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Pollen Morphology of the Genus *Campylotropis* (Leguminosae) in Thailand and Its Systematic Implications

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ABSTRACT.– Pollen grains of seven species of the genus *Campylotropis* in Thailand were described and illustrated based on investigations by light microscopy (LM) and scanning electron microscopy (SEM). The pollen grains were found to be generally monad, isopolar, radially symmetric and prolate. Apertures were tricolporate with lalongate endoapertures. The margo along colpi was psilate, perforate or absent. Exine ornamentation was microreticulate or microreticulate to reticulate, with lumina size diminishing toward the aperture. Types of lumina were a vertical or declined margin. The results of this study illustrated characteristics that can assist investigation of some *Campylotropis* pollen grains at interspecific level: presence and type of margo, type of ornamentation and type of lumina margin. Palynological studies of *Campylotropis bonii*, *C. harmsii* and *C. pinetorum* are firstly reported here. In addition, palynological description of each species, photographs and identification key to species based on palynological evidence are also presented.

KEY WORDS: *Campylotropis*, Leguminosae, palynology, Papilionoideae, Thailand

INTRODUCTION

The genus *Campylotropis* Bunge (Leguminosae, Papilionoideae) comprises about 37 species distributed in temperate and tropical Asia (Iokawa and Ohashi, 2002, 2008; Lewis et al., 2005; Puhua et al., 2010). The genus is morphologically distinguished by pinnately trifoliate leaves, light to dark violet, dark blue or pinkish-white to creamy-white corolla and 1-jointed, 1-seeded pods. In Thailand, seven taxa are currently enumerated on the basis of comparative macro morphology *viz*. *C. bonii* Schindl., *C. capillipes* (Franch.) Schindl. subsp. *prainii* Iokawa and Ohashi, *C. decora* (Kurz) Schindl., *C. harmsii* Schindl., *C. parviflora* (Kurz) Schindl., *C. pinetorum* (Kurz) Schindl. and *C. sulcata* Schindl. (Satthaphorn et al., 2018).

The pollen morphology of the genus was first described by Ohashi (1971) followed by subsequent authors, Mitra and Mondal (1982), Perveen and Qaiser (1998) and Xu et al. (2011). The major palynological study of the genus was conducted by Iokawa and Ohashi (2002) based on 24 species. Pollen grains of *Campylotropis* were reported as having tricolporate aperture with psilate colpi. They were generally prolate, subprolate or prolate spheroidal in shape, isopolar and radially symmetric. Exine sculpturing was noted as fine to coarse reticulate (Mitra and Mondal, 1982; Iokawa and Ohashi, 2002), while Xu et al. (2011) also reported glabrate type in exine ornamentation. However, *Campylotorpis* species have not been delimited by palynological characteristics nor is there a key to species for identifying infrageneric taxa.

Although variations in pollen surface characteristics were recognized as valuable aids in delimiting taxonomic relationships (Van Den Berg, 1984; Rajbhandary et al., 2012), the knowledge of pollen morphology of *Campylotropis*, especially in Thailand, is inadequate due to insufficient sampling. This investigation of pollen flora of the Thai *Campylotropis* and its taxonomic significance aims to clarify details of variations and to construct the a key of pollen. A discussion on the delimitation of Thai *Campylotropis* proposes that some species have been palynologically unknown.

MATERIALS AND METHODS

The pollen grains of all Thai *Campylotropis* species were sampled from herbarium specimens cited in the description (herbarium acronym follows Thiers, 2020). Pollen samples were treated using the acetolysis method following Erdtman (1954). For examination with light microscopy (LM), pollen grains were mounted in glycerine jelly and observed with the Olympus BX43 (Zetter, 1989). The lengths of polar and equatorial axes were measured and the exine thickness including outline, shape and ornamentation were recorded. Measurements were taken from at least 20 grains for each sample and are given with the standard deviation (SD). For examination with scanning electron microscopy (SEM), pollen grains were directly taped onto the specimen stub. The grains were coated with gold (Au) on the stub using an SPI−MODULETM Sputter Coater, SPI 11425. SEM was conducted with the FEI Quanta 400 apparatus and the overview and ornamentation at the center of the equatorial point were photographed. The palynological terminology is based on the criteria of Punt et al. (2007), Hesse et al. (2009) and Halbritter et al. (2018).

