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# A palynological study of the genus Nepeta L. (Lamiaceae)

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Abstract The pollen morphology of forty taxa of the genus Nepeta L. was studied and documented in detail using light microscopy (LM) and scanning electron (SEM) microscopy in this study. Nepeta L. pollen grains are small to large  $(P = 18.64 - 63.46 \,\mu\text{m}, E = 15.62 - 46.33 \,\mu\text{m})$ , suboblate to perprolate (P/E = 0.86-2.09) in shape and hexacolpate (very rarely tetracolpate) with granular membranes. Alternate position of colpi occurs in six Nepeta taxa, N. nuda ssp. glandulifera, N. concolor, N. crinita, N. congesta var. cryptantha, N. stricta var. stricta and N. sibthorpii ssp. tumeniana. In examinations of exine ornamentation with SEM, two types of pollen grains were recognized: (1) type I, with microreticulate sculpture; and (2) type II with bireticulate sculpture, type I and II to be divided into two and five subtypes, respectively. In the two taxa with microreticulate pattern, N. pilinux and N. sulfuriflora, a tendency towards a bireticulum could be recognized due to traces of secondary tectal connections. The bireticulate exine ornamentation is characterized with varying characteristics of the primary muri and secondary reticulum. Pollen morphology within the genus is compared with infrageneric relationships.

**Keywords** Infrageneric classification · Lamiaceae · LM · *Nepeta* · Pollen morphology · SEM

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#### Introduction

*Nepeta* L. (catmint) is one of the largest (ca. 300 spp.) and economically important genera in the Nepetoideae. *Nepeta* species are widely distributed in Eurasia, North Africa, North and Central America and Canary Islands. The greatest diversity and species richness within the genus are found in two regions: South western Asia and the western Himalayas, including the adjacent Hindu Kush (Pojarkova 1954; Hedge 1986; Jamzad et al. 2000).

*Nepeta* species are widely used in folk medicine because of their antispasmodic, expectorant, diuretic, antiseptic, antitussive and antiasthmatic activities. *Nepeta cataria* (Catnip) is the most famous *Nepeta* species which has a long history of use as a tea in Europe before real tea was imported from the orient. The flowering tips of the plant have also been used as a sedative drug (Newall et al. 1996; Baser et al. 2000). Some of the *Nepeta* species are used by bees as a source of pollen and nectar (Sammataro and Avitabile 1998).

Frequent hybridization and introgression, together with substantial age- or habitat-linked variation make *Nepeta* a particularly complex genus. *Nepeta* belongs to the subfamily Nepetoideae, tribe Mentheae (Cantino et al. 1992). There are different infrageneric classifications of *Nepeta* of Boissier (1879), Shishkin (1976), Rechinger (1982), Hedge and Lamond (1982), Budantsev (1997), Dirmenci (2003). These works are mainly based on habit, leaf morphology, inflorescence, calyx and corolla structure, and nutlet characters. The genus *Nepeta* is divided in three informal groups (designated as A, B and C) based largely on flower colour and inflorescence characters by Hedge and Lamond (1982). Group A (14 species); flowers white, yellow or pinkish, nutlets tuberculate throughout or at the apex; group B (16 species); flowers lilac or deep blue, nutlets

tuberculate or smooth and group C (sect. Oxynepeta Benth., three species); flowers white, lilac or purple, nutlets tuberculate, spherical (Hedge and Lamond 1982). The last study related with taxonomy of Nepeta distributed in Turkey was done by Dirmenci (2003, 2005) and Nepeta species in Turkey have been included with 11 sections (sect. Cataria, sect. Macronepeta, sect. Micrantha, sect. Orthonepeta, sect. Oxynepeta, sect. Pycnonepeta, sect. Schizocalyx, sect. Setanepeta, sect. Spicatae, sect. Stenostegiae, sect. Subinterruptae).

Investigations of pollen morphology in Lamiaceae have been essential as an aid to classification within this family. Pollen of Lamiaceae has been studied since Erdtman (1945) suggested a division of the family into two subfamilies based on number of nuclei and aperture number in the pollen grains (Lamioideae: tricolpate and bi-nucleate pollen; Nepetoideae: hexacolpate and tri-nucleate pollen) (Erdtman 1945; Harley et al. 1992; Harley 1992; Abu-Asab and Cantino 1994). However, the tribe Mentheae (Nepetoideae) is still poorly known from a palynological point of view. A few authors have described the pollen of some species of Nepeta. Ubera (1982) studied pollen morphology of twenty Nepeta species in Iberian Penisula. Jamzad et al. (2000, 2003a, b), Azizian et al. (2001) and Ranjbari et al. (2004) studied pollen morphology of some Nepeta species from Iran. Perveen and Qaiser (2003) investigated pollen morphology of Nepeta species in Pakistan. Moon et al. (2008) investigated pollen morphology of 21 Nepeta species with SEM and light microscopy (LM).

This paper presents a detailed account of the pollen morphology of 40 taxa of *Nepeta* collected from Turkey, with 18 species endemic to Turkey, among which 34 species have been investigated palynologically for the first time. The objectives of this paper are to provide a detailed account of the pollen morphology of *Nepeta* L. by LM and scanning electron microscopy (SEM) and to determine the extent to which these palynological data can be used as a taxonomic character in the genus. This data can be useful in other areas such as archeological research since many of the *Nepeta* species are commonly used by humans as food and in medicine, and also in melissopalynological studies since some of *Nepeta* species are used by bees as a source of pollen and nectar.

#### Materials and methods

polar axis and equatorial diameter were based on at least 30 samples and other characters on approximately 20 under the LM  $(1,000\times)$ . All of the measurements were done using CARNOY 2.0 (Schols et al. 2002). The details were given in Tables 1, 2.

For SEM, pollen grains were transferred directly to a stub with double-sided tape and images were obtained using a XL–30 ESEM-FEG/PHILIPS microscope. Selected SEM micrographs were digitized. According to pollen shapes, histograms of frequency of the acetolyzed and non-acetolysed pollen grains in the studied *Nepeta* L. taxa were given in Figs. 1 and 2. In the histograms, frequency of pollen grains was shown as 1–10% rarely present, 11–35% present, <35% dominant.

