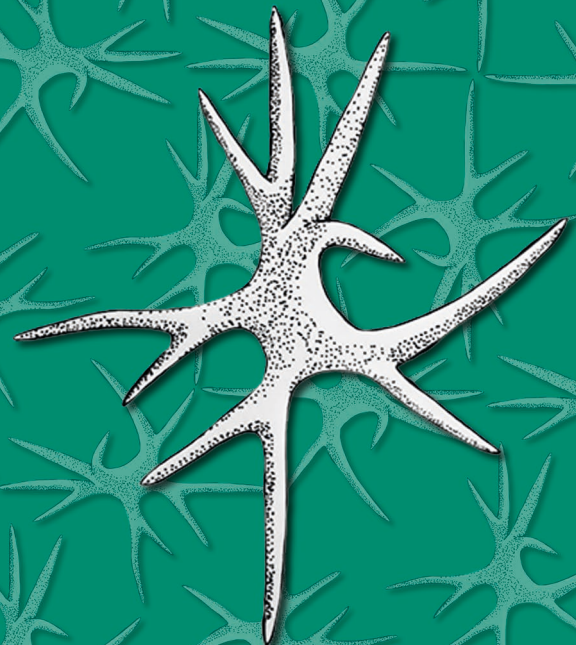
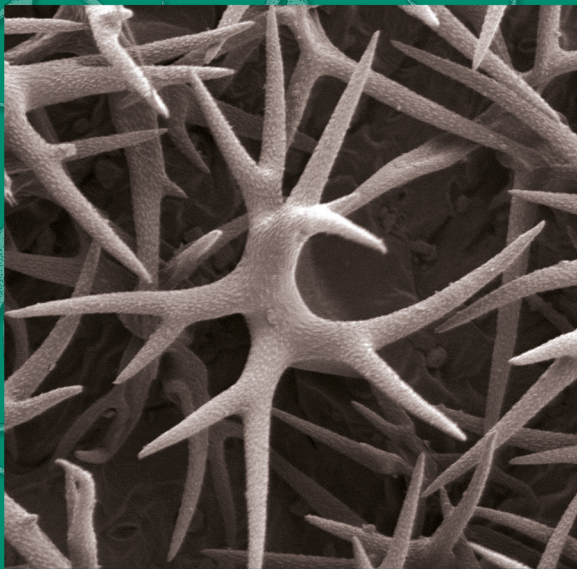


Diversity and taxonomic implications of glands and trichomes in the genus *Matthiola* W.T.Aiton (Anchonieae; Brassicaceae) in the *Flora Iranica* area

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Diversity and taxonomic implications of glands and trichomes in the genus *Matthiola* W.T.Aiton (Anchonieae; Brassicaceae) in the *Flora Iranica* area

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ABSTRACT

Morphology of glands and trichomes of *Matthiola* W.T.Aiton species in the *Flora Iranica* area was examined using stereomicroscope and scanning electron microscope to evaluate their systematic significance and assess infrageneric relationships. The study demonstrated that the general features of the glands and trichomes were constant among different populations of a given species, but they exhibited useful variability in the delimitation of species and their grouping. Reliably diagnostic features include gland-stalk length; distribution of trichome types and glands on various organs; trichome and gland densities; and trichome rays number, length and thickness. Our results confirm the removal of *Matthiola alyssifolia* (DC.) Bornm. from the genus. The species was unique in the distribution of trichomes types and glands on various organs such as stems, pedicels, sepals, and leaves. Other important aspects include the presence vs. absence of glands and trichomes, distribution of simple and 2-4-rayed trichomes and glands on abaxial (vs both) leaf surfaces and leaf margin, and connation of gland stalks. Finally, based on the examination of type specimens and closer studies of trichomes, glands, and other morphological features *Matthiola graminea* Rech.f. is reduced to synonymy of *Matthiola ghorana* Rech.f.

KEY WORDS

Cruciferae,
Matthiola,
indumentum,
trichome,
new synonym.

RÉSUMÉ

Diversité et implications taxonomiques des glandes et trichomes du genre Matthiola W.T.Aiton (Anchonieae; Brassicaceae) dans la région de la Flora Iranica.

La morphologie des glandes et des trichomes des espèces de *Matthiola* W.T.Aiton de la zone couverte par la *Flora Iranica* a été examinée à l'aide d'un stéréomicroscope et d'un microscope électronique à balayage afin d'évaluer leur importance systématique et d'estimer les relations infragénériques. L'étude a démontré que les caractéristiques générales des glandes et des trichomes étaient constantes parmi les différentes populations d'une espèce donnée, mais qu'elles présentaient une variabilité utile pour la délimitation des espèces et leur regroupement. Les caractéristiques permettant un diagnostic fiable sont la longueur du pédoncule des glandes, la répartition des types de trichomes et des glandes sur les différents organes, la densité des trichomes et des glandes, ainsi que le nombre, la longueur et l'épaisseur des rayons des trichomes. Nos résultats confirment le retrait de *Matthiola alyssifolia* (DC.) Bornm. du genre. L'espèce était unique dans la distribution des types de trichomes et des glandes sur divers organes tels que les tiges, les pédicelles, les sépales et les feuilles. Parmi les autres aspects importants, citons la présence ou l'absence de glandes et de trichomes, la répartition des trichomes et des glandes simples et à 2-4 rayons sur les surfaces abaxiales (ou sur les deux) des feuilles et sur le bord des feuilles, et la soudure des pédoncules des glandes. Enfin, sur la base de l'examen des spécimens types et d'études plus approfondies des trichomes, des glandes et d'autres caractéristiques morphologiques, *Matthiola graminea* Rech.f. est mis en synonymie avec *Matthiola ghorana* Rech.f.

MOTS CLÉS

Cruciferae,
Matthiola,
indument,
trichome,
synonyme nouveau.

INTRODUCTION

Matthiola W. T.Aiton (Brassicaceae) is a genus of about 50 species distributed mainly in Africa and Southwest Asia, with fewer species in central Asia and Europe (Zeraatkar *et al.* 2016). On the basis of the latest family phylogenies, the genus is assigned to lineages III and tribe Anchonieae (Nikolov *et al.* 2019, Walden *et al.* 2020). The genus with combinations of characters is distinguished from the rest of tribe Anchonieae (Mahmoodi *et al.* 2016). Some of its species are highly polymorphic and others show a great deal of overlap among them (Chernyakovskaya 1939; Rechinger 1968). The genus is divided into sections by, e.g., Brown (1812), de Candolle (1821), and later Pomel (1874). Nearly all literature have fol-

lowed the de Candolle system (1821). These classifications are clearly artificial, for example, members of the taxon now known as *M. longipetala* (Vent.) DC. have been placed in all four sections designated by de Candolle (1821: 174). On the other hand, the informal classification of Conti (1900) and Gowler (1998) seems partly consistent with molecular studies (Jaén-Molina *et al.* 2009). Moreover, no infrageneric classification of the genus is assigned in the *Flora Iranica* area (Rechinger 1968).

All species have trichomes and many have multicellular glands with multiseriate stalks. These structures are common in many plant families and some authors suggested that they serve as barriers against extreme temperatures, high light intensity, herbivory, and water loss (e.g., Werker 2000; Wagner *et al.* 2004). Moreover, trichomes and glands show high diversity in anatomy and morphology, and therefore, they are taxonomically useful in the delimitation of taxa (e.g., Downing *et al.* 2008; Steyn & Van Wyk 2021). Prantl (1891) relied heavily on trichome types in his upper-level classification of the family, and many authors have recently used it in the delimitation of tribes. Contrary to fruit morphology, which has been extensively used in the delimitation of taxa at all taxonomic levels, the trichomes and glands have been minimally used prior to the recent tribal (Al-Shehbaz *et al.* 2006) or lineage subdivisions (Beilstein *et al.* 2006; Beilstein *et al.* 2008) of the family. In general, however, trichomes and glands characters have been widely used for identification of taxa at lower taxonomic ranks (e.g., Dvořák 1973; Rollins & Banerjee 1976; Al-Shehbaz & Warwick 2007; German 2007; Abdel Khalik 2005; German & Al-Shehbaz 2008; Koch *et al.* 2012; Al-Shehbaz *et al.* 2014). As in other morphological characters, a given trichome type evolved independently several times in the mustard family. For example, malpighiaceus (medifixed, 2-rayed) trichomes are known from over 20 genera and ten tribes (see BrassiBase,

TABLE 1. — Number of investigated individuals and populations of each species of the genus *Matthiola* W.T.Aiton. List of taxa used for the study.

Species	no. of populations	no. of individuals
<i>M. afghanica</i> Rech. f. & Köie	79	202
<i>M. alyssifolia</i> (DC.) Bornm.	145	247
<i>M. chenopodiifolia</i> Fisch. & C.A.Mey.	165	353
<i>M. codringtonii</i> Rech. f.	3	12
<i>M. dumulosa</i> Boiss. & Buhse	18	143
<i>M. farinosa</i> Bunge ex Boiss.	102	311
<i>M. flavida</i> Boiss.	71	219
<i>M. ghorana</i> Rech. f.	2	5
<i>M. incana</i> (L.) W.T.Aiton	10	25
<i>M. longipetala</i> (Vent.) DC.	227	303
<i>M. macranica</i> Rech. f.	2	5
<i>M. tomentosa</i> Bél.	163	238
<i>M. revoluta</i> Bunge ex Boiss.	98	264
<i>Matthiola shiraziana</i> Zeraatkar, Khosravi, F.Ghahrem., Al-Shehbaz & Assadi	14	45
<i>M. spathulata</i> Conti	17	54

