Acta Palaeobotanica 64(1), 60–74, 2024
https://doi.org/10.35535/acpa-2024-0005

e-ISSN 2082-0259
ISSN 0001-6594

Palynological studies of some species of the genus *Cuscuta* with emphasis on taxonomy

ALLA HAYRAPETYAN*, HASMIK SONYAN and ALVARD MURADYAN

Institute of Botany after A. Takhtajan, National Academy of Sciences of the Republic of Armenia, Acharyan 1, 0063, Yerevan, Armenia; e-mails: alla.hayrapetyan.63@gmail.com, ORCID: 0000-0002-8038-7422; hasmiksonyan@gmail.com, ORCID: 0009-0007-9442-3424; alla.muradyan.1991@mail.ru, ORCID: 0009-0003-6271-990X

Received 4 October 2023; accepted for publication 19 June 2024

ABSTRACT. The main objective of this research was to conduct a comparative pollen morphological analysis of some representatives of the genus *Cuscuta* in relation to taxonomy. Investigations of 38 species and 1 variation revealed that not only the number, but the colpi length, as well as the exine ornamentation (at the SEM level), can be regarded as a diagnostic feature. For all the taxa studied, the common zonocolpate type of pollen was observed, represented by three variations: I) colpi long; II) colpi of medium length; III) colpi short. In combination with colpi length, variations in the number of colpi were also identified, such as: I) 3(4)-zonocolpate pollen grains with long colpi (in most of the species studied from subgenera *Grammica* and *Cuscuta*, as well as in *C. monogyna* from the subgenus *Monogynella*); II) 4(3)-zonocolpate pollen grains, with long colpi (*C. cristata* from subgenus *Grammica*); III) 3-zonocolpate pollen grains both with long colpi and colpi of medium length (*C. abyssinica* from subgenus *Cuscuta* and *C. africana*, *C. angulata* from subgenus *Pachystigma*); IV) 3-zonocolpate pollen grains with colpi of medium length were noted for species from all four subgenera (*C. cassytoides*, *C. lupuliformis* from subgenus *Monogynella*, *C. kotschyana* from subgenus *Cuscuta*, *C. nitida* from subgenus *Pachystigma* and *C. jalapensis*, *C. rostrata*, *C. suaveolens* from subgenus *Grammica*); V) 3–4- or 4-zonocolpate, with short colpi (*C. lehmanniana* and *C. gigantea* from subgenus *Monogynella* respectively); VI) 5–6-zonocolpate, with short colpi (*C. reflexa* from subgenus *Monogynella*).

Using SEM, three main types of exine ornamentation were also identified: perforate, foveolate and reticulate. The last type in the vast majority of the cases was presented in combination with echinae (rarely with spines or granules).

The data revealed that the presence of the significant similarity of palyno-morphological characteristics in representatives of the subgenera *Cuscuta*, *Pachystigma* and *Grammica*, with the exception of the species *Lepidanche adpressa* (syn. *C. compacta*), makes it difficult to create an identification key at the level of individual subgenera. Pollen features can be most clearly used only to distinguish the subgenus *Monoginella*, reflecting its certain isolation within the entire *Cuscuta* genus.

The presence of a highly specialized reticulate exine ornamentation in *Lepidanche adpressa* (syn. *C. compacta*), not identified for the pollen of any of the studied taxa of the subgenus *Grammica*, indicates a significant proximity of this species to the subgenus *Monogynella*. For the species *C. reflexa*, the obtained palyno-morphological data are consistent with the previous opinion about the separation of this species, as well as its more advanced position within the genus *Cuscuta*.

KEYWORDS: *Cuscuta*, pollen morphology, aperture, exine ornamentation

INTRODUCTION

The genus *Cuscuta* L. is represented by exclusive annual, rarely overwintering rootless plants with cord-like or filamentous stems that wrap around the plant and stick to them with the help of haustoria. Combining approximately 150 to 200 species, *Cuscuta* is cosmopolitan, however, the predominant number of species (up to 140) occur in the territory of both Americas. Austin (1980) wrote, that the name *Cuscuta* originates from the Arabic word

* Corresponding author

Kushkut which approximately translates as a tangled wisp of hair.

Based on the style and stigma morphology of *Cuscuta* species, three groups are delimited and subsequently ranked in subgenera (Engelmann, 1859; Yuncker, 1932). *Cuscuta* subgenus *Monogyna* species are morphologically characterized by a single whole or partly divided style and stigmas of various forms. The remaining subgenera have two styles and are distinguished by the characteristics of the morphological structure of the stigma: elongated and linear stigmas (*Cuscuta* subgenus *Cuscuta*) vs short and capitated (*Cuscuta* subgenus *Grammica*) (Yuncker, 1932).

With regard to the systematic position of the genus *Cuscuta*, some authors consider this genus in a separate Cuscuteae tribe (Choisy, 1845; Bentham and Hooker, (1873)1876; Baillon, 1891; Hallier, 1893; Peter, 1897) or Cuscutoideae subfamily (Peter, 1891; Melchior, 1964), as a part of the Convolvulaceae family. However, numerous major taxonomists (Dumortier, 1829; Hutchinson, 1926; Dahlgren, 1980; Roberty, 1952, 1964; Austin, 1986; Cronquist, 1988; Takhtajan, 1966, 1987, 1997, 2009; Hu and Yuan, 2002), treat the genus *Cuscuta* as part of a separate family Cuscutaceae, closely associated with Convolvulaceae.

Detailed molecular genetic studies of individual species, as well as subgenera of the genus *Cuscuta* (Stefanović and Olmstead, 2004; Costea et al., 2006a, b, c, d, 2008; García and Martin, 2007, etc.) indicate that this genus is not only a part of the clade Convolvulaceae, but also situated directly within this family, as derived from at least two saprophytic predecessors (Neyland, 2001; Stefanović et al., 2007).

Stefanović et al. (2002) wrote that according to chloroplast DNA sequences, *Cuscuta* is nested within the family Convolvulaceae, although the exact position of this ambiguous and controversial parasitic genus could not be ascertained. According to the authors, this is mainly due to the *Cuscuta* sequences being highly divergent, which possibly indicates their plesiomorphic condition within the family (Stefanović and Olmstead, 2004). In contrast, according to Stefanović et al. (2002), the analysis of the nuclear and plastid DNA sequence of a number of taxa in the Convolvulaceae family is quite consistent with the classical infrageneric division of *Cuscuta* (sensu Yuncker, 1932). All three subgenera were found to be monophyletic, and the subgenus *Monogyna* being recorded as a sister to the rest of the genus (i.e. subgenera *Cuscuta* and *Grammica*) (Stefanović et al., 2002).

However, as a the next steps of molecular investigation, a new molecular dataset consisting of plastid (rbcL) and nuclear ribosomal (nrLSU) DNA sequences was generated (García et al., 2014). According to the authors, "This study represents the most complete molecular phylogenetic hypothesis for *Cuscuta* yet made, including specimens of all the sections and subsections accepted by Yuncker (1932)" (p. 682). These data confirm that subgenera *Monogynella* (the new subgenus name used instead of the previous *Monogyna*) and *Grammica* are monophyletic, but in contrast to previous affirmations, the subgenus *Cuscuta* was confirmed to be *paraphyletic*, with the sister relationship of its South African sect. *Pachystigma* and subgenus *Grammica*. Authors wrote, that as a result, four major, well-supported, and distinct clades were picked out and accepted as four subgenera within the genus *Cuscuta* (*Monogynella*, *Cuscuta*, *Pachystigma* and *Grammica*). At the same time, molecular phylogenetic results show a completely inverted polarity for almost all of the main diagnostic characteristics (i.e. number of styles, stigma shape and fruit dehiscence), proposed by Yuncker (1932).

The logical continuation of these investigations was the work of Costea et al. (2015), where the authors present an infrageneric classification of the genus *Cuscuta* based on the molecular phylogenetic data. A complete species list was also presented for each of the four subgenera of the genus *Cuscuta*. Besides, having separated from the subgenus *Cuscuta* sect. *Pachystigma* (according to the authors, more closely related to subgenus *Grammica*), and by accepting it as a separate subgenus *Pachystigma*, Costea et al. (2015) note the monophyletic nature of all four of the above subgenera.

Palynological studies of *Cuscuta* species using LM have been carried out by Erdtman (1952), Laguardia (1961), Das and Banerji (1966), Heusser (1971), Chiguryaeva (1972), Shimakura (1973), Nair and Rehman (1963), Kupriyanova and Alyoshina (1972), El-Ghazaly (1991), Martin (2001) et al. At the SEM level, the pollen of this genus was studied by Sengupta (1972), Cronk and Clarke (1981), Pedraza (1985), Andres and Heras (1986), Polo

and Diez (1987), Zhang et al. (1991), Severova (1995), Perveen and Qaiser (2004), Hamed (2005), Liao et al. (2005), Welsh et al. (2010) and others.

Sengupta (1972) proposed an evolutionary arrangement of the family Convolvulaceae with four major pollen types based on the number and distribution of apertures. Author also argued, that compared with the 3-colpate pollen encountered in dodder species, the 5–6-colpate grains of *Cuscuta reflexa* are derived. Polo and Diez (1987) revealed that in addition to the basic 3–4-zonocolpate aperture type, for the species *C. epithymum* 5–6-, 8–9-, as well as 12-pantocolpate pollen grains were noted.

Costea et al. (2006a, b, c, d, 2008) conducted taxonomic studies on various species and complexes within the genus *Cuscuta* and also reported on pollen morphology.

