.03±0.22	0.97
T. porphyrocephalus	36.23±2.45	38.61±0.26	0.93
T. rezaiyensis	37.98±1.97	40.02±0.32	0.94

Table 3
Pollen qualitative characters in studied taxa

Species	SPV	SS	STPV	ESP	OS	SO	OP
T. vaginatus	1	1	3	1	1	1	1
T. vvedenskyi	1	1	2	2	2	2	1
T. longirostris	2	2	1	2	1	1	2
T. gongylorrhizus	1	1	3	2	2	1	2
T. buphthalmoides var. *buphthalmoides*	3	2	3	2	1	1	2
T. buphthalmoides var. *latifolius*	3	2	1	2	1	1	2
T. rechingeri	3	2	1	2	1	1	2
T. bornmuelleri var. *bornmuelleri*	1	2	3	2	3	1	1
T. bornmuelleri var. *latifolius*	1	2	3	2	3	1	1
T. acanthocarpus	1	1	1	2	3	1	1
T. graminifolius	3	2	1	1	3	1	1
T. reticulatus	2	1	2	1	2	1	1
T. kotschyi	1	2	2	2	3	2	1
T. marginatus	2	1	2	2	3	1	1
T. coloratus	1	1	2	1	3	1	1
T. pterocarpus	1	2	3	2	1	1	1
T. collinus	3	1	2	2	2	1	2
T. caricifolius	3	2	2	2	2	1	1
T. bakhtiaricus	1	1	1	2	1	1	1
T. gaudanicus	1	2	3	2	2	2	2
T. montanus	1	2	1	3	2	1	1
T. jezdianus	1	2	3	2	2	1	1
T. porphyrocephalus	1	2	2	2	1	1	1
T. rezaiyensis	1	2	2	2	2	1	1

SPV (shape of polar view): 1 = hexagonal, 2 = hexagonal-obtuse, 3 = hexagonal-angle. – SS (shape of spine): 1 = erect, 2 = slightly curved. – STPV (spine type in polar view): 1 = slow, 2 = sharp, 3 = slow-sharp. – ESP (exine surface in polar view): 1 = open pores, 2 = close pores. – OS (opercule surface): 1 = smooth, 2 = twisted. – SO (spinule on the opercule): 1 = yes, 2 = no. – OP (opercule position): 1 = lower, 2 = equal

T. graminifolius was the sister group in this cluster. *T. reticulatus*, *T. marginatus*, *T. kotschyi* were placed in the second cluster and *T. coloratus*, *T. pterocarpus* were the sister groups. *T. vaginatus* and *T. vvedenskyi* were placed close to *T. longirostris* and *T. gongylorrhizus* and formed the third cluster. *T. collinus*, *T. jezdianus*, *T. porphyrocephalus*, *T. rezaiyensis*, *T. bakhtiaricus*, *T. montanus*, *T. caricifolius* and *T. gaudanicus* formed the fourth cluster.