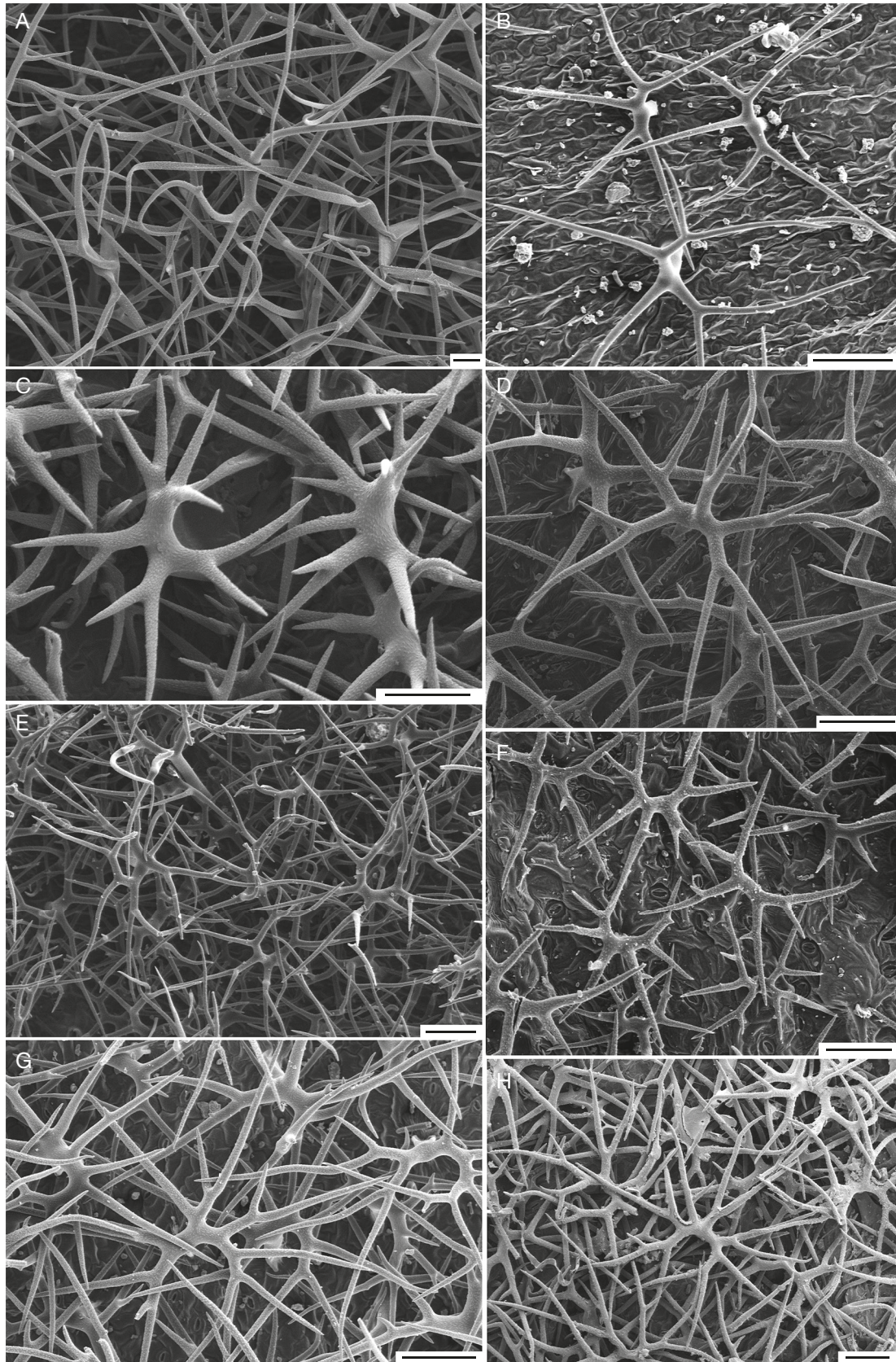


FIG. 1. — SEM images of leaf indumentum of *Matthiola* W.T.Aiton: **A**, *M. dumulosa* Boiss. & Buhse; **B**, *M. longipetala* (Vent.) DC. (same in *M. incana* (L.) W.T.Aiton); **C**, *M. revoluta* Bunge; **D**, *M. afghanica* Rech.f. & Köie; **E**, *M. flavida* Boiss. (same in *M. shiraziana* Zeraatkar, Khosravi, F.Ghahrem., Al-Shehbaz & Assadi, *M. tomentosa* Bél.); **F**, *M. ghorana* Rech.f. (same in *M. graminea* Rech.f.); **G**, *M. spathulata* Conti; **H**, *M. farinosa* Bunge. Scale bars: 90 μ m.

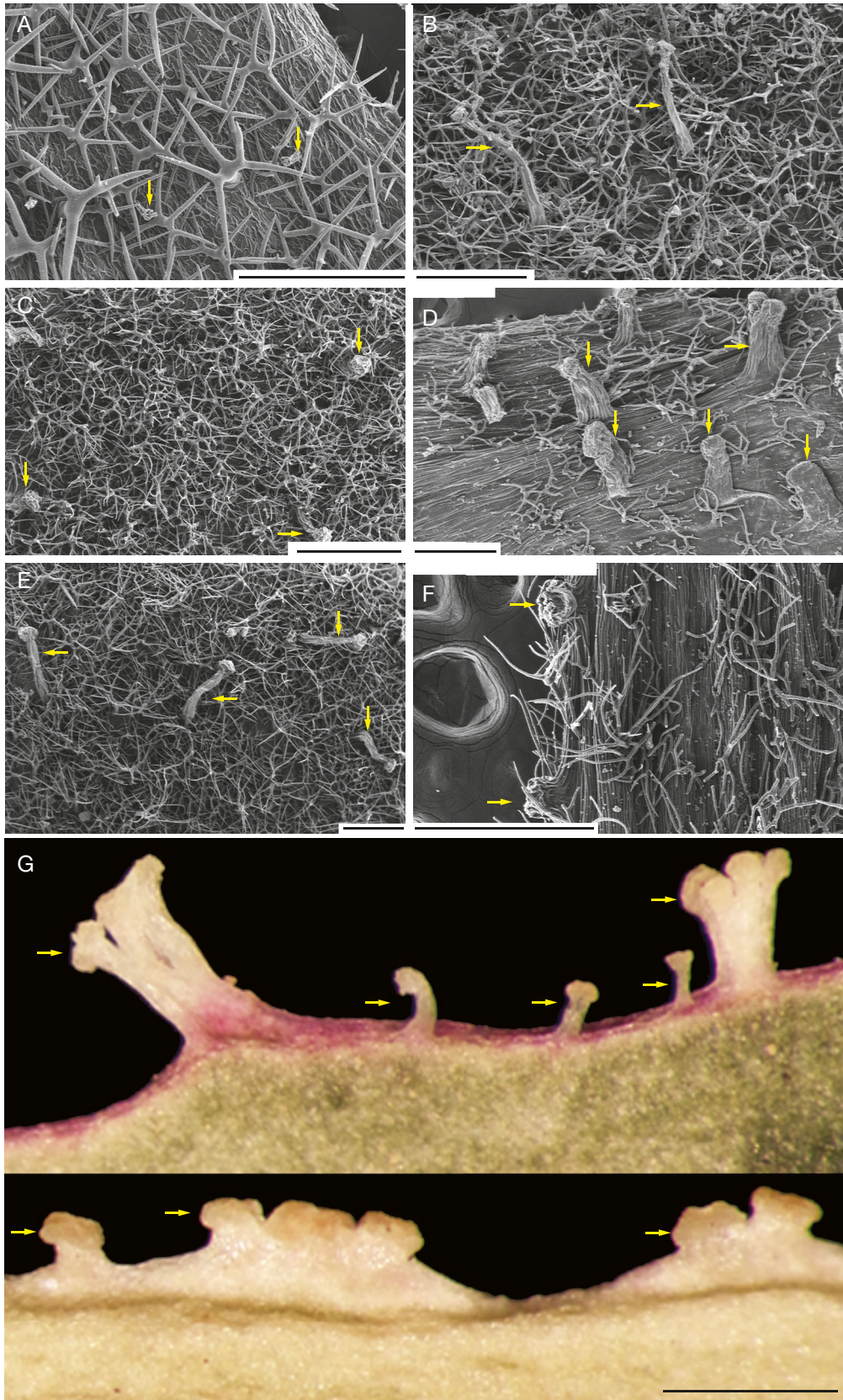


FIG. 2. — Indumentum diversity in *Matthiola* W.T.Aiton, leaf: **A**, *M. chenopodiifolia* Fisch. & C.A.Mey.; **B**, *M. flavida* Boiss.; **C**, *M. codringtonii* Rech.f.; **D**, *M. chenopodiifolia* Fisch. & C.A.Mey. (same in leaf and stem of *M. tomentosa* Bél., *M. farinosa* Bunge, *M. afghanica* Rech.f. & Köie); **E**, *M. shiraziana* Zeraatkar, Khosravi, F.Ghahrem., Al-Shehbaz & Assadi; **F**, *M. longipetala* (Vent.) DC.; **G**, *M. alyssifolia* (DC.) Bornm.. Scale bars: 500 µm. The arrows show glands.

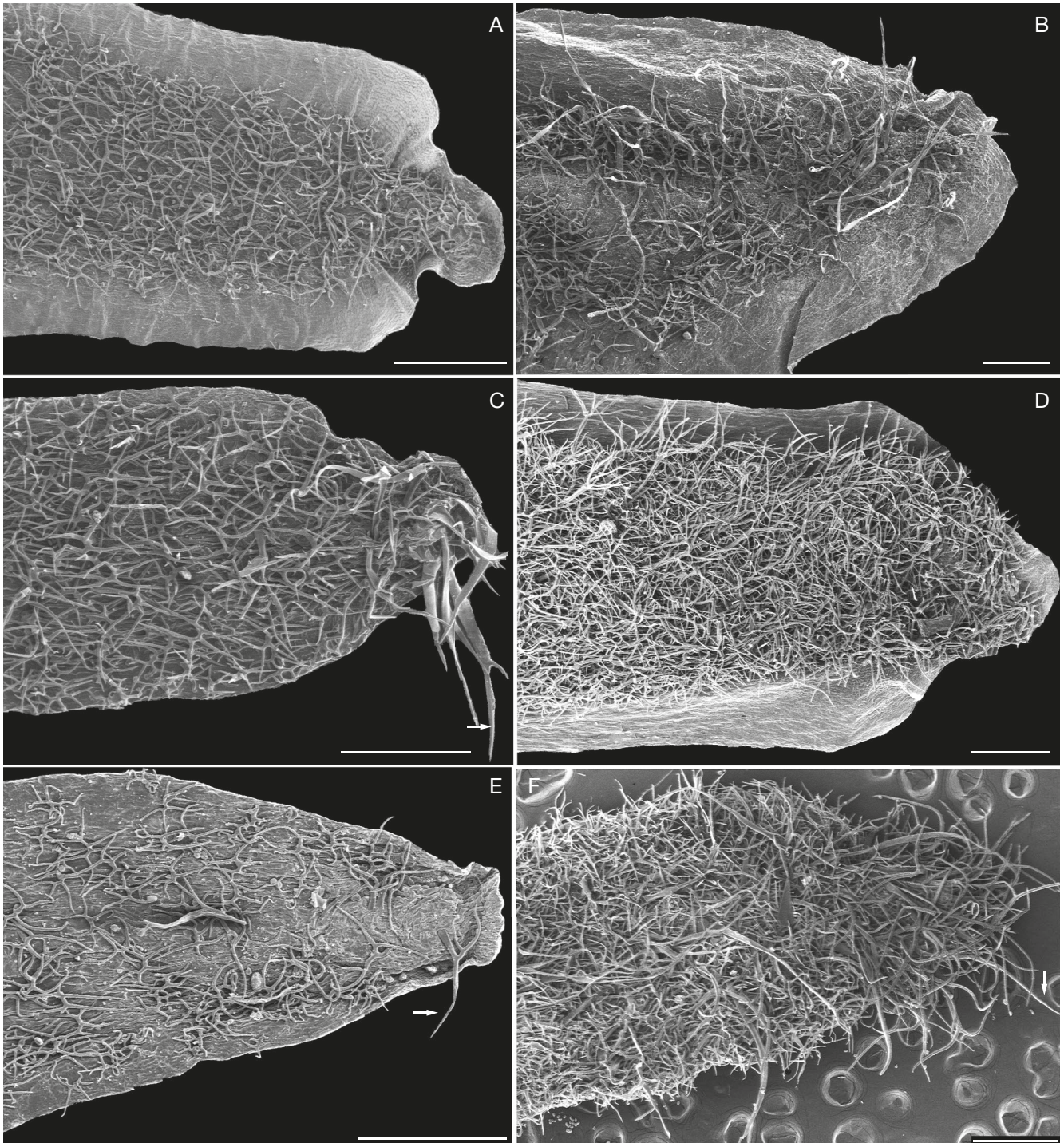


FIG. 3. — SEM images of inner sepal indumentum in *Matthiola* W.T.Aiton: **A**, *M. chenopodiifolia* Fisch. & C.A.Mey.; **B**, *M. alyssifolia* (DC.) Bornm. (same in inner sepal); **C**, *M. chenopodiifolia* Fisch. & C.A.Mey.; **D**, *M. tomentosa* Bél., outer sepal indumentum; **E**, *M. longipetala* (Vent.) DC.; **F**, *M. tomentosa* Bél.. Scale bars: 500 μ m. The arrows show 2-4-rayed (**C**, **E**, **F**).

Kiefer *et al.* 2014; <https://brassibase.cos.uni-heidelberg.de/>). With the exception of many *Descurainia* spp., which have unicellular glandular papillae, glands are restricted to Lineage III and can be either multicellular on a multiseriate stalk (as in most members of the tribes Anchoniae, Buniadeae, Chorisporeae, and Dontostemoneae) or unicellular on a uniseriate stalk (*Hesperis* of Hesperideae) (Al-Shehbaz *et al.*

2006). Our knowledge of the micromorphology of trichomes and glands in the genus of *Matthiola* is limited to a few contradictory studies on a handful of species but without SEM work (Abdel Khalik 2005; Rashid Taranloo *et al.* 2013). The aim of this study is to elucidate the usefulness of trichomes and glands features in identification of species and infrageneric classification of *Matthiola*.