Demir et al. (2017) examined the pollen morphology of the 15 taxa of *Cuscuta* using SEM. For 12 species studied, authors quoted 3-zonocolpate, for *C. campestris* and *C. brevistyla* 3(4)-zonocolpate, and for *C. planiflora* 3(6)-zonocolpate pollen grains. According to Demir et al. (2017), "the apertures of the pollens of these taxa were found scabrate, scabrate-perforate, reticulate and ekinate-reticulate" and "…size and exine can be used to distinguish different *Cuscuta* taxa" (pp. 746 and 750 respectively).

Amini et al. (2018) investigated the molecular and micro-morphological evidence of 12 populations of three species of *Cuscuta* (*C. australis*, *C. campestris* and *C. chinensis*) in Iran. The authors noted that the most important characteristics were pollen shape, ornamentation of the tectum, exine thickness and colpus length.

The study of the overall distribution, morphology, anatomy, and micromorphology of the seeds and pollen of *Cuscuta campestris* was carried out by Zare and Dönmez (2020). The authors characterized the pollen of *C. campestris* as tricolpate with sunken apertures and microechinate perforate exine ornamentation.

Noshad et al. (2020) conducted a detailed comparative palyno-morphological analysis on the species *Cuscuta reflexa* (as a member of Cuscutaceae family) and a few members of Convolvulaceae, using LM and SEM. It has been concluded that "…*Cuscuta refelexa* pollen are exactly similar to *Ipomea arachnosperma* on the bases of pollen morphology and exine" (p. 1215).

The most extensive in terms of the number of studied species and the scope of research was the work of Welsh et al. (2010), which provides palyno-morphological data on 135 species and 13 variations of the genus *Cuscuta* using scanning electron microscopy. The authors noted that "over 95% of the species examined can be characterized as 3-zonocolpate, but this prevalent apertural type may be accompanied in the same anther by a small proportion of 4-, 5- or even 6-zonocolpate grains and, extremely rarely, by pantocolpate grains" (p. 85). The authors also confirmed that pollen grains with a higher number of apertures (5–8) have evolved in *Cuscuta* from the ancestral state with three colpi only in subgenus *Monogynella* (*C. reflexa* and *C. japonica*) and in several South American species belong to subgenus *Grammica*, which can be considered one step above the primitive. As the main diagnostic features of pollen, the authors considered the number of colpi, as well as exine ornamentaion, highlighting 4 types of sculpture: "…imperforate (no perforations present), perforate (tectum with puncta <1 μm), microreticulate (reticulate ornamentation consisting of muri and lumina <1 μm) and reticulate (similar to the previous, but lumina >1 μm)" (p. 84). According to Welsh et al. (2010), the last type is typical only for certain species of the subgenera *Monogyna* (*Monoginella*) and *Grammica*. The authors also defined tectum variation quantitatively as "percent perforation", namely the proportion of the perforation surface (puncta or lumina) from the total surface of the tectum.

In Armenia, Avetisyan and Mekhakyan (1980) investigated the pollen morphology of representatives of the genus *Cuscuta* using LM. Data on pollen features of certain species of this genus using LM and SEM are also available in Hayrapetyan (2010).

The main objective of this research was to conduct a comparative pollen morphological analysis of some representatives of the genus *Cuscuta* in relation to taxonomy.

The subdivision of the genus *Cuscuta* is presented according to Costea et al. (2015).

MATERIAL AND METHODS

Unopened mature flower buds were obtained from 44 specimens of 38 species and 1 variation of *Cuscuta*. Specimens were sampled from ERE and LE (acronyms follow http://sweetgum.nybg.org/science/ih/). All

specimens examined are listed in Table 1 and include information on synonyms according to their location in The Plant List (http://www.theplantlist.org/).

For light microscopy (LM), pollen grains were stained with basic fuchsine (Smolyaninova and Golubkova, 1950), as well as with acetolyzed material (Avetisyan, 1950), and fixed in glycerin jelly. The details of exine structure and ornamentation were studied on acetolyzed pollen grains. Pollen grain shape, size, and aperture structure were studied on non-acetolyzed stained pollen grains.

Measurements were performed under LM using a PZO Warszawa (SK14) and AmScope (2000X LED) binocular microscopes. For SEM, non-acetolyzed dry pollen grains of 16 selected species were placed in a drop of alcohol, mounted on aluminium stubs, and sputter-coated with gold. Samples were observed under a Jeol JSM35 scanning electron microscope run at 15 kV electron beam, and the images were digitized.

Twenty pollen grains were analysed for each investigated specimen, and pollen size (i.e. P × E, where

Table 1. List of investigated species and specimens. The information given in the original herbarium labels is slightly edited, in the original language and with English translation where necessary. ERE – Institute of Botany after A. Takhtajan, National Academy of Sciences, Yerevan, Armenia; LE – Komarov Botanical Institute of the Russian Academy of Sciences, St. Petersburg, Russia; S – specimen

Taxon	Name according to their location in The Plant List (http://www.theplantlist.org/)	S	Herbarium sheet information
C. abyssinica A. Rich.	*C. abyssinica* A. Rich.		Flora von Uzumbara, N 9114, C. Holst (LE)
C. acutiloba Engelm.	*C. acutiloba* Engelm.		Rocky walls of open small canyon, 3000–3200 m. Plants of Peru, dep. Lima, Canta, N 14595, F.W. Pennele (LE)
C. africana Choisy	*C. angulata* Engelm.		Plantarum Africae Australis Extratropicae, N 5730, Burchell (LE)
C. americana L.	*C. americana* L.		Plants of the West Indies, St. Vincent, St. George Parish, N 8246, R. Cooley (LE)
C. angulata Engelm.	*C. angulata* Engelm.		Plantae Schlechterianae Austro-Africanae, N 9506, O. Rivier (LE)
C. arabica Wight.	*C. hyalina* Roth		Arabice "Dan el erneb" loco "Raphidim" Arabiae petraeae, W. Schimper (LE)
C. australis R. Br.	*C. australis* R. Br.		Kt. Tessin, 150 m N vom casino Lido Ascona, (Herb. Polytechnici helvetici turicensis), E.S. Buell (ERE 71577)
C. babylonica Aucher ex Choisy	–		Pl. Palaestinae, Env. of Dead Sea, Kallia, R. Sroclov (ERE 76561)
C. breviflora Vis.	*C. tinei* Insenga		Transcaucasia, Guria, A. Grossheim (ERE 3513)
C. campestris Yunck.	*C. campestris* Yunck.	1	Россия, Рязанск. обл., Спаский р-н, с. Киструс, по лев. бер. Оки, Tichomirov, Ableev, Degtjareva, Djachenko (Russia, Ryazan region, Spassky district, Kistrus village, on the left bank of the Oka River) (ERE 57098)
		2	АрмССР, Азизбек. р-н, с. Караглух, Мулкиджанян, Асланян (ArmSSR, Azizbekov district, Karaglukh village, Mulkidjanian, Aslanyan) (ERE 131835)
C. cassytoides Nees	*C. cassytoides* Nees		Pl. Africae australis, Grahams-town, 800 m, N 2755, R. Schlechter (LE)
C. ceanothi Behr	*C. ceanothi* Behr		USA, California, Marin County, N 69091, L. Rose (LE)
C. chinensis Lam.	*C. chinensis* Lam.		Pl. of the Peoples Rep. of China, Rancho Santa Ana Bot. gard., N 823-21, A. Liston, Li Bosheng, Kong Lingshao, L.Riesberg, Guo Ke, J. Morefield (LE)
C. cristata Engelm.	*C. cristata* Engelm.		Cordoba N 90, Lorentz
C. epilinum Weihe	*C. epilinum* Weihe		Fl. Galliae et Germaniae exs., N 495, F.G. Schultz (LE)
C. epithymum (L.) L.	*C. epithymum* (L.) L.		АрмССР, Егегнадз. р-н, Егегнадзор х Агавнадзор, Я.И. Мулкиджанян (ArmSSR, Yeghegnadzor district, Yeghegnadzor × Aghavnadzor, Ya.I. Mulkidjanian) (ERE 106658)
C. europaea L.	*C. europaea* L.		Россия, Тувинск. АССР, Кызыльский р-н, долина р. Ка-Хем, А. Куминова, С. Кипряенов (Russia, Tuva ASSR, Kyzyl district, valley of the river Ka-Khem, A. Kuminova, S. Kipraenov) (ERE 60665)
C. gigantea Griff.	*C. gigantea* Griff.		Afghanistan, N 5899, Herb. Griffith (LE)
C. *gronovii* Willd. ex Roem et Schult.	**C.** *gronovii* Willd. ex Roem et Schult.		Plantae Quebecenses (Canada), R. Barnabe (LE)
C. indecora Choisy var. *hispidula* (Engelm.) Yunck.	*Cuscuta indecora* Choisy		Flora Texana exsicata, N 664, F. Lindheimer (LE)
C. jalapensis Schltdl.	*C. jalapensis* Schltdl.		Mexique, N 1955, M. Bourgeau (LE)
C. kotschyana Boiss.	*C. europaea* L.		АрмССР, Арташат. р-он, Веди × Гелайсор, Бозбурун, пустыня, А.Л. Тахтаджян, Я. Мулкиджанян, Э. Габриэлян (ArmSSR, Artashat region, Vedi × Gelaisor, Bozburun, desert, A.L. Takhtajan, Y. Mulkidjanian, E. Gabrielian (ERE 64434)