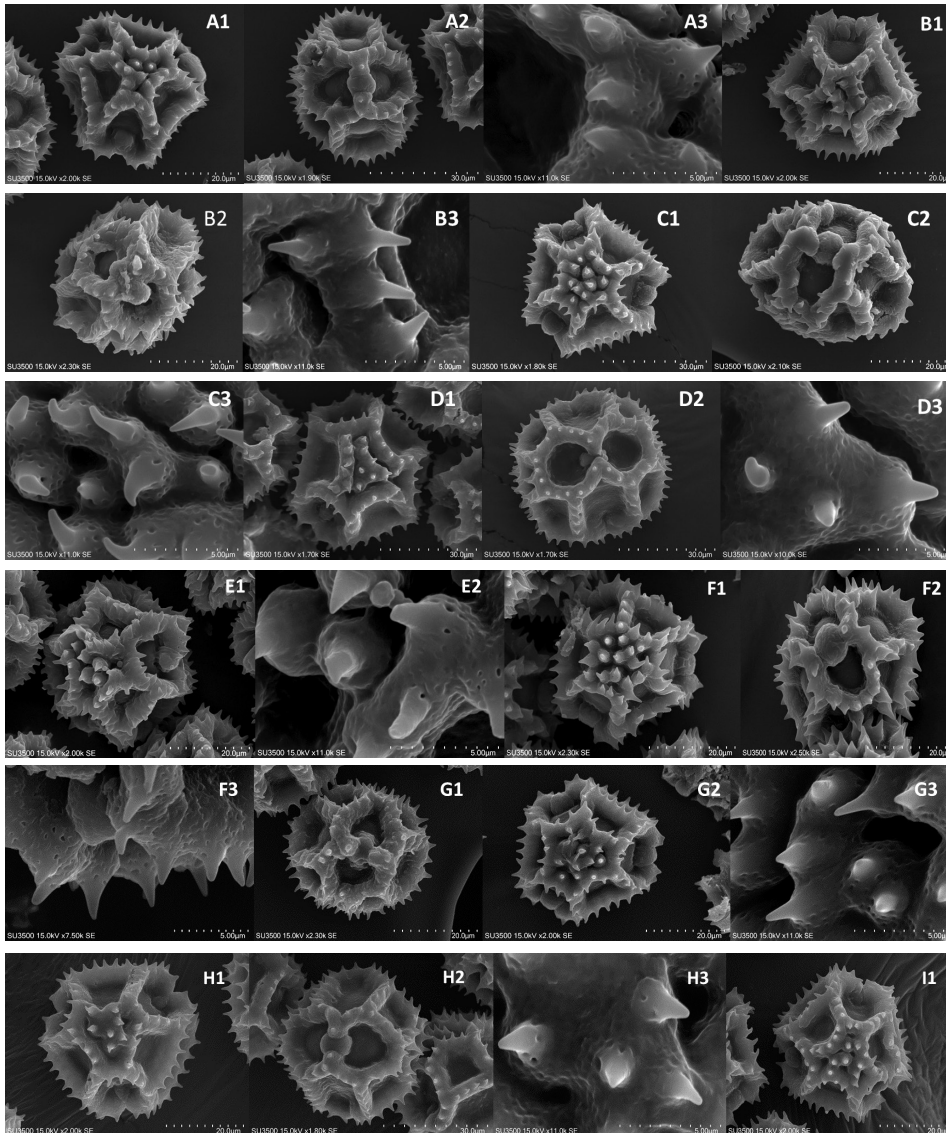

Fig. 1. SEM photographs show pollen grain morphology of the studied species of genus *Tragopogon* L. (Asteraceae). A1–A3: *T. vaginatus*, B1–B3: *T. vvedenskyi*, C1–C3: *T. gaudanicus*, D1–D3: *T. buphthalmoides* var. *buphthalmoides*, E1–E2: *T. reticulatus*, F1–F3: *T. coloratus*, G1–G3: *T. gongylorrhizus*, H1–H3: *T. rechingeri*, I1: *T. acanthocarpus*

DISCUSSION

The influence of pollen morphology in Asteraceae systematics is understood by his comments "...pollen is one of a series of characters such as stylar bases and anther appendages, observable with the compound microscope,