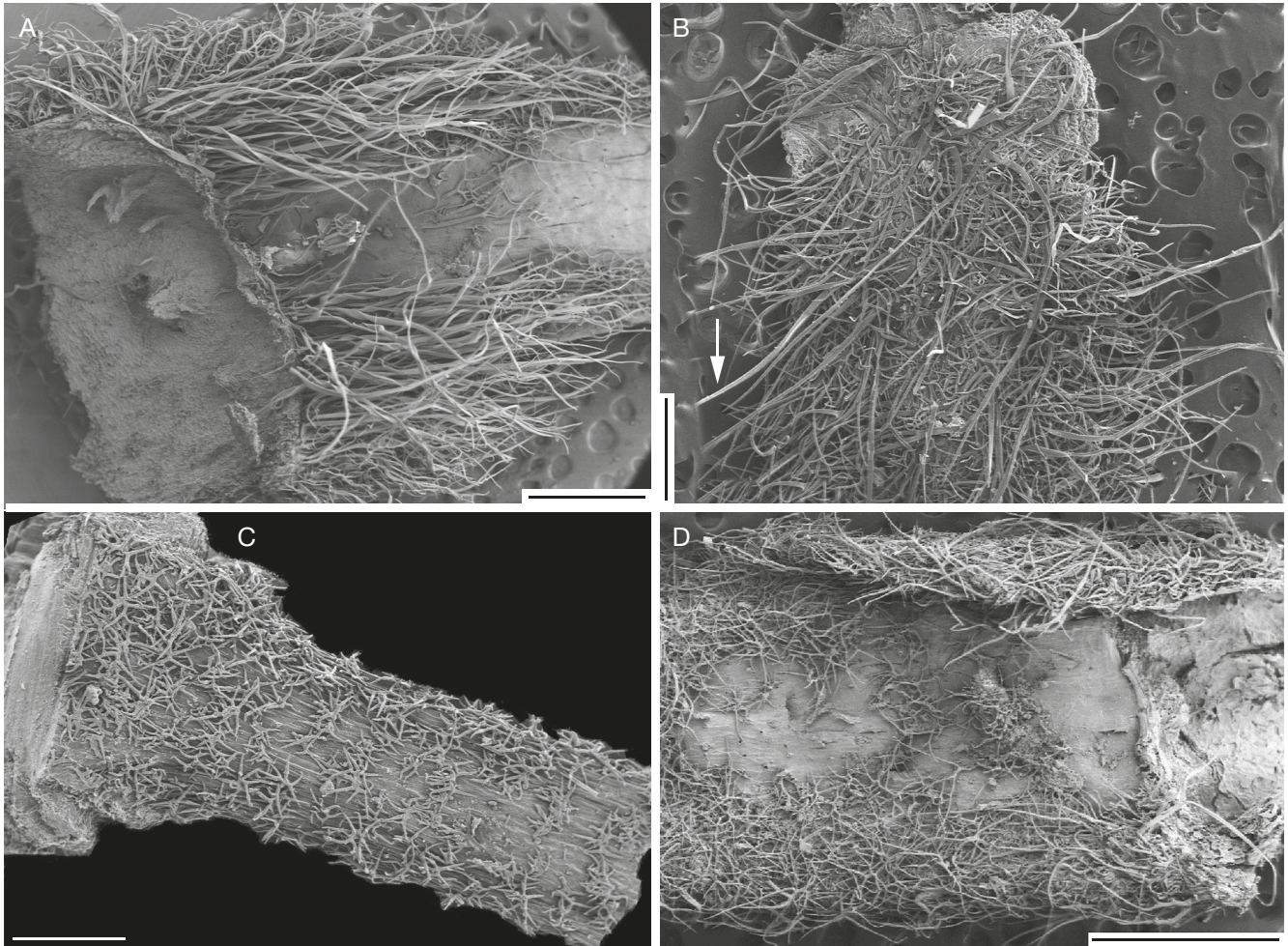


FIG. 4. — SEM image of petiolar leaf base Indumentum in *Matthiola* W.T.Aiton: **A**, *M. spathulata* Conti, pedicel base; **B**, *M. tomentosa* Bél. (same in *M. codringtonii* Rech.f.); **C**, *M. revoluta* Bunge (same in *M. chenopodiifolia* Fisch. & C.A.Mey., *M. graminea* Rech.f., *M. ghorana* Rech.f., *M. macranica* Rech.f.); **D**, *M. farinosa* Bunge (same in all the species except for *M. alyssifolia* (DC.) Bornm. and *M. chenopodiifolia* Fisch. & C.A.Mey. that are glabrous and lacking of 2-4-rayed trichomes, respectively). Scale bars: A, D, 1 mm; B, D, 500 µm. The arrows show 2-4-rayed (**B**).

MATERIAL AND METHODS

SAMPLING

Except for *Matthiola perpusilla* Rech. f., which was not available for this study, the trichomes and glands of the other 16 species of *Matthiola* native to the *Flora Iranica* area, along with the widely cultivated *M. incana* (L.) W.T.Aiton, were studied using stereomicroscopic and scanning electron microscopic methods (Table 1). This study is largely based on 2423 mature specimens in the herbaria DU, E, FAR, FUMH, HUI, HUT, HSU, IRAN, KASH, KUFS, LE, M, MIR, T, TARI, TMRC, W and those of Yasuj University, Agriculture and Natural Resources Researches Center of West Azerbaijan and Hormozgan, and Ferdowsi University of Mashhad (acronyms follow Thiers 2016), as well as fieldwork by the first author in Iran. Additional material from Afghanistan, Turkey, Kashmir, Pakistan, Turkmenistan, Uzbekistan, Spain, and different parts of Iran were also studied. Voucher specimens and their collection data are listed in Tables 1 and 2, Appendix 1.

SCANNING ELECTRON MICROSCOPE (SEM) STUDIES

Small pieces from both the surfaces of adult leaves, abaxial side of sepals, fruit valves, and pedicels were mounted on aluminum stubs and were coated with a layer of gold and examined under SEM (Hitachi SU 3500 of Shahid Beheshti University) at 20-2000 × magnifications. Micrographs of cataphylls and glands of *Matthiola alyssifolia* (DC.) Bornm., fruit, and floral parts were taken under a stereomicroscope (Zeiss Stemi SV8) using a Samsung Powershot WB30F digital camera. Trichome and gland terminology follows Payne (1978) and Beilstein *et al.* (2008).

Because there were no differences in multi-rayed dendritic trichome types among organs of a given plant, the leaves were used to examine the trichomes. Depending on how common a given species was, a minimum of five and maximum of ca. 350 specimens were examined. At least three leaves per specimen were investigated to count the number of rays. A maximum of about 450-830 trichomes were examined to count the numbers of rays. The trichomes were selected from different parts of leaves, and the rays were counted manually under the

TABLE 2. — List of used *Matthiola* W.T.Aiton specimens in SEM along with their voucher specimen, collection site, general distribution, chorotype and life cycle. Abbreviations: **A**, annual; **P**, perennial; **B**, biennial; **IT**, Irano-Turanian region; **Med.**, Mediterranean region; **SS**, Saharo-Sindian region; *, our samples were annual.

Scientific name	Herbarium voucher	Country and locality	General distribution	Chorotype	Life cycle
<i>M. afghanica</i>	16023 (T)	Iran. Khorasan, Robat Sefid, 35°47'42"N, 59°19'41"E, Zeraatkar	NE Iran, Afghanistan, S Turkmenistan	IT	P
<i>M. alyssifolia</i>	7444 (T)	Iran. Tandureh National Park, 37°20'15"N, 58°48'E, Abdolzadeh,	Iran, Afghanistan, S Turkmenistan	IT	P
<i>M. chenopodiifolia</i>	s.n. (HSHU)	Iran. Kerman, Sirjan, 29°29'4"N, 55°47'15"E, Zeraatkar	Iran, Afghanistan, Pakistan, Turkmenistan	IT	A
<i>M. codringtonii</i>	s.n. (HSHU)	Afghanistan. Bamyan, Band-e Gholaman, 34°48'50"N, 67°10'32"E, Ahmadzai	Afghanistan (endemic to Bamyan)	IT	P
<i>M. dumulosa</i>	16024 (T)	Iran. Khorasan, Qayen to Birjand, 33°29'28"N, 59°10'6"E, Zeraatkar	C, NE Iran	IT	P
<i>M. farinosa</i>	16018 (T)	Iran. Semnan, Firuzkuh to Semnan, 35°40'39"N, 53°4'5"E, Zeraatkar	Iran, Afghanistan, S Turkmenistan	IT	P
<i>M. flavida</i>	16013 (T)	Iran. Fars, near Persepolis, Kuh-e Ayub, 30°3'11"N, 52°39'12"E, Zeraatkar	S Iran	IT	P
<i>M. ghorana</i>	19054 (W)	Afghanistan. Ghorat, infra Parjuman, 33°10'N, 63°52'E Rechinger	SW Afghanistan	IT	P
<i>M. incana</i>	s.n. (HSHU)	Iran. Fars, Fasa, Banian, 28°56'N, 53°38'E, Javidi	Coasts of S & W Europe, Cyprus	Med.	P, B, A*
<i>M. longipetala</i>	16041 (T)	Iran. Khuzestan, S Susa, 32°3'55"N, 48°18'15"E, Zeraatkar	C, W Asia; N Africa; Europe	SS, IT, Med.	A
<i>M. macranica</i>	30111 (W)	Pakistan. Makran, 20-30 km Panjgur, 26°58'N, 64°04'E, Rechinger	W Pakistan	IT	A
<i>M. tomentosa</i>	46683 (FAR)	Iran. Tehran, Gisha forest park, 35°44'58"N, 51°21'20"E, Karbaschi	Iran, E Turkey	IT	B or P
<i>M. revoluta</i>	16022 (T)	Iran. Khorasan, Kashmar, Kuh Sorkh, 35°29'42"N, 58°29'17"E, Zeraatkar	Iran, Afghanistan, Turkmenistan, W Pakistan, NW China, Kyrgyzstan, Kashmir, Uzbekistan, Tajikistan	IT	P
<i>M. shiraziana</i>	31348 (TARI)	Iran. Abmalakh, 31°08'N, 51°21'E, Assadi & Mozaffarian	SW Iran (Dena region)	IT	P
<i>M. spathulata</i>	16006 (T)	Iran. Zanjan, Hajibacheh, 36°35'N, 47°57'59"E, Zeraatkar	NW Iran, southern Armenia	IT	P

stereomicroscope. Thickness of trichomes rays was measured at their mid length. Meanwhile, glands and 2-4-rayed trichomes were studied on all organs of all specimens. The length of trichome rays was measured under $\times 250$ magnification from 20 random field images in IMAGEJ (Schneider *et al.* 2012: <http://rsbweb.nih.gov/ij/>). Trichomes and glands were removed from the epidermis, and their stalk length was measured using an eyepiece reticle under a stereomicroscope.

RESULTS

The distribution of various trichomes and glands among the species is summarized in Table 3. Selected stereo- and scanning electron microscopic images are presented in Figs 1-6.

GLANDS

In *Matthiola* species the glands are multicellular-multiseriate and have stalks of various lengths that terminate into a capitate glandular head often wider than the stalk (Tables 3 and 4).

Distribution patterns of glands

The glands appear at an early stage of development. During ovary and leaf enlargement, gland density and their stalk length decrease and increase, respectively. Therefore, the glands are more easily observed on the juvenile leaves and

developing fruits than on mature ones. In general, glands are more common on the petiole and abaxial leaf surface than on the adaxial surface (except for *M. alyssifolia*). The glands were observed on all aboveground organs except stamens and seeds.

Matthiola species in the *Flora Iranica* area fall into two groups based on the presence or absence of glands: a) *M. revoluta* Bunge ex Boiss., *M. macranica* Rech. f., *M. ghorana* Rech. f., *M. graminea* Rech. f., *M. spathulata* Conti, and *M. dumulosa* Boiss. & Buhse are eglandular. Our materials of *M. incana* were eglandular; and b) The remaining nine species are glandular and fall into three subgroups: 1) all aboveground organs are always glandular (*M. codringtonii* and *M. shiraziana*); 2) glands occur at least on one of the aboveground organs (*M. afghanica*, *M. tomentosa*, *M. farinosa*, *M. alyssifolia*, and *M. flavida*); and 3) in *M. longipetala* and *M. chenopodiifolia* both glandular and eglandular individuals were observed within the same population, and in glandular forms, the distal parts (racemes) are glandular and leaves are usually eglandular. By contrast, *M. flavida*, *M. shiraziana*, and *M. alyssifolia* have eglandular ovaries and fruit, compared to *M. tomentosa*, *M. longipetala*, *M. chenopodiifolia*, and *M. afghanica* that are more densely glandular on the reproductive, especially ovaries, than vegetative organs.

