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Pollen Morphology of the Tribe Vernonieae (Compositae) in Thailand

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ABSTRACT.– The pollen morphology of 27 species from five genera in the tribe Vernonieae (Compositae) was examined with light and scanning electron microscopy. Three major pollen types, based on exine sculpturing, could be recognized; subechinolophate, echinolophate and psilolophate. The pollen is spheroidal and isopolar. Most (21/27) of the species' pollen are echinolophate except for four and two species which are subechinolophate and psilolophate, respectively. The pollen, based on aperture type, can be divided into tricolporate, triporate and six-porate. The distribution of triporate and tricolporate pollen between species does not support Robinson's (1999a) notion of restriction to the genera *Elephantopus* and *Vernonia*, respectively, but rather tricolporate and porate grains are found in woody plants and herbs, respectively. The six-porate pollen reported here in the *Vernonia* tribe has not been recorded within the Compositae family before and extends the diversity of pollen morphology and evolution.

KEY WORDS: Pollen morphology, Vernonieae, Compositae, Thailand

INTRODUCTION

Wodehouse (1928) investigated systematic and evolutionary themes based on Vernonieae pollen morphology. He observed the pollen surface morphology in North American *Vernonia* species and recognized two basic forms; echinolophate and subechi-nolophate. The pollen grains varied in size and had exine sculpturing such as lacuna, germinal furrows, spines and other protuberances and ridges or crests. Smith (1969) studied the variation in pollen size and shape of 64 African *Vernonia* species from the *Stenogalia* section using light microscopy (LM), recording that the average pollen diameter was 51.9 μm and that most grains were spheroidal and tricolporate. Jones (1970) also recognized two pollen types in 23 species of North American *Vernonia* using scanning electron microscopy (SEM), and

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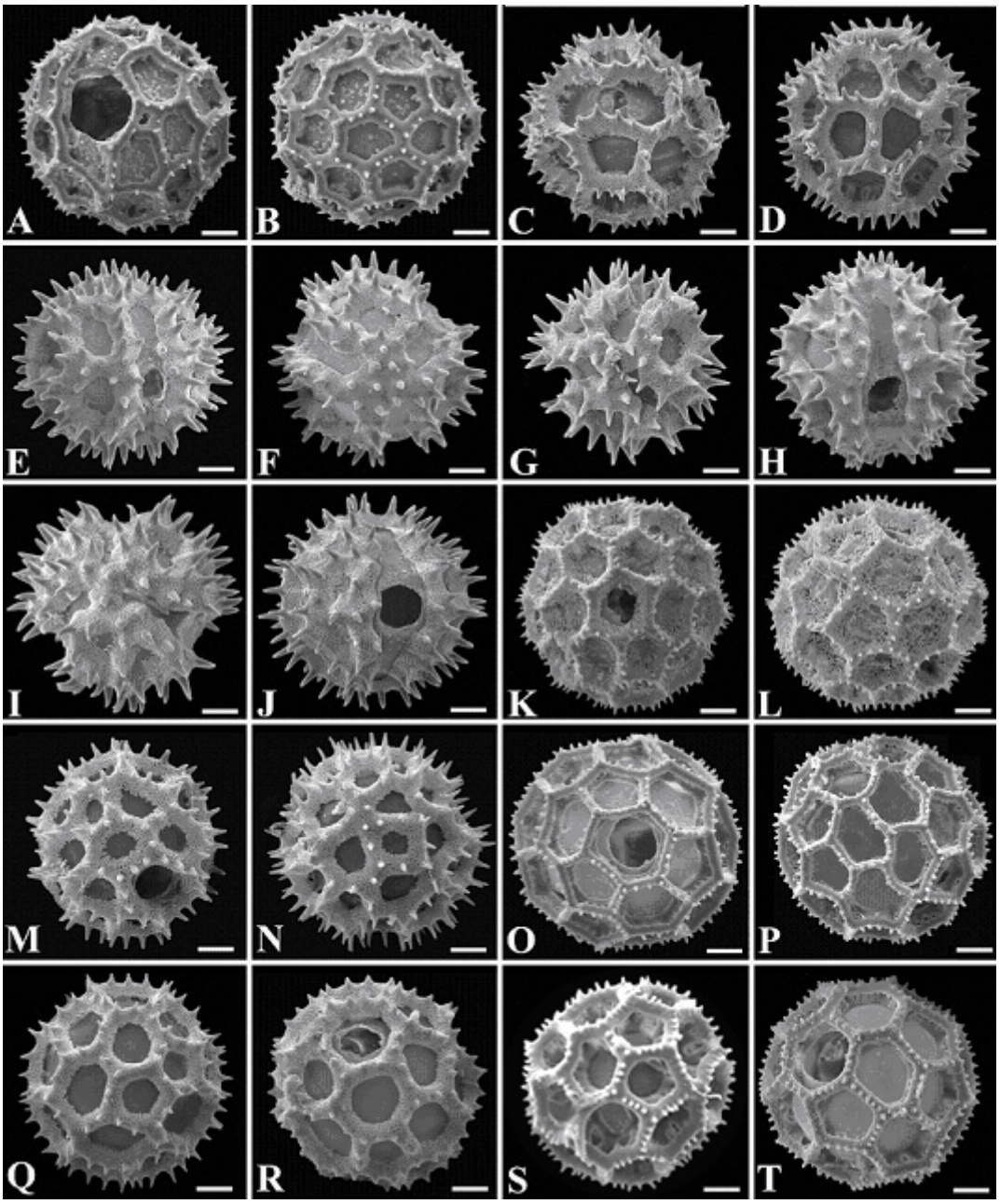