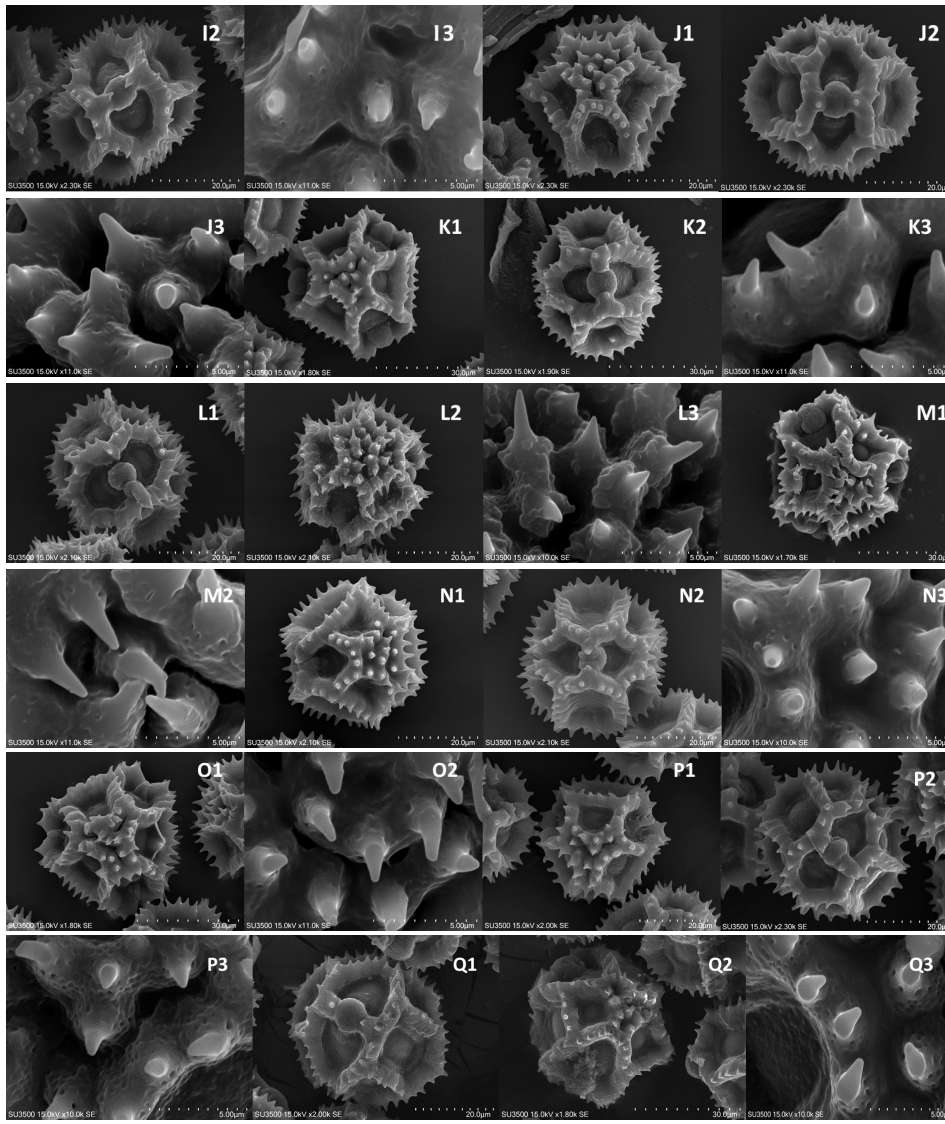

Fig. 2. SEM photographs show pollen grain morphology of the studied species of genus *Tragopogon* L. (Asteraceae). I2–I3: *T. acanthocarpus*, J1–J3: *T. bornmuelleri* var. *bornmuelleri*, K1–K3: *T. bornmuelleri* var. *latifolius*, L1–L3: *T. marginatus*, M1–M2: *T. kotschyi*, N1–N3: *T. collinus*, O1–O2: *T. caricifolius*, P1–P3: *T. graminifolius*, Q1–Q3: *T. bakhtiaricus*

that prove useful in delimiting natural groups. The point has been reached where I believe every taxonomic treatment in the Lactuceae should include mention of pollen type" (Robinson 1992). Later he reinforced these feelings by stating: "The pollen is one of the most useful characters available, and it is inexplicable that taxa would be described at this time without detailed description of the pollen" (Robinson 1992). Similarly, Bolick and Keeley (1994) concluded: "Within the tribe, pollen is a good character for delimiting sections, subsections and series". Based on the sculpturing all pollen grains were echinate in *Tragopogon* (Bolick and Keeley 1994) The young age of the genus