Matthiola alyssifolia is unique among the other 16 species in having leaf glands restricted to the margin, rarely on pedicels,

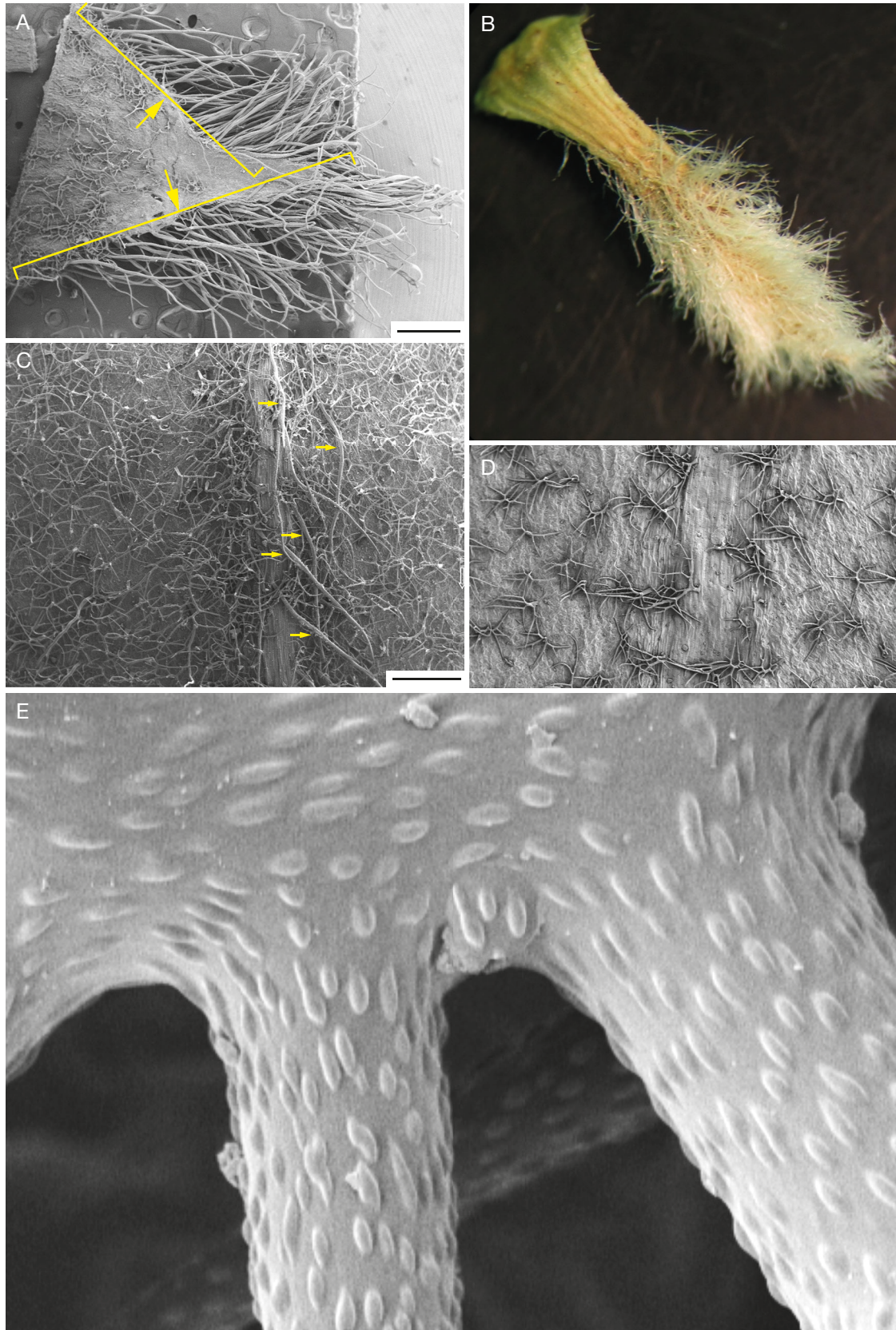


FIG. 5. — **A-D**, *Matthiola alyssifolia* (DC.) Bornm.: **A**, **D**, abaxial side of leaf; **B**, cataphylls covered by simple and 2-4-rayed trichomes; **C**, adaxial side of leaf; **E**, *M. revoluta* Bunge, abaxial side of leaf. Scale bars: A, C, D, 500 μ m; B, 1 cm; E, 20 μ m. The arrow shows 2-4-rayed and simple trichomes (**C**).

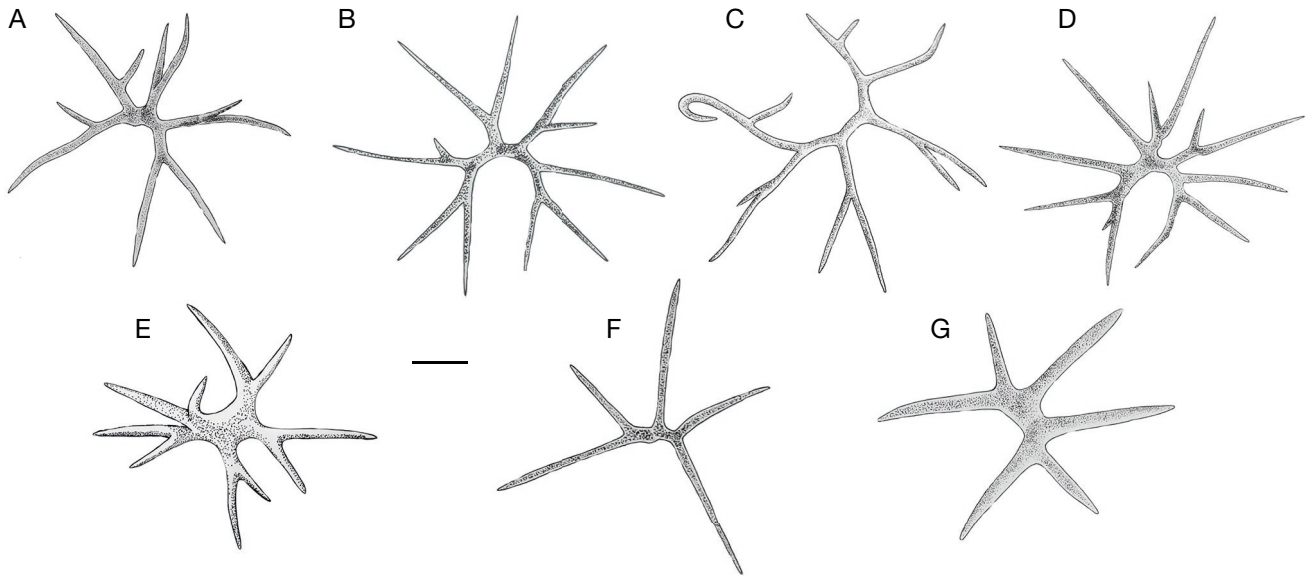


FIG. 6. — Line drawings of trichomes types in *Matthiola* W.T.Aiton: **A**, *M. afghanica*; **B**, *M. farinosa*; **C**, *M. dumulosa*; **D**, *M. spathulata*; **E**, *M. revoluta*; **F**, *M. longipetala*; **G**, *M. chenopodiifolia*. Scale bar: 90 µm.

TABLE 3. — Distribution of trichome types and glands on aboveground organs. Abbreviations: **S**, simple trichome; **Y**, bifurcate trichome; **T**, 3-forked trichome; **C**, cruciform trichome; **G**, gland.; +, presence; -, absence.

Species	Abaxial/ Adaxial leaf blade					Petiole					Pedicel					Outer/Inner sepal					Ovary (Fruit)					Stem					
	S	Y	T	C	G	S	Y	T	C	G	S	Y	T	C	G	S	Y	T	C	G	S	Y	T	C	G	S	Y	T	C	G	
<i>M. afghanica</i>	-/-	-/-	±/±	±/±	±/±	-	±	±	±	-	±	±	±	±	±	±	-/-	+/-	+/-	+/-	±/±	-	±	±	±	±	-	-	-	-	-
<i>M. alyssifolia</i>	+/-	+/-	+/-	+/-	-/-	-	-	-	-	-	±	±	±	±	±	±	±/±	±/±	±/±	±/±	±/±	-	±	±	±	±	-	-	-	-	-
<i>M. chenopodiifolia</i>	-/-	-/-	-/-	-/-	±/±	-	-	-	-	±	-	-	-	-	±	-/-	+/-	+/-	+/-	±/±	-	-	-	-	±	-	-	-	-	-	
<i>M. codringtonii</i>	-/-	-/-	±/±	±/±	±/±	-	+	+	+	+	-	±	±	±	±	+	-/-	+/-	+/-	+/-	+/-	-	-	-	-	+	-	-	-	-	+
<i>M. dumulosa</i>	±/±	+/-	+/-	+/-	-/-	±	+	+	+	-	±	±	±	±	-	±/±	+/-	+/-	+/-	-/-	-	-	-	-	-	±	±	±	±	-	
<i>M. farinosa</i>	-/-	-/-	±/±	±/±	±/±	-	±	±	±	±	-	±	±	±	±	-/-	+/-	+/-	+/-	±/±	-	±	±	±	±	-	-	-	-	-	
<i>M. flavida</i>	-/-	-/-	±/±	±/±	±/±	-	±	±	±	±	-	±	±	±	±	-/-	+/-	+/-	+/-	±/±	-	-	-	-	-(+)	-	-	-	-	-	
<i>M. ghorana</i>	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	
<i>M. incana</i>	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	±	±	±	±	±	-/-	+/-	+/-	+/-	-/-	-	-	-	-	-	-	-	-	-	-	
<i>M. longipetala</i>	-/-	-/-	±/±	±/±	±/±	-	-	-	-	±	-	-	-	-	±	-/-	+/-	+/-	+/-	±/±	-	-	±	±	±	-	-	-	-	-	
<i>M. macranica</i>	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	
<i>M. tomentosa</i>	±/±	+/-	+/-	+/-	±/±	±	+	+	+	±	±	±	±	±	±	-/-	+/-	+/-	+/-	±/±	-	-	-	-	±	±	±	±	±	±	
<i>M. revoluta</i>	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	-/-	-/-	-/-	-/-	-/-	-	-	-	-	-	-	-	-	-	-	
<i>M. shiraziana</i>	-/-	-/-	±/±	±/±	±/±	-	±	±	±	+	-	±	±	±	+	-/-	+/-	+/-	+/-	±/±	-	-	-	-	-(+)	-	-	-	-	+	
<i>M. spathulata</i>	-/-	-/-	-/-	-/-	-/-	+	+	+	+	-	±	±	±	±	±	-/-	+/-	+/-	+/-	-/-	-	-	-	-	-	-	-	-	-	-	

rachis, and sepals, compared to having them on leaf surfaces in other species. Moreover, two or more of its glands are often connate along their stalks (Fig. 2G) whereas in all other species the individual glands are free from each other (Fig. 2A-F).

Gland size

Glands vary in length and can be extremely short and thin (51 µm) as exclusively on leaves of *Matthiola chenopodiifolia* Fisch. & C. A. Mey (Fig. 2A) or larger and thicker elsewhere (Table 4; Fig. 2D). Short-sized glands (mostly 153-245 µm) are found in all aboveground organs *M. longipetala*, *M. alyssifolia*, and *M. codringtonii* Rech. f., and on fruit valves of *M. farinosa* Bunge ex Boiss., *M. tomentosa* Bél. and *M. afghanica* Rech. f. & Köie (Fig. 2C, F, G). Medium-sized glands (mostly 332-446 µm) are found in *M. farinosa*, *M. chenopodiifolia*, *M. afghanica*,

and *M. tomentosa* (Fig. 2D). Gland length differs on fruit and other organs of *M. farinosa*, *M. tomentosa* and *M. afghanica* (subsessile or short stalked (255-296 µm) on fruit valves vs. medium stalked (356-446 µm) on other parts). Long-sized glands (567-675 µm) are found in *Matthiola shiraziana* Zeraatkar, Khosravi, F.Ghahrem., Al-Shehbaz & Assadi and *M. flavida* Boiss. (Fig. 2B, E).