FIGURE 1. Echinolophate type. Subtype I, group 1: tricolporate with oblong colpi, *E. mollis* (**A-B**) and *I. eberhardtii* (**C-D**). Subtype I, group II: tricolporate with elliptic colpi and long spines, *V. cumingiana* (**E-F**), *V. eberhardtii* (**G-H**), *V. garrettiana* (**I-J**). Subtype II, group 1: triporate with discontinuous micropuncta, *S. sparganophorum* (**K-L**), *V. cinerea* (**M-N**), *V. divergens* (**O-P**), *V. patula* (**Q-R**). Subtype II, group II: triporate without micropuncta, *E. scaber* (**S-T**). Scale bars = 6 μm.

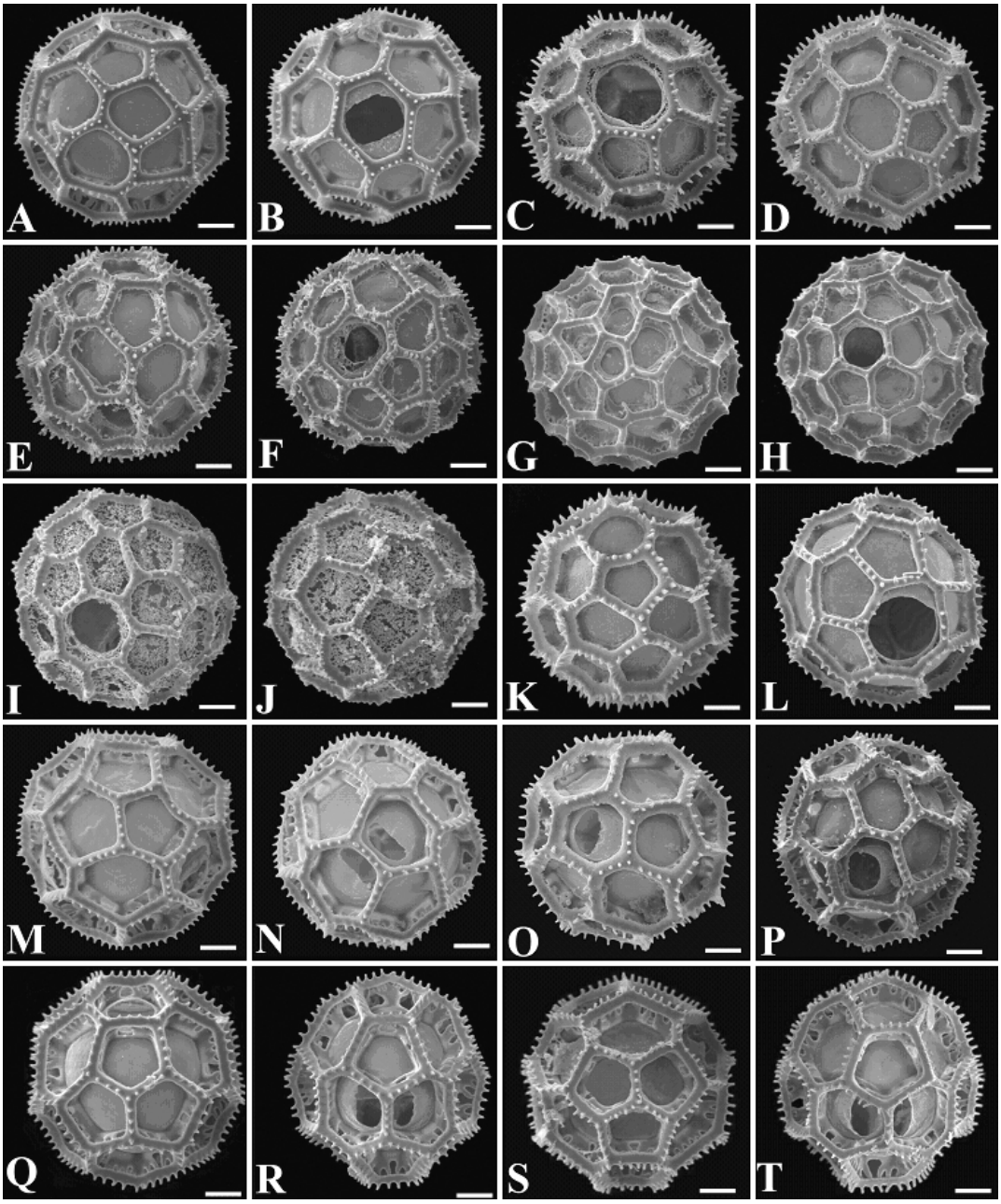

FIGURE 2. Echinolophate type. Subtype II, group II: triporate without micropuncta, *E. spicatus* (**A-B**), *V. attenuata* (**C-D**), *V. kingii* (**E-F**), *V. silhetensis* (**G-H**), *V. squarrosa* (**I-J**), *V. sutepensis* (**K-L**). Subtype III: six-porate without micropuncta, prominent columella, *C. loloana* (**M-N**), *C. pentagona* (**O**), *C. tenuiflora* (**P**), *C. spinulifera* (**Q-R**), *I. gracilis* (**S-T**). Scale bars = 6 μm.

suggested that several species groups showed an evolutionary trend from the subechino-lophate to echinolophate pollen type. Whilst both types showed three germinal pores and furrows, only the subechinolophate grains always show germinal furrows. Kingham (1976) noted six main pollen types (I-VI) in 85 Vernonieae species from tropical Africa and ordered trends from the more primitive echinate or subechinolophate to the more advanced echinolophate and psilolophate. The echinate and subechinolophate grains are always tricolporate with micropuncta, the lophate with micropuncta are confined to American species and tricolporate morphology is more primitive than triporate. Keeley and Jones (1977) investigated the external pollen morphology of 39 species of West Indian *Vernonia* and recognized three distinct pollen types (A-C) and a further three types (D-F) from an extended study of over 500 *Vernonia* species (Keeley and Jones, 1979). They noted that the pollen of many Old world species are spineless, type A pollen, and that this is the most common in Africa and southeastern Asia. The type is subechinolophate tricolporate with continuous micropuncta and is probably the ancestral type for *Vernonia*. Other types show discontinuous micropuncta and well developed columella. In addition, pollen morphology supports a broad generic concept in *Vernonia*. Using the defined six pollen types (A-F) of Keeley and Jones (1977, 1979), Jones (1981) studied the pollen morphology of the Old World *Vernonia* and only found pollen types E and F in this area. Blackmore (1986) examined lophate pollen of the tribes Arctoteae, Lactuceae, Mutisieae and Vernonieae and agreed with Wodehouse (1935) that echinate pollen is the primitive condition in the family and lophate pollen is derived from it. Furthermore, the psilolophate condition is derived by the gradual suppression of spines. Robinson significantly extended the Vernonieae pollen morphological database (Robinson, 1987a,b,c, 1988a,b,c,d, 1990, 1992a,b, 1999a,b; Robinson and Kahn, 1986) and suggested that tricolportae and triportae pollen were restricted to the genera *Vernonia* and *Elephantopus*, respectively (Robinson, 1999a). Skvarla et al. (2005) investigated *Vernonia* and *Elephantopus* pollen using scanning and transmission electron microscopy and found that all *Vernonia* pollen was subechinolophate, as described by Wodehouse (1928), with columella covered by micropuncta. *Elephantopus* pollen was echinolophate and extended the morphological range for this genus. It is clear that only one sculpture pattern, lophate, characterises Vernonieae pollen and that it embraces two forms, subechinolophate and lophate.