Table 1. Continued

Taxon	Name according to their location in The Plant List (http://www.theplantlist.org/)	S	Herbarium sheet information
C. lehmanniana Bunge	*C. lehmanniana* Bunge	1	Узб. ССР, Ферган. обл., Сарикамыш, на р. Сыр-Дарье, В. Дробов (Uzbek SSR, Fergana region, Sarikamysh, on the Syr-Darya river, V. Drobov) (ERE 25726)
		2	Iter Turkestanicum, N 30, Taschkent (LE)
C. leucosphaera Boiss. et Heldr.	–		Flora Graeca exs., N 517, T.G. Orphanides (LE)
C. lupuliformis Krock.	*C. lupuliformis* Krock.		Frankfurt, D. Logger (LE)
C. micrantha Choisy	*C. micrantha* Choisy		Chili, Santiago, in collibus, N 489, Philippi (LE)
C. minor Gilib.	–		Flavigny, France, G Desplantes (LE)
C. mitriformis Engelm. ex Hemsl.	*C. mitriformis* Engelm. ex Hemsl.		Plantae Mexicanae, Maltrata, N 248, E. Kerber (LE)
C. monogyna Vahl	*C. monogyna* Vahl		АрмССР, Кафан. р-н, лев. бер. р. Цав, близ платан. рощи, Мулкиджанян, Асланян (ArmSSR, Kafan district, left bank of the Tsav River, near the plane tree grove, Mulkidjanian, Aslanyan (ERE 64862)
C. nitida E. Mey.	*C. nitida* E. Mey.		Pl. Schlechterianae Austro-Africanae, Terra Capensis, N 7271 (LE)
C. obtusiflora Kunth.	*C. obtusiflora* Kunth.		Boliviensium, Pl. Andium, N 1480, Mandon (LE); var breviflora: Flora Graeca Exsicata, N 1136, T.G. Orphanides (LE)
C. odontolepis Engelm.	*C. odontolepis* Engelm.		N. Mexico, N 1624, C. Wright (LE)
C. odorata Ruíz et Pav.	*C. odorata* Ruíz et Pav.		Pl. of Peru, Dep. of Lima, along Rio Chillon, N 14382, F.W. Pennel (LE)
C. pedicellata Ledeb.	*C. pedicellata* Ledeb.	1	Fl. Palestinae, Shefela, Naama, N. Naftolsky, No. ERE 76562 (LE)
		2	АрмССР, Вединский р-н, с. Байбурт, А.Л. Тахтаджян, Я. Мулкиджанян, Э. Габриэлян (ArmSSR, Vedi district, Bayburt village, A.L. Takhtajan, Y. Mulkidjanian, E. Gabrielian) (ERE 66251)
C. reflexa Roxb.	*C. reflexa* Roxb.		W. Himalaya, N 22072, J.F. Duthie (LE)
C. rostrata Shuttlw. ex Engelm. et A. Gray	*C. rostrata* Shuttlw. ex Engelm. et A. Gray		Fl. of California, Santa Cruz, N 2316, M.A. Jones (LE)
C. salina Engelm.	*C. salina* Engelm.		Flora of California, Santa Cruz. Marcus E. Jones, A.M. (LE)
C. squamata Engelm.	*C. squamata* Engelm.		N. Mexico, N 1628, C. Wright (LE)
C. suaveolens Ser.	*C. suaveolens* Ser.		Fl. Galliae et Germaniae exs., N 152, C. Billot (LE)
C. umbellata Kunth	*C. umbellata* Kunth		Pl. of Arizona, near Tortilla crk., W. Hess, C. Wilhelm (ERE 56098)
Lepidanche adpressa Engelm.	*C. compacta* Juss ex Choisy		N. America, ex Herb. A. Gray (LE)

P – polar axis and E – equatorial diameter; in the case of spheroidal pollen grains – pollen diameter), colpus length, apocolpium diameter, mesocolpium width, exine thickness, ectexine and endexine ratio were measured. The arithmetic mean for pollen size, apocolpium diameter, mesocolpium width, as well as exine thickness were also given (Table 2).

The measurement of colpus length was carried out due to their variation from long to short in individual studied species. Thus, colpi are considered long when the ratio of colpus length to polar axis (C/P ratio) is 4/5–1/1, colpi of medium length – when the ratio of colpus length to polar axis is 2/3–3/4, and in the case of short colpi, the ratio is 1/2–2/5.

A comparative palyno-morphological analysis of the types of exine ornamentation within the genus *Cuscuta* was conducted using SEM data.

The summarized palyno-morphological data are presented in Table 2.

The specimens were examined under LM at the Institute of Botany after A. Takhtajan (Yerevan, Armenia), while SEM studies were carried out at the Komarov Botanical Institute of the Russian Academy of Sciences (St. Petersburg).

The morphological terminology used in our study mainly follows Erdtman (1952), Kuprianova and Alyoshina (1972), Punt et al. (2007) and Halbritter et al. (2018).

Where possible, an identification key for each subgenus of the genus *Cuscuta* has been provided.

RESULTS

Analysis of the data obtained has shown that all the studied species of the genus *Cuscuta* are characterised by the presence of zonocolpate pollen grains, while some variations in the number and length of colpi have been observed. In particular, predominantly 3(4)-zonocolpate pollen grains (colpi long, sometimes of medium length) to 3–4–5–6-zonocolpate (colpi short)

Table 2. Palyno-morphological characteristics of the representatives of the genus *Cuscuta*

Taxon	Pollen size [µm] (P × E)[1]	Aperture	C/P ratio	Colpus		Exine	
				apocolpium diameter [µm]	mesocolpium width [µm]	thickness [µm]	ectexine/ endexine ratio
I. Subgenus *Monogynella*							
C. cassytoides	21.5–24.0/22.8[2] in diameter	3-zonocolpate, colpi of medium length	2/3–3/4	8.6–9.2/9.0	14.0–15.8/14.8	3.5–3.7/3.6	3 : 1
C. gigantea	28.5–30.0/29.3 in diameter	4-zonocolpate, colpi short	1/2–2/5	13.2–13.7/13.5	16.8–17.0/16.9	1.6–1.7/1.6	4 : 1
C. lehmanniana	27.0–28.7/27.9 in diameter	3–4-zonocolpate, colpi short	1/2–2/5	12.0–14.3/13.6	12.0–14.1/13.2	2.8–3.0/2.9	2.5 : 1
C. lupuliformis	37.5–40.2/38.9 in diameter, or 40.0–41.0/40.6 × 36.2–36.7/36.5	3-zonocolpate, colpi of medium length	2/3–3/4	12.8–14.0/13.6	26.2–26.7/26.5	3.4–3.5/3.45	3.5 : 1
C. monogyna	22.5–24.0/23.3 in diameter, or 24.5–25.5/25.1 × 17.2–18.2/17.6	3(4)-zonocolpate, colpi long	4/5–1/1	7.5–9.3/8.5	12.5–15.0/13.8	3.2–3.3/3.26	4 : 1
C. reflexa	24.4–25.7/25.04 in diameter	5–6 zonocolpate, colpi short	1/2–2/5	8.8–9.0/8.9	11.6–12.0/11.7	2.3–2.4/2.35	5 : 1
II. Subgenus *Cuscuta*							
C. abyssinica	21.5–23.0/22.3 × 12.5–14.5/13.6	3-zonocolpate, colpi long or of medium legth	4/5–1/1 or 2/3–3/4	5.0–5.5/3	13.5–14.5/14	1.8–2.2/2.0	2 : 1
C. babylonica	23.5–25.0/24.3 × 12.5–15.5/14.2	3(4)-zonocolpate, colpi long	4/5–1/1	5.5–6.2/5.9	12.6–14.5/13.6	2.1–2.3/2.2	2 : 1
C. epilinum	23.2–25.8/24.6 × 16.8–17.4/17.2	3(4)-zonocolpate, colpi long	4/5–1/1	4.5–5.0/4.8	9.5–10.4/9.8	2.0–2.2/2.1	1 : 1
C. epithymum	22.5–23.0/22.8 in diameter	3(4)-zonocolpate, colpi long	4/5–1/1	8.0–9.0/8.6	14.4–14.7/14.6	2.0–2.3/2.2	2 : 1
C. europaea	16.7–18.9/17.9 × 12.6–14.0/13.4	3(4)-zonocolpate, colpi long	4/5–1/1	4.2–5.4/4.7	8.7–10.8/9.8	1.8–2.0/1.9	2 : 1
C. kotschyana	24.0–24.3/24.2 × 18.0–18.8/18.5	3-zonocolpate, colpi of medium length	2/3–3/4	8.0–9.0/8.4	14.5–14.9/14.7	2.0–2.1/2.05	1 : 1
C. leucosphaera	23.6–24.3/24.0 × 22.0–22.5/22.3	3(4)-zonocolpate, colpi long	4/5–1/1	3.5–4.2/3.9	12.0–12.5/12.3	1.4–1.5/1.45	2.5 : 1
C. pedicellata	17.7–18.5/18.2 × 15.5–17.8/16.8	3(4)-zonocolpate, colpi long	4/5–1/1	5.0–5.5/5.3	10.0–11.6/10.9	1.2–1.5/1.4	2 : 1
III. Subgenus *Pachystigma*							
C. africana	21.5–22.5/22.1 × 17.5–18.0/17.7	3-zonocolpate, colpi long or of medium legth	4/5–1/1 or 2/3–3/4	4.5–5.0/4.8	12.0–12.5/12.3	2.4–2.5/2.45	3 : 1
C. angulata	23.2–25.4/24.2 in diameter	3-zonocolpate, colpi long or of medium legth	4/5–1/1 or 2/3–3/4	7.7–8.4/8.1	19.2–19.9/19.6	2.2–2.3/2.25	3 : 1
C. nitida	20.8–23.0/22.0 × 25.5–28.8/27.0	3-zonocolpate, colpi of medium length	2/3–3/4	10.8–11.0/10.9	17.6–17.9/17.8	1.7–1.8/1.75	1.5 : 1
IV. Subgenus *Grammica*							
Lepidanche adpressa (syn. *C. compacta*)	27.5–28.0/27.7 × 18.5–22.0/19.7	3(4)-zonocolpate, colpi long	4/5–1/1	4.2–5.0/4.6	10.5–11.5/10.9	1.7–2.1/1.9	3 : 1
C. acutiloba	20.0–23.5/21.4 in diameter	3(4)-zonocolpate, colpi long	4/5–1/1	6.6–6.9/6.7	14.4–15.9/15	1.4–1.8/1.6	2.5 : 1
C. americana	15.5–16.8/16.2 × 13.5–14.0/13.7	3(4)-zonocolpate, colpi long	4/5–1/1	5.5–7.0/6.2	10.0–11.0/10.3	ca 2.0	3 : 1
C. arabica (syn. *C. hyalina*)	14.5–20.0/17.5 × 16.8–22.5/19.3	3(4)-zonocolpate, colpi long	4/5–1/1	5.0–6.0/5.4	17.0–20.5/18.6	2.0–2.2/2.06	1 : 1
C. australis	22.5–23.0/22.7 × 15.0–16.5/15.8	3(4)-zonocolpate, colpi long	4/5–1/1	4.5–5.0/4.7	15.0–15.5/15.2	1.9–2.1/1.9	1.5 : 1
C. campestris	17.0–18.5/17.8 × 17.5–20.3/18.9	3(4)-zonocolpate, colpi long	4/5–1/1	7.5–8.2/7.9	12.2–14.0/13	2.4–2.5/2.4	2 : 1
C. ceanothi	16.8–17.2/17 × 21.6–23.0/22.0	3(4)-zonocolpate, colpi long	4/5–1/1	7.2–7.5/7.4	14.7–15.4/15.01	1.6–1.7/1.6	2.5 : 1
C. chinensis	18.5–20.0/19.0 × 17.0–18.0/17.3	3(4)-zonocolpate, colpi long	4/5–1/1	8.6–9.0/8.7	14.0–15.0/14.4	2.4–2.5/2.4	2 : 1