For comparison of P-E axis with sections (Dirmenci 2003) and species groups (Hedge and Lamond 1982) nonparametric tests (Kruskal–Wallis and Mann–Whitney U test) were applied using SPSS 10.0. The pollen terminology in general follows Faegri and Iversen (1975), Harley et al. (1992) and Punt et al. (2007). Pollen grains of the 40 recognized taxa of the genus *Nepeta* were mostly taken from herbarium material housed at the Herbarium of the Uludag University (BULU). Collections examined were listed in Appendix.

#### Results

The morphological variation of pollen grains within *Nepeta* is described for size and shape of pollen grains, number, position and morphology of apertures and exine ornamentation. The pollen size variations and measurements are given in Tables 1, 2 and Fig. 1. Representative pollen characters are illustrated in Figs. 2–161.

The pollen grains are monad, 6-zonocolpate (very rarely intermixed with tetracolpate, less than 1%; e.g. *N. crinita*), and isopolar. *Nepeta* L. pollen is small to large ( $P = 18.64-63.46 \mu m$ ,  $E = 15.62-46.33 \mu m$ ). The shape of the pollen grains in equatorial view ranges from sub-oblate to perprolate (P/E = 0.86-2.09) (e.g. Figs. 3–7–11–15), but most taxa studied are subprolate to prolate (Fig. 1; Table 1). The shape in polar view is more or less circular in all taxa studied (e.g. Figs. 2, 6, 10, 14).

The ectocolpi are distributed symmetrically, elongated, usually shallow and narrowing at the poles (Figs. 2–29, 34–41, 50–97, 102–120, 126–137, 142–161, 175, 176), except six taxa of *Nepeta*. Alternate position of colpi occur in six *Nepeta* taxa, *N. nuda* ssp. glandulifera, *N. concolor* and *N. crinita*, *N. congesta* var. cryptantha and *N. stricta* var. stricta, *N. sibthorpii* ssp. tumeniana (Figs. 2–161, Table 3). Differences between the characteristics of the colpi arrangement were recorded and four different interesting colpi apomorphies were described for six taxa:

Table 1 Morphometric data (with mean values and standard deviations, except exine) of Nepeta species

