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Pollen Morphology and Its Systematic Implications for the Genera *Keiskea* Miq. and *Collinsonia* L. (Elsholtzieae-Lamiaceae)

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The pollen morphology of six species of *Keiskea* and three representative taxa of *Collinsonia* was studied in detail using LM, SEM, and TEM. In both genera, pollen grains are monad, hexa-colpate, and mostly medium in size [P = 28.0 to 37.0 μm, E = 24.3 to 30.7 μm (*Keiskea*); P = 30.0 to 45.0 μm, E = 26.0 to 39.0 μm (*Collinsonia*)]. Polar outlines are of circular or ellipsoid form. Shapes range from primarily oblate-spheroidal to prolate-spheroidal to subprolate, and rarely prolate in the equatorial view. Their exine, including the intine characters, are clearly distinct from each other: *Keiskea*, well-developed bi-reticulate, often forming large lumina by supratectal ridges, unbranched columellae, one-third to one-half of the total exine thickness; versus *Collinsonia*, mostly perforate without supratectal ridges or a faint/very weak bi-reticulate appearance without supratectal ridges, seemingly branched columellae, ca. two-thirds of the total exine thickness. As demonstrated by these current data, the pollen morphology of the two genera is well distinguished, easily supporting the separation of *Keiskea* from *Collinsonia*.

Keywords: Collinsonia, Keiskea, Lamiaceae, pollen morphology, SEM, systematics, TEM

Keiskea Miq., a genus within Lamiaceae, contains six species of mesophytic herbs that are often found in the montane forests of China and Japan, but also are present as one endemic species in Taiwan. Plants are characterized by several floral traits -- a calyx that is somewhat two-lipped and campanulate, with a 3-toothed upper lip and 2-toothed lower lip, plus filaments that are much exserted and rarely included, cymes that are ebracteolate, and usually just one nutlet (Li and Hedge, 1994; Harley et al., 2003).

Masamune (1940) first divided the genus *Keiskea* into two sections: *Macrobracteatae* (bract ovate-rotundate, calyx bilabiate, minutely hairy above) and *Eukeiskea* (linear bract, calyx campanulate, sparsely hairy outside). The section *Macrobracteatae* was created based on one species, *K. macrobracteata* Masam., which is an endemic taxon in Taiwan (Press, 1982; Huang et al., 1998).

Collinsonia L. is an eastern North American genus of perennial herbs in the same family as *Keiskea*. It is usually located in mesophytic, often woodland, habitats, and its center of diversity is in the southeastern United States. Its inflorescence structure, and calyx and corolla morphology are quite similar to those of *Keiskea*. The main difference appears to be in the median lobe of the anterior corolla lip, which is more or less fimbriate in *Collinsonia* and entire to emarginated in *Keiskea*. Four species are commonly recognized and accepted in the former (Harley et al., 2003, 2004; Peirson et al., 2006).

Bentham (1876) first placed *Collinsonia* in tribe Mentheae with primarily east-Asian genera -- *Keiskea*, *Elsholtzia* Willd., *Mosla* (Benth.) Buch.-Ham. ex Maxim., *Perilla* L., and *Perillula* Maxim. Briquet (1895-1897) then assigned *Collinsonia* to tribe Mentheae, and subtribe Collinsoniinae with the genera *Micheliella* Briq., together with *Mosla*, *Perilla*, and *Perillula*.

Wunderlich (1967) later recombined *Collinsonia* and *Micheliella* into the single genus *Collinsonia*, but retained *Keiskea* and *Elsholtzia* in a separate tribe, Elsholtzieae. Recently, Cantino et al. (1992) have revised the classification of all genera in Lamiaceae, and have put *Elsholtzia* into tribe Elsholtzieae, which modifies the circumscription of Wunderlich (1967), but places it together with four other genera (*Collinsonia, Mosla*, *Perilla*, and *Perillula*) besides *Elsholtzia* and *Keiskea*. In fact, the tribe Elsholtzieae sensu Cantino et al. (1992) is the same as Bentham's (1876) unnamed subgroup of subtribe Menthoideae.

Keiskea and *Collinsonia* were previously separated into individual subtribes by Briquet (1895-1897), no doubt because of their seemingly disjunctive distribution. However, the systematics relationship between these two genera has recently been questioned and much debated.

Harley et al. (2003) have included *Keiskea* as a synonym of *Collinsonia*, citing the laciniate lower corolla lobe of *Collinsonia* sensu stricto as the only morphological distinction. In contrast, Peirson et al. (2004) have argued that phylogenetic analysis of their nuclear ribosomal ITS sequence data does not support the merger of *Collinsonia* and *Keiskea* into one genus.