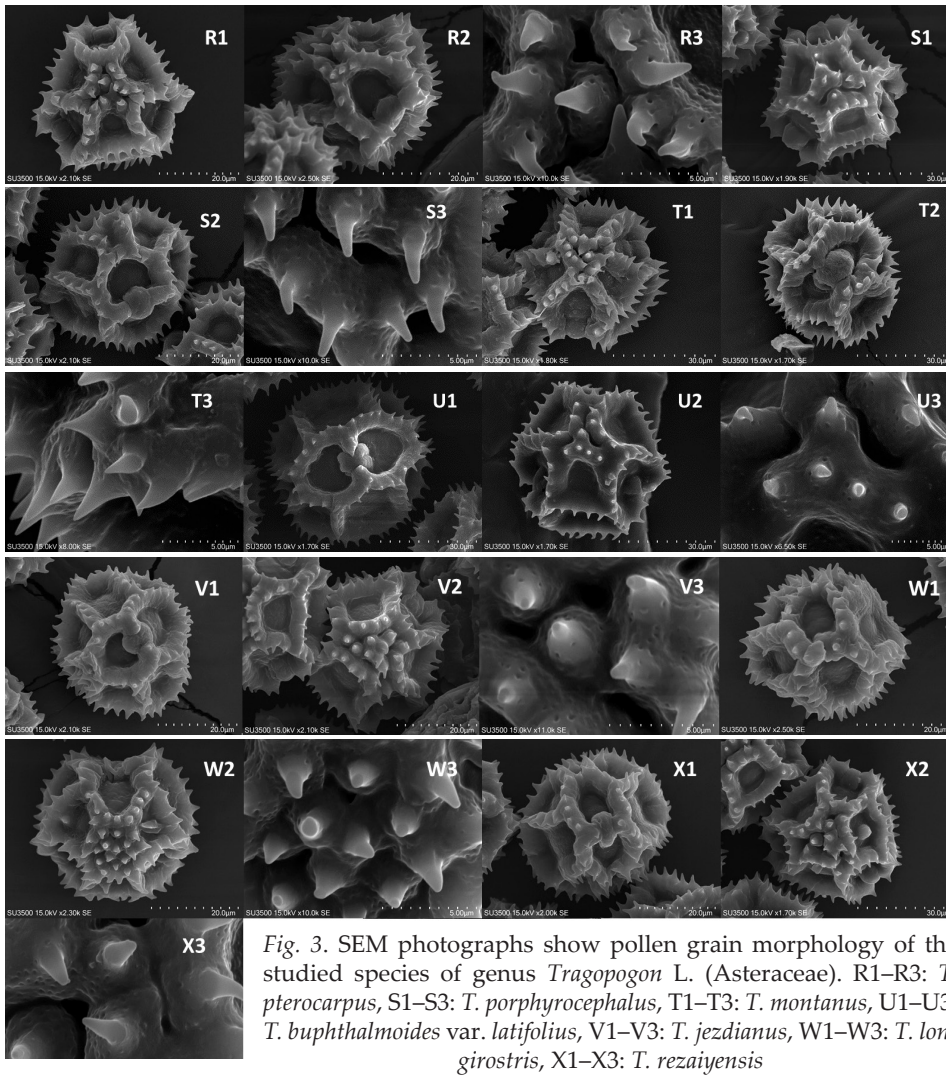

Fig. 3. SEM photographs show pollen grain morphology of the studied species of genus *Tragopogon* L. (Asteraceae). R1–R3: *T. pterocarpus*, S1–S3: *T. porphyrocephalus*, T1–T3: *T. montanus*, U1–U3: *T. buphthalmoides* var. *latifolius*, V1–V3: *T. jezdianus*, W1–W3: *T. longirostris*, X1–X3: *T. rezaiyensis*

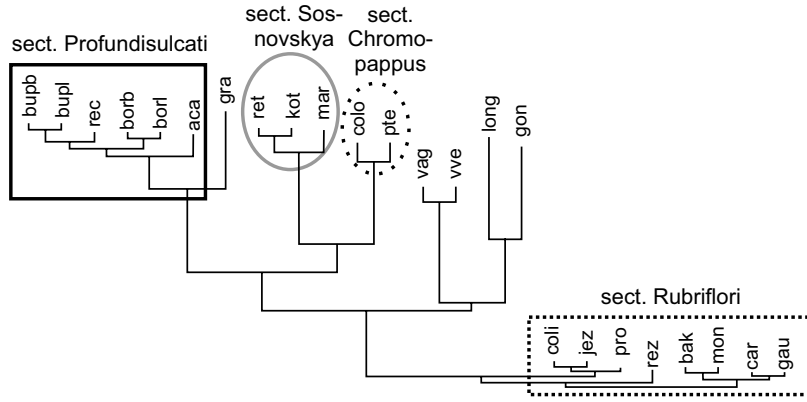

Fig. 4. NJ of *Tragopogon* species studied based on palynological data (buph = *T. buphthalmoides* subsp. *buphthalmoides*, bupL = *T. buphthalmoides* subsp. *latifolius*, rec = *T. rechingeri*, borb = *T. bornmuelleri* subsp. *bornmuelleri*, borL = *T. bornmuelleri* subsp. *latifolius*, aca = *T. acanthocarpus*, gra = *T. graminifolius*, ret = *T. reticulatus*, kot = *T. kotschyi*, mar = *T. marginatus*, colo = *T. coloratus*, pte = *T. pterocarpus*, vag = *T. vaginatus*, vve = *T. vvedenskyi*, lon = *T. longirostris*, gon = *T. gongylorrhizus*, coli = *T. collinus*, jez = *T. jezdianus*, pro = *T. porphyrocephalus*, rez = *T. rezaiyensis*, bak = *T. bakhtiaricus*, mon = *T. montanus*, car = *T. caricifolius*, gau = *T. gaudanicus*)