TRICHOMES

Trichome types

Trichome surface is minutely papillate in the studied species (Fig. 1A-H and Fig. 5E). Trichomes are terete (Fig. 1A-H), flattened (often in *M. alyssifolia*, Fig. 3B) or with flattened stalk and terete rays (Fig. 1A). The trichomes in *Matthiola* are a mixture of simple, 2-4-rayed or dendritic and their

TABLE 4. — Trichome and gland features of *Matthiola* W.T.Aiton species. Abbreviations: **SOF**, stem and ovary, fruit (**P**, pubescent; **G**, glabrous); **TD**, trichome density (**D**, dense, c. 100 trichomes in 1 mm²; **M**, moderate, 20–40 trichomes in 1 mm²; **S**, sparse, 10–15 trichomes in 1 mm²); **G**, glabrescent, < 5 trichomes in 1 mm²). **SMM**, sepal membranous margin; **O/I**, outer/inner (**P**, pubescent; **G**, glabrous); **TS**, trichomes stalk (**M**, medium [116–144 µm]; **L**, long [161–331 µm]; **S**, short [42–79 µm]; **VS**, very short > 20 µm); **ST**, simple trichome; **RT**, ray thickness of trichomes (**M**, medium; **Tn**, thin; **Tc**, thick); **TS**, trichomes stalk (**M**, medium [116–144 µm]; **L**, long [161–331 µm]; **S**, short [42–79 µm]; **VS**, very short > 20 µm)]; columns 1–3, 5–10 and 11 are based on dendritic trichomes; **O**, orientation (**E**, erect; **SE**, suberect; **P**, parallel to epidermis). **BTCT**, **B**, bifurcate trichome; **T**, 3-forked trichome; **C**, cruciform trichome; **R** > 13, the number of rays > 13; **G**, glandulosity. *, the glands are limited to leaves of *M. chenopodiifolia*: +, present; –, absent; ±, glandular and eglandular forms.

	Blade trichomes (number or rays)	Ray length (µm)	Trichome- stalk length (µm)	Gland length (µm)	R									
					SOF	TD	RT	TS	SMM	O/I	13	G	ST	O
<i>M. afghanica</i>	(3-6)-7-12-(13-16)	162.57±6.85	48.71±4.57	356.00±3.53	P	M(S)	Tc	VS	P/G	+	+	–	SE	+
<i>M. alyssifolia</i>	(2-6)-7-9-(10-13)	172.6±44.4	55.75±9.70	206.28±5.40	G	M	Tn	VS	G/G	–	+	+	SE	+
<i>M. chenopodiifolia</i>	(5-6)-7-9-(11)	78.01±4.12	42.30±3.81	360.35±3.83 (51.13±1.51*)	P	M	Tc/M	VS	P/G	–	±	–	SE	+
<i>M. codringtonii</i>	(3-9)-10-13-(14-15)	88.48±1.78	116.08±4.61	245.92±3.92	P	D	Tn	M	P/G	+	+	–	SE	+
<i>M. dumulosa</i>	(2-6)-7-11-(12-15)	435.09±8.30	331.33±4.25	–	P	D	Tc	L	P/G	+	–	+	E	+
<i>M. farinosa</i>	(3-8)-9-12-(13-17)	82.98±7.27	48.59±5.16	348.75±3.70	P	D	M	VS	P/G	+	+	–	P(SE)	+
<i>M. flavida</i>	(3-9)-10-12-(13-18)	168.18±6.16	134.90±2.75	675.15±7.47	P	D	M	M	P/G	+	+	–	E	+
<i>M. ghorana</i>	(5-6)-7-9-(10-12)	46.46±2.15	69.82±3.78	–	P	M (D)	Tc	S	P/G	–	–	–	SE	–
<i>M. incana</i>	(5)-6-9-(10)	161.07±4.30	42.87±2.10	–	P	M	Tn	VS	P/G	–	–	–	SE	+
<i>M. longipetala</i>	(3-4)-5-7-(8-10)	152.98±3.18	46.30±1.81	153.70±3.37	P	S (M)	Tn	VS	P/G	–	±	–	SE	+
<i>M. macranica</i>	(5-6)-7-10-(11)	150.17±4.69	144.05±3.82	–	P	M (S)	M	M	P/G	–	–	–	E	–
<i>M. tomentosa</i>	(2-6)-7-12-(13-14)	170.8±32.5	121.98±7.54	446.85±4.18	P	D	M	M	P/G	+	+	±	E	+
<i>M. revoluta</i>	(5-6)-7-9-(10-12)	64.40±2.77	68.12±3.71	–	P	D	Tc	S	P/G	–	–	–	SE	–
<i>M. shiraziana</i>	(3-9)-10-14-(15-17)	162.57±6.80	128.86±1.44	567.63±4.95	P	D	M	M	P/G	+	+	–	E	+
<i>M. spathulata</i>	(3-9)-10-13-(14-16)	90.77±4.95	79.80±2.32	–	P	D	M	S	P/G	+	–	+	P	+

distribution on various plant parts of a given species is presented in Table 3.

Simple trichomes

This trichome type is found throughout the Brassicaceae, especially in members of Lineage II (Beilstein *et al.* 2006). It may occur on various parts of *Matthiola alyssifolia*, *M. spathulata*, *M. tomentosa*, and *M. dumulosa* (Tables 3 and 4).

2–4-rayed trichomes

These trichomes are found in all studied species except *M. revoluta*, *M. macranica*, *M. graminea*, and *M. ghorana* (Tables 3 and 4). They can be very short (200–400 µm, in *M. longipetala* and *M. incana*), short (400–800 µm, in *M. chenopodiifolia*, Fig. 3C), medium (800–1200 µm, in *M. farinosa*, *M. codringtonii*, *M. tomentosa*, and *M. afghanica*, Fig. 4D), and extremely long 900–3000 µm, in *M. tomentosa*, *M. spathulata*, and *M. alyssifolia*, Figs 4A, B; 5A, B).

Dendritic trichomes

These trichomes type occurs on nearly all aboveground plant parts except the inner side of sepals, stamens, and petals (occasionally few trichomes are present on the petals). They are long stalked on the apex of outer sepals, pedicels, nodes and petiolar leaf bases of most species (except *M. revoluta*, *M. macranica*, *M. graminea* and *M. ghorana*), but all sepals of *M. alyssifolia* and *M. codringtonii*, as well as pedicels of the latter species and *M. tomentosa*, have dense, long-stalked trichomes throughout (Figs 3B; 4B). Outer sepal membranous margin is pubescent in all the species except for *M. alyssifolia*. On the other hand, inner sepal membranous margin is glabrous in all the species (Fig. 3A–F).

The ray number of dendritic trichomes varies among the species and they are fewer in the annual (mostly 5–10-rayed) than in the perennial species (mostly 7–14-rayed). The trichomes are mainly 5–7-rayed in *Matthiola longipetala* or 7–9-rayed in *M. revoluta*, *M. graminea*, *M. chenopodiifolia*, and *M. ghorana* (Table 4; Fig. 1A–H; 2A; 6). Ray thickness also varies, and they are 5–10 µm in *M. incana* (L.) R. Br. in Aiton Brown and *M. longipetala* (Fig. 1B), 10–15 µm in *M. tomentosa* and *M. shiraziana* (Fig. 1E), and 15–20 µm in *M. revoluta*, *M. graminea* and *M. ghorana* (Fig. 1C, F). Ranges of the trichome-stalk length are short (mostly 42–79 µm, in *M. afghanica*, *M. spathulata*, *M. revoluta*, and *M. chenopodiifolia*), medium (mostly 116–144 µm, in *M. shiraziana*, *M. tomentosa*, and *M. flavida*), and long (161–331 µm in *M. dumulosa*). Finally, the rays can be erect in *M. shiraziana*, *M. flavida*, and *M. tomentosa* (Fig. 1E), suberect in *M. afghanica* (Fig. 1D), or parallel to epidermis in *M. farinosa* and *M. spathulata* (Fig. 1G, H; Table 3).

Distribution of trichomes types

The distribution of trichomes types on various parts of investigated species is shown in Tables 3 and 4. Trichomes are usually denser on the abaxial than adaxial leaf surface. The distribution and density of simple, 2–4-rayed and dendritic trichomes differed among species, organs or parts of the same organ. In most species, 2–4-rayed trichomes were restricted to leaf teeth and apex, petiolar leaf bases (Fig. 4A, D), apex of outer sepals (Fig. 3B, C, F) and pedicels (Fig. 4B) but they were on all sepals of *M. alyssifolia* and limited on outer ones of *M. chenopodiifolia* (Fig. 3C).

Simple and 2–4-rayed trichomes were more abundant in *Matthiola alyssifolia* than in the other species. In *M. tomentosa*,

M. dumulosa, and *M. abyssifolia*, these trichomes are found on most organs, though in the last species they were restricted to the abaxial leaf surface and in the other three species to both surfaces (Fig. 5A, C, D; Table 3). In *M. spathulata* the simple and 2–4-rayed trichomes were mainly present on the petiolar leaf bases along lower parts of stem (Fig. 4A). In *M. abyssifolia* such trichomes were also very common on both surfaces of the modified basal leaves “cataphylls” that protect overwintering apical meristem (Fig. 5B) as well as on aborted inflorescences. Also in *M. abyssifolia*, simple and 2–4-rayed trichomes were exclusively located along the leaf midvein, apex and margin of abaxial surface but they were absent elsewhere on the surface (Fig. 5A, C, D). Distribution and types of trichomes were constant in polymorphic species such as *M. farinosa*, *M. revoluta* and *M. longipetala*.

DISCUSSION

TAXONOMIC SIGNIFICANCE OF GLANDS AND TRICHOMES

The current study represents the first comprehensive examination of glands and trichomes in *Matthiola*. Previous floristic treatments (e.g., Chernyakovskaya 1939; Cullen 1965; Rechinger 1968) basically ignored the taxonomic value of these structures. We found that gland length and distribution, as well as trichome type, orientation, curvature, length, and density, and number, thickness of rays are very useful taxonomically. These findings contradict those of Rashid Taranloo *et al.* (2013) who concluded that there were no differences in the trichomes and glands among seven species of *Matthiola* in NE Iran.

We carefully examined the herbarium specimens that Rashid Taranloo *et al.* (2013) have cited in their study and concluded that the species were not identified correctly and that the scientific names of many of them were misidentified. Therefore, incorrect identification of species has caused their study results to be inconsistent with our study.

Except for *Matthiola longipetala* and *M. chenopodiifolia*, the glands show considerable variation among species but are usually constant among individuals of different populations of a given species. As shown in Tables 3 and 4, the glands differed among otherwise morphologically similar species, and nearly a third of the *Flora Iranica* species are eglandular. Abdel Khalik (2005) noted that the lack of glands was valuable for distinguishing *M. fruticulosa* (L.) Maire from the other Egyptian *Matthiola* species. The related *M. flavida* and *M. shiraziana* can be distinguished from *M. tomentosa* by lacking the glands on ovaries and fruit, and the three species can be delimited from each other by the gland size (Zeraatkar *et al.* 2016; Fig. 2B, D, E; Table 3).

Rechinger (1968) relied heavily on fruit morphology and undulation of petal margin to broadly delimit *Matthiola farinosa* that was said to occupy NW Iran. However, plants of that area are *M. spathulata* for their lacking (vs presence) of glands and presence (vs. lacking) of simple trichomes (Tables 3 and 4). He also broadly delimited *M. dumulosa*, but his cited specimens were a mixture of *M. afghanica*, *M. farinosa*, and *M. dumulosa*. Range of the last species somewhat overlaps with *M. afghanica* in NE Iran. However, *M. dumulosa* is eglandular and has simple trichomes, whereas

M. afghanica and *M. farinosa* are glandular and lack simple trichomes. In addition, *M. dumulosa* differs by the length of rays and trichome stalk (Fig. 1A, D, G, H). Furthermore, in that study some specimens cited for *M. tomentosa* belong to *M. revoluta*, *M. shiraziana*, and *M. tomentosa*. As mentioned above, *M. tomentosa* is glandular and has simple and 2–4-rayed trichomes but *M. revoluta* does not. On the other hand, *M. tomentosa* and *M. shiraziana* are distinguishable by the size and distribution of glands and presence/absence of simple and 2–4-rayed trichomes (see above; cf. Zeraatkar *et al.* 2016 and Fig. 2B, E).