Species	Р	Ε	Exine	clg	clt	Mesocolpium	Apocolpium	d
N. aristata	$29.93 \pm 1.69$	$24.82\pm0.82$	1.60	$25.80\pm2.55$	$3.30\pm0.30$	$11.51 \pm 1.11$	$9.17\pm0.68$	$4.36\pm0.54$
N. baytopii	$37.19\pm2.49$	$26.73\pm1.83$	1.41	$30.50\pm2.15$	nm	$11.68\pm3.20$	$10.30\pm2.44$	$4.81\pm0.63$
N. betonicifolia	$35.00\pm2.80$	$25.10\pm1.73$	0.82	$25.08\pm2.81$	$2.50\pm0.40$	$11.49\pm2.13$	$10.10\pm1.67$	$4.96\pm0.88$
N. cadmea	$27.20\pm2.83$	$34.31\pm3.62$	1.45	$34.31\pm3.62$	$1.60\pm0.50$	$11.51 \pm 1.71$	$9.95 \pm 1.38$	$4.23\pm0.72$
N. caesarea	$37.00\pm2.70$	$24.10\pm1.95$	1.05	$30.20\pm2.22$	$1.50\pm0.09$	$12.14\pm2.18$	$13.30\pm2.33$	$6.14 \pm 1.12$
N. cataria	$33.00\pm3.40$	$25.60\pm3.18$	1.87	$24.76\pm3.31$	$2.10\pm0.70$	$9.78 \pm 1.31$	$10.90\pm1.38$	$5.58\pm0.64$
N. cilicia	$35.70\pm3.08$	$32.56\pm3.76$	1.79	$32.40\pm2.32$	$4.60\pm1.70$	$13.44 \pm 1.43$	$9.09 \pm 1.29$	$4.44\pm0.72$
N. concolor	$35.90\pm2.87$	$27.45\pm2.49$	1.69	$27.50\pm1.54$	$3.70\pm1.00$	$10.92\pm2.56$	$7.13 \pm 0.76$	$3.37\pm0.65$
N. conferta	$33.00\pm2.60$	$27.70\pm2.66$	1.88	$28.93  \pm  1.43$	$3.20\pm0.90$	$11.74\pm2.03$	$8.07\pm1.06$	$4.04\pm0.83$
N. congesta var. congesta	$29.34\pm3.67$	$25.74\pm2.26$	2.22	$21.70\pm3.79$	$2.30\pm0.40$	$8.98 \pm 1.25$	$9.77 \pm 1.30$	$4.92\pm0.89$
N. congesta var. cryptantha	$33.41\pm2.27$	$29.30\pm2.52$	2.11	$26.70\pm1.09$	$2.20\pm0.30$	$10.94\pm1.42$	$10.00\pm0.48$	$4.60\pm1.03$
N. crinita	$30.00\pm2.20$	$25.90\pm2.26$	0.81	$24.50\pm2.13$	$3.60\pm1.00$	$11.34\pm1.39$	$9.72\pm0.50$	$4.70\pm1.23$
N. fissa	$29.09\pm2.61$	$27.15\pm1.86$	1.70	$23.90\pm2.59$	$4.10\pm0.60$	$10.74\pm1.45$	$9.23\pm1.08$	$4.35\pm0.69$
N. flavida	$34.00\pm1.00$	$31.20\pm 6.40$	2.15	$25.40\pm1.14$	$3.80\pm0.70$	$12.42\pm0.80$	$9.41\pm1.28$	$4.88\pm0.60$
N. glomerata	$33.58\pm2.48$	$27.53\pm3.07$	0.88	$27.10\pm2.80$	$2.20\pm0.90$	$9.06 \pm 1.08$	$9.13 \pm 0.86$	$4.34\pm0.73$
N. heliotropifolia var. heliotropifolia	35.36 ± 4.53	$26.84\pm3.27$	1.53	$25.80\pm2.73$	2.70 ± 0.50	9.64 ± 2.23	$13.02 \pm 2.76$	6.03 ± 1.19
N. humulis	$32.04\pm1.64$	$26.36\pm1.80$	1.79	$25.80\pm2.73$	$2.70\pm0.50$	$9.51\pm0.94$	$8.96 \pm 1.25$	$4.47\pm0.62$
N. isaurica	$35.00\pm3.20$	$22.90\pm1.84$	0.66	$29.56\pm2.45$	$2.40\pm0.25$	$12.40\pm2.15$	$12.10\pm3.90$	$5.77\pm1.72$
N. italica	$34.00\pm4.80$	$26.70\pm3.45$	2.27	$25.26 \pm 3.45$	$4.40\pm1.80$	$12.38\pm1.66$	$10.40\pm1.32$	$4.75\pm0.99$
N. lamiifolia	$30.55\pm2.20$	$29.78\pm0.81$	1.72	$23.10\pm1.23$	$3.10\pm0.90$	$8.81\pm0.89$	$8.63\pm1.21$	$4.28\pm0.52$
N. macrosiphon	$35.55\pm2.50$	$28.02\pm2.68$	1.65	$27.40\pm4.15$	$3.60\pm0.90$	$9.66 \pm 1.07$	$9.05\pm1.03$	$4.18\pm0.87$
N. meyeri	$32.81\pm2.18$	$29.09\pm1.52$	1.57	$26.10\pm3.70$	$2.20\pm0.20$	$11.17\pm2.12$	$11.19\pm1.01$	$5.56\pm0.71$
N. nuda ssp. albiflora	$34.00\pm5.10$	$26.90\pm1.57$	1.82	$29.73\pm3.00$	$2.80\pm1.00$	$9.60\pm1.64$	$11.20\pm1.06$	$5.42\pm0.65$
N. nuda ssp. glandulifera	$29.00\pm3.10$	$26.90\pm1.57$	1.10	$22.01\pm1.45$	$2.00\pm0.30$	$12.82\pm3.57$	$12.90\pm2.91$	$5.54 \pm 1.32$
N. nuda ssp. lydiae	$32.00\pm0.90$	$23.80\pm1.94$	1.81	$28.96\pm0.26$	$3.30\pm0.50$	$11.04\pm1.56$	$10.40\pm1.51$	$4.94\pm0.71$
N. nuda ssp. nuda	$32.00\pm4.20$	$26.50\pm2.76$	2.14	$21.25\pm1.44$	nm	$11.89\pm0.11$	nm	nm
N. obtusicrena	$31.82\pm0.99$	$24.80\pm1.46$	1.49	$27.00\pm2.94$	$2.40\pm0.08$	$9.06\pm3.08$	$9.55\pm0.85$	$4.39\pm0.41$
N. phyllochlamys	$33.00\pm2.20$	$25.60\pm1.42$	1.51	$25.21\pm1.69$	$2.10\pm0.28$	$11.12\pm1.32$	$9.59 \pm 1.08$	$4.27\pm0.57$
N. pilinux	$33.00\pm3.60$	$25.20\pm2.88$	2.16	$27.61\pm3.03$	$3.70\pm1.30$	$10.33\pm2.03$	$8.77 \pm 0.89$	$4.11 \pm 0.73$
N. racemosa	$32.00\pm2.70$	$27.40\pm1.87$	0.98	$27.80\pm2.73$	nm	$10.80\pm1.65$	$8.43\pm1.18$	$4.30\pm0.57$
N. sibthorpii subsp. tumeniana	$35.69\pm2.12$	$26.60\pm4.00$	1.79	$29.30\pm2.79$	$2.40\pm0.30$	$10.97\pm1.89$	$8.30 \pm 1.39$	$4.18\pm0.66$
N. sorgerae	$37.00\pm2.60$	$25.90\pm2.26$	0.92	$28.80\pm3.48$	$2.60\pm0.20$	$11.95\pm1.48$	$8.79\pm1.29$	$4.14\pm0.83$
N. stenantha	$33.40\pm 6.12$	$22.63\pm4.00$	0.95	$25.10\pm5.51$	$3.40\pm0.70$	$7.95\pm2.49$	nm	$4.27\pm0.65$
N. stricta var. curvidens	$32.01\pm2.84$	$26.96\pm2.76$	1.67	$22.40\pm0.29$	$4.80\pm0.40$	$10.91\pm1.78$	$10.06\pm1.32$	$4.78\pm0.68$
N. stricta var. stricta	$20.99\pm1.85$	$23.69\pm2.81$	1.20	$19.18\pm3.07$	$3.22\pm0.70$	$10.34\pm2.32$	$9.44 \pm 0.97$	$4.53\pm1.09$
N. sulfuriflora	$29.00\pm3.60$	$27.10\pm2.54$	2.05	$22.18\pm3.59$	$2.60\pm0.50$	$10.45\pm1.38$	$9.59 \pm 1.23$	$4.56\pm0.70$
N. supina	$40.20\pm3.82$	$31.25\pm3.89$	1.74	$29.10\pm5.05$	$2.50\pm1.00$	$13.71\pm1.81$	$12.38\pm1.64$	$5.63 \pm 0.97$
N. trachonitica	$35.75\pm2.37$	$27.88 \pm 1.85$	1.80	$30.70\pm1.59$	$5.00\pm0.05$	$11.04 \pm 1.64$	nm	$4.50\pm2.11$
N. transcaucasica	$41.00\pm4.70$	$27.50\pm0.60$	1.82	$37.21 \pm 1.55$	$2.60\pm0.26$	$10.36\pm0.96$	$9.74 \pm 1.05$	$4.83\pm0.59$
N. viscida	$36.00\pm1.00$	$32.10\pm2.08$	1.07	$28.83  \pm  1.25$	$4.20\pm0.20$	$11.27\pm1.79$	$10.80\pm1.89$	$5.19 \pm 1.11$

(P) Polar axis, (E) equatorial axis, (clg) colpus length, and (clt) width, (d) ratio of the distance between the apices of two ectocolpi, (nm) non-measured, all measurements in  $\mu$ m

- 1. Three narrow mesocolpia, alternate between three wide mesocolpia are observed in *N. concolor* (Figs. 30–33).
- 2. In *N. congesta* var. *cryptantha* and *N. stricta* var. *stricta*, the colpi apices in the apocolpial area differ,

one being more narrow than the other (Figs. 42–45, 138–141).

3. Opposite mesocolpia are shown as two wide and the other four narrow or two narrow and the other four wide in *N. nuda* ssp. *glandulifera* (Figs. 98–101).

