IRANIAN JOURNAL OF BOTANY 30 (2), 2024
DOI: 10.22092/ijb.2024.366712.1484

SYSTEMATIC APPLICATION OF ANDROECIUM MORPHOLOGY AT THE INFRA-GENERIC CLASSIFICATION OF THE GENUS FRITILLARIA (LILIACEAE)

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Received 2024.08.18; accepted for publication 2024.11.03

Mohsennezhad, F. & Bakhshi Khaniki, Gh. 2024.12.30: Systematic application of androecium morphology at the infra-generic classification of the genus *Fritillaria* (Liliaceae). -*Iran. J. Bot. 30 (2): 155-172*. Tehran.

The systematic state of the genus *Fritillaria* at the subgeneric level has been the subject of long debate. The genus was classified into various subgenera ranging from two to ten in different morphological e.g., bulbs, style, nectaries, and capsule, Karyological, and molecular studies. In this study scanning electron microscopy imaging of the filament and anther was used to revise the systematics of the genus at the subgeneric level. Several quantitative and qualitative characteristics including filaments' morphology, length, color, ornaments, and anthers' length, color, and attachment were studied in 27 *Fritillaria* species. For the species under study, a clustering dendrogram was constructed based on these characters, and a phylogenetic tree was built using a phylogenetic backbone based on the botanical nomenclature of The Plant List in R software. The results showed some correspondence between the dendrogram and phylogenetic tree, indicating the relative usefulness of filament and anthers' ultrastructure characters in the systematics of *Fritillaria* at the subgeneric level. Moreover, both trees were correspondent in suggesting that the members of subgenus *Fritillaria* were not monophyletic, and a sister relationship between the subgenera *Petilium* and *Theresia*.

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Keywords: *Fritillaria*; Liliaceae; filament; anther; classification; SEM

کاربرد سیستماتیک مورفولوژی نافه گل در سطح زیر جنس در **Fritillaria (Liliaceae)**

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وضعیت سیستماتیک جنس Fritillaria در سطح زیرجنس موضوع بحث‌های طولانی بوده است. این جنس از نظر ریخت‌شناسی پیاز، خامه، نوش‌جای و کپسول، مطالعه هسته و تیمارهای مولکولی به دو تا ده زیرجنس طبقه‌بندی شده است. در این مطالعه از میکروسکوپ الکترونیکی روبشی میله پرچم و بساک برای بازنگری سیستماتیک جنس در سطح فرعی استفاده شد. چندین ویژگی کمی و کیفی از جمله طول میله پرچم، ریخت‌شناسی، رنگ، تزئینات و طول، رنگ و چسبندگی بساک‌ها در۲۷ گونه از جنس Fritillaria مورد بررسی قرار گرفت. برای گونه‌های مورد مطالعه، یک دندروگرام خوشه‌بندی براساس این صفات ساخته شد و یک درخت فیلوژنتیک با استفاده از ستون فقرات فیلوژنتیکی براساس نام‌گذاری گیاه‌شناسی فهرست گیاهان در نرم‌افزار R صورت گرفت. نتایج نشان داد که تناظری بین دندروگرام و درخت فیلوژنتیک وجود دارد که نشان‌دهنده سودمندی نسبی ویژگی‌های فراساختاری میله و بساک در سیستماتیک Fritillaria در سطح زیرجنس است. علاوه بر این، هر دو درخت نشان دادند که اعضای زیرجنس Fritillaria تک‌نیا نیستند و یک رابطه خواهری بین زیرجنس‌های Petilium و Theresia وجود دارد.

INTRODUCTION

The genus *Fritillaria* L. (Liliaceae) includes about 140 geophytic species (Rix & al. 2001) and is one of the most complex genera in the family. The plants are distributed in the temperate climatic regions of the Northern Hemisphere (Rønsted & al. 2005), mainly throughout Europe, West and East Asia, Mediterranean, and North America (Beetle 1944; Tomović & al. 2007; Tekşen & al. 2011). Nineteen species were reported from Iran, of which at least 10 are endemic to the country (Rix 1977; Rechinger 1990; Bakhshi Khaniki 1997; Rix & al. 2001; Kiani et & al. 2017). Bakhshi Khaniki did the last revision of the genus *Fritillaria* in Iran in Flora of Iran (Bakhshi Khaniki 2023).

The systematic status of the genus *Fritillaria* at the subgeneric level has been the subject of long debate. Since Linnaeus 1753, several treatments have been proposed for the subgeneric classifications of *Fritillaria*. Based on the morphology of bulbs, style, nectaries (Khaniki & Persson 1997), and capsule. (Baker 1874) divided the genus into 10 subgenera. *Fritillaria* was divided into two subgroups by Boissier (1884) based on style morphology, entire or trifid. Komarov (1935) Losina-Losinskaya (1935) recognized the two subgenra *Korolkowia* and *Rhinopetalum* of Baker's systems (Baker 1874) as distinct genera. Bakhshi Khaniki (1997), Khaniki and Persson (1997) studying the morphology of floral nectaries, distinguished *Rhinopetalum* group as a separate genus. Losina-Losinskaya (1935), Khaniki & Persson (1997) and Bakhshi Khaniki (2007) supporting the treatment of Komarov (1935). Karyological studies indicated that the Old World taxa had little or no heterochromatin, while New World taxa showed abundant heterochromatin (Darlington & Wylie 1955; Darlington & Wylie 1956). The latest revision of *Fritillaria* belongs to Rix & al. (2001), in which eight subgenera including *Davidii*, *Liliorhiza*, *Japonica*, *Fritillaria*, *Rhinopetalum*, *Petilium*, *Theresia*, and *Korolkowia* were recognized. The taxonomic relevance of stem and leaf anatomy in 10 endemic *Fritillaria* species from the Mediterranean region was studied by Kandemir & al. (2024).

Several molecular studies based on analysis of sequences of different regions of genomic and organelle DNA were conducted to elucidate the taxonomic issues of *Fritillaria* (Rønsted & al. 2005; Day& al. 2014). Based on analyses of DNA sequences of matK, trnK intron, intron ribosomal coding rpl16 gene, and rDNA-ITS (Rønsted & al. 2005), two main clades were defined within the genus, one including the subgenus *Liliorhiza* and the second comprising members of the remaining seven subgenera. In addition, a phylogenetic tree based on matK and rpl16 sequences did not support *Fritillaria* as a monophyletic genus (Day & al. 2014).

This study aimed to investigate the systematic applicability of the filament and anther characters at the subgeneric level of the genus *Fritillaria* based on SEM studies.

MATERIALS AND METHODS

Species studied

27 species from four out of 10 known subgenera of *Fritillaria*, *Rhinopetalum* Fisch., *Theresia* Koch, and *Petilium* L. Endl. from the genus *Fritillaria* were included in the study. Plant materials were collected by the authors in Iran or obtained from cultivated plants in Goteborg Botanical Garden, Sweden. Vouchers are deposited in the Herbarium of the Goteborg University GB Sweden. Each population in the following is assigned a collection number preceded by the abbreviation GBK which stands for author name (Table 1). The scientific names of the plants were standardized based on The Plant List http://www.theplantlist.org and Royal Botanic Gardens-Kew Plants of the World: https://powo.science.kew.org/. A minimum number of four samples were randomly studied for each species, and the average value was used.

Microscopic studies

The shape, size, and pubescence of filaments were studied on fresh material by light microscope. Filaments and anthers were also fixed in FAA 5 vol. Formalin 40%; 5 vol. Acetic acid, glacial; 90 vol. Ethanol 50% in the greenhouse. Materials for SEM studies were prepared as follows: Mature and well-developed filaments and anthers were separated from the flower and transferred to 70% alcohol for 2 days. Then the material was transferred in 70% acetone followed by dehydration in a graded acetone series 90% and 95%; 15 min each, and was further double-dehydrated in 100% acetone for 20 min each time. The material was subjected to critical-point drying BALZERS CPD 030 with liquid CO2 as a transitional fluid and thereafter coated with gold 50 nm thick, BALZERS UNION 010. The prepared slides containing the anther and filament were studied using a Zeiss scanning electron microscope SEM, ZEISS DSM 940. These steps were part of the sample preparation in Sweden.