Investigation of the pollen morphology within the Lamiaceae has been essential for elaborating on the system of

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Appendix: Abbreviated collection data for voucher specimens studied. *Keiskea australis* C. Y. Wu & H. W. Li: China, without detailed locality and date, Anonym. s.n. (PE). - *K. elscholtzioides* Merrill: China, Jiangsi, Xiu-Shiu County, 16. IX. 1989, Liu 890032 (GH). - *K. glandulosa* C. Y. Wu: China, without detailed locality, 27. X. Anonym. 6044 (KUN). - *K. japonica* Miq.: Japan, Hondo, Tokyo Pref., Nerima-ku, Ooizumi, 29. IX. 1928, Makino 14858 (S). - *K. sinensis* Diels: China, without detailed locality, 4. X. 1957, Li 1524 (PE). - *K. szechuanensis* C. Y. Wu: China, Yunnan, X. 1958, Li 980 (KUN). - *Collinsonia canadensis* L.: U.S.A., New York state, Tompkins County, Cornell University Campus, Beebe Lake, 30. VII. 1913, Palmer 1057 (S). - *C. scabriuscula* Aiton: U.S.A., Alabama, Evergreen, 1. X. 1900, Anonym. 2029a (S). - *C. verticillata* Baldwin ex Elliott: U.S.A., Tennessee, V. 1895, Ruth s.n. (S).

this family (Erdtman, 1945; Harley et al., 1992; Pozhidaev, 1989, 1992; Abu-Asab and Cantino, 1992, 1994). However, that of *Keiskea* and *Collinsonia* has been poorly studied and little is known about it. Trudel and Morton (1992) have presented a short pollen description of *C. canadensis* L., while Wagstaff (1992) has examined the pollen morphology of the tribe Mentheae sensu Bentham, but treated only one taxon (*C. canadensis*). Zhou et al. (1997) have documented pollen data (size and SEM photos) for both *C. canadensis* and *K. elsholtzioides* Merr. to infer the systematics position of a related genus, *Mosla*, for comparison. Finally, Huang et al. (1998) have illustrated the pollen grains as well as the habits of *K. macrobracteata* as part of the Flora of Taiwan, but have published no formal description or notes.

Therefore, the objectives of the research presented here were to provide, for the first time, a detailed account of the pollen morphology of *Keiskea and Collinsonia* using light microscopy (LM), scanning electron microscopy (SEM), and, for some selected taxa, transmission electron microscopy (TEM). The results were then used to determine the extent to which these pollen morphological data could serve as systematics characters, as well as to clarify the generic relationships between these two.

MATERIALS AND METHODS

Pollen grains from six species of the genus *Keiskea* plus three representative taxa of *Collinsonia* were obtained primarily from materials at the following herbaria: GH, KUN, PE, and S. All acronyms followed those of Holmgren et al. (1990), with vouchers listed in Table 1 and the Appendix. A lack of available materials precluded an examination of the Taiwan endemic taxon, *K. macrobracteata*.

Fully matured anthers were removed from the specimens and prepared by the standard acetolysis method (Erdtman, 1960). They were mounted in glycerin jelly and sealed with paraffin for light microscopy (LM). Morphological observations were made with an Olympus BX-41 microscope, and polar axis (P) and equatorial diameters (E) were measured from 10 pollen grains per species (× 1000). The quotient P/E is given in Table 1.

For scanning electron microscopy (SEM), acetolyzed pollen grains in a 70% ethanol solution were pipetted directly onto aluminum stubs with double-sided cellophane tape, then air-dried at room temperature (RT) under an inverted flask. Specimens were coated with platinum (Pt) using a JFC-1100E ion sputter before being examined in a JEOL JSM-5200 at 20 kV and photographed.

For transmission electron microscopy (TEM), anthers from three taxa (*K. japonica, K. elsholtzioides*, and *C. canadensis*) were maintained for 50 h in TAG-solution (1% tannic acid + glutaraldehyde in 0.1 M phosphate buffer; pH 7.4). Following dehydration in alcohol solutions (Ruzin, 1999), the pollen grains were positioned in araldite resin using a rapid embedding technique described by Skvarla (1966). Sections were cut with a Sovall MT 6000 ultramicrotome, then stained with 1% aqueous uranyl acetate for 20 min at RT and with lead citrate for 5 min. These sections, on copper grids, were examined with an Hitachi H7100 microscope. More detailed methods for SEM and TEM are provided by Hong et al. (2005) and Jang and Heo (2005).