MATERIALS AND METHODS

Pollen from 27 species in the tribe Vernonieae were examined by LM and SEM. Pollen was obtained from field collections around Thailand by the first author and from herbarium specimens. Voucher specimens, along with author citations for taxa, are listed in the appendix. Pollen samples for LM and SEM were acetolyzed following the technique of Erdtman (1960). For LM, acetolyzed pollen was mounted in silicone oil and sealed with paraplast. At least 15 pollen grains per species were used to measure the pollen size, spine, pore, furrow and exine

thickness. For SEM, acetolysed pollen was freeze dried by the critical point drying (CPD) method, placed on specimen stubs with double sided silver tape and sputter-coated with gold. Photomicrographs were taken with SEM (LEO, 1450VP). Pollen terminology follows that of Wodehouse (1928, 1935) and Punt et al. (1994).

Results and Discussions

The pollen grains have polar axes that range from 25-56 μm, equatorial diameters that range from 27-58 μm, and are spheroidal (P/E = 0.91–1.06) (Table 1). All species examined are monad, isopolar and generally spheroidal in shape. Exine thickness ranges from 2-8 μm, spine length ranges from 0-6 μm; grains of some species are spineless, pore diameter varies from 3-15 μm and is usually circular, colpi range from 8-38 μm and varies from both oblong to elliptic. The apertures exist in three types; tricolporate, triporate and six-porate. Three exine sculpturing patterns are present within the group studied; subechinolophate, echinolophate and psilolophate.

Echinolophate type has the highest variation in aperture types and can be divided into three subtypes: tricolporate, triporate and six-porate.

Tricolporate subtype exhibits a great deal of variation in the shape of the colpus and polar lacuna, and can be subdivided into two groups. Group I have a tricolporate grain with a short oblong colpi and a polar lacuna; *E. mollis* and *I. eberhardtii*. The pollen is similar to pollen type C (Jones, 1977, 1981; Keeley and Jones, 1977, 1979) and pollen type IV (Kingham, 1976). *E. mollis* is a scandent perennial herb with rhizomes and differs from other members in this genus by its distinct colpi of the pollen. Group II is a tricolporate grain with long elliptic colpi and without polar lacuna. The polar area of *V. cumingiana* is wide with 3-4 rows of spines, but narrow with only one row of spines in *V. eberhartii* and *V. garrettiana*. The pollen of this group has conspicuous micropuncta (net-like tecta) on muri that hide its columella. The pollen of this group is similar to pollen type B (Jones, 1977, 1981; Keeley and Jones, 1977, 1979) and pollen type IV (Kingham, 1976).

Triporate subtype is subdivided into two groups. Group I is triporate with discontinuous micropuncta and unexposed columella which occur in *S. spargano-phorum*, *V. cinerea*, *V. divergens* and *V. patula* (Fig. 1). These characteristics belong to pollen type D (Jones, 1977, 1981; Keeley and Jones, 1977, 1979), pollen type II (Kingham, 1976) and pollen of *V. cinerea* type (Blackmore, 1986). Group II is triporate with a well exposed columella. There are blunt spinules less than 1.5 μm in *V. silhetensis* and *V. squarrosa*. *E. scaber* var. *scaber*, *E. scaber* var. *penicillatus*, *E. spicatus* and *V. divergens* are grouped by having a point spinule. The spines of *V. attenuata*, *V. kingii* and *V. sutepensis* are acute and longer than 1.5 μm (Fig. 2). The pollen of this group is similar to pollen type E (Jones, 1977, 1981; Keeley and Jones, 1977, 1979) and pollen type I (Kingham, 1976).