Filament and anthers characters

Several quantitate and qualitative characters of filament and anthers including filament length, morphology, color, ornaments, and anthers' length, color, and attachment were recorded in samples of 27

Fritillaria species. Table 2 assesses the systematic usefulness of filament and anthers characters. The average values were used for filaments and anthers length of several samples. For various variants of a given qualitative character numbers 1, 2, 3, … were used. Filament morphology (Rix 1977): 1- Subulate, 2- Slender, 3- Stout. Filament color: 1 - Orange-yellowish, 2 - Pale yellow, 3- Brown-yellowish, 4- Yellow-purplish, 5- Yellowish green, 6- Purplish. Filament ornaments 1- Glabrous, 2- Papillose, 3 - Densely papillose, 4- Sparsely papillose, 5- Minutely papillose but narrowly glabrous toward apex, 6- Densely papillose in the upper part and glabrous at the base, 7- Papillose below. Anther color: 1- Pale yellow, 2- Yellow-purplish, 3- Yellow, 4- Greenish, 5- Purplish, 6 - Brown-purplish, 7- Purple. Anther attachment (There are generally two kinds of attachment, basifixed and dorsifixed (Rix 1977): 1- Basifixed, 2 - Shortly dorsifixed.

A clustering dendrogram was constructed based on a combination of quantitative and qualitative variables of filament and anthers using Principal Component Analysis in R software 4.3.2. In addition, a phylogenetic tree was built for the species under study using a phylogenetic backbone based on the botanical nomenclature of The Plant List using R package phylomaker based on a mega tree (Rønsted & al. 2005, Day & al. 2014). The obtained dendrogram based on stamen characters was compared to the phylogenetic tree to assess the systematic usefulness of stamen characters.

Table 1. The source of *Fritillaria* materials used in the current study GBK= Gholamreza Bakhshi Khaniki.* Plant materials collected from cultivated plants in Göteborg Botanical Garden.
Vouchers are deposited in the Herbarium of the Goteborg University GB Sweden. Each population in the following is assigned a collection number preceded by the abbreviation GBK which stands for the author.

No	Species	subgenus	Locality
1	*Fritillaria ariana* (Losinsk. & Vved.) Rix	*Rhinopetalum*	Iran: Khorasan, Torbat-e Jam, Salehabad 1500 m, GBK 42
2	*F. armena* Boiss. *	*Fritillaria*	Turkey: Erzurum, east of Kop pass, SØNDERHOUSEN 1134
3	*F.* assyriaca Baker*	*Fritillaria*	Turkey: Agri, Tahir Da. pass, SØNDERHOUSEN 1106
4	*F. atrolineata* Bakhshi Khan.	*Fritillaria*	Iran: W. Azarbaijan, Urmiah, Ghasemlu, 1500 m, GBK 63
5	*F. bucharica* Regel	*Rhinopetalum*	Tadjikistan: Hissar mountains, 1400 m, VACRATOT
6	*F. caucasica* Adams	*Fritillaria*	Iran: E. Azarbaijan, Tabriz to Ahar, 1800 m, GBK 70
7	*F. chlorantha* Hausskn. & Bornm.	*Fritillaria*	Iran: Khoramabad, Oshtoran Kuh, 2400 m, GBK 88
8	*F. chlororhabdota* Bakhshi Khan.	*Fritillaria*	Iran: W. Azarbaijan, Urmiah, Sir Mt., 1800 m, GBK 65
9	*F. crassifolia* subsp. *crassifolia*	*Fritillaria*	Turkey: Denizli, Honaz Dag, STEVENS
10	*F. crassifolia* subsp. *kurdica* (Boiss. & Noë) Rix	*Fritillaria*	Iran: West AzarbijanSalmas, Ghooschi pass, 1900 m, GBK 67
11	*F. gibbosa* Boiss.	*Rhinopetalum*	Iran: Tehran, Karadje, Park-e Chitgar, 1400 m, GBK 1
12	*F. hermonis* subsp. amana* Rix	*Fritillaria*	Turkey: Hatay, 5 km before Belen, 1300 m, SØNDERHOUSEN 1055
13	*F. imperialis* L.	*Petilium*	Iran: Esfahan, Khunsar, Golestan Kuh, 2600 m, GBK 16
14	*F. kotschyana* subsp. *grandiflora* (Grossh.) Rix*	*Fritillaria*	Turkmenistan: Talysh, Pagum Lerik, 1100 m, FURSE 3520
15	*F. kotschyana* subsp. *kotschyana*	*Fritillaria*	Iran: Tehran, Shemshak, Elborz mtns., 2800 m, GBK 98
16	*F. michailovskyi* Fomin*	*Fritillaria*	Turkey: Kars, Sarikamis, Yenikoy, 2300 m, SØNDERHOUSEN 893

17	*F. minima* Rix*	*Fritillaria*	Turkey: Van, Kavussahap Dag, MATHEW
18	*F. minuta* Boiss. & Noë *	*Fritillaria*	Turkey: Van, Tatvan, 2510 m, FURSE 7241
19	*F. olivieri* Baker	*Fritillaria*	Iran: Hamadan, Kuh-e Elvand, 2500 m, GBK 60
20	*F. persica* L.	*Theresia*	Iran: Esfahan, Khunsar, Golestan Kuh, 2600 m, GBK 90
21	*F. pinardii* Boiss.*	*Fritillaria*	Turkey: Eskisehir, 22 km north of Eskisehir, SØNDERHOUSEN 1219
22	*F. poluninii*(Rix) Bakhshi Khan. & K.M.Perss. *	*Fritillaria*	Iran: Kermanshahan, Kuh-e Owraman, pass between Daraki and Nowsud, 2500-2600 m, WENDELBO
23	*F. raddeana* Regel	*Petilium*	Iran: Gorgan, Golestan Forest, Almeh, 1650 m, GBK 48
24	*F. reuteri* Boiss.	*Fritillaria*	Iran: W. Azarbaijan, Urmiah, Kuh-e Sir, 2100 m, GBK 94
25	*F. stenanthera* (Regel) Regel *	*Rhinopetalum*	Turkmenistan: near Askabad, CUBA
26	*F. straussii* Bornm.	*Fritillaria*	Iran: Kermanshah, Ghallajeh pass, 1700 m, GBK 51
27	*F. uva-vulpis* Rix *	*Fritillaria*	Iraq: Rowandooz, Haji Omran, TUBERGEN
28	*F. zagrica* Stapf	*Fritillaria*	Iran: Arak, Soltanabad village, 1700-1900 m, GBK 33

RESULTS

The SEM micrographs of anther and filaments of species under study were of high quality for comparison and scoring of quantitative and six qualitative characters (Figs. 1 – 10). Two quantitative and six qualitative characters of filament and anthers measured in 27 species of the genus *Fritillaria* are indicated in Table 2. On average the filament length ranged from 5 to 31.5 mm mean= 9.6, StDev = 5.3. This range for anthers was 2 - 9.5 mean 4.9, StDev=1.8.