RESULTS

The results of palynological investigation of Thai *Campylotropis* are summarized in Table 1 and Figures 1–5. Pollen grains of *Campylotropis* were monad, isopolar, radially symmetric and prolate. The outline was convex triangular in polar view and elliptic in equatorial view. The length of the polar axis ranged from 19.8 µm (*C. bonii*) to 40.0 µm (*C. harmsii*) and the length of the equatorial axis from 15.6 µm (*C. bonii*) to 37.0 µm (*C. harmsii*). Apertures were tricolporate with lalongate endoapertures. The margo along colpi was psilate (*C. bonii* and *C. sulcata*) or perforate (*C. capillipes* subsp. *prainii*, *C. decora*, *C. harmsii* and *C. parviflora*), but absent in *C. pinetorum*. The length of colpi ranged from 15.4 µm (*C. bonii*) to 25.6 µm (*C. decora*). Protrusions at aperture were found in *C. harmsii*, *C. parviflora* and *C. pinetorum*, but were absent in the other species. Exine thickness ranged from 0.8 µm (*C. pinetorum* and *C. sulcata*) to 1.8 µm (*C. bonii* and *C. decora*). Exine ornamentation was microreticulate (*C. bonii*, *C. decora*, *C. parviflora* and *C. pinetorum*) and microreticulate to reticulate (*C. capillipes* subsp. *prainii*, *C. harmsii* and *C. sulcata*). Size of lumina was smaller towards the aperture. Margin of lumina was vertical in most species except declined in *C. capillipes* subsp. *prainii* and *C. decora*. Lumina diameter ranged from 0.2 µm (*C. decora*) to 2.0 µm (*C. harmsii*) with perforation at the base. The width of muri ranged from 0.2 µm (*C. bonii*, *C. capillipes* subsp. *prainii* and *C. pinetorum*) to 0.6 µm (*C. decora*, *C. parviflora* and *C. sulcata*). The identification key of Thai *Campylotropis* presented below is based on pollen morphology and a description of each species is appended.

TABLE 1. Investigation of pollen grains of *Campylotropis* in Thailand

Taxa	Polar axis (µm) min–max (average)	Equatorial axis (µm) min–max (average)	Colpi length (µm)	Margo	Orna-mentation type	Lumina margin	Lumina width (µm)	Muri width (µm)	Exine thickness (µm)	Voucher specimens
C. bonii	19.8–24.5 (22.4±1.2)	15.6–21.3 (19.3±1.2)	15.4–18.2	psilate	micro-reticulate	vertical	0.4–0.6	0.2–0.4	1.0–1.8	*Satthaphorn* and *Leeratiwong 81* (**PSU**)
C. capillipes subsp. *prainii*	24.5–30.0 (27.5±1.7)	19.6–26.3 (23.9±1.5)	17.3–21.1	perforate	micro-reticulate to reticulate	declined	0.5–1.1	0.2–0.5	0.9–1.3	*Satthaphorn* and *Leeratiwong 90* (**PSU**)
C. decora	22.5–32.5 (29.1±2.1)	19.6–27.5 (24.8±2.0)	20.6–25.6	perforate	micro-reticulate	declined	0.2–0.9	0.4–0.6	1.1–1.8	*Satthaphorn* and *Leeratiwong 91* (**PSU**)
C. harmsii	25.4–40.0 (31.7±3.7)	20.7–37.0 (27.6±3.6)	22.8–24.5	perforate	micro-reticulate to reticulte	vertical	0.8–2.0	0.3–0.5	1.0–1.2	*Satthaphorn* and *Leeratiwong 88* (**PSU**)
C. parviflora	25.0–30.0 (27.8±1.5)	18.4–23.8 (21.8±1.3)	20.9–22.9	perforate	micro-reticulate	vertical	0.3–0.9	0.3–0.6	0.9–1.3	*Satthaphorn* and *Leeratiwong 92* (**PSU**)
C. pinetorum	23.8–29.5 (26.2±1.7)	19.5–25.0 (22.3±1.5)	19.5–21.6	absent	micro-reticulate	vertical	0.4–0.9	0.2–0.3	0.8–1.3	*Satthaphorn* and *Leeratiwong 84* (**PSU**)
C. sulcata	22.4–28.5 (24.8±1.6)	17.9–24.5 (21.2±1.6)	18.9–22.0	psilate	micro-reticulate to reticulate	vertical	0.3–1.3	0.4–0.6	0.8–1.5	*Satthaphorn 75* (**PSU**)