Matthiola porphyrantha Rech. f., Aellen & Esfand. was reduced to the varietal rank under *M. chenopodiifolia* Fisch. & C.A.Mey. by Léonard (1983). Additionally, the names *M. tenera* Rech. f. and *M. integrifolia* Kom. are currently treated as synonyms of *M. chorassanica* Bunge ex Boiss. in some studies and global databases (Zhou *et al.* 2001; The Plant List 2013). The present trichome and gland study provides further support that *M. tenera* and *M. integrifolia* are conspecific with *M. chorassanica* (synonym of *M. revoluta*, see below) and also *M. porphyrantha* is a synonym of *M. chenopodiifolia*.

TAXONOMIC CONSIDERATIONS

Trichome and gland features along with other morphological characters of the types and numerous other specimens clearly show that *M. graminea* is indistinguishable from *M. ghorana*. Therefore, they are reduced to synonymy as follows:

Family BRASSICACEAE Burnett
Genus *Matthiola* W.T.Aiton

Matthiola ghorana Rech. f.

Anzeiger der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse 101: 422 (Rechinger 1964). — Type: **Afghanistan**. Ghorat, in faucibus calc. infra Parjuman (Partcheman), c. 33°10'N, 63°52'E, c. 1850 m, *K. H. Rechinger 19054* (holo-, W[W19660006885]!; iso-, B[B100241930], E[E00386179], G[G00371813], K[K000693506], LE[LE00013101], W[W19670001971]!).

Matthiola graminea Rech. f., *Anzeiger der Österreichische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse* 101: 423 (Rechinger 1964), **syn. nov.** — Type: **Afghanistan**. Ghazni, in valle fluvii Arghandab prope Sang-i Masha, 33°15'N, 67°10'E, 2400 m, *K. H. Rechinger 17518* (holo-, W[W19660006884]!; iso-, E[E00377251], G[G00371811], W[W19690001298]!).

DESCRIPTION

The above two species were described based on few specimens collected from adjacent localities. A critical examination of all material used in the descriptions of *M. ghorana* and *M. graminea* showed that there is a considerable overlap in every morphological character, including petal and pedicel length, leaf shape, and fruit and seed size.

The only differences between *Matthiola ghorana* and *M. revoluta* are the longer pedicels and linear or narrowly oblong-lanceolate leaves in *M. ghorana*. However, we observed some specimens of *M. revoluta* from Iran and Afghanistan that have the same characters. In our opinion, *M. ghorana* represents only one of numerous ecological variants that occur throughout the range of *M. revoluta*. However, further collections from their type localities and nearby areas are necessary before their status can be fully assessed.

TAXONOMIC SIGNIFICANCE OF INDUMENTUM IN INFRAGENERIC CLASSIFICATION

The type and distribution of glands and trichomes correlate reasonably well with species grouping as suggested below. All groups share dendritic-stalked trichomes and multicellular-multiseriate glands.

GROUP I

Matthiola incana and *M. longipetala* are quite diverse morphologically, but they are almost identical in trichome and gland features. They are characterized by thin, mostly 5-7-rayed (*M. longipetala*) or 6-9-rayed (*M. incana*) and rarely 2-4-rayed trichomes, minute glands (mainly 153 µm long in *M. longipetala*) and glandular or eglandular plants. Both of them are annual, but *M. longipetala* is easily recognised from *M. incana* by petal, fruit and flowering size as well leaf shape. *Matthiola incana* and *M. longipetala* are mostly distributed in Mediterranean and Saharo-Sindian regions, respectively, whereas all other studied species are distributed in Irano-Turanian region (see Table 2). The group members are distinguished from others by fruits with a horned stigma, terete in cross-section, frequent stipulelike glands and four nectar glands.

GROUP II

This group includes only *Matthiola alyssifolia*. Distribution and micromorphology of trichome and gland distinctly differ from those of other species (see above, Tables 3, 4). The species is also unrelated in terms of nectary morphology to any other member of the genus in the *Flora Iranica* area (Zeraatkar *et al.* 2022). In the molecular studies of Warwick *et al.* (2007) and Khosravi *et al.* (2009), the species did not form a monophyletic genus, and German (2019) excluded *Matthiola alyssifolia* from the genus and along with *Iskandera alaica* (Korsh.) Botsch. et Vved. assigned to *Dvorakia*. Comprehensive molecular phylogenetic sampling of all extant species and the related genera is needed to establish whether or not it belongs to *Matthiola* or a new monophyletic genus.

GROUP III

The group includes *Matthiola flavida*, *M. shiraziana*, *M. tomentosa*, *M. farinosa*, *M. codringtonii*, *M. dumulosa*, *M. afghanica*, and *M. spathulata*. Morphologically the spe-

cies are sisters of Central Asia species and species distributed into Caucasus and east Turkey such as *M. superba* Conti, *M. odoratissima* (Pall.) W. T. Aiton, *M. obovata* Bunge, *M. robusta* Bunge, *M. tatarica* (Pall.) DC., *M. montana* Boiss., *M. anchoniifolia* Hub.-Mor., *M. tianschanica* Sarkisova, *M. daghestanica* (Conti) N.Busch, *M. caspica* (N.Busch) Grossh., *M. taurica* (Conti) Grossh. and *M. fragrans* (Fisch.) Bunge. Most important characters for the group are the presence of <13-rayed dendritic trichomes and glands often 245-446 µm long. However, in *M. shiraziana* and *M. flavida* glands are up to 675 µm long, and *M. dumulosa* and *M. spathulata* are eglandular. The lack of glands within some members of the Anchonieae and the other tribes is likely a derived state in lineage III (Al-Shehbaz 2012). The group is characterized by often sordid yellow or brown petals outrolled from the apex and capitate, 2-lobed stigmas (except for *M. codringtonii*).

GROUP IV

This group includes only *Matthiola chenopodiifolia*, which has mostly 7-9-rayed trichomes, 2-4-rayed trichomes confined to outer sepal apex, two gland sizes (ca. 51 µm and ca. 360 µm long). Both glandular and eglandular forms are found in the species. The species has a twisted petal (rarely channelled) and a conical, 2-lobed stigma, and it lacks the stipulelike glands. *M. chenopodiifolia* is most similar to *M. stoddartii* Bunge distributed in Central Asia.

GROUP V

This group comprises *Matthiola revoluta*, *M. macranica*, and *M. ghorana*. It lacks 2-4-rayed trichomes and glands and has minute, thick-walled (except *M. macranica*) and mostly 7-9-rayed trichomes. The group also has circinate involute petals and conically 2-lobed stigmas (capitate, 2-lobed in *M. macranica*).

Our results on diversity and taxonomic implications of indumentum are nearly completely in line with findings of Gowler (1998) who used most morphological characters together with phenetic numerical analysis to grouping of *Matthiola* species. Moreover, like molecular phylogenetic analysis carried out by Jaén-Molina *et al.* (2009), *Matthiola alyssifolia*, *M. longipetala* and *M. revoluta* are separated from other species (Group III).

As the taxonomy of *Matthiola* is still controversial at the infrageneric level, our informal grouping remains to be tested against thorough molecular studies that we intend to conduct in the future.

CONCLUSION

The gland and trichome morphologies of *Matthiola* exhibit tremendous diversity that provides features suitable for the identification of species. As shown above, *M. alyssifolia* is quite distinct morphologically from the others, and our findings support previous molecular studies that suggest its exclusion from the genus. The number of tri-

KEY TO THE *MATTHIOLA* W.T.AITON SPECIES MOSTLY BASED ON GLANDS AND TRICHOMES MORPHOLOGY

- 1a. Plants annual 2
 — Plants perennial or biennial 3
- 2a. Trichomes mostly 7-9-rayed, ±thick; glands usually 360 µm long, stipulelike glands absent
 *Matthiola chenopodiifolia* Fisch. & C.A.Mey.
 — Trichomes mostly 5-7-rayed, thin; glands usually 153 µm long, stipulelike glands always present
 *Matthiola longipetala* (Vent.) DC.
- 3a. Plants eglandular 4
 — Plants glandular 7
- 4a. 2-4-rayed trichomes absent, petals circinate involute at apex 5
 — 2-4-rayed trichomes present, petals revolute at apex 6
- 5a. Trichomes sparse, thin, stalk mostly 144 µm long, plants 8-15 cm long, stigma capitate-bilobed
 *Matthiola macranica* Rech.f.
 — Trichomes usually dense, thick, stalk mostly ca. 70 µm long, stigma conical-bilobed, plants longer.....
 *Matthiola ghorana* Rech.f./*Matthiola revoluta* Bunge
- 6a. Simple trichomes frequent, restricted to petiolar leaf bases on proximal part of stem, trichomes up to 169 µm long, rays parallel to epidermis, basal leaves present, 5-14.5 cm long *Matthiola spathulata* Conti
 — Simple trichomes sparse nearly throughout, trichomes up to 766 µm long, rays erect, basal leaves absent or significantly shorter *Matthiola dumulosa*
- 7a. Ovary, fruit and stem glabrous, glands exclusively limited to margins of uppermost cauline leaves
 *Matthiola alyssifolia* (DC.) Bornm.
 — Ovary, fruit, and stem pubescent; glands on both leaf surfaces 8
- 8a. Glands (300) 600-700 (920) µm long, usually absent on ovaries and fruits, petals margin smooth 9
 — Glands (200-) 300-500 µm long, present on ovaries and fruits, petals margin undulated 10
- 9a. Leaves and stems always glandular (in both flowering and fruiting periods), glands abundant, (300-) 500-600 (700) µm long, leaves broadly elliptic or elliptic-ob lanceolate
 *Matthiola shiraziana* Zeraatkar, Khosravi, F.Ghahrem., Al-Shehbaz & Assadi
 — Leaves and stems eglandular in the time of fruit maturity, glands usually sparse, (300) 600-700 (920) µm long, leaves lanceolate, sometimes sublyrate *Matthiola flavida* Boiss.
- 10a. 2-4-rayed trichomes present in intercostal fields of leaves, simple trichomes occasionally present, biennial or sometimes short-lived perennial, petals margin proximally revolute and distally curved backwards
 *Matthiola tomentosa* Bél.
 — 2-4-rayed trichomes rare and at leaf apex, simple trichomes absent, perennial, petals margin curved backwards proximally (not revolute) 11
- 11a. Glands moderate or dense on all organs; long-stalked trichomes present on pedicel and sepal throughout, rays usually curved, petals violet *Matthiola codringtonii* Rech.f.
 — Glands usually sparse or absent at least from some organs; long-stalked trichomes restricted to below receptacle, petiolar leaf base and outer sepal apex, rays usually straight, petals pale brown or sordid yellow 12
- 12a. Trichomes moderate, rays suberect; glands often dense on distal third of plant, especially fruits, flowering pedicels sessile or 0.5-1 (2.5) mm, fruit apex usually the same width as the rest of fruit
 *Matthiola afghanica* Rech.f. & Köie
 — Trichomes always dense, rays often parallel to epidermis; glands sparse throughout, flowering pedicels (0.5-1.5-) 0.2-4 (6) mm, fruit apex usually attenuate *Matthiola farinosa* Bunge

chome rays is fewer in the annual than in the perennial species. However, this hypothesis remains to be tested in a broader systematic context along with other taxa of Brassicaceae. Similar morphological studies should be carried out on the remaining 32 species of the genus along with comprehensive molecular phylogenetic studies to obtain meaningful conclusions about the generic limits and character evolution.

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APPENDIX 1. — Selected of voucher specimens used for gland and trichome studies. The following abbreviations designate the herbaria without index: Yasouj University herbarium (YUH); Agriculture and Natural Resources Researches center of Urmia and Hormozgan herbaria (ANRRU and ANRRH, respectively); Department of Science, Ferdowsi University of Mashhad (FUM); Herbarium of Isfahan University of Technology (HIUT).