Intergeneric classifications in the tribe Elsholtzieae followed those of Cantino et al. (1992). General pollen terminology was used according to Harley (1992), Harley et al. (1992), and Punt et al. (2007).

RESULTS

Representative pollen grains are illustrated in Figures 1 to 3; size and shape measurements, including voucher information of the taxa examined here, are provided in Table 1. General descriptions of the pollen grains from *Keiskea* and *Collinsonia* are as follows:

Keiskea (Figs. 1A-P; 2A-Q)

Pollen grains are monad, hexa-colpate. The colpi are distributed symmetrically, elongated, usually shallow, narrowing at the poles (Figs. 1C, G, K, O; 2C, F, G). Grains are mostly medium in size: P (polar axis) = 28.0 to 37.0 µm, E (equatorial diameter) = 24.3 to 30.7 µm. Their polar outlines are circular or ellipsoid (Figs. 1B, F, N; 2B). In the equatorial view, the shapes are mostly oblate-spheroidal to prolate-spheroidal, except for *K. sinensis*, in which they are subprolate (Fig. 1M; cf. Table 1). The exine is ca. 1ß¦ thick; its surface sculpture is well-developed bi-reticulate with frequent large lumina by supratectal ridges (Figs. 1C, G, K, O; 2F, G).

Table 1. Pollen morphological data for examined *Collinsonia* and *Keiskea* species. P = Polar axis; E = Equatorial diameter; P/E = ratio of polar axis to equatorial diameter. - (N = 10; units for P and E = µm; * for TEM).

Species	Collector and locality	P	E	P/E
Keiskea australis	Anon. s.n. (PE), China	34.0 (35.4) 37.0	35.0 (36.0) 38.0	0.94 (0.99) 1.00
*K. elsholtzioides**	Liu 890032 (GH), China	30.0 (31.3) 32.0	27.0 (28.3) 29.0	1.07 (1.11) 1.14
K. glandulosa	Anon. 6044 (KUN), China	30.5 (31.6) 32.0	29.0 (29.8) 30.7	1.03 (1.06) 1.10
*K. japonica**	Makino 14858 (S), Japan	30.0 (30.6) 32.0	28.0 (29.8) 30.2	1.04 (1.06) 1.07
K. sinensis	Li 1524 (PE), China	32.0 (32.2) 33.0	24.3 (26.0) 27.0	1.18 (1.25) 1.32
K. szechuanensis	Li 980 (KUN), China	28.0 (29.8) 31.0	29.5 (30.5) 31.0	0.95 (0.97) 1.00
*Collinsonia canadensis**	Palmer 1057 (S), USA	30.0 (33.3) 36.0	30.0 (31.1) 32.6	0.97 (1.08) 1.13
C. scabriuscula	Anon. 2029a (S) USA	32.0 (36.4) 40.0	26.0 (30.0) 32.0	1.19 (1.23) 1.26
C. verticillata	Ruth s.n. (S), USA	40.0 (42.6) 45.0	32.0 (34.0) 39.0	1.15 (1.26) 1.34

However, the distribution of perforations and supratectal ridges varies among species (Figs. 1D, H, L, P; 2D, H, I-N). In *K. australis* and *K. sinensis*, the muri that form the supratetal ridges are continuous (Fig. 1I, K. M, O; 2G, H), whereas in the others they are somewhat discontinuous (cf. Figs. 1C-D, G-H; 2C-D, F-G). The supratectal ridges in *K. australis* are much thicker than those in the remaining taxa (Figs. 1K-L; 2K). Perforations tend to be circular and more or less angular (Fig. 2I-N). TEM details of the pollen wall ultrastructure for *K. japonica* and *K. elsholtzioides* include columellae that are more or less loosely spaced, much longer than both the tectum and the foot layer, and seemingly unbranched (Fig. 2O-Q). The foot layer is discontinuous, slightly thick in places where it anastomoses with the base of the bacula. The endexine is darkly staining, discontinuous, and much thinner than the foot layer. The intine comprises one-third to one-half of the total exine thickness, and is usually bizonal in its staining, with the lower zone denser than the upper one.