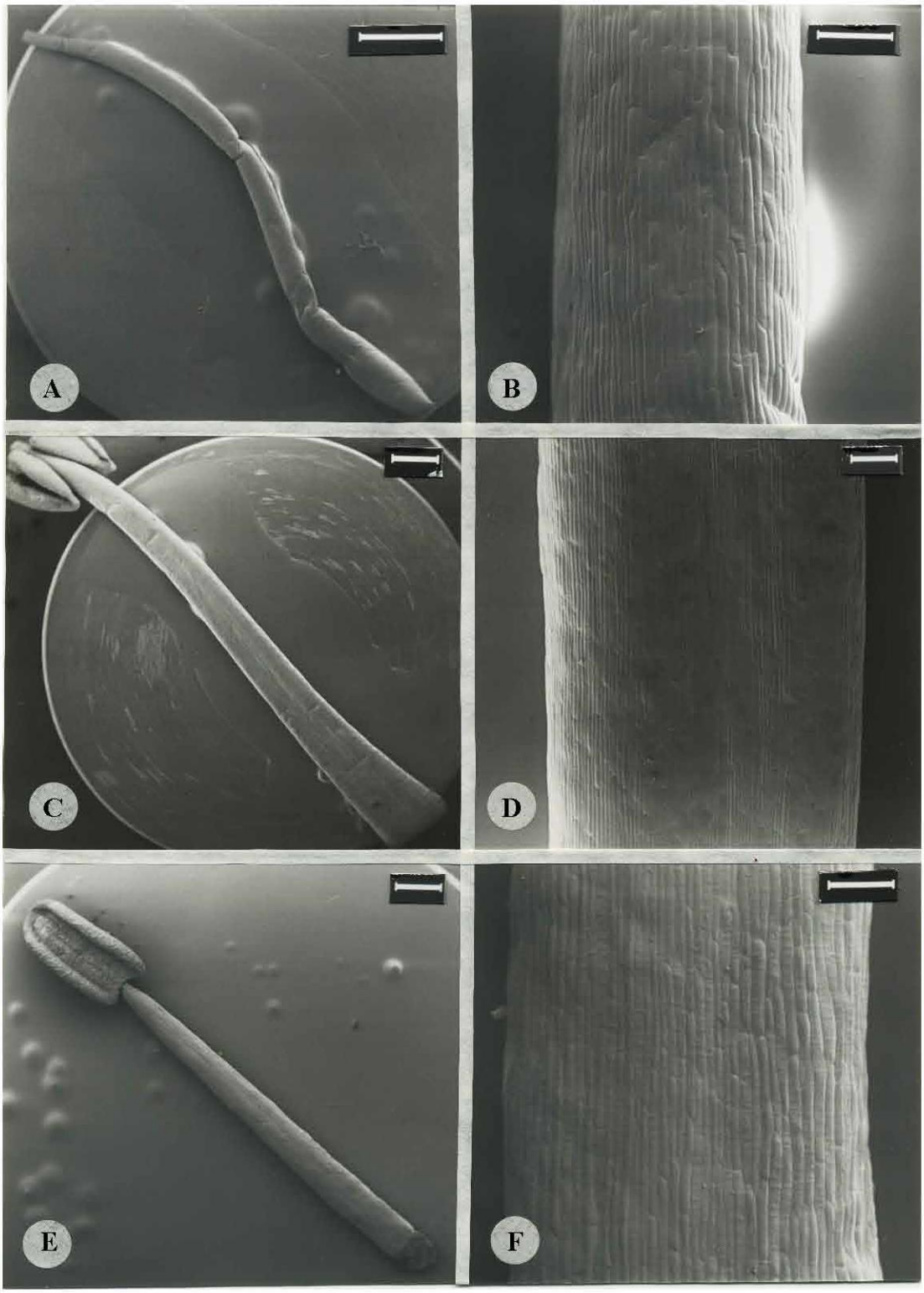

Fig. 1. SEM micrographs of *Fritillaria imperialis*: A, filament; B, filament base. *Fritillaria raddeana*: C, filament; D, filament base. *Fritillaria persica*: E, filament; F filament base. Scales: A, 2 mm; B, 200 µm; C, 2 mm; D, 200 µm; E, 1 mm; F, 100 µm.

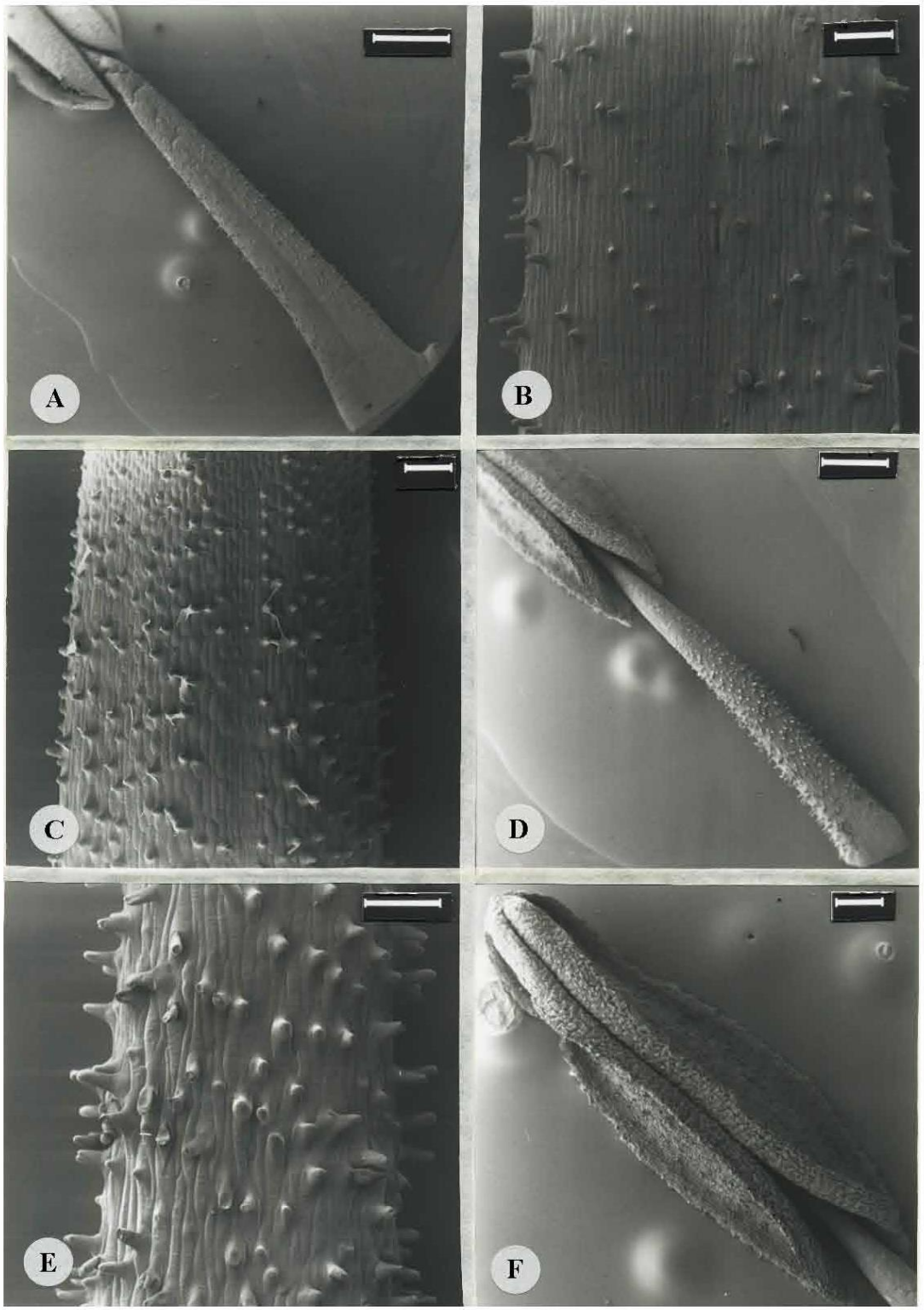

Fig. 2. SEM micrographs of *Fritillaria crassifolia* ssp. *crassifolia*: A, filament; B, filament base. *Fritillaria crassifolia* ssp. *kurdica*: C, filament base. *Fritillaria poluninii*: D filament; E, filament base; F, anther. Scales: A, C, E-F, 200 µm; B, D, 1 mm.