Table 2 Morphometric data of Nepeta L. species (all measurements in µm)

Species	Reticule number in 1 $\mu m^2$	Lumina diameter	Lumina shape	Reticule number in lumina	Sculpture type
N. aristata	5–9	1.77-5.96	Circular or long	8–21	Bireticulate
N. baytopii	3–4	1.84-7.91	Long	8-60	Bireticulate
N. betonicifolia	4–6	1.11-3.70	Irregular	6–16	Bireticulate
N. cadmea	2–11	-	-	-	Mikroreticulate
N. caesarea	3–6	1.81-3.47	Circular	6–33	Bireticulate
N. cataria	4–6	-	-	-	Mikroreticulate
N. cilicia	-	-	-	-	Bireticulate
N. concolor	3–4	-	-	-	Bireticulate
N. conferta	2–3	-	-	-	Bireticulate
N. congesta var. congesta	1–3	-	-	-	Mikroreticulate
N. congesta var. cryptantha	2–4	-	-	-	Mikroreticulate
N. crinita	5–11	0.77-1.54	Irregular	12–33	Bireticulate
N. fissa	4–6	1.77-4.88	Long	18-80	Bireticulate
N. flavida	3–5	_	-	-	Mikroreticulate
N. glomerata	3–6	2.53-4.18	Irregular	11–25	Bireticulate
N. heliotropifolia var. heliotropifolia	1–7	_	-	-	Bireticulate
N. humulis	5-12	3.46-10.22	Long	40-160	Bireticulate
N. isaurica	4–7	1.37-2.44	Irregular	13–26	Bireticulate
N. italica	6–9	-	Irregular	3–20	Bireticulate
N. lamiifolia	11–13	_	-	-	Bireticulate
N. macrosiphon	4–7	2.63-4.64	Circular	6–40	Bireticulate
N. meyeri	4–5	1.18-4.15	Circular or long	6–26	Bireticulate
N. nuda ssp. nuda	4–7	0.74-1.27	-	3–7	Bireticulate
N. nuda ssp. albiflora	3–4	_	-	-	Mikroreticulate
N. nuda ssp. glandulifera	3–6	_	-	-	Bireticulate
N. nuda ssp. lydiae	2–4	-	-	-	Bireticulate
N. obtusicrena	5–8	1.87-4.64	Angular	15–31	Bireticulate
N. phyllochlamys	3–5	_	-	-	Bireticulate
N. pilinux	1–3	-	-	-	Mikroreticulate
N. racemosa	3–7	1.41-1.89	Polygonal	9–16	Bireticulate
N. sibthorpii subsp. tumeniana	2–7	1.24-1.70	Circular	3–10	Bireticulate
N. sorgerae	6–12	1.46-2.96	Irregular	18–33	Bireticulate
N. stenantha	4-8	1.59-3.80	Irregular	5-34	Bireticulate
N. stricta var. curvidens	3–5	_	-	-	Bireticulate
N. stricta var. stricta	3–4	_	-	-	Mikroreticulate
N. sulfuriflora	1–2	_	-	-	Mikroreticulate
N. supina	5–6	2.01-6.16	Long	35-60	Bireticulate
N. trachonitica	3–4	1.99-3.22	Angular	_	Bireticulate
N. transcaucasica	_	1.17-1.52	Circular		Bireticulate
N. viscida	4–5	0.90-2.06	Circular	4–5	Bireticulate

4. In pollen grains of *N. sibthorpii* ssp. *tumeniana*, three mesocolpia with a perforate-reticulate exine alternating with three mesocolpia with a bireticulate exine are observed (Figs. 122–125).

range of colpi width of all studied taxa is  $1.50-5.00 \mu m$ and the range of colpi length of all studied taxa is  $19.18-37.21 \mu m$  (Table 1). The length of colpi is not correlated with the whole pollen size. The range of mesocolpial area and apocolpium diameter of studied taxa is 6.17-13.16 and  $6.65-14.32 \mu m$ , respectively. All

In all the investigated taxa the colpus membrane is finely or coarsely granular (Figs. 163, 165, 176). The



Fig. 1 Histograms of frequency of the acetolyzed pollen grains in the studied Nepeta L. taxa, according to pollen shapes

palynological data of investigated *Nepeta* species are given in Tables 1, 2.

In examinations of exine ornamentation with SEM, two types of pollen grains were recognized as microreticulate and bireticulate, respectively. Exine thickness varies between 0.66 and 2.27  $\mu$ m (Table 1; Figs. 162–180).

1. Type I, Microreticulate sculpture: the microreticulate sculpture has to be divided into two subtypes according to the secondary tectal connections. The simple microreticulate pattern is found in *N. cadmea*, *N. cataria*, *N. congesta* var. *congesta*, *N. congesta* var. *cryptantha*, *N. flavida*, *N. stricta* var. *stricta* and *N. nuda* ssp.

**Figs. 2–29** LM micrographs of pollen grains of *Nepeta*. 2–5: *N. aristata*; 6–9: *N. baytopii*; 10–13: *N. betonicifolia*; 14–17: *N. cadmea*; 18–21: *N. caesarea*; 22–25: *N. cataria*; 26–29: *N. cilicia*. 2, 6, 10, 11, 18, 22, 26: equatorial view and high focus; 3, 7, 11, 15, 19, 23, 27: equatorial view and low focus; 4, 8, 12, 16, 20, 21, 28: polar view and high focus; 5, 9, 13, 17, 21, 25, 29: polar view and low focus; *scale bar* 10 μm



Figs. 30–57 LM micrographs of pollen grains of Nepeta. 30–33: *N. concolor*; 34–37: N. conferta; 38–41: N. congesta var. congesta; 42–45: N. congesta var. cryptantha; 46-49: N. crinita; 50-53: N. fissa; 54-57: N. flavida. 30, 34, 38, 42, 46, 50, 54: equatorial view and high focus; 31, 35, 39, 43, 47, 51, 55: equatorial view and low focus; 32, 36, 40, 41, 48, 52, 56: polar view and high focus. 33, 37, 41, 45, 49, 53, 57: polar view and low focus; scale bar 10 μm