***Collinsonia* (Fig. 3A-N)**

Pollen grains are monad, hexa-colpate. The colpi are distributed symmetrically, elongated, usually shallow, narrowing at the poles or sometimes developing granular membranes (Figs. 3C, G, K). Grains are mostly medium in size: P (polar axis) = 30.0 to 45.0 μm, E (equatorial diameter) = 26.0 to 39.0 μm. In the equatorial view, the shape is mostly oblate-spheroidal to subprolate, rarely prolate (cf. Table 1). The exine is 1 to 2 μm thick, with that of *C. verticillata* being about twice as thick as from *C. canadensis* (Fig. 3M-N). The surface sculpture of the exine surface is mostly perforate without supratectal ridges, or else has a faint/very weak bi-reticulate appearance without supratectal ridges (Fig. 3D, H, L). TEM details of the exine in *C. canadensis* include a tectum that is slightly thicker than the foot layer, and columellae that are longer than the tectum, somewhat densely packed, and sparsely branched (Fig. 3M-N). The foot layer is about one-fourth of the total wall thickness, discontinuous,

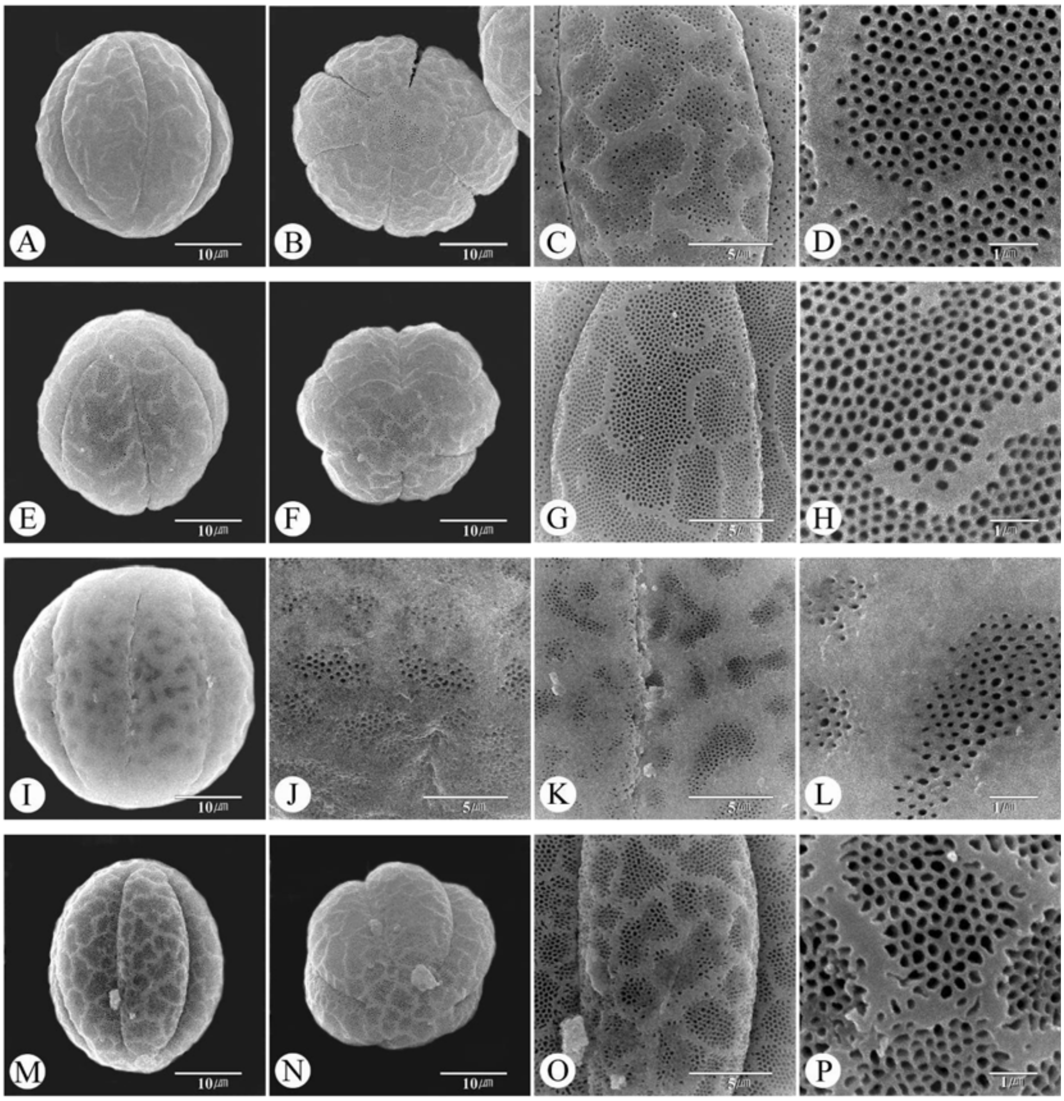

Figure 1. SEM micrographs of pollen from genus *Keiskea*. A-D, *K. japonica*; E-H, *K. elsholtzioides*; I-L, *K. australis*; and M-P, *K. sinensis*. Whole grain in equatorial view (A, E, I, M), and in polar view (B, F, J, N); exine ornamentation of mesocopium and colpus margin (C, G, K, O) and detailed observations (D, H, L, P), and exine ornamentation of apocolpium (J).