Six-porate subtype comprises all species of *Camchaya* and *I. gracilis* which are recognized by its conspicuous pairs of germinal pores in side-by-side lacuna (Fig. 2). The features of those pores are incomplete openings in a half to nearly

TABLE 1. Pollen measurements of Vernonieae. (Measurements represent mean, low and high values, P = polar axis, E = equatorial axis, P/E = ratio of polar axis and equatorial axis; 0.88 – 1.14 = spheroidal, SL = spine length, ET = exine thickness, PD = pore diameter, CL = colpus length, MP = micropuncta, PL = polar lacuna, + = present, - = absent. All units in μm)

Species	P	E	P/E	SL	ET
Camchaya loloana Kerr	42.5(38-48)	43(41-45)	0.99	1.0-2.0	5.0-7.0
C. pentagona H.Koyama	42.4(39-49)	42.9(37-48)	0.99	1.0-1.5	4.0-7.0
C. spinulifera H.Koyama	45.1(42.5-47.5)	45.4(41.2-47.5)	0.99	1.5-2.5	5.0-6.5
C. tenuiflora Kerr	44.5(38-48)	42.9(37-48)	1.04	1.0-1.5	5.0-7.0
Elephantopus mollis H.B.K.	33.1(29-36)	31.6(29-35)	1.05	1.0-1.5	2.0-4.0
E. scaber L.	30.1(25-35)	32.3(27.5-35)	0.93	1.0 -1.5	3.0-5.0
E. scaber var. *penicillatus* Gagnep.	32.7(30-35)	33(32-35)	0.99	0.5-1.0	3.0-5.0
E. spicatus Aubl.	37.7(31-42)	38.5(31-42)	0.98	1.0-1.0	4.0-5.0
Iodocephalus eberhardtii Gagnep.	44.3(37.5-47.5)	46.5(37.5-50)	0.95	2.5-3.0	5.0-7.5
I. gracilis Thorel et Gagnep.	43.4(37-48)	44.6(40-50)	0.97	1.0-2.0	5.0-8.0
Struchium. sparganophorum (L.) Kuntze	32.93(28-39)	31.8(27.5-36)	1.04	1.0-1.5	3.0-4.5
Vernonia arborea Buch.-Ham.	31.8(27-35)	31.7(29-37)	1.00	3.5-5.0	2.0-4.0
V. attenuata DC.	40.3(37.5-42.5)	40.3(37.5-42.5)	1.00	2.0-2.5	2.0-2.0
V. cinerea var. *montana* (C.B.Clake) Koster	29.3(27.5-30)	30.4(28-33)	0.96	1.5-2.0	2.0-4.0
V. cumingiana Benth.	37.4(35-40)	41.4(35-48)	0.90	4.0-5.0	3.0-5.0
V. divergens (DC.) Edgew.	35.4(30-40)	34.2(32.5-37)	1.04	1.0-1.5	2.5-5.0
V. eberhardtii Gagnep.	34.7(32.5-37.5)	33.3(32.5-35)	1.04	3.0-5.0	3.0-6.0
V. elliptica DC.	29.8(29-33)	31.4(29-35)	0.95	4.0-6.0	3.0-5.0
V. extensa DC.	36(33-37)	37.5(34-44)	0.96	4.0-6.0	4.0-7.0
V. garrettiana Craib	39.2(38-40)	42.9(38-46)	0.91	4.0-6.0	3.0-6.0
V. kingii C.B.Clake	46.8(37-53)	45.1(40-54)	1.04	1.0-2.0	3.0-5.0
V. parishii Hook.f.	39.8(32.5-47.5)	39.5(35-45)	1.01	0	5.0-7.5
V. patula (Dryand.) Merr.	30.4(30-31)	28.95(27-30)	1.05	1.0-1.5	3.0-4.0
V. silhetensis (DC.) Hand.-Mazz.	52.9(38-56)	54.7(50-58)	0.97	0.5-1.0	5.0-7.5
V. solanifolia Benth.	31.8(27-37)	32.7(29-36)	0.97	3.0-6.0	3.0-5.0
V. squarrosa Less.	47.25(45-50)	46.63(45-50)	1.01	0.5-1.0	5.0-7.5
V. sutepensis Kerr	38.8(32.5-45)	36.6(35-40)	1.06	1.0-2.5	2.5-5.0
V. volkameriifolia DC.	41.3(37.5-45)	44.5(42.5-47.5)	0.93	0	5.0-7.5