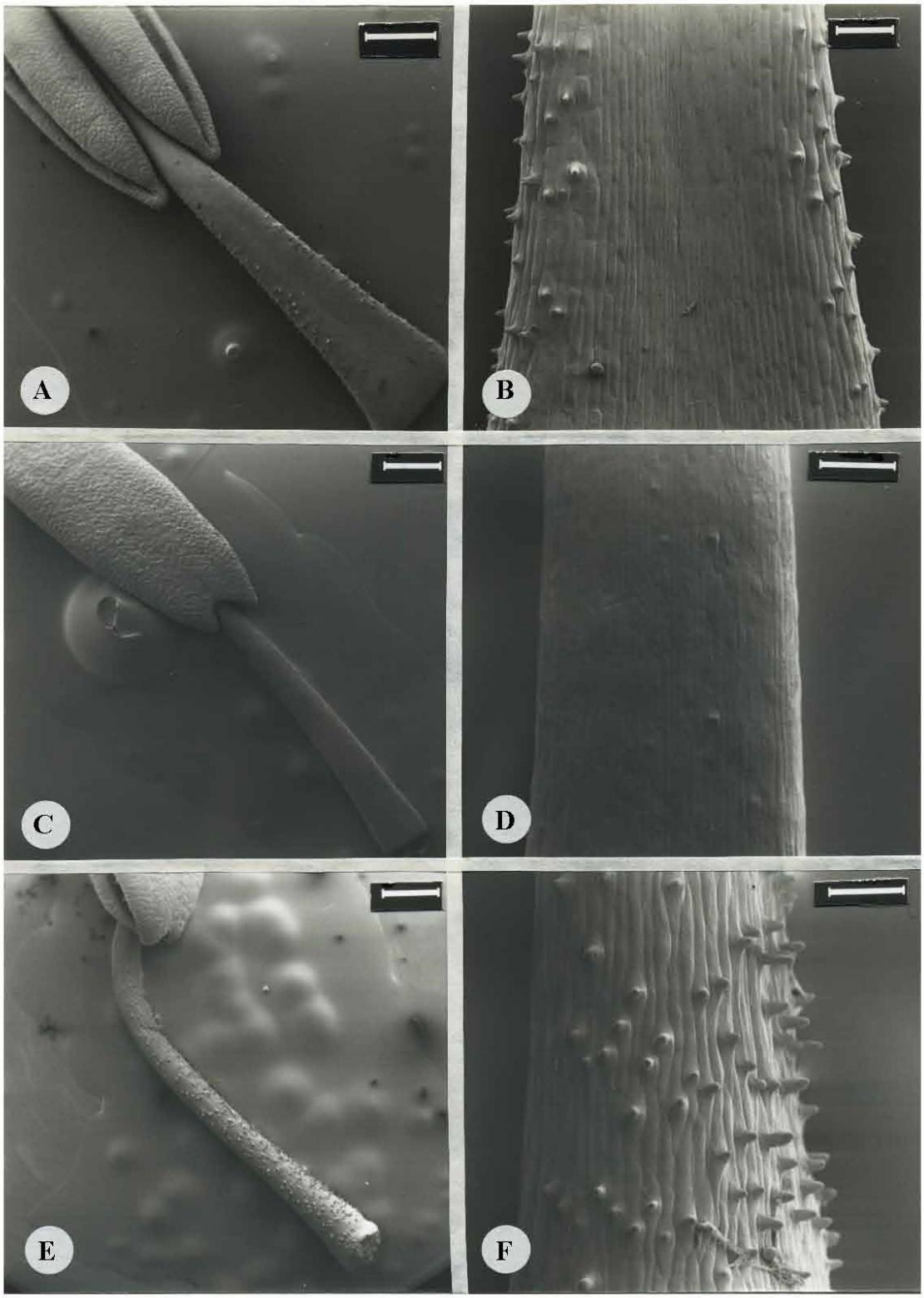

Fig. 3. SEM micrographs of *Fritillaria michailovskyi*: A, filament; B, filament base. *Fritillairia reuteri*: C, filament; D, filament base. *Fritillaria straussii*: E, filament; F, filament base. Scale bars: A, C, E, 1 mm; B, D, F, 200 μm.

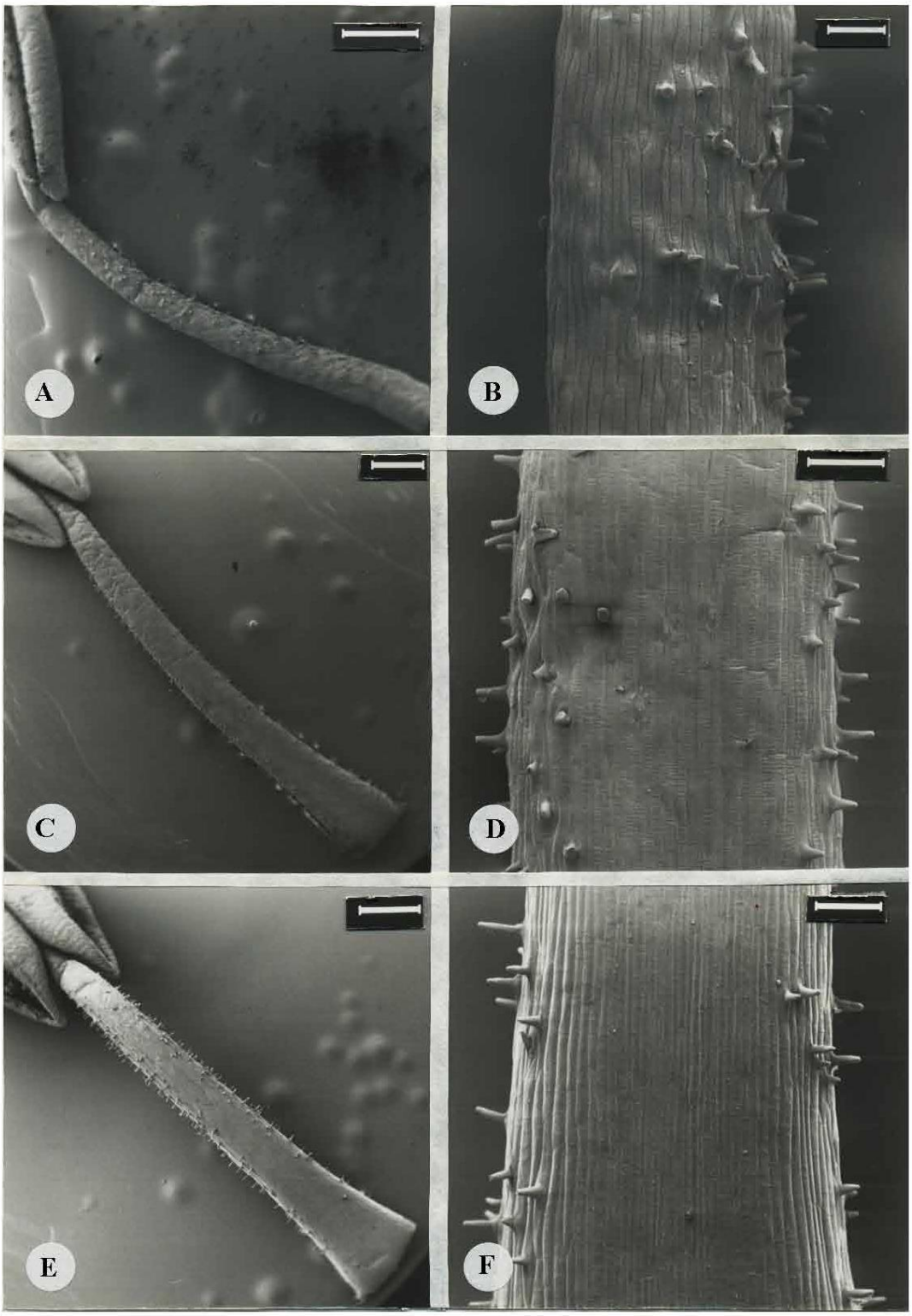

Fig. 4. SEM micrographs of *Fritillaria kotschyana* ssp. *kotschyana*: A, filament; B, filament base. *Fritillaria kotschyana* ssp. *grandiflora*: C, filament; D, filament base. *Fritillaria hermonis* ssp. *amana*: E, filament; F, filament base. Scale bars: A, D, 1 mm; B, C, E, 200 µm; F, 100 µm.

