Introduction of seed and capsule micromorphological features of the genus Scrophularia (Scrophulariaceae) in Iran

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Abstract. In the present study, seed surface ornamentations in 31 species (34 populations) and the capsule surface sculpturing in five species of the genus Scrophularia L. distributed in Iran were examined using Scanning Electronic Microscopy. Based on the published seed surface terminologies, all examined seeds show the reticulate pattern with scalariform inner ornamentations. However, there is enough but untrustworthy variations in epidermal cell shapes and the walls’ characteristics to divide the seed surface sculpturing patterns into four different groups: (1) cells with completely irregular shape; (2) cells without distinct shape so that their boundaries are not clear; (3) reticulate polygonal cells bordered with distinct walls neither undulate nor vesiculate, divided in two subgroups; forming elongated narrow cells and wide cells; (4) reticulate polygonal cells bordered with undulated or sometimes vesiculate walls divided in two subgroups; forming elongated narrow cells and wide cells. In addition, all the species’ seeds can be alveolate, ridged or without distinct alveoli or ridges regarding their surfaces. There have also been variations in size, shape and color of the seeds even in a single individual. There are no applicable features of capsule surface sculpturing analyzed here, based on which species could be classified in certain groups.

Keywords. alveolate, microscope, ornamentation, reticulate, Verbaseae
INTRODUCTION

Scrophularia L. (commonly known as figwort) with about 250 taxa (Judd et al., 2008) worldwide and about 60 species in Iran (Bayat & Attar, 2016; Ranjbar & Rahchamani, 2018, 2019), is among the largest genera of Scrophulariaceae sensu stricto which belongs to one of the taxonomically most difficult groups in the family (Attar & Hamzhee, 2006; Attar et al., 2011; Ranjbar et al., 2017; Maaberley, 2018).

The genus is mostly found throughout the Northern Hemisphere (Heywood, 1985), but concentrated in Asia with only a few species in Europe and North America. The genus Scrophularia grows in different ecological habitats in Iran. Although it occurs throughout mountainous regions (e.g. S. azerbajanica Grau), it can be found in forests (e.g. S. megalantha Rech.f.), riversides (e.g. S. subaphylla Boiss.), and rarely along the roadsides (e.g. S. variegata M.Bieb.). Scrophularia, morphologically, is characterized by opposite or alternate leaves, open two-lipped flowers and compound cymes at the end of the stems which can be frondose (having leaves along the peduncles) or non frondose. The most important problem in the taxonomy of the genus is the unclear borders among several species.

Moreover, the importance of several characters such as shape of corolla and staminods in the systematics of the genus is still ambiguous. Based on a comprehensive phylogenetic study, the family Scrophulariaceae s.s. is delimited into seven tribes (Stevens, 2017), according to which Scrophularia and Verbascum L. form one well-supported clade called the tribe Scrophularieae. Very closely related to Scrophularia are Verbascum and Oreosolen Hook. F. (Oxelman et al., 2005). Scrophularia and Verbascum were placed in the tribe Verbascceae (Freeman & Scogin, 1999). However, they were all transferred into Scrophularieae (Olmstead et al., 2001; Oxelman et al., 2005; Stevens, 2017).

The close relationship between Scrophularia and Verbascum has been suggested by previous molecular studies (Gahremaninejad et al., 2014; Riahi & Gahremaninejad, 2019), as well as similarities in seed and embryo characters (Thieret, 1967) and leaf anatomy (Lersten & Curtis, 1997).

Seed micromorphology of some Scrophulariaceae genera such as Striga Lour. (Jones & Safa, 1982), Paulownia Siebold & Zucc. (Vujčič et al., 1993), Cordylanthus Nutt. & Benth. (Chuang & Heckard, 1972), Orthocarpus Nutt. (Chuang & Heckard, 1983), Kickxia Dumort. (Juan et al., 1998) and Verbascum (Juan et al., 1997; Attar et al., 2007) has been the subject of study. In general, and according to Chuang and Heckard (1983), the seed shape is directly related to the insertion point in the fruit. It is proved that there are some striking similarities between the species of the genus Orobanche L. and some species of Scrophularia in some morphological characters especially some of the seed features, such as the terminal insertion and the reticulate ornamentation (Juan et al., 2000) which shows the closeness of the two families. Based on the features of the tangential wall in the seeds epidermal cells of the genera of the family Scrophulariaceae studied by Juan et al. (2000), two groups were established from which Verbascum and Scrophularia are in the first group with membranous walls.