**Figs. 58–85** LM micrographs of pollen grains of *Nepeta*. 58–61: *N. glomerata*; 62–65: *N. heliotropifolia* var. *heliotropifolia*; 66–69: *N. humulis*; 70–73: *N. isaurica*; 74–77: *N. italica*; 78–81: *N. lamiifolia*; 82–85: *N. macrosiphon*. 58, 62, 66, 70, 74, 78, 82: equatorial view and high focus, 59, 63, 67, 71, 75, 79, 83: equatorial view and low

focus; 60, 64, 68, 72, 76, 80, 84: polar view and high focus; 61, 65, 69, 73, 77, 81, 85: polar view and low focus; *scale bar* 10 μm





**Figs. 86–113** LM micrographs of pollen grains of *Nepeta*. 86– 89: *N. meyeri*; 90–93: *N. nuda* spp. *lydiae*; 106–109: *N. obtusicrena*; 110–113: *N. phyllochlamys*. 86, 90, 91, 98, 102, 106, 107: equatorial view and high focus; 87, 91, 95, 99, 103, 107, 111: equatorial view and low focus; 88, 92, 96, 100, 104, 108, 112: polar view and high focus; 89, 93, 97, 101, 105, 109, 113: polar view and low focus; *scale bar* 10 μm



Figs. 114-141 LM micrographs of pollen grains of Nepeta. 114–117: N. pilinux; 118-121: N. racemosa; 122-125: N. sibthorpii subsp. *tumeniana*; 126–129: N. sorgerae; 130–133: N. stenantha; 134–137: N. stricta var. curvidens; 138-141: N. stricta var. stricta. 114, 118, 122, 126, 130, 134, 138: equatorial view and high focus; 115, 119, 123, 127, 131, 135, 139: equatorial view and low focus; 116, 120, 124, 128, 132, 136, 140: polar view and high focus; 117, 121, 125, 129, 133, 137, 141: polar view and low focus; scale bar 10 µm



**Figs. 142–161** LM micrographs of pollen grains of *Nepeta.* 142–145: *N. sulfuriflora*; 146–149: *N. supina*; 150–153: *N. trachonitica*; 154–157: *N. transcaucasica*; 158–161: *N. viscida*; 142, 146, 150, 154, 158: equatorial view and high focus; 143, 147, 151, 155, 159: equatorial view and low focus; 144, 148, 152, 156, 160: polar view and high focus; 145, 149, 153, 157, 161: polar view and low focus; *scale bar* 10 μm



*albiflora* (Type I-a; Figs. 162–164), while *N. pilinux* and *N. sulfuriflora* possess microreticulate pattern with secondary tectal connections of round lumina. The secondary reticulum is more or less present and primary lumina are subdivided into 2 or 4 smaller units (Type I-b; Figs. 165, 166).

2. Type II, bireticulate sculpture: the bireticulate exine ornamentation is characterized having varying characteristics of the primary muri and secondary reticulum. Type II can be divided into five subtypes based on thickness of primary muri, appearance of primary lumen, shape and number of secondary lumina, and varying characteristics of the secondary reticulum. *N. stenantha*, *N. cilicia*, *N. glomerata*, *N. aristata*,

*N. caesarea*, *N. baytopii*, *N. meyeri*, *N. trachonitica*, *N. transcaucasica*, *N. heliotrophifolia* var. *heliotrophifolia* and *N. macrosiphon* have bireticulate exine ornamentation, which is characterized by the primary lumen of angular shape with well defined secondary reticulum (Type II-a; Figs. 167, 168). The primary muri are irregular in shape and sometimes discontinuous; the secondary reticulum consists of more than 15 rounded lumina in *N. fissa*, *N. obtusicrena*, *N. lamiifolia* and *N. concolor* (Type II-b; Figs. 169–171). The primary muri are elongated in shape with some discontinuous irregular shape in *N. supina* and *N. humilis* with distinct secondary reticulum (Type II-c; Figs. 172–175). The primary muri are thicker than the secondary muri in

 Table 3 Figure numbers of light microscopy (LM) and scanning electron microscopy (SEM) of Nepeta species

Species	LM	SEM
N. aristata	2–5	_
N. baytopii	6–9	167-168
N. betonicifolia	10-11	-
N. cadmea	14–17	-
N. caesarea	18–21	-
N. cataria	22–25	-
N. cilicia	26–29	-
N. concolor	30–33	-
N. conferta	34–37	-
N. congesta var. congesta	38-41	162
N. congesta var. cryptantha	42–45	163–164
N. crinita	46-49	_
N. fissa	50-53	171
N. flavida	54–57	_
N. glomerata	58-61	_
N. heliotropifolia var. heliotropifolia	62–65	_
N. humulis	66–69	174–175
N. isaurica	70–73	_
N. italica	74–77	176–177
N. lamiifolia	78-81	169–170
N. macrosiphon	82-85	-
N. meyeri	86–89	-
N. nuda ssp. nuda	90–93	-
N. nuda ssp. albiflora	94–97	-
N. nuda ssp. glandulifera	98-101	-
N. nuda ssp. lydiae	102-105	-
N. obtusicrena	106-109	-
N. phyllochlamys	110-113	-
N. pilinux	114–117	165
N. racemosa	118-121	-
N. sibthorpii subsp. tumeniana	122-125	178–179
N. sorgerae	126–129	180
N. stenantha	130–133	-
N. stricta var. curvidens	134–137	-
N. stricta var. stricta	138–141	-
N. sulfuriflora	142-145	166
N. supina	146–149	172–173
N. trachonitica	150–153	-
N. transcaucasica	154–157	-
N. viscida	158–161	-

*N. italica*, *N. viscida* and *N. nuda* ssp. *nuda* (Type II-d; Figs. 176–177). *N. sibthorphii* ssp. *tumeniana* has heteromorphic exine ornamentation; three mesocolpia with a microreticulate exine alternate with the others with a bireticulate exine (Figs. 178, 179). All of the remaining studied taxa have wide primary muri with a

very shallow secondary reticulum in the primary lumen (Type II-e; Fig. 180).