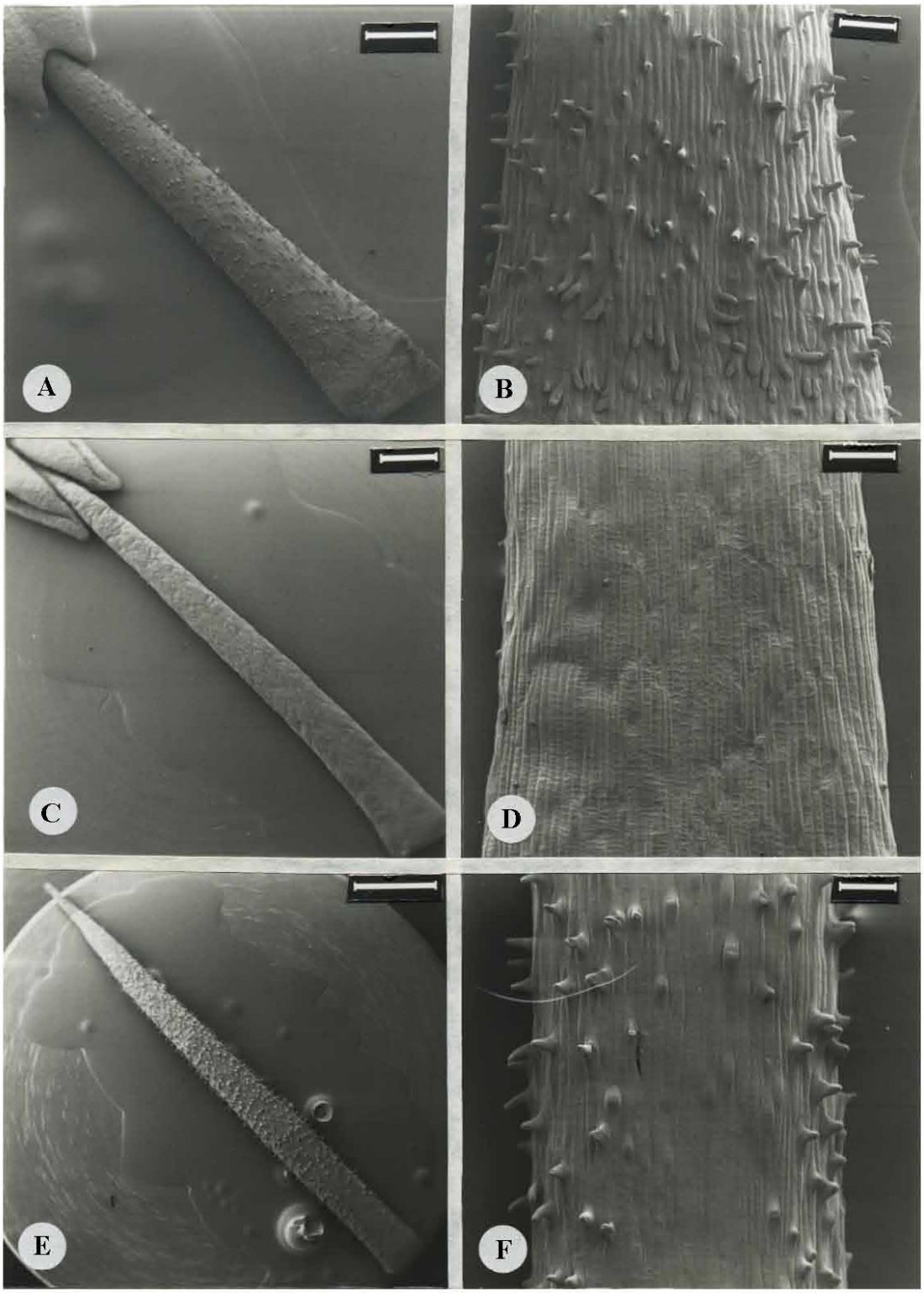

Fig. 5. SEM micrographs of *Fritillaria olivieri*: A, filament; B, filament base. *Fritillaria whittallii*: C, filament; D, filament base. *Fritillaria caucasica*: E, filament; F, filament base. Scale bars: A, C, 1 mm; E, 2 mm; B, D, F, 200 µm.

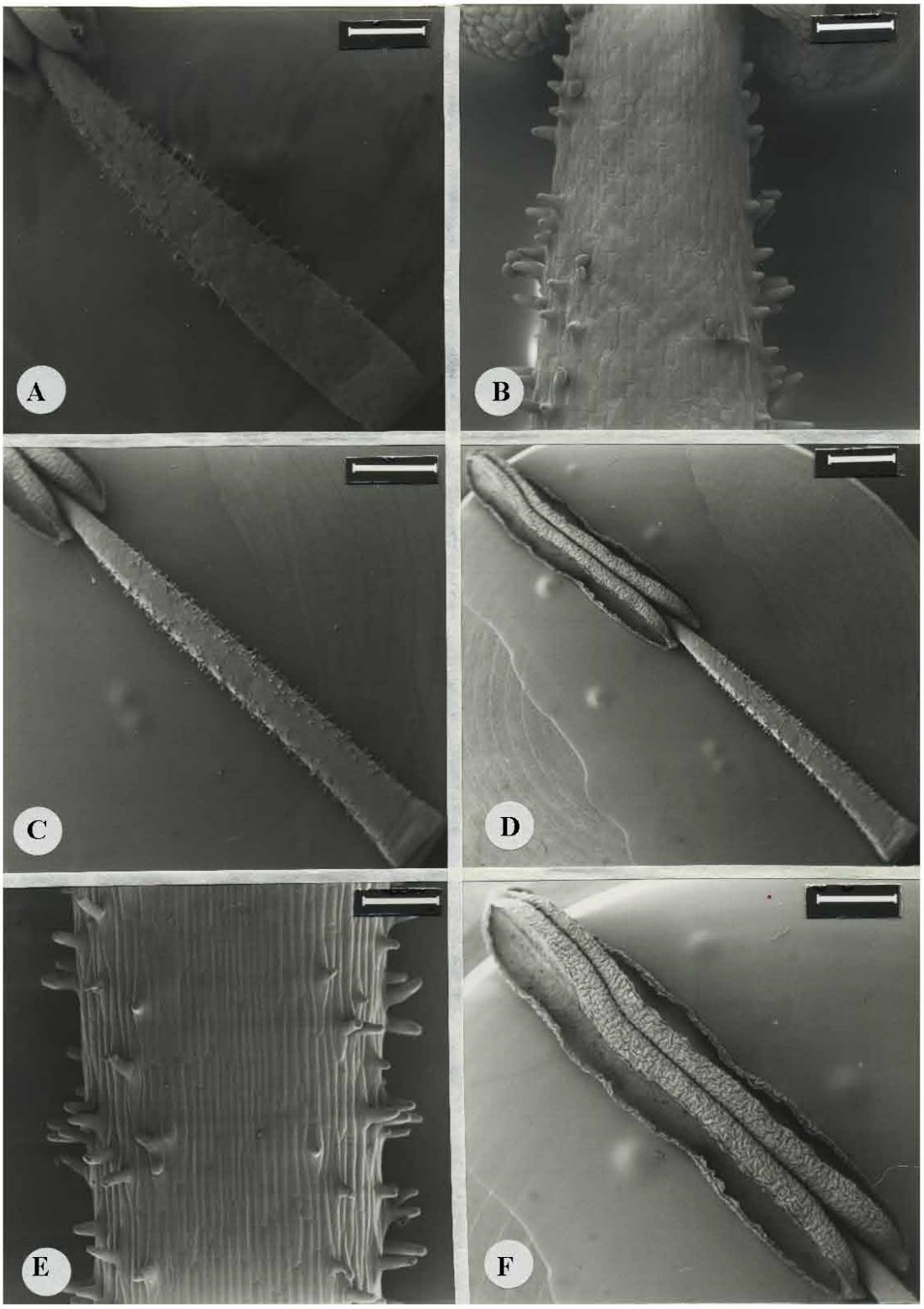

Fig. 6. SEM micrographs of *Fritillaria armena*: A, filament; B,filament base. *Fritillaria minima*: C, filament; D, filament and anther; E, filament base; F, anther. Scale bars: A, C, F, 1 mm; B; 2 mm; B, D, E, 200 μm.