The aim of the present study is to screen the seed and capsule surface ornamentation in order to see if they are appropriate for a reliable classification of the genus at the infrageneric level.

MATERIALS AND METHODS

All the analyzed information on the species, collection data and the vouchers used are given in Table 1. Seeds were collected from living plants whenever possible, otherwise from herbarium specimens. The species of the genus Scrophularia examined here (including 31 species with some populations of the six species), are deposited at HKS, IRAN and TUH (acronyms according to Holmgren et al., 1990). The species which are not included in this analysis are closely similar to species examined, some of them are rare and some others are collected from the samples that possess no seeds. For the SEM studies, clean seeds were fixed on aluminum stubs using double-sided adhesive and were coated with a thin layer (ca. 25 nm) of gold-palladium. The SEM micrographs were taken by a Zeiss SEM-960A (Germany) from the middle of the seeds, mostly at magnification of 600x. At least, four seeds from each specimen were scanned to ensure the consistency of seed coat ornamentations. 10 seeds at least were measured to record the accurate information about morphology and size parameters. The terminology of Sutton (1988) and Juan et al. (1997) have been used to describe the seed surface patterns. Regarding capsule surface ornamentation, all the species were taken from the same samples as mentioned.
Table 1. Voucher information and results of seed micromorphological characters for the studied specimens.