## Discussion

The shape of the pollen grains varies from suboblate to perprolate (P/E = 0.86 - 2.09) in equatorial view and circular in the polar view. Pollen grains are usually radially symmetrical, isopolar, hexacolpate with microreticulate or mostly bireticulate sculpture. The pollen grain sizes obtained are comparable to the few previously published data. Pollen sizes of the following species are given for *N. cataria* by Ubera;  $P = 28.80-36.60 \ \mu m$ , E = 28.80-40.80 µm (Ubera 1982); Perveen and Oaiser (2003); Ranjbari et al.;  $P = 40.80 \ \mu\text{m}$ ,  $E = 28.60 \ \mu\text{m}$  (Ranjbari et al. 2004). Jamzad et al. (2000) provided pollen data of annual species of Nepeta. Pollen sizes of N. meyeri are given by Jamzad et al. (2000) as  $P = 36.00 \ \mu m$ ,  $E = 36.00, 37.00 \ \mu\text{m}$ . Among the investigated taxa in this study, pollen grains of N. congesta var. cryptantha, N. heliotropifolia, N. isaurica, N. cataria, N. meyeri and N. fissa were investigated by Jamzad et al. (2003b), and N. cataria, N. nuda, N. racemosa, N. viscida were investigated by Moon et al. (2008). Most of the taxa they investigated had more or less similar pollen morphologies to those examined by us, except for the differences in size and in the ratio of the polar axis-equatorial diameter and sculpture types. The values are a little different from those given in the present paper. It is possible that the slight variation is due to differences in preparation.

Pollen data were statistically evaluated to ascertain the value of pollen characters in the taxonomy of Nepeta. Comparing the Nepeta pollen types and subtypes derived from pollen analysis with the previous "sectional classifications" by Boissier (1879), Shishkin (1976), Rechinger (1982), Budantsev (1997), Hedge and Lamond (1982) and Dirmenci (2003) reveals that most pollen types contain members of more than one section. There are no similarities between pollen types/subtypes and other sectional classifications (Table 4). Two scatter plots were prepared to show polar axis-equatorial diameter and sections/ groups (Figs. 181, 182). There are no differences between polar axes (Kruskal Wallis, P > 0.05) of different groups (Hedge and Lamond 1982) and also sections (Dirmenci 2003), but for equatorial axis, the only significant difference between groups was found between Group B and Group C were identified (Mann-Whitney U test, P < 0.05).

In the pollen grains of investigated *Nepeta* species, the exine sculpture is microreticulate or bireticulate. These features are common in most of the pollen of species of subfamily Nepetoideae as well as other Lamiaceae

Figs. 162-171 SLM micrographs of pollen grains of Nepeta. 162: N. congesta var. congesta, 163-164: N. congesta var. cryptantha, 165: N. pilinux, 166: *N. sulfuriflora*, 167–168: N. baytopii. 163, 165, 168, 169: equatorial view of pollen grains; 162-166: microreticulate exine ornamentation 167-171, variations of bireticulate exine ornamentation. Scale bar 163, 163 165, 168, 169, 10 µm; 162, 170, 171, 5 µm, remainder 2 µm 165

(Wagstaff 1992; Abu-Asab and Cantino 1992, 1994; Jamzad et al. 2000; Celenk et al. 2008; Moon et al. 2008). In most of the investigated taxa, exine ornamentation is bireticulate,

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which characterized by showing varying characteristics of the primary muri and secondary reticulum. The bireticulate type can be divided into several subtypes.





Pollen type	Species	1	2	3	4	5	6
Ia	Nepeta cadmea <sup>a</sup>	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group A	Sect. Pycnonepeta
	Nepeta cataria	Sect. Eunepeta, Ss: Catariae	Sect. Cataria	Sect. Cataria	Sect. Nepeta	Group A	Sect. Cataria
	Nepeta congesta var. congesta <sup>a</sup>	N.I.	N.I.	N.I.	N.I.	Group C	Sect. Oxynepeta
	Nepeta congesta var. cryptantha	Sect. Eunepeta, Ss: Oxynepeta	N.I.	N.I.	N.I.	Group C	Sect. Oxynepeta
	Nepeta stricta var. stricta	Sect. Eunepeta, Ss: Oxynepeta	N.I.	N.I.	N.I.	Group C	Sect. Oxynepeta
	Nepeta flavida	N.I.	N.I.	N.I.	N.I.	Group A	Sect. Pycnonepeta
	Nepeta nuda ssp. albiflora	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group A	Sect. Orthonepeta
I b	Nepeta sulfuriflora <sup>a</sup>	N.I.	N.I.	N.I.	N.I.	Group A	Sect. Pycnonepeta
	Nepeta pilinux <sup>a</sup>	N.I.	N.I.	N.I.	N.I.	Group A	Sect. Pycnonepeta
II a	Nepeta stenentha	Sect. Eunepeta, Ss: Stenostegiae	N.I.	Sect. Stenostegiae	Sect. Nepeta	Group B	Sect. Stenostegiae
	Nepeta cilicia	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	Sect. Schizocalyx	Group B	Sect. Macronepeta
	Nepeta glomerata	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group B	Sect. Macronepeta
	Nepeta aristata <sup>a</sup>	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group B	Sect. Setanepeta
	Nepeta caeserea <sup>a</sup>	N.I.	N.I.	N.I.	Sect. Setanepeta	Group A	Sect. Setanepeta
	Nepeta baytopii <sup>a</sup>	N.I.	N.I.	N.I.	N.I.	Group B	Sect. Schizocalyx
	Nepeta meyeri	Sect. Eunepeta, Ss: Micranthae	Sect. Micranthae	Sect. Micranthae	Sect. Micranthae	Group B	Sect. Micrantha
	Nepeta trachonitica	N.I.	N.I.	Sect. Psilonepeta	Sect. Setanepeta	Group B	Sect. Setanepeta
	Nepeta transcaucasica	N.I.	Sect. Cataria	N.I.	N.I.	Group B	Sect. Stenostegiae
	Nepeta heliotropifolia var. heliotropifolia	Sect. Eunepeta, Ss: Micranthae	N.I.	Sect. Oxynepeta	N.I.	Group C	Sect. Oxynepeta
	Nepeta macrosiphon	Sect. Eunepeta, Ss: Longiflorae	N.I.	Sect. Schizocalyx	Sect. Schizocalyx	Group B	Sect. Schizocalyx
II b	Nepeta fissa	Sect. Eunepeta, Ss: Longiflorae	Sect. Schizocalyx	Sect. Schizocalyx	N.I.	Group B	Sect. Schizocalyx
	Nepeta obtuscrena <sup>a</sup>	N.I.	N.I.	N.I.	N.I.	Group B	Sect. Schizocalyx
	Nepeta lamiifolia	Sect. Eunepeta, Ss: Longiflorae	Sect. Schizocalyx	N.I.	Sect. Schizocalyx	Group B	Sect. Schizocalyx
	Nepeta concolor <sup>a</sup>	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group B	Sect. Macronepeta
II c	Nepeta supina	Sect. Eunepeta, Ss: Catariae	Sect. Spicatae	N.I.	N.I.	Group B	Sect. Spicatae
	Nepeta humilis	Sect. Eunepeta, Ss: Stenostegiae	N.I.	Sect. Micranthae	N.I.	Group B	Sect. Micrantha
II d	Nepeta italica	Sect. Eunepeta, Ss: Microstegiae	N.I.	Sect. Macrostegiae	Sect. Macrostegiae	Group A	Sect. Pycnonepeta
	Nepeta nuda ssp. nuda	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group A	Sect. Orthonepeta
	Nepeta viscida <sup>a</sup>	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	Sect. Subinteruaptae	Group A	Sect. Subinterruptae