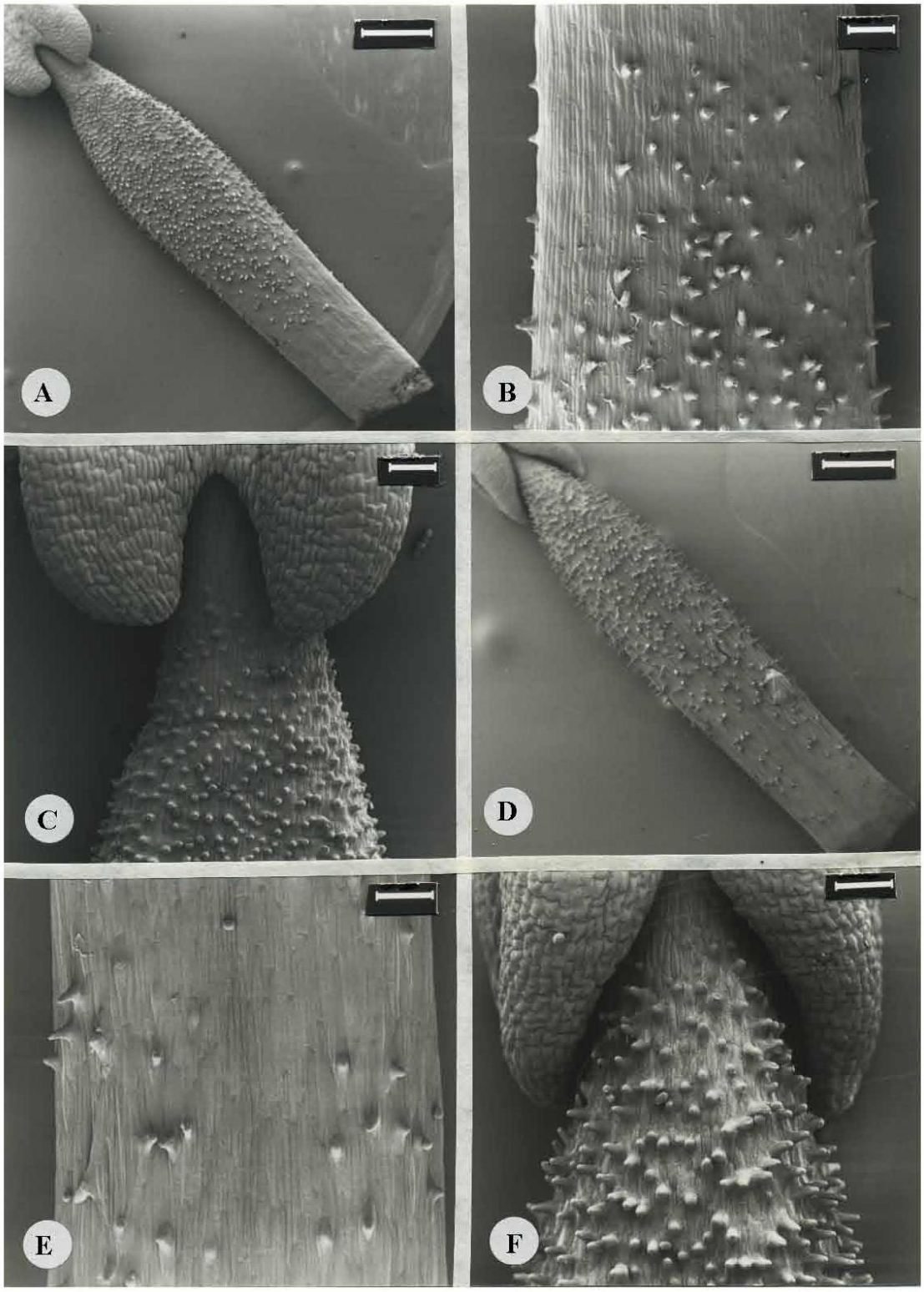

Fig. 7. SEM micrographs of *Fritillaria pinardi*: A, filament; B, filament base; C, attachment of the filament to anther. *Fritillaria uva-vulpis*: D, filament; E, filament base; F, attachment of the filament to anther. Scale bars: A, C, 1 mm; B, F, 200 µm; D, E, 500 µm.

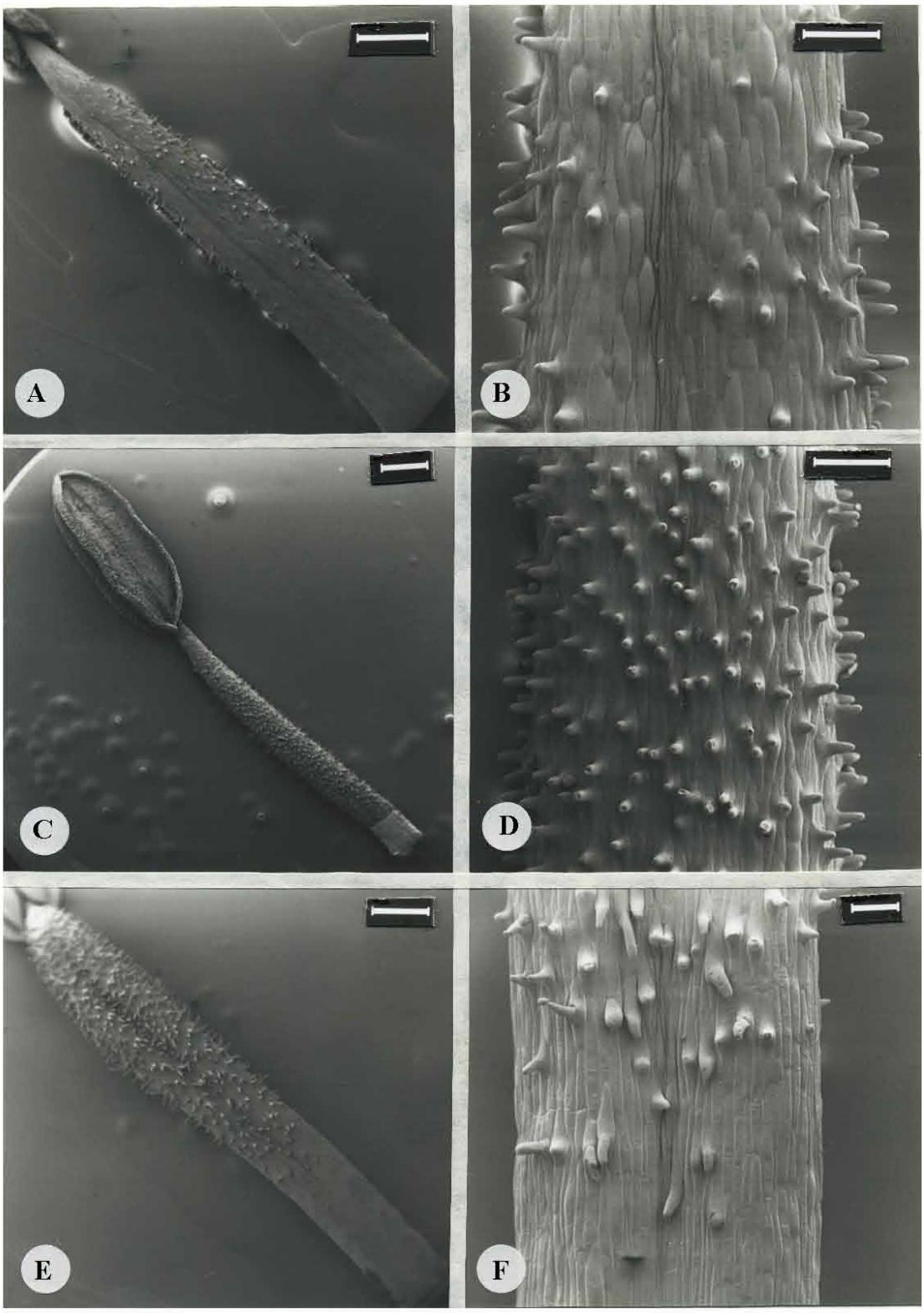

Fig. 8. SEM micrographs of *Fritillaria chlorantha*: A, filament; B, filament base. *Fritillaria zagrica*: C, filament; D, filament, and anther. *Fritillaria atrolineata*: E, filament; F, filament base. Scale bars: A, C, E, 1 mm; B, D, F, 200 µm.