Table 2. Continued

Taxon	Pollen size [µm] (P × E)[1]	Aperture	C/P ratio	Colpus		Exine	
				apocolpium diameter [µm]	mesocolpium width [µm]	thickness [µm]	ectexine/ endexine ratio
C. cristata	24.4–25.0/24.5 × 30.0–31.2/30.4	4(3)-zonocolpate, colpi long	4/5–1/1	4.8–5.3/5.1	14.0–14.5/14.2	1.6–1.7/1.6	2 : 1
C. gronovii	26.8–29.5/28.2 × 25.6–27.0/26.1	3(4)-zonocolpate, colpi long	4/5–1/1	9.3–10.4/9.7	18.7–20.0/19.3	1.2–1.4/1.3	2 : 1
C. indecora var. *hispidula*	26.0–27.1/26.5 × 22.3–23.7/23	3(4)-zonocolpate, colpi long	4/5–1/1	6.8–7.1/6.9	20.9–21.9/21.4	1.6	2.5 : 1
C. jalapensis	22.0–27.0/24.6 × 21.0–27.9/24.5	3-zonocolpate, colpi of medium length	2/3–3/4	11.6–11.8/11.7	15.0–15.4/15.2	2.7–2.8/2.7	3 : 1
C. micrantha	25.0–25.2/25.1 × 20.0–20.3/20.12	3(4)-zonocolpate, colpi long	4/5–1/1	4.7–4.8/4.6	9.5–9.6/9.5	1.4–1.5/1.4	3.5 : 1
C. mitriformis	23.2–25.2/24.1 in diameter	3(4)-zonocolpate, colpi long	4/5–1/1	8.8–9.0/8.6	16.5–16.7/16.6	2.2–2.3/2.2	2 : 1
C. obtusiflora	24.0–25.0/24.4 in diameter, or 23.2–27.7/25.1 × 23.5–25.5/24.4	3(4)-zonocolpate, colpi long	4/5–1/1	8.0–8.2/8.1	20.0–20.2/20.1	2.5 –2.6/2.5	4 : 1
C. odontolepis	20.0–20.5/20.2 × 23.1–23.5/23.3	3(4)-zonocolpate, colpi long	4/5–1/1	8.1–8.2/8.15	13.5–14.0/13.8	1.5–1.6/1.55	1.5 : 1
C. odorata	29.2–30.0/29.5 in diameter	3(4)-zonocolpate, colpi long	4/5–1/1	6.4–6.5/6.45	14.4–15.1/14.6	2.4–2.5/2.45	2 : 1
C. rostrata	27.6–28.0/27.8 × 22.0–22.3/22.2	3-zonocolpate, colpi of medium length	2/3–3/4	12.0–12.5/12.2	13.7–15.0/14.4	2.0–2.1/2,04	2 : 1
C. salina	24.3–25.4/24.7 in diameter, or 24.0–24.4/24.2 × 26.1–26.4/26.2	3(4)-zonocolpate, colpi long	4/5–1/1	7.2–7.4/7.3	12.4–12.8/12.5	2.2–2.3/2.25	1.5 : 1
C. squamata	15.5–18.9/17.3 × 14.0–16.5/15.3	3(4)-zonocolpate, colpi long	4/5–1/1	7.5–8.4/7.8	11.5–12.0/11.8	3.2–3.3/3.25	1.5 : 1
C. suaveolens	20.5–22 /21.3 in diameter, or 20.4–20.7/20.5 × 22.0–22.5/22.3	3-zonocolpate, colpi of medium length	2/3–3/4	8.0–8.4/8.2	10.8–11.5/11.2	1.6–1.7/1.65	2 : 1
C. umbellata	23.5–26.7/24.7 × 20.5–22.0/21.3	3(4)-zonocolpate, colpi long	4/5–1/1	8.0–8.2/8.1	17.5–18.1/18	2.3–2.4/2.35	2.5 : 1

[1] P – polar axis, E – equatorial diameter.
[2] Averaged data, obtained by measuring 20 pollen grains, are presented in the table after the forward slashes.

pollen grains have been identified. Pollen of all species studied small or of medium size; the form of pollen grains varies from prolate to oblate spheroidal.

I. Subgenus *Monogynella*

Fig. 1

Pollen size of representatives of this subgenus varies from 21.5–24.0 µm in diameter (*C. cassytoides*) to 40.0–41.0 × 36.2–36.7 µm (P × E) in *C. lupuliformis*. Regarding the shape of the pollen grains of most of the species studied, spheroidal, in species C. *lupuliformis* and *C. monogyna* also prolate pollen grains were observed. Pollen of *C. cassytoides*, *C. lupuliformis* is characterized by the presence of 3-zonocolpate, that of *C. monogyna* by 3(4)-zonocolpate and that of *C. lehmanniana* by 3–4-zonocolpate apertures. In the species *C. gigantea* 4-zonocolpate, and in *C. reflexa* 5–6-zonocolpate apertures were revealed. With the exception of *C. monogyna*, where the long colpi were revealed, in the pollen of the other species colpi of medium length or short were noted. The latest aperture variation within the genus *Cuscuta* is typical only for species of this subgenus. Exine thickness varies from 1.6–1.7 µm in *C. gigantea* to 3.5–3.7 µm in *C. cassytoides*; ectexine 2.5 to 5 times thicker than endexine; columellae separated, with spherical or claviform heads. Exine ornamentation reticulate (LM); ornamentation under SEM reticulate, and excrescences of various shapes (granules, spinules, spines) on the reticulum muri were noted.

– Pollen grains 3(4)-zonocolpate
  – Pollen grains 3(4)-zonocolpate, colpi long . . . . . *C. monogyna*
  – Pollen grains 3-zonocolpate, colpi of medium length . . . . . *C. cassytoides*, *C. lupuliformis*