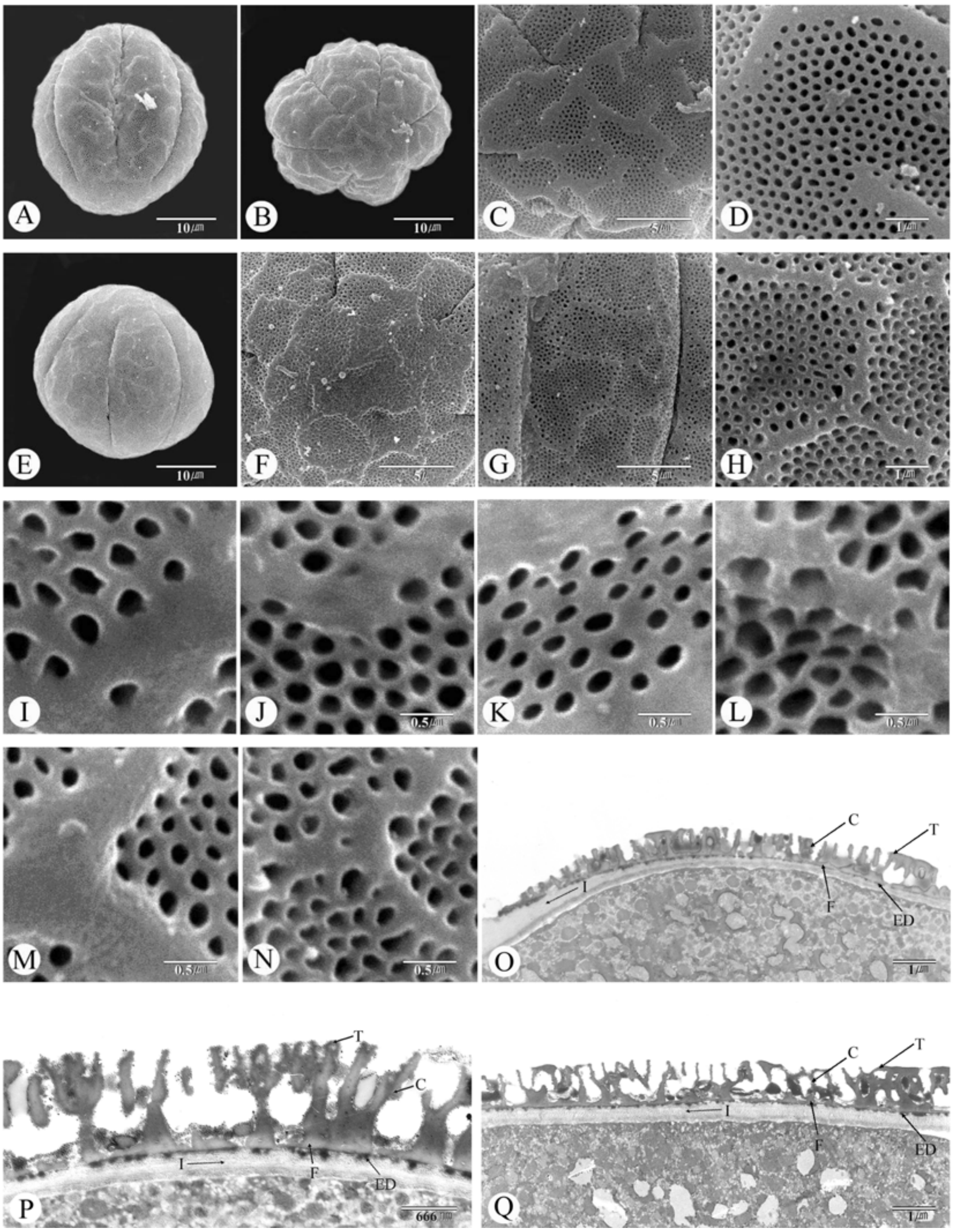

Figure 2. SEM and TEM micrographs of pollen in genus *Keiskea*. A-D, M, *K. glandulosa*; E-H, N, *K. szechuanensis*; I, *K. japonica*; J, *K. elsholtzioides*; K, *K. australis*; and L, *K. sinensis*. Whole grain in equatorial view (A, E), and in polar view (B). Exine ornamentation of mesocopium and colpus margin (G) and at apocolpium (C, F), and detailed observations (D, H). TEM: O-P, *K. japonica*; and Q, *K. elsholtzioides*. T: Tectum; C: Columella; F: Foot layer; ED: Endexine, I: Intine.

cone-shaped, and slightly thick in places where it anastomoses with the base of the bacula. The endexine is darkly staining, somewhat continuous, and much thinner than the foot layer, while the intine is very thick, accounting for about two-thirds of the total exine thickness.