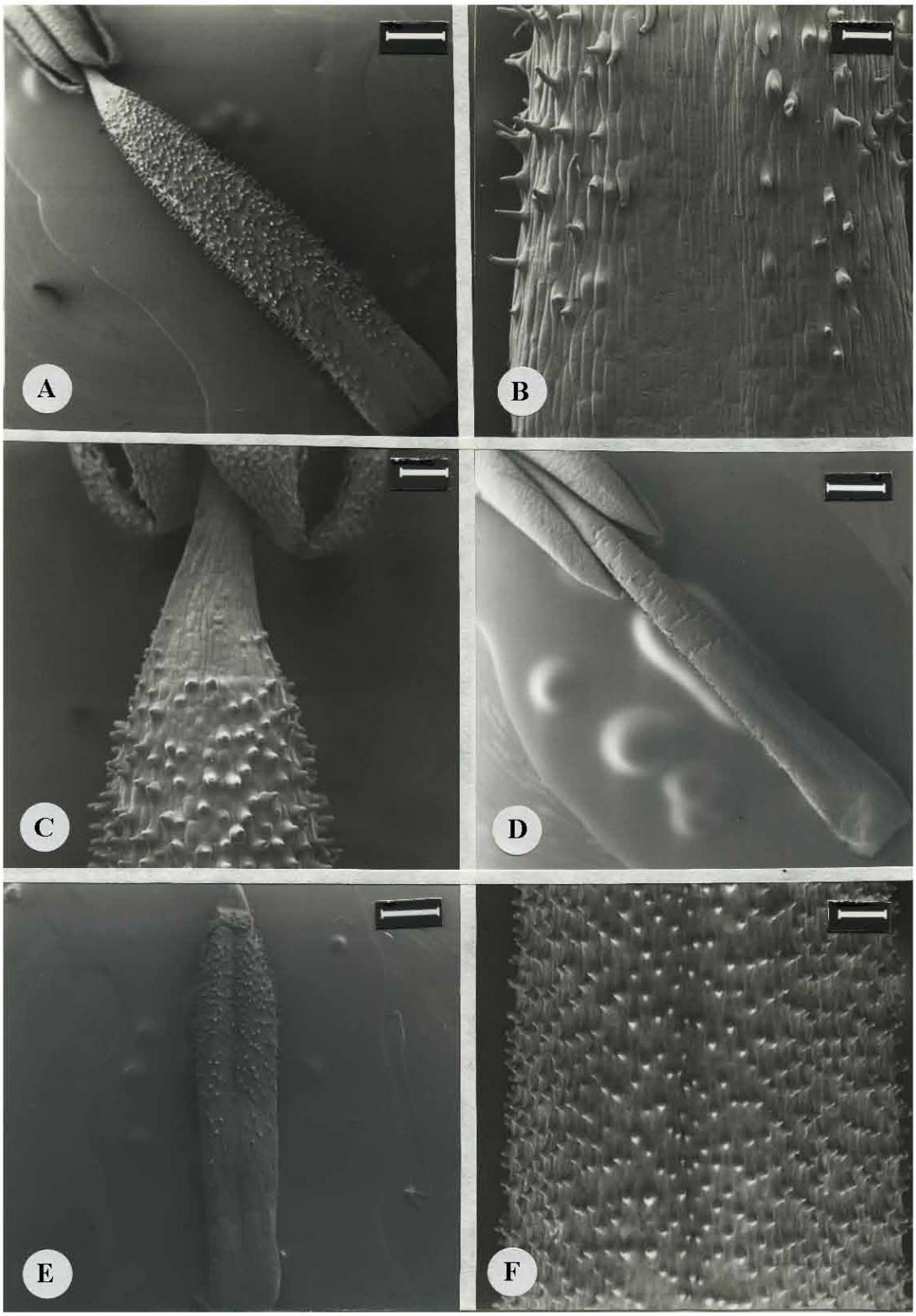

Fig. 9. SEM micrographs of *Fritillaria assyriaca*: A, filament; B, filament base; C, attachment of the filament to anther. *Fritillaria minuta*: D, filament. *Fritillaria chlororhabdota*: E, filament; F, upper part of filament. Scale bars: A, D, E, 1 mm; B, C, F, 200 µm.

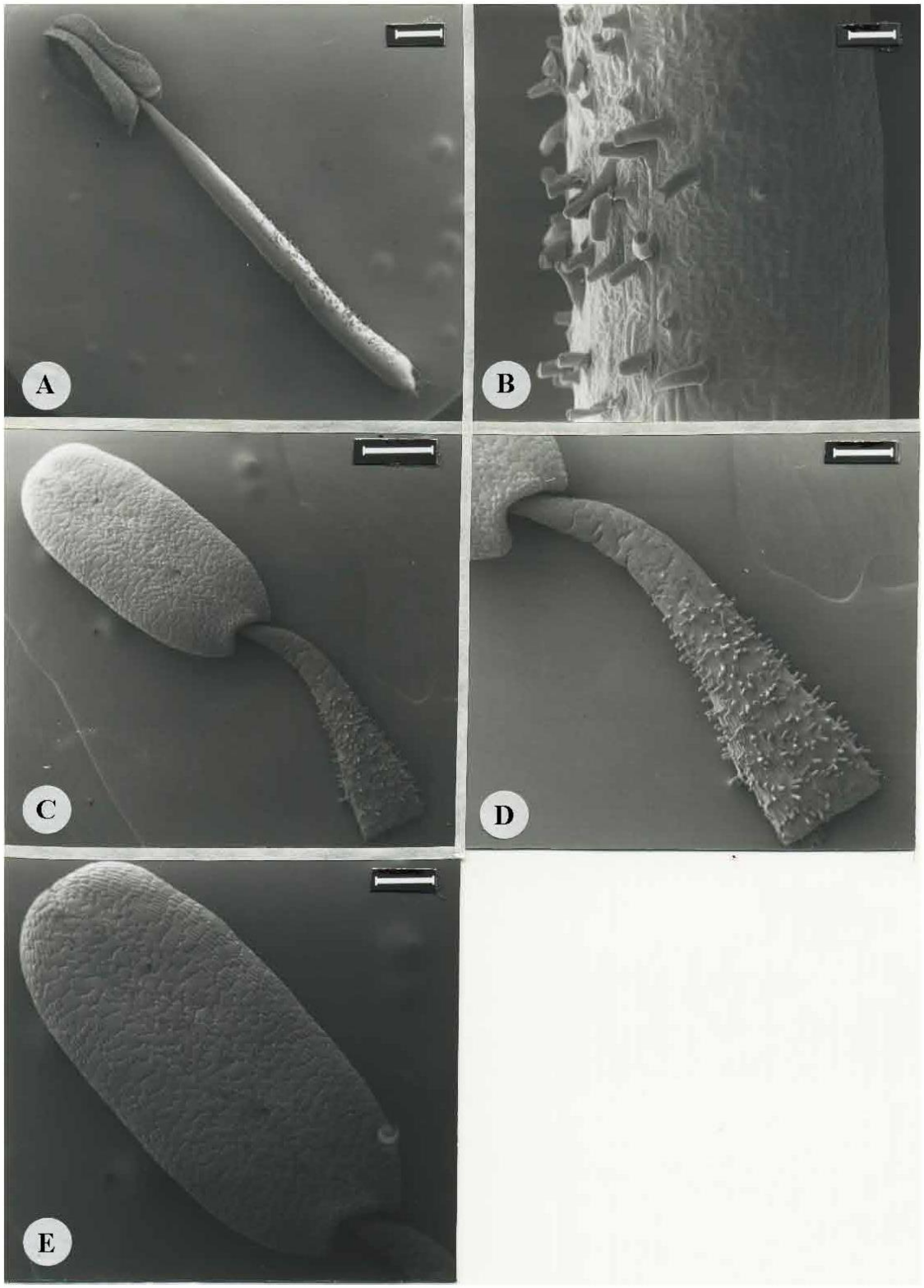

Fig. 10. SEM micrographs of *Fritillaria gibbosa*: A, filament; B, filament base. *Fritillaria ariana*: C, androecium; D, filament; E, anther. Scale bars: A, C, 1 mm; B, 100 µm; D, E, 500 µm.

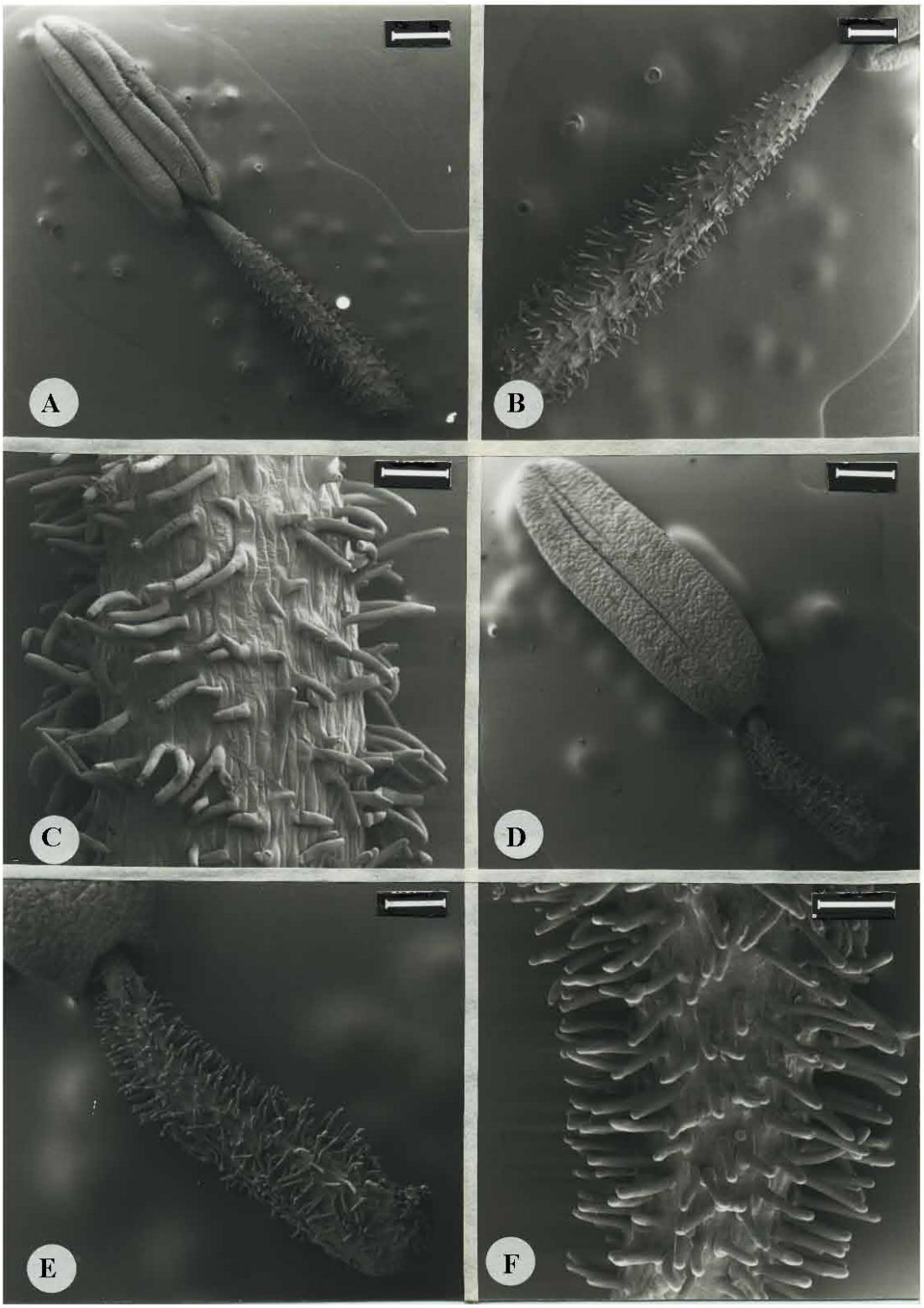

Fig. 11. SEM micrographs of *Fritillaria stenanthera*: A, androecium; B, filament; C, filament base. *Fritillaria bucharica*: D, androecium; E, filament; F, filament base Scale bars; A, D, 1 mm; B, D, 500 μm; C, F, 100 μm.