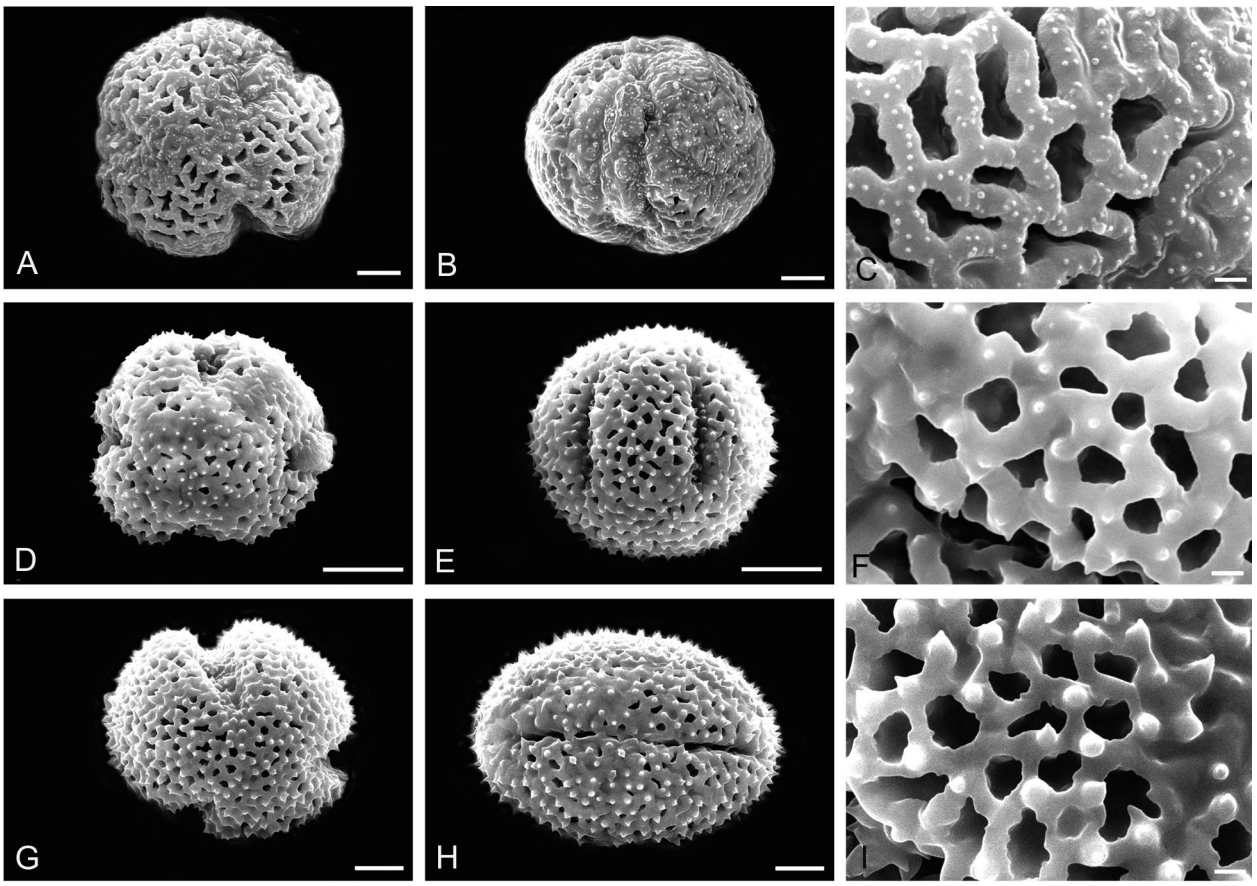

Figure 1. Pollen grains of the representatives of the subgenus *Monogynella* (SEM micrographs). **A–C**. *C. cassytoides*; **D–F**. *C. lehmanniana*; **G–I**. *C. monogyna* (A, D, G – polar view; B, E, H – equatorial view; C, F, I – exine ornamentation). Scale bar = 10 μm in D, E; 5 μm in A, B, G, H; 1 μm in C, F, I

– The number of colpi varies, colpi short
  – Pollen grains 3–4-zonocolpate
    – Pollen grains 3–4-zonocolpate, pollen size 37.5–40.2 μm in diameter, or 40.0–41.0 μm × 36.2–36 μm . . . . . *C. lehmanniana*
    – Pollen grains 4-zonocolpate, pollen size 28.5–30.0 μm in diameter . . . . . *C. gigantea*
  – Pollen grains 5–6-zonocolpate . . . . . *C. reflexa*

II. Subgenus *Cuscuta*

Fig. 2A–L

Pollen grains of all 8 studied species are 3(4)-zonocolpate, from prolate to spheroidal. The size of pollen grains varies from 16.7–18.9 × 12.6–14.0 μm in *C. europaea* to 24.0–24.3 × 18.0–18.8 μm in *C. kotschyana*. Colpi long (in the vast majority of species) or of medium length (*C. kotschyana*), in the pollen of *C. abyssinica*, both aperture variations were observed simultaneously; in width colpi sometimes narrow, almost slit-like, often operculate: the colpus edges are generally slightly undulate, the ends pointed. The exine thickness varies from 1.2–1.5 μm (*C. pedicellata*) to 2.1–2.3 μm (*C. babylonica*); ectexine is quite often 1.5 to 2.5 times thicker than endexine; columellae separated, thin or thick, quite often thickened at the ends, sometimes also with enlarged bases. Exine ornamentation is predominately finely reticulate (LM); ornamentation under SEM is echinate perforate, sometimes echinate perforate tuberculate (*C. babylonica*).

– Colpi long
  – Exine ornamentation echinate perforate . . . . . *C. epilinum*, *C. epithymum*, *C. europaea*, *C. leucosphaera*, *C. pedicellata*
  – Exine ornamentation echinate perforate tuberculate . . . . . *C. babylonica*
– Colpi long or of medium length . . . . . *C. abyssinica*
– Colpi of medium length . . . . . *C. kotschyana*

III. Subgenus *Pachystigma*

Fig. 2M–O

Pollen grains are 3-zonocolpate, prolate in *C. africana*, spheroidal in *C. angulata* and oblate spheroidal in *C. nitida*. Pollen grains of all three studied species are approximately the same in size (Table 2). Colpi of medium length (*C. nitida*), in the pollen of *C. africana*, and *C. angulata*, both long and medium length aperture variations were observed simultaneously;

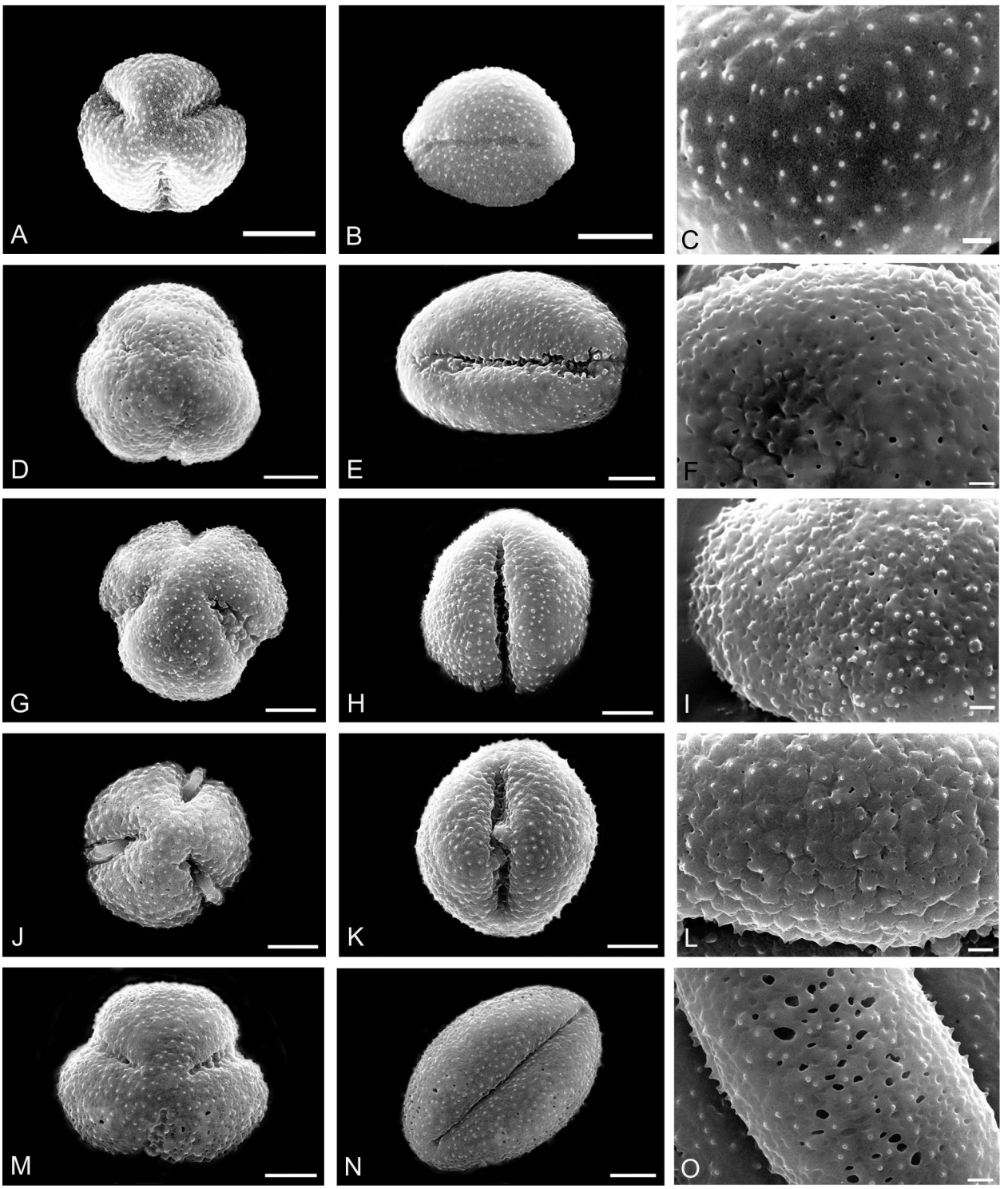

Figure 2. Pollen grains of the representatives of the subgenera *Cuscuta* and *Pachystigma* (SEM micrographs). **A–L**. Subgenus *Cuscuta*; **A–C**. *C. abyssinica*; **D–F**. C. *epilinum*; **G–I**. C. *europaea*; **J–L**. *C. pedicellata*; **M–O**. Subgenus *Pachystigma*, *C. africana* (A, D, G, J, M – polar view; B, E, H, K, N – equatorial view; C, F, I, L, O – exine ornamentation). Scale bar = 10 μm in A, B; 5 μm in D, E, G, H, J, K, M, N; 1 μm in C, F, I, L, O

in width colpi sometimes narrow, almost slit-like: the colpus edges are generally slightly undulate, the ends pointed. The exine thickness varies from 1.7–1.8 μm (*C. nitida*) to 2.4–2.5 μm (*C. africana*); ectexine is quite often 1.5 to 3 times thicker than endexine; columellae separated, thin or thick, quite often thickened at the ends. Exine ornamentation is predominately finely reticulate (LM); ornamentation under SEM is echinate foveolate (*C. africana*).