DISCUSSION

In the all examined taxa from both *Keiskea* and *Collinsonia*, the pollen grains are monad and hexa-colpate, traits shared with other genera of the tribe Elsholtzieae sensu Cantino et al. (1992). Although the pollen of *Collinsonia* is slightly larger, that size difference is not significant (cf. Table 1, Figs. 1-3). Among the *Keiskea* species, *K. australis* has the largest grains on average (35.4 × 36.0 μm; Fig. 1I), while *K. szechuanensis* has the smallest pollen (29.8 × 30.5 μm; Fig. 2E). In the genus *Collinsonia*, the largest grains on average are observed in *C. verticillata* (42.6 × 34.0 μm; Fig. 3I-J). The

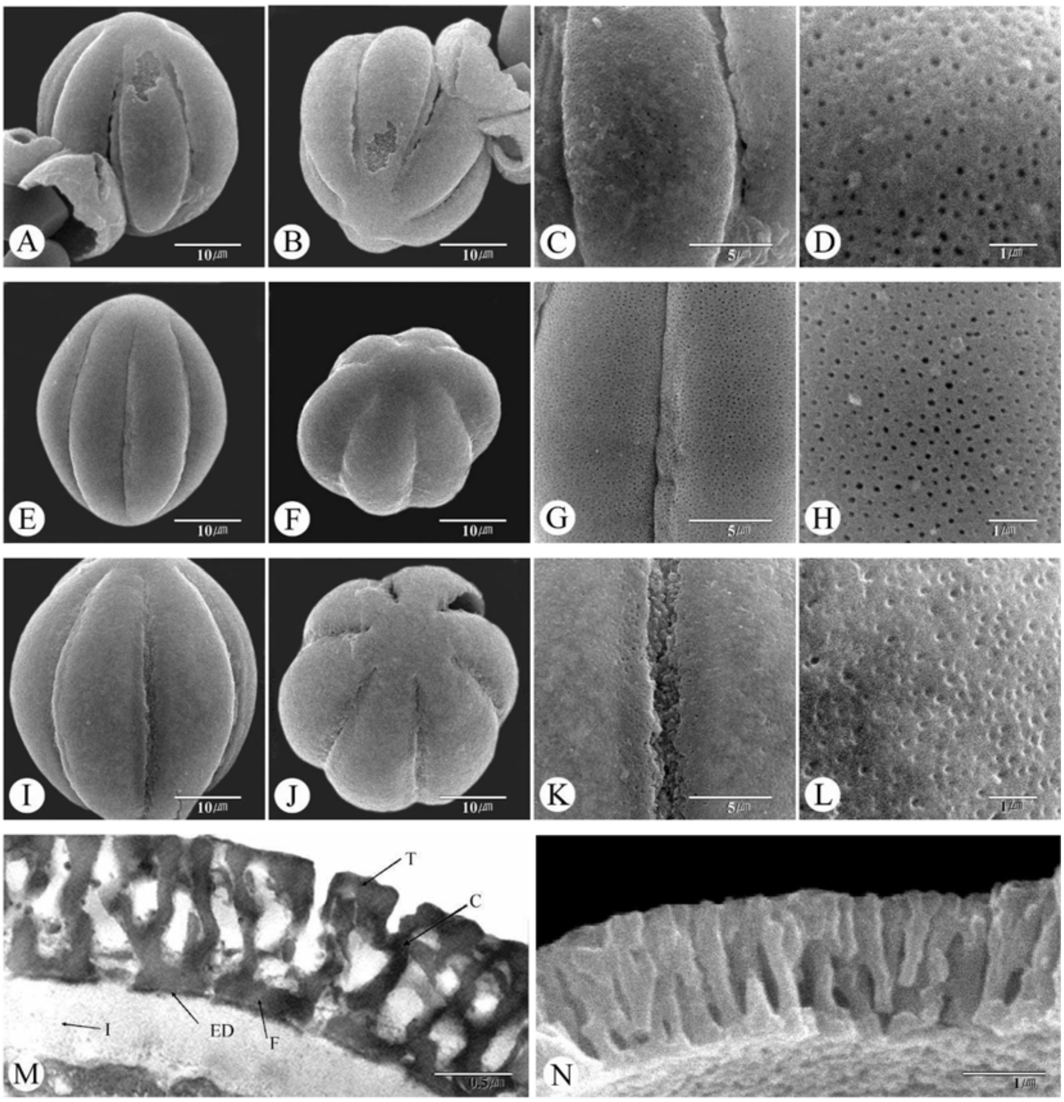

Figure 3. SEM and TEM micrographs of pollen in genus *Collinsonia*. A-D, M, *C. canadensis*; E-H, *C. scabriuscula*; and I-L, N, *C. verticillata*. Whole grain in equatorial view (A, E, I), viewed from the bottom (B), and in polar view (F, J). Exine ornamentation of mesocopium and colpus margin (C, G, K), and detailed observations (D, H, L). TEM: Ultrastructure of pollen wall at mesocopial regions (M), and fractured exine through mesocolpium region (N). T: Tectum; C: Columella; F: Foot layer; ED: Endexine, I: Intine.

pollen of *K. elsholtzioides* measured here is slightly larger than that described by Zhou et al. (1997). Thus far, chromosome numbers have been reported for only one taxon, *C. canadensis* (2n = 50, 52; Keener, 1979; Gill, 1981; Peirson et al., 2006; cf. IPCN - http://mobot.mobot.org/W3T/Search/ipcn.html), which makes it difficult to ascertain whether that size difference is related to either geographical variations or chromosome number.

The shapes of the pollen in equatorial view vary among taxa, with those of *Keiskea* being mostly oblate-spheroidal to prolate-spheroidal, except for *K. sinensis*, in which they are subprolate. In contrast, the grains of *Collinsonia* are primarily oblate-spheroidal to subprolate, and rarely prolate (cf. Table 1). It is, however, noteworthy that pollen shape in the Lamiaceae is often affected by the state of hydration and/or fixation (Demissew and Harley, 1992; Harley et al., 2004). Grains in that family frequently undergo dramatic changes in their shapes because of the loss of the colpal membrane during acetolysis. As a result of hot acid treatment, a naturally hydrated, oblate, or suboblate grain often becomes subprolate or prolate because, in the absence of the colpal membranes, the inter-colpal areas of the tectum tend to close in (Harley, 