circular shape. The six-porate echinolophate pollen is new pollen phenotype (character) within both the Vernonieae tribe and Compositae family. Until now taxonomists have only recognized the aperture type of Vernonieae triporate and tricolporate forms (Wodehouse, 1928, 1935; Erdtman, 1952; Smith, 1969; Jones, 1970, 1977, 1981;

PD	CL	Habit	Pollen type	Exine sculpture	MP	PL
8.0-13.0	-	herb	6-porate	Echinolophate	-	+
4.0-12.0	-	herb	6-porate	Echinolophate	-	+
7.5-8.5	-	herb	6-porate	Echinolophate	-	+
5.0-10.0	-	herb	6-porate	Echinolophate	-	+
5.0-8.0	9-11	herb	3-colporate	Echinolophate	-	+
5.0-10.0	-	herb	3-porate	Echinolophate	-	+
4.0-9.0	-	herb	3-porate	Echinolophate	-	+
7.0-12.0	-	herb	3-porate	Echinolophate	-	+
10.0-12.5	22-27	herb	3-colporate	Echinolophate	+	+
7.0-10.0	-	herb	6-porate	Echinolophate	-	+
5.0-10.0	-	herb	3-porate	Echinolophate	+	+
3.0-6.0	20-27	tree	3-colporate	Subechinolophate	+	-
5.0-10.0	-	herb	3-porate	Echinolophate	-	+
7.0-11.0	8-13	herb	3-porate	Echinolophate	+	+
6.5-10.0	25-35	woody scandent	3-colporate	Echinolophate	+	-
6.5-12.0	-	herb	3-porate	Echinolophate	-	+
3.0-10.0	30-35	woody scandent	3-colporate	Echinolophate	+	-
6.0-10.5	18-20	woody scandent	3-colporate	Subechinolophate	+	-
6.5-8.0	30-35	small shrub	3-colporate	Subechinolophate	+	-
10.0-12.0	35-38	woody scandent	3-colporate	Echinolophate	+	-
10.0-14.0	-	herb	3-porate	Echinolophate	-	+
8.5-13.0	26-32	Small shrub	3-colporate	Psilolophate	-	+
4.5-7.0	-	herb	3-porate	Echinolophate	+	+
6.0-15.0	-	herb	3-porate	Echinolophate	-	+
8.0-14.0	25-30	woody scandent	3-colporate	Subechinolophate	+	-
8.5-14.0	-	herb	3-porate	Echinolophate	-	+
4.5-15.0	-	herb	3-porate	Echinolophate	-	+
5.0-10.0	28-35	tree	3-colporate	Psilolophate	-	+

Keeley and Jones, 1977, 1979; Kingham, 1976; Blackmore, 1986; Robinson and Kahn, 1986; Skvarla et al., 2005).