Key to the species based on pollen morphology

1. Margo present
    2. Margo psilate
        3. Ornamentation microreticulate……………………………………………1. ***C. bonii***
        3. Ornamentation microreticulate to reticulate……………………………..7. ***C. sulcata***
    2. Margo perforate
        4. Lumina margin declined
            5. Ornamentation microreticulate……………………………………3. ***C. decora***
            5. Ornamentation microreticulate to reticulate…....2. ***C. capillipes*** subsp. ***prainii***
        4. Lumina margin vertical
            6. Ornamentation microreticulate……………………………..………..5. ***C. parviflora***
            6. Ornamentation microreticulate to reticulate……………….……..4. ***C. harmsii***
1. Margo absent……………………………………………………………..6. ***C. pinetorum***

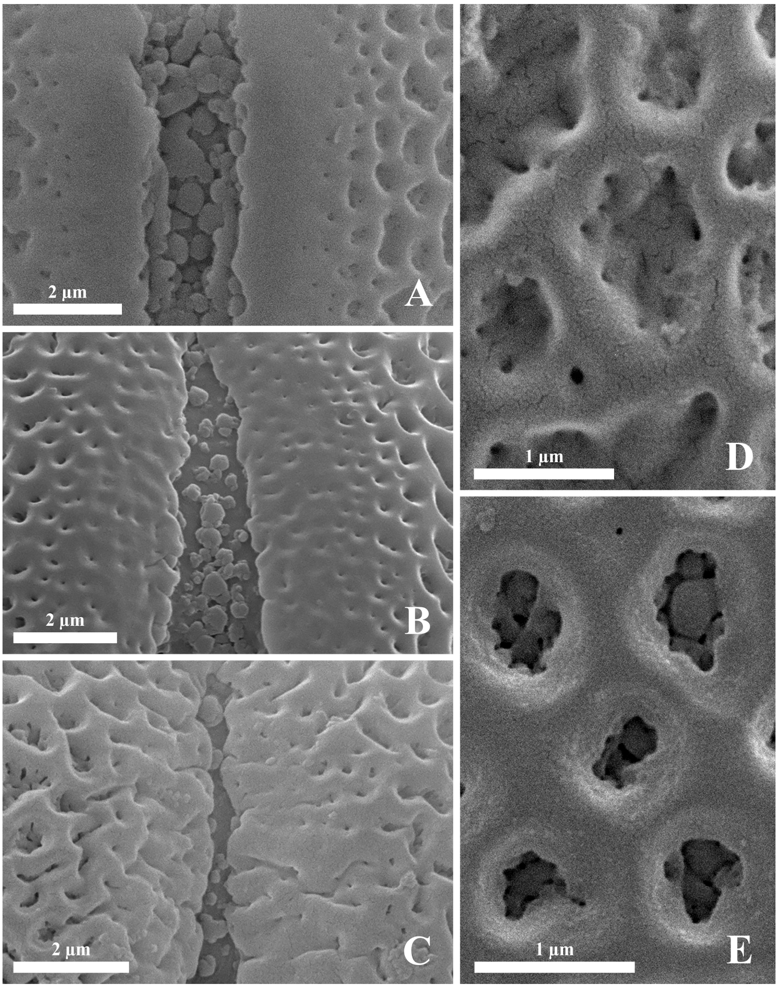

FIGURE 1. Significant characters that identify *Campylotropis* species in Thailand: A, psilate margo and absence of protrusion (*C. bonii*); B, perforate margo (*C. capillipes* subsp. *prainii*); C, absence of margo (*C. pinetorum*); D, vertical margin of lumina (*C. harmsii*); E, declined margin of lumina (*C. capillipes* subsp. *prainii*)

Pollen description of Thai *Campylotropis*

Pollen grains monad, isopolar, radially symmetric prolate; outline convex triangular in polar view, elliptic in equatorial view; tricolporate, margo psilate, perforate or absent; endoaperture lalongate; exine ornamentation microreticulate or microreticulate to reticulate; lumina margin vertical or declined, base perforate.