Matthiola afghanica Rech.f. & Köie. **Iran. Khorasan:** Robot sefid, 1649 m, *Zeraatkar 16023* (T); 80 km Mashhad from Sabzevar, 1107 m, *Zeraatkar 16020* (T); Robot Sefid, 1694 m, *Zeraatkar 16039* (T); S Ataiyeh, 1591 m, *Zeraatkar 16019* (T); Taghestan-e Nowzar, 900 m, *Faghihnia & Zangooei 22870* (FUMH); SW Taybad, Karat Mt., 894 m, *Faghihnia 34797* (FUMH); Torbat Heydariyeh, 1050 m, *Joharchi & Zangooei 19946* (FUMH); between Saleh Abad & Polkhatoon, 500 m, *Faghihnia & Zangooei 22705* (FUMH); Akhلامad, 1380 m, *Ayatollahi & Rezaie 12726* (FUMH); Tangal-e Bardoo, 1666 m, *Johrachi & Zangooei 15407* (FUMH); Mazdavand, 950 m, *Joharchi & Zangooei 16737* (FUMH); Tandureh National Park, 1862 m, *Vaezi & Tabasi 89232, 89237* (FUM); Torbat Heydariyeh to Khaf, 1319 m, *Anonymous s.n.* (FUM); Baghcheh-Mashhad highway, 1036 m, *Anonymous s.n.* (FUM); Mirabad, 1800-2000 m, *Assadi & Massoumi 21253* (TARI); 70 km from Neyshabour to Kashmar, 1550-1950 m, *Assadi & Mozaffarian 35451* (TARI); Torbat-e Jam to Bakhazr, 1770 m, *Assadi & Amirabadi 84597* (TARI); N Robot Sefid, 1700-2000 m, *Runemark & Sandabi 23515* (TARI); ca. 63 km Neyshabour from Kashmar, 1600 m, *Assadi 95831* (TARI); Robot Sefid, 1700-1900 m, *Assadi & Mozaffarian 35864* (TARI); ca. 25 Mashhad to Fariman, 990 m, *Mozaffarian 67523* (TARI). **Afghanistan. Bamian:** In jugo Shibar, 2400 m, *Neubauer 4692* (KUFS). **Herat:** 1500 m, *Köie 3849* (W); 23 km N Herat and der straÙe nach Toraghundi, 1330 m, *Podlech & Yarmal 29412* (KUFS); Kuh-e Zayarat, 1200-1400 m, *Jarmal & Podlech 29299* (M).

Matthiola alyssifolia (DC.) Bornm. **Iran. Khorasan:** E Quchan, 1650 m, *Faghihnia & Zangooei 27491* (FUMH); E Birjand, 2400 m, *Faghihnia & Zangooei 32073* (FUMH); Bojnurd, Qaleh Sheykh to Sorkhzo, 1300 m, *Faghihnia & Zangooei 21659* (FUMH); E Birjand, 2300 m, *Faghihnia & Zangooei 30308* (FUMH); Kalat, 1200 m, *Lotfi & Mousavi 2643* (TARI); ca. 50 km Mashhad, 1600 m, *Paryab & Shirdel 7291* (TARI); Dargaz, 1300 m, *Mousavi et al 7343* (TARI); Tandoureh National Park, 1520 m, *Vafae & Mohammadzadeh 479* (TARI); Akhلامad, 1600-1800 m, *Mozaffarian 48779* (TARI); Chalpoo, 1550 m, *Amirabadi & Abbasi 4409* (TARI); Gonabad to Ferdos, 2090 m, *Amirabadi & Ranjbar 2495* (TARI); Birjand, 1800 m, *Shad & Vafae 931* (TARI). **Gorgan:** Between Azadshahr & Shahrud, 2000 m, *Assadi 85659* (TARI); S Kordkoy, 1700 m, *Massoumi 55969* (TARI); Golestan National Park, 1450 m, *Wendelbo et al. 11086* (TARI). **Hamadan:** Yalfan, 1940 m, *Termeh & Mousavi 16059* (TARI); **Esfahan:** Mouteh, 1990 m, *Amin & Mousavi 6336* (TARI); Kashan, 1800 m, *Iranshahr 16079* (TARI); Tiran, 2200 m, *Nouroozi 5240* (TARI); Darband, *Iranshahr 15951* (TARI); Golpayegan, 2210 m, *Etemadi & Movahedi 3122* (TARI). **Yazd:** Shirkuh, 2400 m, *Mozaffarian 77678* (TARI); S Yazd, Shirkuh, 2800 m, *Mousavi & Tehrani 16071* (TARI). **Kohgiluyeh & Boyer-Ahmad:** Yasuj, 2030 m, *Fasibi 24499* (TARI). **Chaharmahal & Bakhtiari:** 32 km Shahrkor,

2300 m, *Iranshahr 15958* (TARI); Kuh-e Shahidan, 2300-3000, *Mozaffarian 58097* (TARI); Tang-e Sayyad national park, 2400 m, *Mozaffarian 62123* (TARI). **Fars:** Khorambid, near Gooshti village, 2560 m, *Khosravi & Farahmand s.n.* (SUH). **Kerman:** 70 km NW Ravar, 2400-3200 m, *Assadi & Bazgosha 56159* (TARI); Pabdana, 2275 m, *s.n.* (SUH); Rafsanjan to Zarand, 1800 m, *Saber & Ghonchei 88* (TARI); Kerman, *Babankhanloo 24007* (TARI). **Semnan:** 49 km Azadshahr to Shahrud, 1000 m, *Assadi & Wendelbo 29617* (TARI); Mehmandust, 1800-2200 m, *Termeh & Zargani 15954* (TARI); 35 km N Damghan, 1950 m, *Assadi & Wendelbo 29491* (TARI). **Tehran:** Karaj, 1700 m, *Termeh 15953* (TARI); Karaj, Kalak, 1800 m, Mousavi 16074 (TARI); Kuhdashteh, 2500 m, Parsa 12398 (TARI); Mardabad, 1800 m, *Gaubia 16076* (TARI); Garmdareh, 2000 m, *Assadi 27534* (TARI); Khojir, *Hamzeh & Shirvani 95184* (TARI). **Arak:** Arak to Mahalat, 2500 m, *Massoumi & Mozaffarian 47931* (TARI). **Afghanistan. Ghorat:** Ghorat, 2400 m, *Podlech 21839* (M).

Matthiola chenopodiifolia Fisch. & C.A.Mey. **Iran. Khorasan:** Beshruyeh to Ferdows, 800 m, *Khosravi s.n.* (SUH); Nehbandan to Sefidayeh, 1000 m, *Hojjat & Zangooei 24844* (FUMH); SE Tous, 850 m, *Rafeie & Zangooei 26199* (FUMH); N Gonabad, 880 m, *Joharchi & Zangooei 17226* (FUMH); E Sabzevar, 900 m, *Joharchi & Zangooei 11281* (FUMH); Torbat Hedarieyeh to Gonabad, 1087 m, *Ayatollahi & Zangooei 13705* (FUMH); Jajarm, 900 m, *Joharchi & Zangooei 11348* (FUMH). **Esfahan:** NE Kashan, 870 m, *Babakhanloo & Amin 17808* (TARI); Shahrreza to Abadeh, 1900 m, *Nouroozi & Shams 12359* (TARI). **Yazd:** Nodoushan, 1991 m, *Hadi 19253 & 19252* (FAR); Bafq, 1350 m, *Assadi & Bazgosha 56019* (TARI); Bahramabad, 1500 m, *Rech. & Esf. 15970* (TARI). **Hormozgan:** Hajiabad to Bandar, 1200 m, *Rech. & Esf. 15973* (TARI); between Gahkom & Tarom, 800 m, *Mozaffarian 52262* (TARI). **Kerman:** Ravar to Chatrud, 1500 m, *Assadi & Bazgosha 56306* (TARI); near Mahan, 1700 m, *Haravi 649* (TARI); Mamanak, 1000 m, *Mousavi & Termeh 15976* (TARI). **Baluchistan:** Zahedan, 1500 m, *Massoumi 1038* (TARI); Zahedan to Mirjaveh, 1690 m, Sandughdaran 942 (TARI). **Semnan:** Mayamey to Damqan, 1339 m, *Zeraatkar 16042* (T); Garm-sar to Semnan, 1200 m, *Iranshahr 15984* (TARI); N Shahrud, 1100 m, *Freitag & Mozaffarian 28410* (TARI). **Fars:** Abadeh to Esfahan, 2098 m, *Ghorbani 102* (TMRC); Abadeh, *Farrokh s.n.* (SUH). **Tehran:** Saveh to Tehran, 1170 m, *Foroughi 4490* (TARI); Siahkuh, 1000 m, *Wendelbo & Assadi 16069* (TARI). **Pakistan. Baluchistan:** 8k to Warechah, *Martin L. Grant 15331* (SUH); Makran, Panjgur area, *Riedl & Rafiq PG-98-027* (W).

Matthiola codringtonii Rech.f. **Afghanistan. Bamian:** Band-e Amir, Band-e Gholaman, 3057 m, *Abmadzai s.n.* (SUH); Band-e Amir, 2900 m, *Hedge & Wendelbo 4779* (E, photo); Band-e Amir, 1800 m, *Rech. f. 18485* (E, photo).

APPENDIX 1. — Continuation.

Matthiola dumulosa Boiss. & Buhse. **Iran. Khorasan:** Qayen to Birjand, 1837 m, *Zeraatkar* 16024 (T); W of Jajarm, Daraq, 900 m, *Joharchi* 11388 (FUMH); Qayen to Birjand, 1703 m, *Basiri* 1570, 19991, 19992, 19994 (FUM); Qayen to Birjand, 2 km to Khezri, 1718 m, *Basiri* 17181 (FUM); ca. 1 km after Darq from Jajarm, 1101 m, *Zeraatkar* 16043 (T, SUH); ca. 38 km E Torbat-e Jam, 700 m, *Assadi & Amirabadi* 66788 (TARI). **Semnan:** Dehmolla & Salehabad to Kavir, 1200 m, *Mozaffarian* 72671 (TARI); 33 km Shahrud to Sabzevar, 1500 m, *Assadi & Abouhamzeh* 40074 (TARI).

Matthiola farinosa Bunge ex Boiss. **Iran. Khorasan:** Baba Aman, 1216 m, *Zeraatkar* 16035 (T). Saluk, 1357 m, *Ezazi* 5402 (T); Bar, 2046 m, *Zeraatkar* 16025 (T); Chamanbid, 1608 m, *Zeraatkar* 16037 (T); Behkadeh, 1608 m, *Zeraatkar* 16036 (T); SE Bojnurd, 1500 m, *Rafeie & Zangoeei* 31557 (FUMH); S Dargaz, 1800 m, *Joharchi & Zangoeei* 18685 (FUMH); N Faruj, 1400 m, *Faghihnia & Zangoeei* 31244 (FUMH). **Semnan:** Bashm, 2600 m, *Assadi & Mozaffarian* 40337 (TARI); Tang-e Parvar, 2200 m, *Assadi & Mozaffarian* 40750 (TARI); above Touye, 2000 m, *Assadi & Wendelbo* 29490 (TARI). **Gorgan:** after Golestan tunnel, 999 m, *Zeraatkar* 16056 (T); E Maraveh Tappeh, 300 m, *Assadi & Massoumi* 55478 (TARI); Tilabad, 1000 m, *Wendelbo & Assadi* 29599 (TARI).