IV. Subgenus *Grammica*

Fig. 3

Pollen grains of the vast majority of the species studied are 3(4)-zonocolpate, with the exception of *C. jalapetsis*, *C. rostrata*, *C. suaveolens* (3-zonocolpate) and *C. cristata* with 4(3)-zonocolpate apertures. The shape of the pollen grains is oblong, broadly ellipsoidal, spheroidal or oblate spheroidal, and variations in the shape can be observed even within the same sample. Pollen size (P × E) varies from 15.5–16.8 µm × 13.5–14.0 µm (*C. americana*) to 24.4–25.0 µm × 30.0–31.2 µm (*C. cristata*). Colpi in the pollen of most of the species are long (in species *C. jalapensis*, *C. suaveolens*,

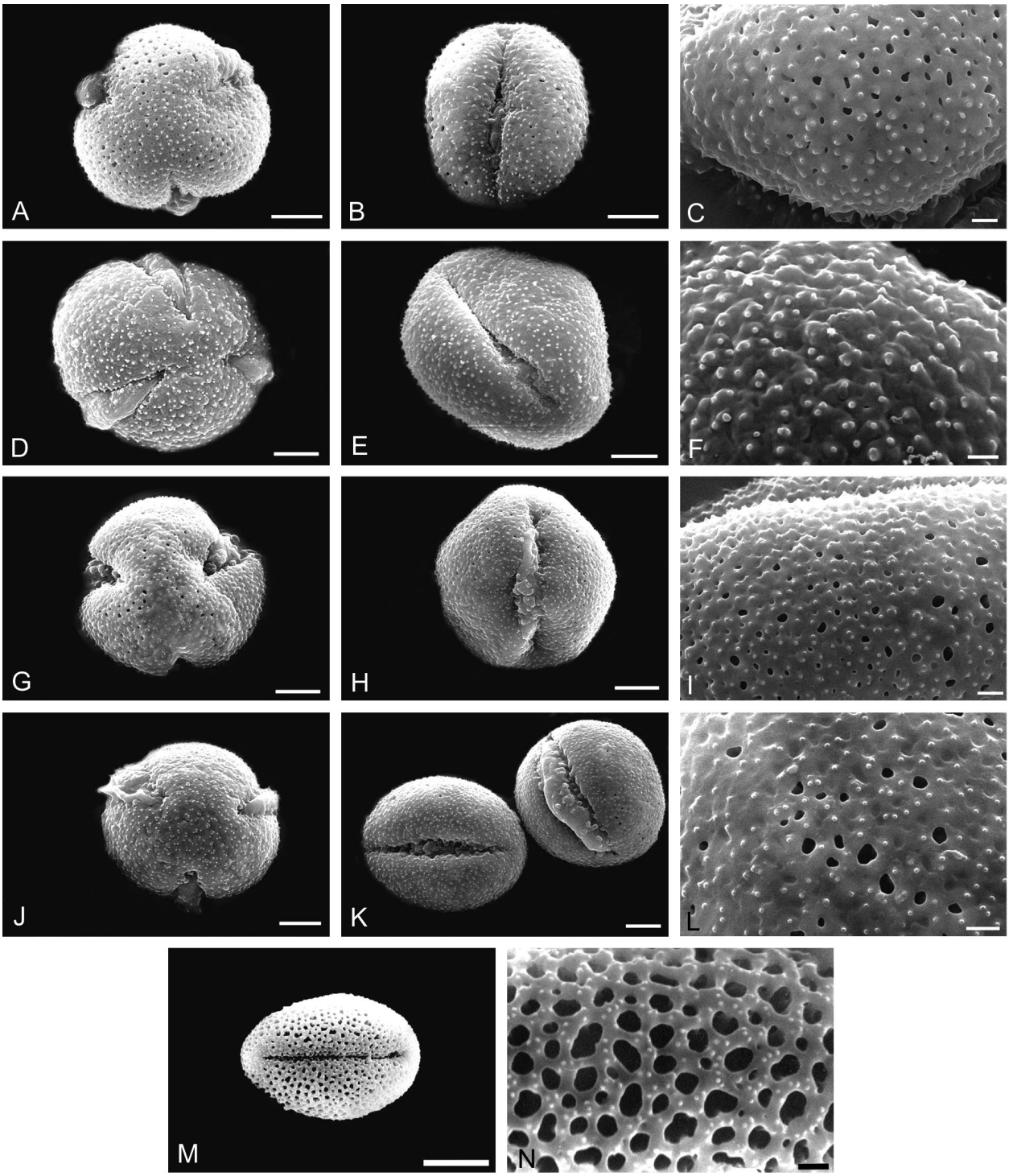

Figure 3. Pollen grains of the representatives of the subgenus *Grammica* (SEM micrographs). **A–C**. *C. americana*; **D–F**. *C. arabica*; **G–I**. *C. campestris*; **J–L**. *C. squamata*; **M**, **N**. *Lepidanche adpressa* (A, D, G, J – polar view; B, E, H, K, M – equatorial view; C, F, I, L, N – exine ornamentation). Scale bar = 10 µm in M; 5 µm in A, B, D, E, G, H, J, K; 1 µm in C, F, I, L, N

and *C. rostrata* of medium length), quite often operculate, from narrow, almost slit-like to wide, with smooth or slightly wavy margins; colpi ends pointed or slightly rounded. The thickness of the exine layer varies from 1.2–1.4 µm (*C. gronovii*) to 2.7–2.8 µm (*C. jalapensis*); ectexine is 1.5 to 3.5 times thicker than endexine; columellae separated, thin or thick, quite often thickened at the ends, sometimes also with enlarged bases. Exine ornamentation is finely reticulate (LM); ornamentation under SEM for a number of species is predominantly echinate perforate foveolate or echinate perforate tuberculate; in the species *Lepidanche adpressa* (syn. *C. compacta*), reticulate ornamentation with granules on the reticulum muri was revealed (Fig. 3N).

– Exine ornamentation reticulate . . . . . *Lepidanche adpressa* (syn. *C. compacta*)
– Exine ornamentation echinate perforate foveolate (tuberculate) . . . . . other taxa studied

DISCUSSION

Analysis of derivations from various types of colpate apertures (colpate, colporate, etc.) to porate ones revealed, that the essential features include not only the *number* but also the *length* of the colpi (Takhtajan, 1966; Van Campo, 1976). On the whole, in the presence of the common zonocolpate aperture type of pollen in the genus *Cuscuta*, the following aperture subtypes were discovered:

– 3(4)-zonocolpate pollen grains with long colpi (in most of the species studied from subgenera *Grammica* and *Cuscuta*, as well as in *C. monogyna* from the subgenus *Monogynella*);

– 4(3)-zonocolpate pollen grains, with long colpi (*C. cristata* from subgenus *Grammica*);

– 3-zonocolpate pollen grains both with long colpi and colpi of medium length (*C. abyssinica* from subgenus *Cuscuta* and *C. africana*, *C. angulata* from subgenus *Pachystigma*);

– 3-zonocolpate pollen grains with colpi of medium length were noted for species from all four subgenera (*C. cassytoides*, *C. lupuliformis* from subgenus *Monogynella*, *C. kotschyana* from subgenus *Cuscuta*, *C. nitida* from subgenus *Pachystigma* and *C. jalapensis*, *C. rostrata*, *C. suaveolens* from subgenus *Grammica*);

– 3–4- or 4-zonocolpate, with short colpi (*C. lehmanniana* and *C. gigantea* from subgenus *Monogynella* respectively);

– 5–6-zonocolpate, with short colpi (*C. reflexa* from subgenus *Monogynella*).

In our investigations of the genus *Cuscuta*, three main types of pollen sculpture were also identified: perforate, foveolate and reticulate. The last sculpture type in the vast majority of the samples was present in combination with echinae (rarely with spines or granules). For the species *C. americana*, *C. chinensis* (subgenus *Grammica*), as well as *C. epilinum* (subgenus *Cuscuta*) echinate perforate foveolate, and for *C. arabica* (subgenus *Grammica*), as well as for *C. babylonica* (subgenus *Cuscuta*) echinate perforate tuberculate types of pollen sculpture were noted.

The analysis of the data obtained was used to compile a brief summary of the palyno-morphological characteristics for each of the subgenera of the genus *Cuscuta*.

Within the subgenus *Monogynella* a variety of zonocolpate apertures both in length (colpi long, colpi of medium length, short colpi) and in their number (mainly 3 or 4, in *C. reflexa* – 5–6) was noted. A significant variability in the size of pollen grains in individual species (from 21.5 to 41.0 µm, i.e. almost double) was also identified. The presence of such a wide range of variability in pollen characteristics provided the basis for an identification key within this subgenus (see above). At the same time, pollen of representatives of this subgenus is uniform in the type of exine ornamentation (reticulate with excrescence of various forms); only the sizes of the lumina vary.