1992). León-Arencibia and La-Serna Ramos (1992) have reported similar observations of certain intraspecific heterogeneity for pollen shape in the genus *Lavandula* L. Therefore, one might conclude that differences in shapes among the pollen grains from the taxa studied here are neither particularly significance nor even applicable for the taxonomy. To preserve a more natural form, however, more careful processing is required, including critical point-drying of fresh material.

In all these examined taxa of *Keiskea* and *Collinsonia*, palynological diversity is evident, especially in their exine sculpture and structure, with clearly distinct patterns between the two. For example, pollen grains from *Keiskea* are well-developed and bi-reticulate, often forming large lumina by supratectal ridges. In contrast, the exine surface of *Collinsonia* pollen is mostly perforate without supratectal ridges, or else has a faint/very weak bi-reticulate appearance without supratectal ridges (cf. Figs. 1-3). Such grains are considered unique, and have been labeled by Wagstaff (1992) as autoapomorphic characters in the tribe Mentheae sensu Bentham. Although there are some variations in perforation on the *Keiskea* pollen grains, most generally have none (Fig. 2I-K, M) or only an occasional few on the ridges (Fig. 2L, N). Zhou et al. (1997) also have reported that *K. elsholtzioides* lacks perforations on its supratectal ridges, which agrees with the data presented here (cf. Figs. 1H, 2J). Huang et al. (1998) have illustrated pollen grains of *K. macrobracteata* that show continuous supratectal ridges, with muri resembling those found in *K. australis, K. sinensis*, and *K. szechuanensis* (cf. Figs. 1I-P, 2E-H). Masamune (1940) previously divided the genus *Keiskea* into two sections -- *Macrobracteatae* and *Eukeiskea* -- based on calyx characters. However, that earlier infrageneric treatment is not well supported by the current pollen data and those illustrations by Huang et al. (1998). Likewise, Press (1982) has suggested that the calyx characters used to distinguish those sections of *Keiskea* are non-applicable. This is agreed by the present author. It is noteworthy that the exine ornamentation of *Keiskea* is more similar to that of the genera *Elsholtzia* and *Perilla*, which is finely and well-developed bi-reticulate with polygonal or sometimes irregular supratectal ridges. Hong and Jeon (manuscript submitted) also have now described the pollen data for 18 species of *Elsholtzia*.