Matthiola flavida Boiss. **Iran. Fars:** near Persepolis, Kuh-e Ayub, 1746 m, *Zeraatkar* 16014 (T); Kavar, 2175 m, *Sobrabie s.n.* (SUH); Shiraz, Derak Mt, 1640 m, *Khosravi s.n.* (SUH); Kharameh, Khaneh Kat Mt., 1620 m, *Khosravi & Biglari s.n.* (SUH); Dokuhak, 1765 m, *Khosravi s.n.* (SUH); Jahrom, Kuh-e Sur, 2101 m, *Mohammadi s.n.* (SUH); N Shiraz, 1600 m, *Kamali s.n.* (SUH). **Kohgiluyeh & Boyer-ahmad:** Dehdasht, *Taghizadeh s.n.* (SUH); Sogh, *Panahi s.n.* (SUH). **Kerman:** E Kerman, 1842 m, *Naderi s.n.* (SUH); Shahr-e Babak to Meymand village, 1919 m, *Abbasi s.n.* (SUH); Rafsanjan, Gurchupan, 2400 m, *Emamipur s.n.* (SUH); Lalehzar, 2600 m, *Foroughi & Assadi* 17898 (TARI). **Hormozgan:** S Genou, 1600 m, *Wendelbo & Foroughi* 15500 (TARI); Qotbabad, 1200 m, *Wendelbo & Foroughi* 15775 (TARI); Bokhvan, 1500 m, *Mozaffarian* 44721 (TARI); SE Jakdan, 1200 m, *Mozaffarian et al.* 39390 (TARI). **Baluchistan:** Taftan, 2700-3800 m, *Mozaffarian* 53077 (TARI); Taftan region, 2200 m, *Mozaffarian* 52982 (TARI); Khash, 2500 m, *Assadi* 22840 (TARI).

Matthiola ghorana Rech.f. **Afghanistan. Ghorat:** infra Parjuman, *Rech.* 19054 (W). **Ghazni:** In valle fluvii Arghandab prope Sang-i Masha, 2400 m, *Rech.* 17518 (W); Sang-i Masha, in saxosis ad fluv. Arghandab, 2500 m, *Rech.* 17468 (W).

Matthiola incana (L.) W.T.Aiton. **Iran. Azerbaijan:** Mianeh, 1100 m, *Illegible* 19273 (T, cult.). **Mazandaran:**

Amol, 95 m, *Ebrahimi* 7224 (T, cult.). **Tehran:** Park-e Daneshjoo, 1150 m, *Zeraatkar* 16021 (T, cult.). **Kerman:** Bam, 1150 m, *Zare s.n.* (SUH, cult.). **Fars:** Mamassani, 1820 m, *Akbari s.n.* (SUH, cult.).

Matthiola spathulata Conti. **Iran. Azerbaijan:** Asalem to Khalkhal, *Assadi* 86500 (TARI); 22 km SW Ahar, 1550 m, *Illegible* 26885 (TARI); ca. 18 km NW Marand, 1500 m, *Assadi & Shabsavari* 65444 (TARI); W Bazargan, 1500-1700 m, *Assadi & Mozaffarian* 30200 (TARI); Khoy to Shahpur, 1200 m, *Wendelbo & Assadi* 19263 (TARI); Tabriz to Marand, 1500 m, *Assadi & Mozaffarian* 29812 (TARI). **Qazvin:** Abgarm, Kharamaghan, 1735 m, *Mozaffarian* 87297 (TARI). **Zanjan:** Hajibacheh, 1900 m, *Zeraatkar* 16006 (T, SUH); 50 km on the Zanjan-Dandi, 1908 m, *Mahmoodi* 99568 (T, TARI); between Gowjeh Qaya and Gholtugh, 1902 m, *Mahmoodi* 100456 (T, TARI); 4 km before Ghezel-Ozan river, 1450 m, *Mahmoodi* 100458 (T, TARI). Haji-Bache 1908 m, *Mahmoodi* 100457 (T, TARI).

Matthiola longipetala (Vent.) DC. **Iran. Hormozgan:** Tashkuye village, 668 m, *Zeraatkar* 16044 (T); 2169 m, Geno Mt., *Zarrin & Ghahremaninejad* 322651 (T); 22 km Senderk to Darpahn, 550 m, *Mozaffarian, Banihashemi & Shahinzadeh* 39258 (TARI). **Bushehr:** 61 km Kazerun to Dalaki, 250 m, *Runemark & Mozaffarian* 26837 (TARI); 70 Bushehr to Ameri, 3 m, *Runemark & Mozaffarian* 27058 (TARI); 2 N Khormuj, 150 m, *Runemark & Mozaffarian* 27182 (TARI). **Khuzestan:** Andimeshk to Khoramabad, Pol-e Zal, 350 m, *Mozaffarian* 53780 (TARI); 10 km Bagh Malek to Haftkel, 500 m, *Assadi & Abouhamzeh* 38872 (TARI); S Susa, 63 m, *Zeraatkar* 16041 (T); 55 km Behbahan to Ramhormoz, 240 m, *Runemark & Mozaffarian* 30921 (TARI); Masjed soleyman, 278 m, *Arabi* 46391 (T); Bagh Malek, 750 m, *Mozaffarian* 53595 (TARI); Susangerd, Bostan, Alahoakbar, 60 m, *Mozaffarian* 62658 (TARI); Behbahan, Khyrudkenar, 470 m, *Foroughi* 2938 (TARI). **Fars:** Shiraz, Bamu National Park, 1900 m, *Dehbozorgi* 32824 (TARI); 22 km from Fahlian to Rashk, 900 m, *Mozaffarian* 45960 (TARI); Darab, Rostagh neck, 1200 m, *Riazi* 4599 (TARI). **Kohgiluyeh & Boyer-Ahmad:** 5 km Shamsabad to Basht, 700 m, *Assadi & Abouhamzeh* 38614 (TARI). **Chaharmahal & Bakhtiari:** Lurdegan, Sarkhun, 1200 m, *Mozaffarian* 45960 (TARI). **Hamedan:** Asadabad neck, 2030 m, *Riazi* 4696 (TARI). **Kermanshah:** Bisetun to Kermanshah, Rahimabad, 1358 m, *Hamzeh & Asri* 87772 (TARI). **Kordestan:** ca. 15 km N Sanandaj, 1700 m, *Wendelbo & Assadi* 16913 (TARI). **Kordestan:** Sanandaj, Cheno village, 1250 m, *Fatahi & Khaledian* 199 (TARI). **Tehran:** 40 km to Qom, 200 m, *Ghafari* 120/64 (TARI). **Tehran:** 55 km N Tafresh, 1300 m, *Amin & Bazargan* 18797 (TARI). **Markazi:** Save, 985 m, *Nazemi-Karami* 58040 (T). **Ilam:** Mehran, 155m, *Jafari* 25973 (T).

Matthiola tomentosa Bélang. **Iran. Mazandaran:** Sangdeh, 1315 m, *Doumanchick 31295* (TARI). **Markazi:** 50 km to Delijan, after Ghoragchi neck, *Zeraatkar 16055* (T, TARI); Gharghabad, 1500 m, *Amin & Bazargan 8207* (TARI); Khomyn to Mahalat, 1700 m, *Nowroozi 4540* (TARI); Golpayegan, 1860 m, *Jalali 19257* (FAR). **Chaharmahal & Bakhtiari:** Shahidan Mt., 2208 m, *Mozaffarian 58106* (TARI); Boroujen, Baraftab Mt., 2109 m, *Mozaffarian 54780* (TARI); Shalamazar, 2064 m, *Mozaffarian 54614* (TARI). **Yazd:** Taft, Deh Bala, 2203 m, *Zeraatkar 16007* (T); near Taft, 1469 m, *Zeraatkar 16045* (T); S Yazd, 1285 m, *Nowroozi & Feyzi 5991* (TARI). **Esfahan:** 30 km Shahreza from Semirum, 2322 m, *Zeraatkar 16046* (T); Tiran, 2057 m, *Nowroozi & Feyzi 5434* (TARI); Chadegan, Zayandehrood, 2098 m, *Assadi & Khatamsaz 76403* (TARI). **Qazvin:** Alamut, 1494 m, *Khaleghi & Imani s.n.* (FAR). **Tehran:** Sarbandan, 2469 m, *Zeraatkar 16010* (T); Ghuchak, 1960 m, *Mousavi 22832* (TARI); Lashgarak, 1500 m, *Dini 9024* (TARI); Mardabad, 1250 m, *Hedge, Wendelbo & Froughi 14697* (TARI); Gisha, 1366 m, *Karbaschi s.n.* (FAR). **Semnan:** Aho-van neck, 1939 m, *Zeraatkar 16012* (T); N Sorkheh, 1400 m, *Wendelbo & Assadi 29429* (TARI); SW Semnan, 1100 m, Pabot 26879 (TARI); N Garmsar, 1000 m, *Amin & Bazargan 19052* (TARI). **Fars:** Safashahr to Surmaq, 1827 m, *Zeraatkar 16008* (T); Bel Mt., 2540 m, *Sadri s.n.* (SUH). **Hormozgan:** Bandar Abbas, 0 m, *Mobayan 7981* (ANRRU, fragment).

Matthiola revoluta Bunge ex Boiss. **Iran. Khorasan:** Sabzevar from Esfarayen, 1109 m, *Zeraatkar 16052* (T); Robot Sefid, 1694 m, *Zeraatkar 16053* (T); S Ataiyeh, 1591 m, *Zeraatkar 16054* (T); near Khezri Dashtebayaz, 1583 m, *Zeraatkar 16049* (T); Neyshabour, kuh-e Binaloud, 1500-2700 m, *Mozaffarian 49000* (TARI); Garmab, 1668 m, *Zeraatkar 16051* (T). **Yezd:** near Abarkooh, 1566 m, *Zeraatkar 16048* (T); near Arij, 1762 m, *Zeinali s.n.* (SUH); Dehshir to Taft,

1750 m, *Khosravi s.n.* (SUH). **Esfahan:** Niasar, 1504 m, *Naderi s.n.* (DU); Sangab, 2200 m, *Yousefi 1144* (TARI); Ravand, 1550 m, *Dini & Bazargan 8016* (TARI). **Fars:** near Eqlid, 2128 m, *Zeraatkar 16017* (T); N Izadkhast, 2050, *Khosravi s.n.* (SUH). **Baluchistan:** Sarbaz to Iranshahr, 979 m, *Ghorbani 939* (TMRC); 18 km Khash-Iranshahr road to Irandegan, 1500 m, *Mozaffarian 42852* (TARI); 65 km Khash to Zahedan, Mortak, 2100 m, *Mozaffarian 53395* (TARI). **Semnan:** N Semnan, 1400-1500 m, *Wendelbo & Assadi 29747* (TARI); Delbar, 2200-2300 m, *Freytag 13916* (TARI); Shahrud, 1400 m, *Freytag & Mozaffarian 28575* (TARI). **Tehran:** Damavand, Eivanakey to Bulan, 1600 m, *Mozaffarian 54057* (TARI). **Afghanistan. Gardez:** Safed Kuh, 2600-2700, *Rech. 31972* (W). **Bamian:** Band-e Amir, Band-e Panir, 2959 m, *Ahmadzai s.n.* (SUH); Band-e Gholaman, 3057 m, *Ahmadzai s.n.* (SUH). **Uzbekistan.** Peti village, 6000 ft., *Komarov s.n.* (LE).

Matthiola shiraziana Zeraatkar, Khosravi, F.Ghahreman., Al-Shehbaz & Assadi. **Iran. Esfahan:** Esfahan to Vanak road, 2200 m, *Parishani 14363* (HIUT); Semirum, Padena to Sisakht, Gardaneh Rigan (probably Bijan) 2600 m, *Nowrooz 4678* (HIUT); Khafr, Dena Mt., 3700 m, *Riazi 6890* (TARI); Semirum, Vanak, 2250 m, *Mozaffarian 62152* (TARI); Semirum, Padena to Sisakht, Gardan-e Bizhan, 2600 m, *Nowroozi 2863* (TARI). **Fars:** Shiraz, Ghalat village, 2420 m, *Jowkar s.n.* (SUH); 20 km W Shiraz, Ghalat village, 2100 m, *Sarafraz s.n.* (SUH). **Kohgiluyeh & Boyer-Ahmad:** 27 km of N Sisakht, 2428 m, *Jamzad et al. 69446* (TARI); SE Yasuj, 15 km to Ardakan, Moleye Balout, Torbekestan Mt., 2510 m, *Moazzeni & Pirani 2210* (TMRC, FUMH); *Yasouj*, the old road of Kakan, 2078 m, 30 May 2013, *Hosseini s.n.* (YUH). **Chaharmahal & Bakhtiari:** Farsan, 2220 m, *Mozaffarian 96682* (TARI).