For subgenus *Cuscuta*, in the presence of a common 3(4)-zonocolpate aperture type, some variability in the length of pollen apertures was revealed. Colpi are mainly long, however, in *C. kotschyana* they are of medium length, and in *C. abyssinica* both long and medium length colpi were found. Exine ornamentation in most studied species is echinate perforate (in *C. babylonica* echinate perforate tuberculate). The data received provided the basis for an identification key within this subgenus (see above).

For three studied representatives of the subgenus *Pachystigma* (previously considered one of the sections of the subgenus *Cuscuta*), a common 3-zonocolpate type of pollen aperture with a variation in length of colpi (long or of medium) was noted; sculpture is echinate foveolate.

In the most studied (in terms of the number of taxa) subgenus *Grammica*, significant

palyno-morphological uniformity was revealed both in the number of pollen apertures (mainly 3(4)-zonocolpate) and in the length of colpi (long). Except for the pollen of *Lepidanche adpressa* (syn. *C. compacta*) with reticulate pollen sculpture, an echinate perforate foveolate (tuberculate) exine ornamentation was noted, that provided the basis for a short identification key (see above).

Our research has confirmed the significant palyno-morphological proximity of the subgenera *Grammica* and *Cuscuta*. Pollen grains of the vast majority of investigated representatives of both subgenera were characterized by common 3(4)-zonocolpate pollen (colpi long, sometimes of medium length) and a similar exine ornamentation, exactly, echinate perforate, sometimes echinate perforate foveolate or echinate perforate tuberculate. The data obtained are consistent with molecular phylogenies that resolved subgenera *Cuscuta* and *Grammica* as sister clades Stefanović et al., 2002; Revill et al., 2005).

In contrast, the presence of a common echinate foveolate type of pollen ornamentation in the species *C. africana* from the subgenus *Pachystigma* and some species from the subgenus *Grammica* (*C. campestris*, *C. americana*, *C. squamata*) indicates a certain proximity of these two subgenera. It is also interesting that due to the reticulate type of pollen sculpture in the species *Lepidanche adpressa* (syn. *C. compacta*), the subgenus *Grammica* is also close to the subgenus *Monogynella*.

In the subgenus *Grammica*, the presence of almost all types of pollen exine ornamentation (echinate perforate foveolate, echinate perforate tuberculate, as well as reticulate ones), typical for the genus *Cuscuta* as a whole possibly indicates its central (or intermediate, transitional) position, allowing the formation of certain relationships with all three other subgenera. It can be argued that the suggestion of Telleria and Daners (2003) about the significant taxonomic significance of exine ornamentation is quite clearly expressed within the genus *Cuscuta*.

CONCLUSION

For all studied species, three variations in the common zonocolpate aperture type of pollen were recognized (colpi long, colpi of medium length, short colpi); variations in the number of apertures were also identified. The data obtained is consistent also with earlier views of Welsh et al. (2010) on the presence of pollen aperture polymorphism in the genus *Cuscuta*.

In contrast, the significant similarity of pollen characteristics in representatives of the subgenera *Cuscuta*, *Pachystigma* and *Grammica* (with the exception of the species *Lepidanche adpressa* (syn. *C. compacta*)) makes it difficult to create an identification key at the level of individual subgenera. Thus, pollen morphological results are largely inconsistent with the existing infrageneric classification.

Pollen characteristics are most applicable to the subgenus *Monoginella*, reflecting its somewhat isolated position within the genus *Cuscuta*. The data obtained were consistent with the results on the structure of the seed coat, the comparative embryology and karyology of the genus *Cuscuta* (Tiagi, 1951; Hutchison and Ashton, 1979; Aryavand, 1987; Terekhin and Kotov, 1988), as well as molecular studies that resolved subgenus *Monogynella* as the sister of the rest of the genus (Stefanović et al., 2002; Revill et al., 2005).

The presence of a reticulate exine ornamentation, not identified for the pollen of any of the studied taxa of the subgenus *Grammica*, indicates a significant proximity of the species *Lepidanche adpressa* (syn. *C. compacta*) to the subgenus *Monogynella*.

For the species *C. reflexa*, the obtained palyno-morphological data are consistent with the opinion of Sengupta (1972) about the isolation of this species, as well as its more advanced position.

ACKNOWLEDGEMENTS

We thank L. Kartzeva for assistance with SEM photography.

We are also grateful to the anonymous referees for their suggestions, which helped to substantially improve the original manuscript.

ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors have declared that no competing interests exist.

ETHICAL STATEMENT. No ethical statement was reported.

FUNDING. No.

REFERENCES

Amini, E., Nasrollahi, F., Sattarian, A., Kor, S., Boozarpour, S., 2018. Molecular and micro-morphological evidences of the genus *Cuscuta* in Iran. Rostaniha 19(2), 113–129.

Andres, I.M., Heras, J.G., 1986. Estudios polinicos de la flora Valenciana: Convolvulaceae. Lazaroa 9, 83–95.

Aryavand, A., 1987. The chromosome numbers of some *Cuscuta* L. (Cuscutaceae) species from Isfahan, Iran. Iranian Journal of Botany 3(2), 177–182.

Austin, D.F., 1980. Studies of the Florida Convolvulaceae III. *Cuscuta*. Florida Scientist 43, 294–302.

Austin, D.F., 1986. Cuscutaceae. In: Brooks, R.E., Schofield, E.K., McGregor, R.L., Barkley, T.M. (eds), Flora of the Great Plains. Great Plains Flora Association. University Press of Kansas, Lawrence, Kansas.

Avetisyan, E.M., 1950. Uproshchenny atsetolizny metod obrabotki pil'tsi. Botanicheskii Zhurnal 35(4), 385–387 (in Russian).

Avetisyan, E.M., Mekhakyan, A.K., 1980. Opisanie pil'tsi semeystva Cuscutacae. In: Takhtajan, A.L. (ed.), Flora Armenii, 7. Akademiya Nauk ArmSSR, Yerevan (in Russian).

Baillon, H., 1891. Convolvulacées. Histoire des plante, Paris, France: Librairie Hachett and Cie.

Bentham, G., Hooker, J.D., (1873)1876. Convolvulaceae. Genera Plantarum. London 2 (2), 864–869.

Chiguryaeva, A.A., 1972. K morfologii pil'tsi Parnolistnikovikh, Kazuarinovikh, Vyunkovikh. In: Flora i rastitel'noct' Yugo-vostoka, 2. Saratov (in Russian).

Choisy, J.D., 1845. Convolvulaceae. In: De Candolle, A.P. (ed.), Phrodromus Systematic Regni Vegetables. Annals And Magazine of Natural History, Paris, pp. 323–465.

Costea, M., Nesom, G.L., Stefanović, S., 2006a. Taxonomy of *Cuscuta pentagona* complex (Convolvulaceae) in North America. SIDA Contribution to Botany 22, 151–175.

Costea, M., Nesom, G.L., Stefanović, S., 2006b. Taxonomy of *Cuscuta salina-californica* complex (Convolvulaceae) in North America. SIDA Contribution to Botany 22, 176–195.

Costea, M., Nesom, G.L., Stefanović, S., 2006c. Taxonomy of *Cuscuta gronovii* and *Cuscuta umbrosa* (Convolvulaceae). SIDA Contribution to Botany 22, 197–207.

Costea, M., Nesom, G.L., Stefanović, S., 2006d. Taxonomy of *Cuscuta indecora* complex (Convolvulaceae) in North America. SIDA Contribution to Botany 22, 209–225.

Costea, M., Aiston, F., Stefanović, S., 2008. Species delimitation, phylogenetic relationships, and two new species in the *Cuscuta gracillima* complex (Convolvulaceae). Botany 86, 670–681. https://doi.org/10.1139/B08-030

Costea, M., García, M.A., Stefanović, S., 2015. A phylogenetically based infrageneric classification of the parasitic plant genus *Cuscuta* (Dodders, Convolvulaceae). Systematic Botany 40(1), 269–285. https://doi.org/10.1600/036364415X686567

Cronk, Q.C.B., Clarke, G.S.C., 1981. The Northwest European pollen flora, 28. Convolvulaceae. Review of Palaeobotany and Palynology 33(1), 117–135. https://doi.org/10.1016/0034-6667(81)90086-5

Cronquist, A., 1988. The evolution and classification of flowering plants. The New York Botanical Garden. Bronx, NY, USA.

Dahlgren, R.M.T., 1980. A revised system of classification of the angiosperms. Botanical Journal of the Linnean Society 80(2), 91–124. https://doi.org/10.1111/j.1095-8339.1980.tb01661.x

Das, S., Banerji, M., 1966. Pollen morphology of a new speies of *Cuscuta*. Current Science (India) 3, 105–106.

Demir, I., Kaya, I., Benli, M., Altınoglu, M.K., 2017. Investigation of palinological features of taxa belonging to the genus *Cuscuta* distributed in Turkey. International Journal of Agriculture and Biology 19, 746–750. https://doi.org/10.17957/IJAB/15.0349

Dumortier, B.C., 1829. Analyse des families des plantes avec l'indication des principaux genres quis'y rattachent. Tournay.

El-Ghazaly, G.A., 1991. Pollen flora of Qatar. University of Qatar.

Engelmann, G., 1859. Systematic arrangement of the species of the genus *Cuscuta* with critical remarks on old species and description of new ones. Transactions of the Acadademy of Science of St. Louis 1, 453–523.

Erdtman, G., 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist et Wiksell, Stockholm.