| Taxon                           | Voucher data                        | Seed length (mm) | Seed width (mm) | Seed pattern         |
|---------------------------------|-------------------------------------|------------------|-----------------|----------------------|
| *S. amplexicaulis*              | Lorestan: Khorramabad, 24147-TUH    | 1±0.2            | 0.5±0.1         | - / 4a               |
| *S. atropatana*                 | Azarbayejan: Khoi, Forouagh, Shurik, 69952-TUH | 0.75±1.5        | 0.5±0.1         | Alveolate/4b         |
| *S. azerbajaniaca*              | Azarbayejan: Arasbaran, Khodafarin, 17356-TUH | 1±0.1            | 0.5±0.1         | Alveolate/4a         |
| *S. chlorantha*                 | Kordestan: Maryvand to Saghez, Agieh village, 387-HKS | 0.5±0.1          | 0.3±0.1         | - / 4b               |
| *S. crassicaulis*               | Tehran: Shemshak to Dizin, 14536-TUH | 1.4±0.1          | 0.6±0.1         | - / 4b               |
| *S. crassiuscula*               | Bakhtiari: Borujen, to Dorahan, Doudelu Mountain, 57239-TUH | 0.8±0.2          | 0.5±0.1         | Alveolate/2          |
| *S. crenophila*                 | Kordestan: Divandareh to Saghez, Irankhah pass, 7604-HKS | 0.7±0.3          | 0.4±0.2         | Alveolate/4a         |
| *S. deserti*                   | Baluchestan: 50 km to Bazman from Bampour, 21540-TUH | 1.4±0.5          | 0.5±0.3         | Alveolate/4b         |
| *S. farinosa*                   | Kohkilouyeh-Boyer Ahmad: Dehdasht, Toyeh-Sh, 46914-IRAN | 1.15±0.15        | 0.7±0.2         | -                    |
| *S. frigida* subsp. frigida¹    | Khorasan: Neyshabur, Soumeh, Binaloud, 39129-IRAN | 1.25±0.25        | 0.7±0.2         | Alveolate/4b         |
| *S. frigida* subsp. frigida²    | Kerman: Baft, Gughder, Bondar, 31979-TUH | 1.4±0.1          | 0.5±0.1         | Alveolate/4b         |
| *S. frigida* subsp. haussknechtii¹ | Kerman: Hezar Mountain, 39138-IRAN | 1.4±0.3          | 0.5±0.2         | Alveolate/4b         |
| *S. frigida* subsp. haussknechtii² | Markazi: Arak, Sefidkhani elevation, 10633-TUH | 1±0.1            | 0.5±0.1         | Alveolate/4b         |
| *S. gauvae¹*                    | Mazandaran: Sang-Deh, 30 km S.E. Pole-Sefid, 39381-IRAN | 1±0.7            | 0.6±0.1         | Alveolate/3b         |
| *S. gauvae²*                    | Gilan: Amarlou, Barreh-Sar to Damash, 39224-IRAN | 1.25±0.15        | 0.75±0.15       | Alveolate/3b         |
| *S. glauca*                     | Fars: Shiraz, Sabzpushan Mountain, 39145-IRAN | 0.8±0.1          | 0.5±0.1         | - / 2                |
| *S. ilwensis*                   | Azarbayejan: Kalbar, Nabijan, Kalan Mountain, 39416-IRAN | 0.85±0.15       | 0.6±0.1         | Ridged/4b            |
| *S. kardica*                    | Azarbayejan: Urumieh, Band, 70083-TUH | 0.9±0.1          | 0.4±0.1         | - / 4a               |
| *S. leucoclada*                 | Kerman: Between Doulatabad and Sirueh, 70177-TUH | 2±0.1            | 1.1±0.1         | Ridged/4b            |
| *S. libanotica*                 | Esfahan: Akhore mountain, 39168-IRAN | 1.1±0.2          | 0.5±0.1         | Alveolate/3a         |
| *S. megalantha*                 | Mazandaran: Ramsar, Neydasht, 8409-TUH | 0.5±0.1          | 0.4±0.1         | Alveolate/1           |
| *S. mesopotamica*               | Kordestan: Saghez to Mrivan, Heshlagh Pol village, 4237-HKS | 0.6±0.1          | 0.4±0.1         | Alveolate/3b         |
| *S. nervosa* subsp. boissieri¹   | Kordestan: Bidjar, Hamzeh-Arab Mountain, 39178-IRAN | 1.5±0.2          | 0.7±0.1         | Alveolate/4b         |
| *S. oxysepala*                  | Ardebil: Ghotur_Sou, Sabalan Mountains, 39198-IRAN | 0.9±0.2          | 0.5±0.1         | Ridged/4b            |
| *S. pruinosa*¹                   | Kordestan: 55 km to Baneh from Marivan, 36346-TUH | 1.8±0.2          | 0.75±0.15       | Alveolate/3b         |
| *S. pruinosa*²                   | Kermanshah: 7 km after Paveh to Ravansar, 17837-TUH | 1±0.2            | 0.65±0.15       | Alveolate/4a         |
| *S. pruinosa*²                   | Mazandaran: Rudehen elevations, 10623-TUH | 1.3±0.1          | 0.7±0.1         | Alveolate/4a         |
| *S. sanguinea*                  | Lorestan: Oshtoran- Kooh, Saravand to Gahar lake, 39234-IRAN | 1.3±0.2          | 0.6±0.2         | Alveolate/4a         |
| *S. scoparia*                   | Khorassan: Sabzehvar, Soltan Abad to Ghochan, 39230-IRAN | 1.1±0.2          | 0.55±0.25       | Alveolate/1           |
| *S. scopoli¹*                    | Gilan: Ispili, Larekhani, 18473-TUH | 0.8±0.1          | 0.4±0.1         | - / 1                |
| *S. scopoli²*                    | Gilan: Asalem to Khalkhal (forest), 39232-IRAN | 0.85±0.15       | 0.4±0.1         | - / 1                |
| *S. striata*¹                    | Yazd: Tarzian, 28175-TUH | 1.3±0.1          | 0.7±0.1         | Ridged/4b            |
| *S. striata*²                    | Markazi: Arak, Emarat elevation, 10645-TUH | 1.45±0.15       | 0.8±0.1         | Ridged/4a            |
RESULTS