Subechinolophate type is tricolporate consisting of continuous micropuncta and exhibits both narrow and broad polar areas. The polar areas of *V. arborea* and *V.*

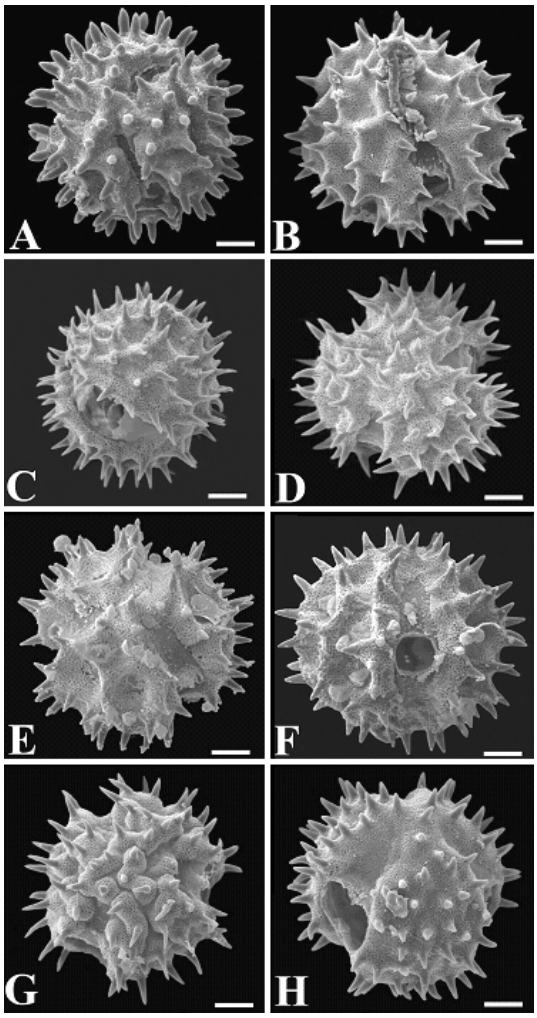

FIGURE 3. Subechinolophate type. Tricolporate, present polar area, continuous micropuncta, long and pointed spine. *V. arborea* (**A-B**) and *V. elliptica* (**C-D**) are narrow polar areas. *V. extensa* (**E-F**) and *V. solanifolia* (**G-H**) are broad polar areas. Scale bars = 6 μm.

extensa are narrow with a single row of spines, whereas *V. elliptica* and *V. solanifolia* show a broad polar area with 2-4 rows of acute spines (Fig. 3). These features are similar to the descriptions of subechinolophate pollen (Wodehouse, 1928; Erdtman, 1952; Skvarla, 2005), pollen type

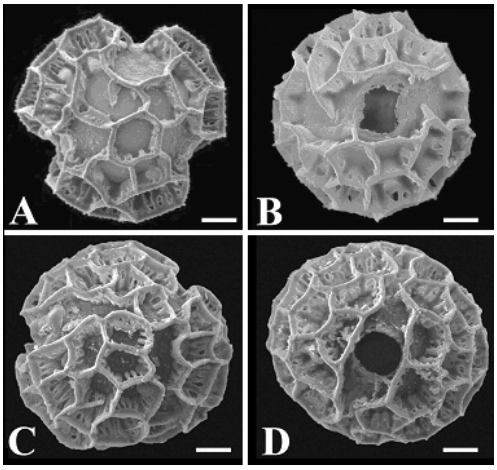

FIGURE 4. Psilolophate type. Tricolporate without micropuncta. *V. parishii* (**A-B**) has 3-4 polar lacunae. *V. volkameriifolia* (**C-D**) has single polar lacunae and approximately 40 lacunae. Scale bars = 6 μm.

A (Jones, 1977, 1981; Keeley and Jones, 1977, 1979) and pollen type VI (Kingham, 1976).

Psilolophate type is also tricolporate but with elliptic colpi without spines on muri. *V. parishii* has 3-4 polar lacunae, whereas *V. volkameriifolia* has a single one (Fig. 4). These features are similar to the description of pollen type III (Kingham, 1976). In contrast, Jones (1981) described pollen of *V. volkameriifolia* as pollen type B and *V. parishii* as type F. The exine sculpturing of *V. volkameriifolia* in Thailand is unique in that it has a single polar lacuna, well exposed unbranched columella, without micropuncta, and approximately 40 lacunae per grain. The grains of Thai *V. parishii* are thus quite different from pollen type F (Jones, 1981) and distinguished by their conspicuous long elliptic colpi. Pollen type F, however, has inconspicuous colpi and only muri interrupted by pores.

TABLE 2. Pollen grouping of Vernonieae in Thailand.