Table 4 Proposed informal taxonomic scheme for Nepeta compared with previous infrageneric classifications

Pollen type	s Species	1	2	3	4	5	6
II e	Nepeta sibthorpii ssp. tumeniana <sup>a</sup>	T'N	N.I.	.I.N	TN	N.I.	Sect. Pycnonepeta
	Nepeta sorgerae <sup>a</sup>	T.N.	N.I.	N.I.	N.I.	Group A	Sect. Subinterraptae
	Nepeta conferta <sup>a</sup>	T.N.	N.I.	N.I.	N.I.	Group A	Sect. Setanepeta
	Nepeta betonicifolia	Sect. Eunepeta, Ss: Stenostegiae	Sect. Cataria	Sect. Stenostegiae	Sect. Nepeta	Group B	Sect. Stenostegiae
	Nepeta stricta var. curvidens	Sect. Eunepeta, Ss: Oxynepeta	N.I.	N.I.	N.I.	Group C	Sect. Oxynepeta
	Nepeta nuda ssp. glandulifera <sup>a</sup>	T'N	N.I.	N.I.	N.I.	Group A	Sect. Orthonepeta
	Nepeta nuda ssp. lydiae <sup>a</sup>	T'N	N.I.	N.I.	N.I.	Group A	Sect. Orthonepeta
	Nepeta crinita <sup>a</sup>	Sect. Eunepeta, Ss: Catariae	N.I.	N.I.	N.I.	Group B	Sect. Setanepeta
	Nepeta isaurica <sup>a</sup>	Sect. Eunepeta, Ss: Stenostegiae	N.I.	N.I.	N.I.	Group A	Sect. Pycnonepeta
	Nepeta racemosa	Sect. Eunepeta, Ss: Stenostegiae	N.I.	Sect. Stenostegiae	Sect. Nepeta	Group B	Sect. Stenostegiae
	Nepeta phyllochlamys <sup>a</sup>	T'N	N.I.	N.I.	Sect. Macrostegiae	Group A	Sect. Pycnonepeta
N.I. not ind	licated. <i>sect.</i> section. <i>ss.</i> subsection 1: Bois	sier (1879): 2: Shishkin (1976): 3: Re	schinger (1982): 4:	Budantsev (1997): 5:	Hedge and Lamond 19	82: 6: Dirm	enci (2003)

Endemic for Turkey

a

Table 4 continued



**Fig. 181** Scatter plot for polar axis (*B*), Sections (*A* Dirmenci 2003) and Groups (*C* Hedge and Lamond 1982). Numbers in axis *A*: 1 = sect. Setanepeta, 2 = sect. Schizocalyx, 3 = sect. Stenostegiae, 4 = sect. Pycnonepeta, 5 = sect. Cataria, 6 = sect. Macronepeta, 7 = sect. Oxynepeta, 8 = sect. Micrantha, 9 = sect. Orthonepeta, 10 = sect. Subinterruptae, 11 = sect. Spicatae; numbers in axis *C*: 2 = Group B, 3 = Group C; measurements for *B* axis was given in  $\mu m$ 



**Fig. 182** Scatter plot for equatorial axis (*D*), Sections (*A* Dirmenci 2003) and Groups (*C* Hedge and Lamond 1982). Numbers in axis *A*: 1 = sect. Setanepeta, 2 = sect. Schizocalyx, 3 = sect. Stenostegiae, 4 = sect. Pycnonepeta, 5 = sect. Cataria, 6 = sect. Macronepeta, 7 = sect. Oxynepeta, 8 = sect. Micrantha, 9 = sect. Orthonepeta, 10 = sect. Subinterruptae, 11 = sect. Spicatae; numbers in axis *C*: 2 = Group B, 3 = Group C; measurements for *B* axis was given in  $\mu$ m

In six taxa of the investigated genus, N. nuda ssp. glandulifera, N. concolor, N. crinita, N. congesta var. cryptantha, N. stricta var. stricta, N. sibthorpii ssp. tumeniana, colpi have different shapes like many hexacolpate Lamiaceae pollen grains. In these taxa, the colpi are not distributed symmetrically. The alternation of narrow and wide mesocolpia is a common phenomenon in the family Lamiaceae. Different colpi apomorphies were recorded by Pozhidaev (1992) in the subfamily Saturejoideae. Pozhidaev (1992) states that there is no reason to regard this feature as characteristic of the most primitive forms of six-colpate pollen grains. The data of Cantino and Sanders (1986) show that the change of number of colpi in deviating pollen grains is not accompanied by a change of number of their cells. Hexazonocolpate pollen probably represents a synapomorphy in this order comprising the subfamily Nepetoideae (Cantino and Sanders 1986; Abu-Asab and Cantino 1992, 1994). Furthermore, pollen with a tectate-perforate to reticulate exine structure and a surface ornamented with a network of supratectal ridges surrounding polygonal lumina is hypothesized to be a plesiomorphic condition within the subfamily Nepetoideae, where it occurs, for example, in the tribe Mentheae: Perilla, Elsholzia, Perillula, Hyssopus, Monardella and Satureja mimoloides (Wagstaff 1992). It is characteristical of Nepeta pollen that it has a two different exine ornamentation characterized by the partial reduction of the tectum in N. sibthorpii ssp. tumeniana. Similar to pollen grains of *N. sibthorpii* ssp. *tumeniana*, an apomorphy for pollen grains of *Nepeta amoena* was observed by Jamzad et al. (2000). Three narrow mesocolpia with a perforatereticulate exine, alternate with three wide mesocolpia that are bireticulate. Heteromorphic sexine ornamentation has been recorded in *Agastache scrophulariifolia* by Moon et al. (2008). Alternate position of colpi has been recorded in the genera *Endostemon* (Paton et al. 1994), *Lycopus* (Moon and Hong 2003) and *Mentha* (Celenk et al. 2008) although in *Endostemon, Lycopus* and *Mentha* the exine ornamentation is similar for both the narrow and the wide mesocolpia.