Seed shape and surface

As it is observed in Figures, *S. pruinosa* (Fig. 1), *S. azerbajianiaca* Grau (Fig. 2) and *S. deserti* Del. (Fig. 3) show the alveolate type, whereas *S. leucoxoclada* Bunge (Fig. 4) and *S. striata* Boiss. (Fig. 5) show the ridged type and *S. chlorantha* Kotschy & Boiss. (Fig. 6), *S. umbrosa* Dumort. (Fig. 7) and *S. umbrosa* (Fig. 8) do not have a clear alveoli or ridge. *S. pruinosa* (Fig. 9), *S. frigida* Boiss. subsp. *haussknechtii* Borrm. ex Grau (Fig. 10), *S. frigida* subsp. *frigida* (Fig. 11), *S. frigida* subsp. *frigida* (Fig. 12), *S. variegata* M.Bieb. subsp. *cinerascens* (Boiss. in Tchihat.) Grau (Fig. 13), *S. variegata* subsp. *variegata* (Fig. 14), *S. variegata* subsp. *rupestris* (M.Bieb.) Grau (Fig. 15) are some more examples of alveolate type. Seed surface ornamentations have been also examined. As it is shown in Figures, *S. megalantha* (Fig. 16) possesses irregular cells, *S. glauca* Deene. ex Bentham (Fig. 17) has shapeless cells and *S. kurdica* Eig (Fig. 18), *S. syriaca* Bentham (Fig. 19), *S. pruinosa* (Fig. 20), *S. leucoxoclada* (Fig. 21) and *S. pruinosa* (Fig. 22) all contain reticulate cells. The seeds vary from oblong (e.g. *S. pruinosa*) to elliptic (e.g. *S. umbrosa*) and prismatic (e.g. *S. frigida* subsp. *frigida*) in shape (see Figs. 1, 7, 11). It is important to mention that all the types could be found in all the species’ capsules. Among the studied species, the size of seed ranges from 0.3 (e.g. *S. megalantha*) to 0.9 mm (e.g. *S. umbrosa*) in width and from 0.7 (e.g. *S. atropatana* Grossh.) to 1.9 mm (e.g. *S. leucoxoclada*) in length (Table 1). Some seeds have an attenuate (e.g. *S. azerbajianiaca*), truncate (e.g. *S. leucoxoclada*), apiculate (e.g. *S. chlorantha*), obtuse (e.g. *S. umbrosa*), or rounded (e.g. *S. variegata* subsp. *variegata*) beak (see Figs. 2, 4, 6, 8, 14 respectively), whether in all dimensions or two, although it can be in one as well. The spectrum of mature seed color ranges from dark brown (e.g. *S. megalantha*) to black (e.g. *S. leucoxoclada* – data not shown).

However, orange to light brown colors are recognized in immature seeds. Given the fact that three different types of seed surface patterns are identified for species in the present study, we can make a relatively thorough artificial classification, based on which seed coat can be alveolate (Figs. 1-3), ridged (Figs. 4-5) - which are arranged longitudinally in numerous rows, or without distinct alveoli or ridges sometimes forming clear longitudinal undulate walls (Figs. 6-8). As the alveoli show significant differences in depth and slight differences in length and width among the species, the ridges demonstrate some differences which can help classify the species into different types as discussed later. If the ratio of length to width calculated in each species is 1.8 ± 0.4 mm, it is considered as ridge and if the ratio is 4.5 ± 0.5 mm, it represents alveolus (measuring at the same magnification). The seed coat is far deeply alveolate in *S. pruinosa*, *S. scoparia* Pennell, *S. svartiana* Gabrielian, *S. syriaca*, *S. mesopotamica* Boiss. and *S. crassiuscula* Grau, whereas *S. azerbajianiaca*, *S. gaubae* Bornm., *S. libanotica* Boiss., *S. nervosa* Bentham., *S. sanguinea* Grau., *S. subaphylla* Boiss., *S. variegata* subsp. *variegata* are deeply alveolate and *S. atropatana* Grossh., *S. crenophila* Boiss., *S. deserti*, *S. frigida*, *S. megalantha*, *S. variegata* subsp. *rupestris*, *S. variegata* subsp. *cinerascens* are shallowly alveolate (see Figs. 1-3 and also 9-15).