Type	Sculptural type	Subtype	Group	species
1	Echinolophate	I (tricolporate)	I	*E. mollis*, *I. eberhardtii* (2 spp.)
			II	*V. cumingiana, V. eberhardtii*, *V. garrettiana* (3 spp.)
		II (triporate)	I	*S. sparganophorum, V. cinerea*, *V. divergens*, *V. patula* (4 spp.)
			II	*E. scaber, E. spicatus, V. attenuata, V. kingii, V. silhetensis, V. squarrosa*, *V. sutepensis* (7 spp.)
		III (six-porate)	-	*C. loloana, C. pentagona, C. spinulifera, C. tenuiflora*, *I. gracilis* (5 spp.)
2	Subechinolophate	-	-	*V. arborea, V. elliptica, V. extensa*, *V. solanifolia* (4 spp.)
3	Psilolophate	-	-	*V. parishii*, *V. volkameriifolia* (2 spp.)

CONCLUSION

The pollen of Vernonieae in Thailand is divided into three major sculptural types. The Echinolophate type can be further subdivided into three subtypes (tricolporate, triporate and six-porate) and within that divided into five groups. The distribution of tricolporate and triporate grains in these Thai samples does not conform to the restricted taxa distribution of *Vernonia* and *Elephantopus*, respectively (Robinson, 1999a), but rather tricolporate and porate grains are confined to woody plants and herbs, respectively. The six-porate pollen type is a new phenotype and systematic character for the Vernonieae (Table 2).

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APPENDIX

Pollen of taxa are listed in alphabetical order and deposited at KKU (Khon Kaen University herbarium), BK (Bangkok herbarium, Department of Agriculture) and QBG (Queen Sirikit Botanical Garden herbarium, Chiang Mai). Specimens marked with an asterisk (*) were collected from dried materials.

Camchaya loloana Kerr, *S. Bunwong* 37 (KKU); *C. pentagona, H. Koyama*, *S. Bunwong* 29 (KKU); *C. spinulifera H. Koyama, S. Bunwong* 11 (KKU); *C. tenuiflora* Kerr, *S. Bunwong* 48 (KKU); *Elephantopus mollis* H.B.K., *S. Bunwong* 9 (KKU); *E. scaber* L., *S. Bunwong* 10

(KKU); *E. scaber* var. *penicillatus* Gagnep., *S. Bunwong* 34 (KKU); *E. spicatus* Aubl., *S. Bunwong* 42 (KKU); *Iodocephalus eberhardtii* Gagnep., *S. Bunwong* 12 (KKU); *I. gracilis* Thorel et Gagnep., *S. Bunwong* 33 (KKU); *Struchium sparganophorum* (L.) Kuntze, *S. Bunwong* 28 (KKU); *Vernonia arborea* Buch.-Ham., *W. Nanakorn* 7163 (QBG)*; *V. attenuata* DC., *S. Bunwong* 15 (KKU); *V. cinerea* var. *montana* (C.B.Clake) Koster, *S. Bunwong* 62 (KKU); *V. cumingiana* Benth., *Winit* 1287 (BK)*; *V. divergens* (DC.) Edgew., *S. Bunwong* 59 (KKU); *V. eberhardtii* Gagnep., *S. Bunwong* 67 (KKU); *V. elliptica* DC., *S. Bunwong* 69 (KKU); *V. extensa* DC., *S. Bunwong* 76 (KKU); *V. garrettiana* Craib, *S. Bunwong* 75 (KKU); *V. kingii* C.B.Clake, *S. Bunwong* 51 (KKU); *V. parishii* Hook.f., *S. Bunwong* 72 (KKU); *V. patula* (Dryand.) Merr., *Sakol* 1875 (BK)*; *V. silhetensis* (DC.) Hand.-Mazz., *S. Bunwong* 49 (KKU); *V. solanifolia* Benth., *S. Bunwong* 70 (KKU); *V. squarrosa* Less., *S. Bunwong* 20 (KKU); *V. sutepensis* Kerr, *S. Bunwong* 71 (KKU); *V. volkameriifolia* DC., *S. Bunwong* 60 (KKU).