Briquet (1895-1897) separated *Collinsonia* into two genera, *Collinsonia* and *Micheliella*. The latter, *Micheliella* sensu Briquet, consisted of *M. anisata* (Sims) Briq. and *M. verticillata* (Elliott) Briq. Later, Wunderlich (1967) again recombined the above two into that single genus of *Collinsonia*. No clear distinctions were found among the present examined taxa, including *M. verticillata*, thereby confirming that Wunderlich recombination. Peirson et al. (2004) also have mentioned that recognition of the genus *Micheliella* is not supported by ITS molecular analysis.

Using TEM here, the pollens of *Keiskea* have been shown to possess loosely spaced columellae, seemingly unbranched compared with the grains of *Collinsonia*, which are somewhat densely packed and show sparse branching (cf. Fig. 3M-N). Such branched columellae are considered an advanced pollen character in Lamiaceae (Abu-Asab and Cantino, 1992, 1994). In *Collinsonia*, the intine seems to be thick, about two-thirds of the entire exine thickness. It is interesting to note that pollen grains with unbranched columellae are considered to be in a plesiomorphic condition, and found in most gynobasic-styled Lamiaceae (Abu-Asab and Cantino, 1992; Wagstaff, 1992). Wagstaff (1992) has suggested that the tectate-perforate pollen grains of *Collinsonia* have evolved through a different process-reduction in the height of the supratectal ridges, meaning that the grains of *Keiskea* are more primitive based on pollen data. This is agreed by the present author. That hypothesis is also supported by their distributional patterns (i.e., *Collinsonia* in eastern North America versus *Keiskea* in eastern Asia). One might assume that the former is possibly derived from the stock of a common ancestor for the east-Asian *Keiskea*.

Harley et al. (2003) are insistent that there is a strong tendency within these genera for fewer ripe nutlets, with the characteristic globose to subglobose nutlets having a small abscission scar, and often being reduced to one through abortion (Hong, unpublished nutlet anatomy and SEM data). The structure of the inflorescence, calyx and corolla morphology, and the arrangement of the stamens are all very similar. The main difference appears to be in the median lobe of the anterior corolla lip, which is entire to emarginated in *Keiskea* and more or less fimbriate in *Collinsonia*. Therefore, based on such similarities, Harley et al. (2003, 2004) have included *Keiskea* as a synonym of *Collinsonia*.

However, Peirson et al. (2004) have argued that phylogenetic analysis of nuclear ribosomal ITS sequence data does not support this merger of *Collinsonia* and *Keiskea* into one genus. The pollen morphology of these two is well distinguished, as demonstrated by the present data, and clearly indicates that *Keiskea* is separate from *Collinsonia*. If one follows the premature ITS data of Peirson et al. (2004), then *Keiskea* and *Perilla* form a well-supported clade (96% bootstrap support), as do *Keiskea*, *Perilla*, and *Collinsonia* (92% bootstrap support). Although the genus *Elsholtzia* has been shown to be a sister to the other genera of the tribe Elsholtzieae, Peirson et al. (2004) have used only one representative each of *Keiskea*, *Perilla*, and *Elsholtzia* for ITS analysis. Furthermore, because of such small sample sizes, one cannot absolutely claim that a more exact systematics relationship exists between *Collinsonia* and *Keiskea*. It is also noteworthy that the pollen morphology of *Keiskea* is closer to that of the genus *Elsholtzia*, which is finely well-developed bi-reticulate with polygonal or sometimes irregular supratectal ridges (Hong, unpublished data). Zhou et al. (1997) also have mentioned that *Elsholtzia* and *Keiskea* and, possibly, *Perillula* are similar to each other based on their pollen ornamentations. Therefore, further detailed study of pollen morphology as well as other informative characters (including molecular data from a more expanded taxa) will enable us to elucidate the important intergeneric relationships within the tribe Elsholtzieae.

In conclusion, exine and intine characters are clearly distinct between *Keiskea* (well-developed bi-reticulate, often forming large lumina by supratectal ridges, unbranched columellae, one-third to one-half of the total exine thickness) and *Collinsonia* (mostly perforate without supratectal ridges or a faint/very weak bi-reticulate appearance without supratectal ridges, seemingly branched columellae, about two-thirds of the total exine thickness). These pollen traits appear to be more relevant from a systematics point of view than any others. This distinction is well supported by data from the present study of morphologies from these two genera.

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