### Table 1. continued.

| Species                  | Location Description                                                                 | Length (mm) | Width (mm) | Surface Pattern    |
|--------------------------|--------------------------------------------------------------------------------------|-------------|------------|--------------------|
| *S. striata* ³            | Khorassan: Qucan, Chenaran, Akhamad fall, 27512-TUH                                  | 1.2±0.1     | 0.5±0.1    | Ridged/3a          |
| *S. subaphylla*           | Esfahan: Khansar, Ghale-Bala-Mohammad Mt., 39318-IRAN                                | 1.5±0.1     | 0.6±0.1    | Alveolate/4a       |
| *S. svartiana*            | Azarbayejan: 15 km after Salmas to Urumieh, 39302-IRAN                               | 0.9±0.1     | 0.6±0.1    | Alveolate/4b       |
| *S. syriaca*              | Semnan: 8 km N.E. of Momen-Abad, 39300-IRAN                                          | 1.5±0.1     | 0.8±0.1    | Alveolate/3b       |
| *S. umbrosa* ¹            | Mazandaran: Karaj, Chalus road, Pole Zanguleh, Kamarbon, 33296-TUH                    | 1±0.1       | 0.5±0.1    | -/4b               |
| *S. umbrosa* ²            | Golestan: Golestan park, after Mirza Baylu to Sulgerd, 25445-TUH                     | 0.8±0.1     | 0.5±0.1    | -/3b               |
| *S. variegata* subsp. *rupestris* | Mazandaran: Kelardasht to Pit-Sara, 39324-IRAN                                      | 1.5±0.1     | 0.6±0.1    | Alveolate/3b       |
| *S. variegata* subsp. *cinerascens* | Mazandaran: Ilka, Varvasht mountain to Kamarbon, 39316-IRAN                  | 1.25±0.25   | 0.5±0.1    | Alveolate/3b       |
| *S. variegata* subsp. *variegata* | Gilan: Talesh, Aghvelar village, 28978-TUH                                        | 1.5±0.1     | 0.6±0.1    | Alveolate/3b       |
| *S. vernalis* ¹           | Golestan: Gorgan, Shamshak forest, 47677-IRAN                                        | 0.9±0.1     | 0.4±0.1    | -/4b               |
| *S. vernalis* ²           | Mazandaran: Tunekebon, Jannat-Rudbar, 21238-TUH                                      | 1.2±0.1     | 0.7±0.1    | -/3b               |
| *S. xylobasis*            | Fars: Estahbanat, Chute mountain, 39397-IRAN                                        | 1.4±0.1     | 0.6±0.1    | -/2                 |
Figures 1-15. Alveolate types. 1. *S. pruinosa*¹ (far deeply). 2. *S. azerbaijanica* (deeply). 3. *S. deserti* (shallowly). 4,5. ridged type: 4. *S. leucoclada* (far deeply) and as the largest seed, 5. *S. striata*² (deeply). 6-8. without alveoli or ridges type and sometimes longitudinally undulate: 6. *S. chlorantha* (as the smallest seed). 7,8. *S. umbrosa*¹². 9. *S. pruinosa*³, 10. *S. frigida* subsp. *haussknechti*². 11. *S. frigida* subsp. *frigida*². 12. *S. frigida* subsp. *frigida*¹. 13. *S. variegata* subsp. *cinerascens*. 14. *S. variegata* subsp. *variegata*. 15. *S. variegata* subsp. *Rupestris*
Figures 16-27. Seed surface ornamentation and capsule surface. 16-22. Seed surface ornamentation, scale bar = 20 µm. Irregular cells. 16. S. megalantha; shapeless cells. 17. S. glauca; reticulate cells. 18. S. kurdica. 19. S. syriaca. 20. S. pruinosa³. 21. S. leucoclada. 22. S. pruinosa¹. 23-27. Capsule surface, scale bar = 10 µm. 23. S. amplexicaulis. 24. S. atropatana. 25. S. azerbaijanica. 26. S. crassicaulis. 27. S. striata².

Some species such as S. leucoclada can be far deeply ridged while S. ilwensis C.Koch, S. oxysepala Boiss. and S. striata are deeply ridged (see Figs. 4, 5). In some species such as S. amplexicaulis Benth., S. chlorantha, S. crassicaulis Boiss., S. glauca, S. kurdica, S. scopolii Hoppe, S. umbrosa and S. vernalis L., no distinct alveoli or ridges are observed, which form the third group sometimes including longitudinal undulate walls (see Figs. 6-8). Sometimes significant differences
are found in subspecies or populations of the same species. For example, the seed surface patterns are the same in two far distant populations of S. umbrosa and S. pruinosa. On the other hand, three subspecies of S. variegata show some differences in their shapes and patterns.

Based on the seed surface ornamentation, another classification is also considered which divide all the species into four groups;
(1) cells with completely irregular shape (e.g. S. megalantha),
(2) cells without distinct shape so that their boundaries are not clear (e.g. S. glauca),
(3) reticulate polygonal cells bordered with distinct walls neither undulate nor vesiculate, consisting two subgroups a- forming elongated narrow cells (e.g. S. kurdica), b- forming wide cells (e.g. S. syriaca),
(4) reticulate polygonal cells bordered with undulate or sometimes vesiculate walls, consisting two subgroups a- forming elongate narrow cells (e.g. S. pruinosa), b- forming wide cells (e.g. S. leucoclada) (see Figs. 16-22).