García, M.A., Martin, M.P., 2007. Phylogeny of *Cuscuta* subgenus *Cuscuta* (Convolvulaceae) based on nrDNA ITS and chloroplast trnL intron sequences. Systematic Botany 32(3), 899–916.

García, M.A., Costea, M., Kuzmina, M., Stefanović, S., 2014. Phylogeny, character evolution, and biogeography of *Cuscuta* (dodders; Convolvulaceae) inferred from coding plastid and nuclear sequences. American Journal of Botany 101(4), 670–690. https://doi.org/10.3732/ajb.1300449

Halbritter, H., Ulrich, S., Grímsson, F., Weber, M., Zetter, R., Hesse, M., Buchner, R., Svojtka, M., Frosch-Radivo, A., 2018. Illustrated Pollen Terminology (Second edition). Springer Open. Switzerland. https://doi.org/10.1007/978-3-319-71365-6

Hallier, H., 1893. Versuch einer natürlichen Gleiderung der Convolvulaceen auf morphologischer und anatomischer Grundlage. Botanische Jahrbücher fur Systematik 16, 453–591.

Hamed, K.A., 2005. Pollen and seed characters of certain *Cuscuta* species growing in Egypt with a reference to a taxonomic treatment of the genus. International Journal of Agriculture & Biology 7(3), 325–332.

Hayrapetyan, A., 2010. Pollen morphology of the genus *Cuscuta* L. Proceedings of the YSU, Chemistry and Biology 1, 42–49 (in Russian).

Heusser, C.I., 1971. Pollen and spores of Chile. Modern types of the Pteridophyta, Gymnospermae and Angiospermae. Tucson, Arizona.

Hu, S.-Y., Yuan, Z.-F., 2002. Distribution of the cytoplasmic DNA in male cells of the Convolvulaceae and its systematic significance. Acta Phytotaxonomica Sinica (Journal of Systematics and Evolution) 40(6), 511–516.

Hutchinson, J., 1926. The families of flowering plants. I. Dicotyledons. Arranged according to a new system based on their probable phylogeny, 1 ed. London: MacMillan.

Hutchison, J.M., Ashton, F.M., 1979. Effect of desiccation and scarification on the permeability and structure of the seed coat of *Cuscuta campestris*. American Journal of Botany 66(1), 40–46.

Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. https://sweetgum.nybg.org/science/ih/; accessed 27 september 2023.

Jones, A., 1968. Chromosome numbers in *Ipomoea* and related genera. The Journal of Heredity 59, 99–102.

Kuprianova, L.A., Alyoshina, L.A., 1972. Pyl'tsa i spory rasteni flori Yevropeyskoy chasti SSSR (Pollen and spores of plants of the flora of the European part of USSR), I. Akademiya Nauk SSSR, BIN, Leningrad (in Russian).

Laguardia, A.M., 1961. Morfologia del grano de pollen de algunas Convolvulaceaes Uruguayas. Boletin de la Sociedad Argentina de Botanica 9, 187–197.

Liao, G.I., Chen, M.Y., Huoh, C.S., 2005. Pollen morphology of *Cuscuta* (Convolvulaceae) in Taiwan. Botanical Bulletin of Academia Sinica 46, 75–81.

Martin, H.A., 2001. The family Convolvulaceae in the Tertiary of Australia: evidence from pollen. Australian Journal of Botany 49, 221–234.

Melchior, H., 1964. Convolvulaceae. In: Engler A. (ed.). Syllabus der Pflanzenfamilien 2. 12th ed. Berlin.

Nair, P.K.K., Rehman, K., 1963. Pollen grains of Indian plants – VI. Bulletin, National Botanic Gardens, Lucknow 83, 1–17.

Neyland, R., 2001. A phylogeny inferred from large ribosomal subunit (26S) rDNA sequences suggests that *Cuscuta* is a derived member of Convolvulaceae. Brittonia 53, 108–115.

Noshad, Q., Ajaib, M., Kiran, A., 2020. Comparative investigation of palynological characters of *Cuscuta reflexa* and few memebers of Convolvulaceae. The Journal of Animal & Plant Sciences 30(5), 1215–1223. https://doi.org/10.36899/JAPS.2020.5.0139

Pedraza, R.A., 1985. Estudio palinologico de la familia Convolvulaceae de Mexico II. Biotica 10(2), 175–187.

Perveen, A., Qaiser, M., 2004. Pollen flora of Pakistan – XLI. Cuscutaceae. Pakistan Journal of Botany 36(3), 475–480.

Peter, A., 1891. Convolvulaceae. In: Engler, A., Prantl, K. (eds), Die natürlichen Pflanzenfamilien. Bd. 3a. Leipzig: Engelmann, pp. 1–40.

Peter, A., 1897. Convolvulaceae. In: Engler, A., Prantl, K. (eds), Die Natürlichen Pflanzenfamilien (Appendix) 3.

Polo, J.M., Diez, M.J., 1987. Cuscutaceae. In: Valdes, B., Diez, M.J., Fernandez, I. (eds), Atlas polinico de Andalucia Occidental. Universidad de Sevilla.

Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., Le Thomas, A., 2007. Glossary of pollen and spore terminology. Review of Palaeobotany and Palynology 143, 1–81. https://doi.org/10.1016/j.revpalbo.2006.06.008

Revill, M.J.V., Stanley, S., Hibberd, J.M., 2005. Plastid genome structure and loss of photosynthetic ability in the parasitic genus *Cuscuta*. Journal of Experimental Botany 56, 2477–2486. https://doi.org/10.1093/jxb/eri240

Roberty, G., 1952. Genera Convolvulacearum. Candollea 14, 11–60.

Roberty, G., 1964. Les genres de Convolvulacées (esquisse). Boissiera 10, 129–156.

Sengupta, S., 1972. On the pollen morphology of Convolvulaceae with special reference to taxonomy. Review of Palaeobotany and Palynology 13, 157–212.

Severova, E.E., 1995. Palinomorphological features of Russian dodders (*Cuscuta*). Byulleten' Moskovskogo obshchestva ispitateley prirodi. Otdeleniye Biologii 100(1), 65–73 (in Russian).

Shimakura, M., 1973. Palynomorphs of Japanese plants. Special Publication of Osaka Museum of Natural History 5, 1–60.

Smolyaninova, L.A., Golubkova, V.F., 1950. K metodike issledovaniya pil'tsi. Dokladi Akademii Nauk SSSR 75(1), 125–126 (in Russian).

Stefanović, S., Krueger, L., Olmstead, R.G., 2002. Monophyly of the Convolvulaceae and circumscription of their major lineages based on DNA sequences of multiple chloroplast loci. American Journal of Botany 89, 1510–1522. https://doi.org/10.3732/ajb.89.9.1510

Stefanović, S., Olmstead, R.G., 2004. Testing the phylogenetic position of a parasitic plant (*Cuscuta*, Convolvulaceae, Asteridae): Bayesian inference and the parametric bootstrap on data drawn from three genomes. Systematic Biology 53(3), 384–399. https://doi.org/10.1080/10635150490445896

Stefanović, S., Kuzmina, M., Costea, M., 2007. Delimitation of major lineages within *Cuscuta* subgenus *Grammica* (Convolvulaceae) using plastid and nuclear DNA sequences. American Journal

of Botany 94(4), 568–589. https://doi.org/10.3732/ajb.94.4.568

Takhtajan, A., 1987. Sistema Magnoliofitov (Systema Magnoliophytorum). Nauka, Leningrad (in Russian).

Takhtajan, A., 1997. Diversity and classification of flowering plants. New York.

Takhtajan, A., 2009. Flowering Plants (Second edition). Springer Science+Business Media B.V. https://doi.org/10.1007/978-1-4020-9609-9

Takhtajan, A.L., 1966. Sistema i filogeniya tsvekovikh rasteni (Systema et Phylogenia Magnoliophytorum). Nauka, Moskva, Leningrad (in Russian).

Tellería, M.C., Daners, G., 2003. Pollen types in southern New World Convolvulaceae and their taxonomic significance. Plant Systematics and Evolution 243, 99–118. https://doi.org/10.1007/s00606-003-0069-z

Terekhin, E.S., Kotov, V.A., 1988. Embryology of *Cuscuta japonica*. Botanicheskii Zhurnal 73(2), 222–230 (in Russian).

The Plant List http://www.theplantlist.org/

Tiagi, B., 1951. A contribution to the morphology and embryology of *Cuscuta hyalina* Roth. and *C. planiflora* Tenore. Phytomorphology 1, 2–21.

Van Campo, M., 1976. Patterns of pollen morphological variation within taxa. In: Ferguson, I.K., Muller, J. (eds), The evolutionary significance of the exine. Academic Press, London, 125–137.

Welsh, M., Stefanović, S., Costea, M., 2010. Pollen evolution and its taxonomic significance in *Cuscuta* (dodders, Convolvulaceae). Plant Systematics and Evolution 285, 83–101. https://doi.org/10.1007/s00606-009-0259-4

Yuncker, T.G., 1932. The genus *Cuscuta*. Memoirs of the Torrey Botanical Club 18(2), 113–331.

Zare, G., Dönmez, A.A., 2020. *Cuscuta campestris* Yunck. morphology, anatomy and traditional use in Turkey. Hacettepe University Journal of the Faculty of Pharmacy 40(1), 1–10.

Zhang, Z., Cheng, G., Zhongwu, S., Chenghu, L., 1991. Scanning electron microscope observation on pollen morphology of *Cuscuta* in China. Guihaia 11(4), 308–311.