Table 2: The quantitative and qualitative characters of filament and anthers of 27 species belonging to four subgenera of the genus *Fritillaria*.

Species	Filament length	Anther length	Filament shape	Filament color	Filament ornaments	Anther color	Anther attach
Fritillaria ariana	7	2.5	2	2	6	7	1
F. armena	7.5	3.75	2	4	3	5	2
F. assyriaca	8	4.25	3	2	3	3	1
F. bucharica	5	2	2	4	3	8	1
F. caucasica	14	6.5	2	2	2	3	1
F. chlorantha	6.25	6	2	5	2	3	1
F. chlororhabdota	6	4.2	3	4	6	6	1
F. gibbosa	9	2.25	1	1	5	5	1
F. hermonis	9	7	1	2	2	3	2
F. imperialis	31.5	9.5	1	1	1	1	1
F. kotschyana ssp. *grandiflora*	11	6.75	2	2	2	3	1
F. michailovskyi	8	5	1	2	2	3	1
F. minima	9	4.75	2	3	2	3	1
F. minuta	8	4.5	2	3	5	1	1
F. olivieri	9.5	7	2	2	4	3	1
F. persica	7.5	4	2	1	1	2	1
F. pinardii	8	4	3	2	2	3	1
F. poluninii	6	3.5	2	3	2	3	1
F. raddeana	20	6.5	2	2	1	1	1
F. reuteri	8.5	6	2	3	1	3	1
F. ssp. *kotschyana*	8	5.25	1	3	3	3	1
F. stenanthera	8	2	2	3	3	6	1
F. straussii	9	3.75	2	1	2	1	2
F. uva-vulpis	8.5	6.5	3	2	3	3	1
F. whittallii	10	6.5	2	3	2	4	1
F. zagrica	8	3.75	2	6	3	5	1

Filament shape (Rix 1977)	Filament color (Rix 1977)	Filament ornaments (Rix 1977)	Anther color (Rix 1977)	Anther attachment (Rix 1977)
1 - Subulate 2 - Slender 3 - Stout	1 - Orange-yellowish 2 - Pale yellow 3 - Brown-yellowish 4 - Yellow-purplish 5 - Yellowish green 6 - Purplish	1 - Glabrous 2 - Papillose 3 - Densely papillose 4 - Sparsely papillose 5 - Minutely papillose but narrowly glabrous toward the apex 6 - Densely papillose in the upper part and glabrous at the base 7 - Papillose below	1 - Pale yellow 2 - Yellow-purplish 3 - Yellow 4 - Greenish 5 - Purplish 6 - Brown-purplish 7 - Purple	1 - Basifixed 2 - Shortly dorsifixed

A clustering dendrogram based on a combination of quantitative and qualitative characters of filaments and anthers was concurrent with the phylogenetic tree based on Mega tree Fig. 12.

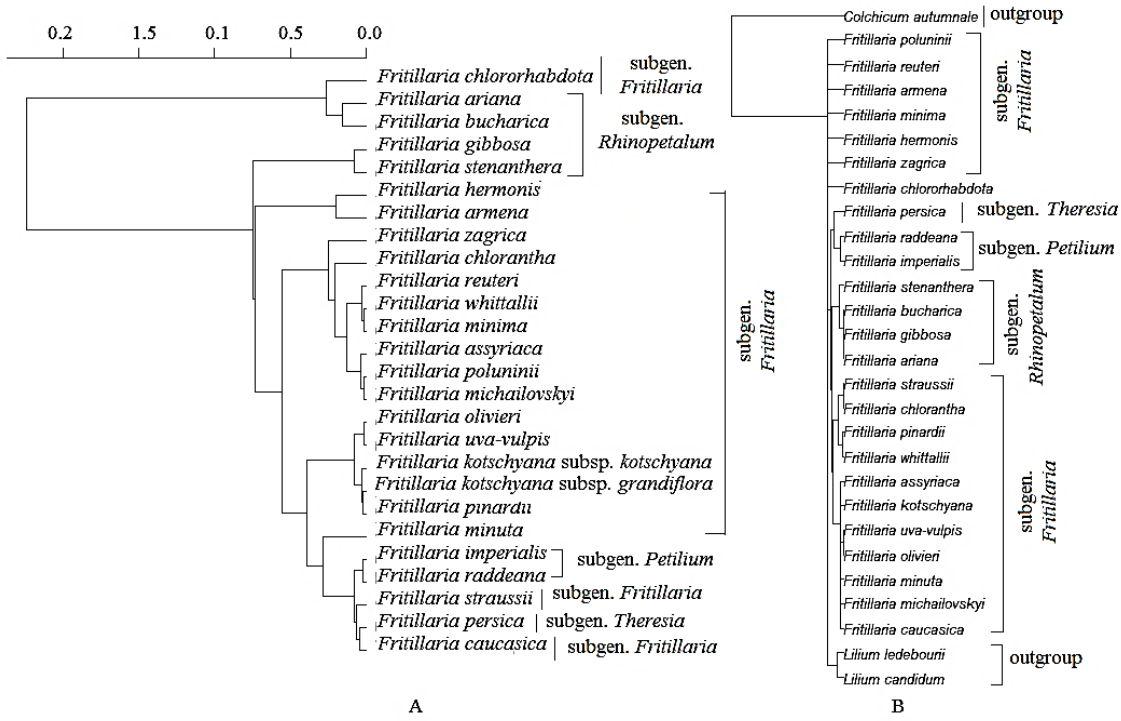

Fig 12. Comparison of the phylogenetic relationship among 27 species belonging to four subgenera of the genus *Fritillaria*: A, the clustering dendrogram based on the combination of quantitative and qualitative characters of filament and anthers, and B, the phylogenetic tree constructed based on a mega tree in R software.

DISCUSSION

The high-level congruence between the dendrogram based on filament-anthers' characters and the phylogenetic tree of *Fritillaria* species supports the usefulness of these characters in the infra-generic classification of *Fritillaria* (Advay & al. 2016). In both trees, the members of subgenera *Rhinopetalum* and *Petilium* were located in their own clusters. Moreover, both trees were correspondent in indicating that the members of subgenus *Fritillaria* were not monophyletic. In addition, both the dendrogram and phylogenetic tree showed a sister relationship between subgenera *Petilium* and *Theresia*. However, there was a contradiction between the trees, since the phylogenetic tree showed the monophyly of subgenus *Rhinopetalum*, but the dendrogram presented paraphyletic status for this group. Moreover, stamen position and anthesis type were shown to have systematic and evolutionary importance in the tribe Myrteae so that the three patterns of stamen position corresponded to the phylogeny of the tribe (Vasconcelos & al. 2015). Systematic analysis of morphological quantitative characters of floral parts carried out on 10 species of *Fritillaria* was reported to be consistent with sectional classification of these species (Advay & al. 2016). Our study and other studies (Rønsted & al. 2005, Day & al. 2014) support the systematic application of ultrastructure characters of filament, anther at infra-genus and infra-tribal levels. The surface structure of the filament papillose or glabrous is taxonomically important and useful for subgeneric classification. All species of subgenus *Fritillaria* except *F. reuteri* have ± papillose filaments, but filaments are glabrous in subgenera *Petillium* and *Theresia* species. All *Rhinopetalum* species have± papillose filaments. The shape, size, and color of filaments seem taxonomically unimportant (Bakhshi Khaniki 1998).

ACKNOWLEDGMENTS

We appreciate the support of Payame Noor University (PNU), Department of Biology for this project.

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