However, the first classification is artificially applicable for classifying the species. It is noticeable that neither of two classifications suggested here, verify each other.

Capsule surface

Since there are no helpful features in capsule surface ornamentations, the examined species could not be classified into some artificial certain groups. Although, some different ornamentations on capsule surfaces could be recognized. Some of the micrographs are illustrated in Figures 23-27. As it is shown, capsule surfaces can be longitudinally striate forming almost orbicular chambers (e.g. S. amplexicaulis, Fig. 23), horizontally striate forming various grooves (e.g. S. atropatana, Fig. 24), smooth with no special sculpturing (e.g. S. azerbajiana, Fig. 25), irregularly striate forming more clear chambers (e.g. S. crassicaulis, Fig. 26), unclearly striate forming irregularly small chambers (e.g. S. striata, Fig. 27).

DISCUSSION

According to Juan et al. (2000), the indumentum, capsule dehiscence, structure of the endocarp, seed coat ornamentation, and inner structure of the seeds were the most useful features to determine relationships among the different genera included in the family Scrophulariaceae. Despite the utility of fruit and seed characters for distinguishing the genera in Scrophulariaceae by Juan et al. (2000), seed features are unlikely to classify the species of Scrophularia in an accurate way based on the present study. In addition, phenoetic analysis of 58 characters revealed that several groups of genera in Scrophulariaceae are closely related on the basis of their fruit and seed features (Juan et al., 2000) which is not true regarding the species of Scrophularia using micromorphological features of seed and pollen grains (Daemi, 2009; Rahchamani, 2018). Similarly, seed micromorphological studies on Verbascum as the closest genus to Scrophularia could not present a complete classification for the genus (Attar et al., 2007). Also, in the family Orobanchaceae as a close family to Scrophulariaceae, characters such as size, shape and ornamentation of the seeds were not found to be very useful in differentiation of taxa; however, other characters of the epidermal seed coat cells confirm the usefulness of seed characters to identify most of the studied species of Orobanche (Plaza et al., 2004). Moreover, Verbascum and Celsia L. also belong to the Scrophularia type of the alveolate seeds, characterized by endothelium arranged in ribs and penetrate in endosperm (based on the classification presented by Hartl, 1959). Contrary to most other genera in the family Scrophulariaceae, Scrophularia, Verbascum and Oreocephalum are all mainly distributed in Northern Hemisphere -confirming their close relationship biogeographically. Although, they are not surprisingly from the same morphological point of view, their seed surface ornamentations are more or less similar to each other which makes it difficult to make a classification.

As a result, having a short look at Figures 1-15 shows the difficulties in differentiating the species having the alveolate type. It is also shown obviously that S. pruinosa (Figs. 1, 9) with two populations from two different locations have almost the same alveoli but different seed surface ornamentations. In S. frigida two populations of the same subspecies and the subspecies show variations in their size, shape and particularly in surface (see Figs. 10-12). Likely, three subspecies of S. variegata have alveolate seeds, but there are clear differences in their surfaces (see Figs. 13-15). Given the fact that reticulate seed coats have been observed in several genera belonging to different tribes, such as Digitaleae (Juan et al., 2000), some of the species examined here show reticulate sculpturing. However, this is not a reliable character for identifying the species of Scrophularia. Only Verbascum and Scrophularia have seeds with longitudinal rows of alveoli or ridges (Juan et al., 2000). According to study on Verbascum seeds (Attar et al., 2007) on Verbascum and our current data on Scrophularia, it seems that seed and capsule surface ornamentations show homoplasy and are not suitable to be relied on. Therefore, the information given here on both seed surface patterns and ornamentations is not helpful. For example,
although seed surface patterns in *S. pruinosa* (Figs. 1, 9) are the same, their ornamentations (Figs. 20, 22) put them more or less in different groups. Although capsule dehiscence in *Scrophularia* is septicidal, which has been proved to have a high systematic value, they do not allow us to put the species even in artificial groups. The results of this study indicate that the characters of seed surface and capsule sculpturing do not provide any diagnostic features useful in separation of the species of *Scrophularia* and presenting natural grouping in the genus. Therefore, these characteristics are not reliable to indicate the homogeneity of the group and probably its monophyly.

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