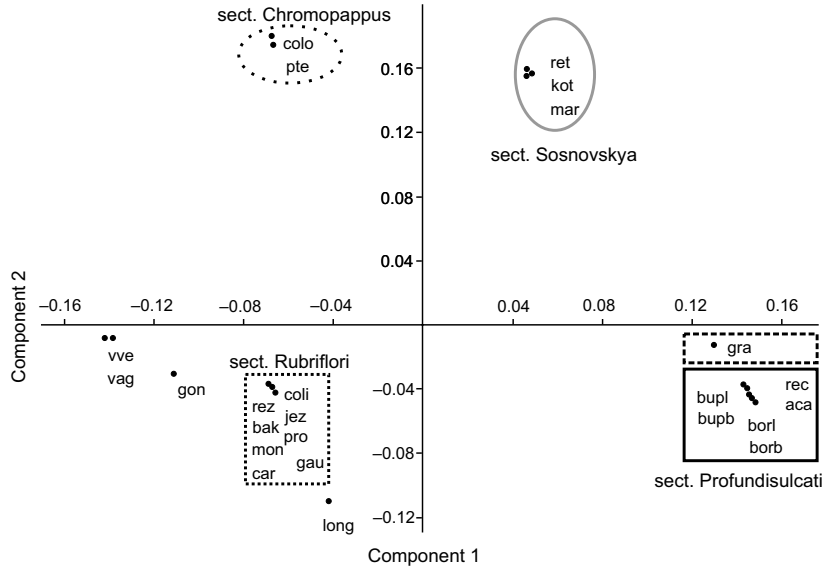

Fig. 5. PCA of *Tragopogon* species studied based on palynological data (buph = *T. buphthalmoides* subsp. *buphthalmoides*, bupL = *T. buphthalmoides* subsp. *latifolius*, rec = *T. rechingeri*, borb = *T. bornmuelleri* subsp. *bornmuelleri*, borL = *T. bornmuelleri* subsp. *latifolius*, aca = *T. acanthocarpus*, gra = *T. graminifolius*, ret = *T. reticulatus*, kot = *T. kotschyi*, mar = *T. marginatus*, colo = *T. coloratus*, pte = *T. pterocarpus*, vag = *T. vaginatus*, vve = *T. vvedenskyi*, lon = *T. longirostris*, gon = *T. gongylorrhizus*, coli = *T. collinus*, jez = *T. jezdianus*, pro = *T. porphyrocephalus*, rez = *T. rezaiyensis*, bak = *T. bakhtiaricus*, mon = *T. montanus*, car = *T. caricifolius*, gau: *T. gaudanicus*)

(Bell *et al.* 2012), in combination with high species richness, indicates a rapid diversification of *Tragopogon* (Bell *et al.* 2012) and therefore seems to be the best explanation for the poor resolution of the molecular-evidence tree.

Others have similarly proposed that "soft" incongruence between multiple single-gene trees might also be a result of rapid diversification (reviewed in Wendel and Doyle 1998). For example, rapid evolutionary radiations have been proposed to explain poorly resolved phylogenies in many groups of organisms from insects to flowering plants (reviewed in Wendel and Doyle 1998, Whitfield and Lockhart 2007). Furthermore, with low rates of molecular evolution, as in *Tragopogon*, some relationships may receive support simply by chance (Downarowicz *et al*. 2008) molecular phylogenetic investigation of *Tragopogon* provide support for the monophyly of several sections of *Tragopogon*, although relationships among sections are not always clear or well supported (Mavrodiev *et al*. 2004, 2005).

Based on Shishkin'n concept Rechinger (1977) divided the genus into 13 sections and 37 species in Flora Iranica, 26 species (11 species endemic) of them exist in the flora of Iran. Safavi *et al*. (2014) divided it into 26 species without sections in the Iran flora. In this study based on palynological characters showed separation of the species of the sections *Majores*, *Profundisulcati*, *Sosnovsky*, *Chromopappus*, *Rubriflori* according to Flora Iranica from the other species of *Tragopogon*. The species of section *Sosnovskya* with the species of section *Chromopappus* according to Flora Iranica are sister groups. Relationship between section of *Majores* with section of *Angustissima* and section of *Krascheninnikovia* with section of *Tuberosi* are according to Flora Iranica.

Position of *T. jezdianus*, *T. porphyrocephalus*, *T. rezaiyensis* is unclear in Flora Iranica. However, based on the molecular data (seven nuclear genes) have classified *T. rezaiyensis* in clade B, *T. jezdianus* in clade C, *T. stroterocarpus* in clade D, *T. porphyrocephalus* in clade of F. (Mavrodiev *et al.* 2012). Based on ITS-ETS studies, the species *T. jezdianus* is classified in section of *Collini* (Mavrodiev *et al*. 2005). Based on a current palynology study, it is suggested that *T. jezdianus*, *T. porphyrocephalus*, *T. rezaiyensis* should be included in section *Rubriflori*. In our study, palynological characters could delimit the studied *Tragopogon* species and pollen characters (like exine surface in polar view, spinule on the opercule, opercule position and polar diameter/equatorial diameter) proved to be useful characters for classification. The results of these studies are consistent with the introduced sections by Rechinger in Flora Iranica. Therefore palynological studies could help to resolve problems related to the taxonomy of *Tragopogon*.

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