The tendency towards reduction of tectum is characteristic for many other genera and species in the tribe Mentheae, for example: *Origanum* (Husain and Heywood 1982), *Thymbra* (Morales-Valverde 1987), *Micromeria* (Morales-Valverde 1990) and is generally interpreted as an evolutionary trend.

In conclusion, studies in the genus of *Nepeta* so far indicate that additional sources of potentially very useful characters are available from pollen morphology. As with any morphological study the more complete the data the more convincing the subsequent analyses are regarding phylogeny and relationships.

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#### Appendix

Voucher specimens of the genus Nepeta L. which are examined in the present study

Species	Voucher information
N. aristata Boiss. et Kotschy ex Boiss.	Kesis Mountain-Malatya, 17.07.2002. Dirmenci 24333
N. baytopii Hedge and Lamond	Diyarbakir, 16.07.2001. Dirmenci 24348
N. betonisifolia C. A. Meyer	Erzurum, 16.06.2002. Yildiz and Dirmenci 24321
N. cadmea Boiss.	Honaz Mountain-Denizli, 30.06.1999. Dirmenci 24286
N. caesarea Boiss.	Icel, 06.08.2002. Yildiz and Dirmenci 24310
N. cataria L.	Malatya, 11.08.2001. Dirmenci 24296
N. cilicia Boiss.	Kahramanmaraş, 15.07.2002. Dirmenci 24327
N. concolor Boiss. and Heldr.	Geyik mountain-Antalya, 10.08.2002. Dirmenci 24329
N. conferta Hedge and Lamond	Ciglikara Forest-Antalya, 29.06.2000. Dirmenci 24295
N. congesta Fisch. et Mey. var. cryptantha (Boiss.) Hedge and Lamond	Van, 08.06.2001. Dirmenci 24352
N. congesta Fisch. et Mey. var. congesta Fisch. and Mey.	Eskisehir, 31.05.2002. Yildiz and Dirmenci 24351
N. crinita Montbret and Aucher ex Bentham	Kube Mountain-Malatya, 18.07.2002. Dirmenci 24312
N. fissa C.A. Meyer	Sivas, 23.07.2002. Yildiz and Dirmenci 24341
N. flavida HubMor	Osmaniye, 15.07.2002. Dirmenci 24292
N. glomerata Montbret et Aucher ex Bentham	Antalya, 13.07.2002. Dirmenci 24330
N. heliotropifolia Lam. var. heliotropifolia Lam.	Kars, 13.06.2002. Dirmenci 24356
N. humilis Benth.	Hakkari, 09.06.2002. Dirmenci 24358
N. isaurica Boiss. and Heldr	Geyik Mountain-Antalya, 22.07.1999. Yildiz and Dirmenci 24308

Species	Voucher information
N. italica L	Balikesir, 30.05.2001. Dirmenci 24280
N. lamiifolia Wild	Suphan Mountain-Bitlis, 23.07.2001. Dirmenci 24339
N. macrosiphon Boiss.	Kambos Mountain-Bitlis, 30.07.2001. Dirmenci 24347
N. meyeri Bentham	Erzurum, 06.06.2001. Dirmenci 24349
N. nuda L. ssp. albiflora (Boiss.) Gams	Kars, 22.07.2000. Yildiz and Dirmenci 24301
N. nuda L. ssp. nuda L.	Balikesir, 05.07.2000. Dirmenci 24298
N. nuda L. ssp. glandulifera HubMor and Davis	Icel, 10.07.2001. Dirmenci 24303
N. nuda L. ssp. lydiae Davis	Denizli, 28.06.1999. Dirmenci 24304
N. obtusicrena Boiss. et Kotschy ex Hedge	Bitlis, 18.07.2001. Dirmenci, 24346
N. phyllochlamys P. H. Davis	Antalya, 02.06.2002. Yildiz and Dirmenci 24306
N. pilinux P. H. Davis	Antalya, 10.08.2002. Dirmenci 2429
N. pilinux P. H. Davis	Antalya, 10.08.2002. Dirmenci 24294
N. racemosa Lam.	Kars, 12.06.2002. Dirmenci 24314
N. sibthorpii subsp. tumeniana B. Yildiz and T. Dirmenci	Kaz Mountain-Balikesir, 15.07.2003. Dirmenci 24366
N. sorgerae Hedge and Lamond	Malatya, 18.07.2002. Dirmenci 24313
N. stenantha Kotschy and Boiss. ex Boiss.	Erzurum, 30.07.2001. Dirmenci 24323
N. stricta (Banks and Sol.) Hedge and Lamond var. curvidens (Boiss and Bal) Hedge and Lamond	Agri, without date. Dirmenci 24355
N. stricta (Banks and Sol.) Hedge and Lamond var. stricta (Banks and Sol.) Hedge and Lamond	Eskisehir, 31.05.2002. Yildiz and Dirmenci 24354
N. sulfuriflora P. H. Davis	Antalya, 07.07.2000. Dirmenci 24290
N. supina Steven	Buyuk Agri Mountain-Igdir, 01.08.2002. Dirmenci 24326
N. trachonitica Post	Hakkari, 19.6.2004. Dirmenci 24324
N. transcaucasica Grossh.	Agri, 06.06.2001. Dirmenci 24316
N. viscida Boiss.	Balikesir, 05.07.2000. Dirmenci 24309

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