1. ***Campylotropis bonii*** (Figs. 2A–2D)

Description.— Length of polar diameter 19.8–24.5 µm; length of equatorial diameter 15.6–21.3 µm; margo psilate, colpi 15.4–18.2 µm long; endoaperture 4.5–5.6 µm long, 6.2–7.8 µm wide; exine 1.0–1.8 µm thick, microreticulate; lumina margin vertical, 0.4–0.6 µm wide with perforation, muri 0.2–0.4 µm wide.

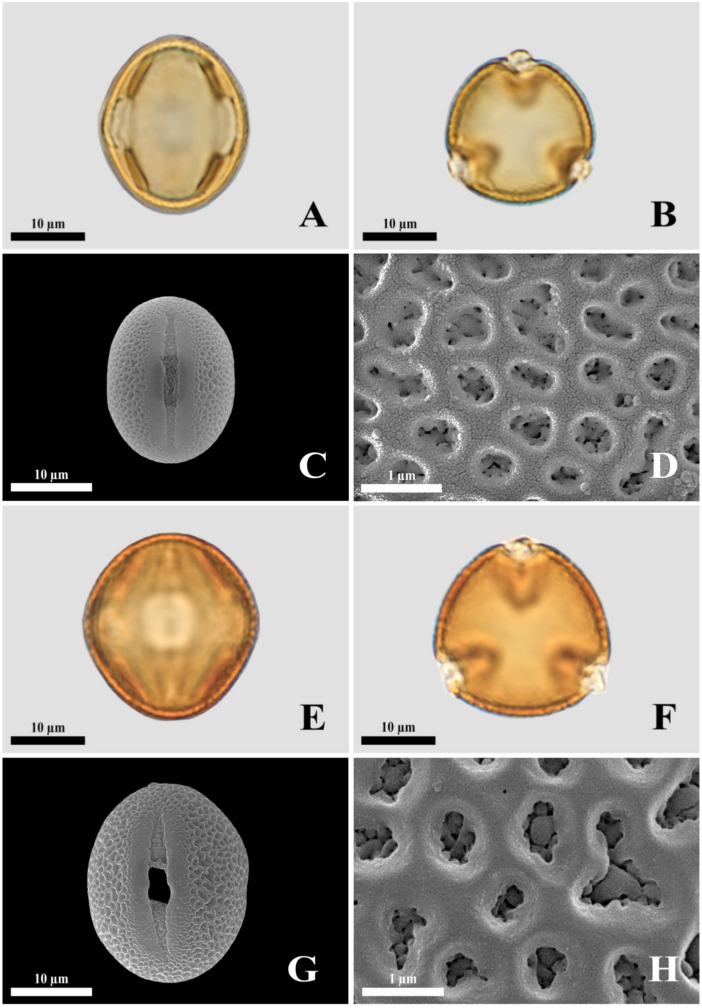

FIGURE 2. Pollen morphology of Thai *Campylotropis*: A-D, *C. bonii*; E-H, *C. capillipes* subsp. *prainii*; A & E, equatorial view; B & F, polar view; C & G, SEM overview of grains; D & H, SEM showing the ornamentation

Voucher specimen.— *Satthaphorn and Leeratiwong 81* (**PSU**).

Note. — Pollen grains of *C. bonii* are resembled to pollen grains of those *C. sulcata* in having a psilate margo along colpi but exine sculpturing is different. Microreticulate ornamentation can be found in *C. bonii*, whereas *C. sulcata* exhibits microreticulate to reticulate ornamentation.

2. ***Campylotropis capillipes*** subsp. ***prainii*** (Figs. 2E–2H)

Description.— Length of polar diameter 24.5–30.0 µm; length of equatorial diameter 19.6–26.3 µm; margo perforate, colpi 17.3–21.1 µm long; endoaperture 6.6–7.4 µm long, 7.7–8.0 µm wide; exine 0.9–1.3 µm thick, microreticulate to reticulate; lumina

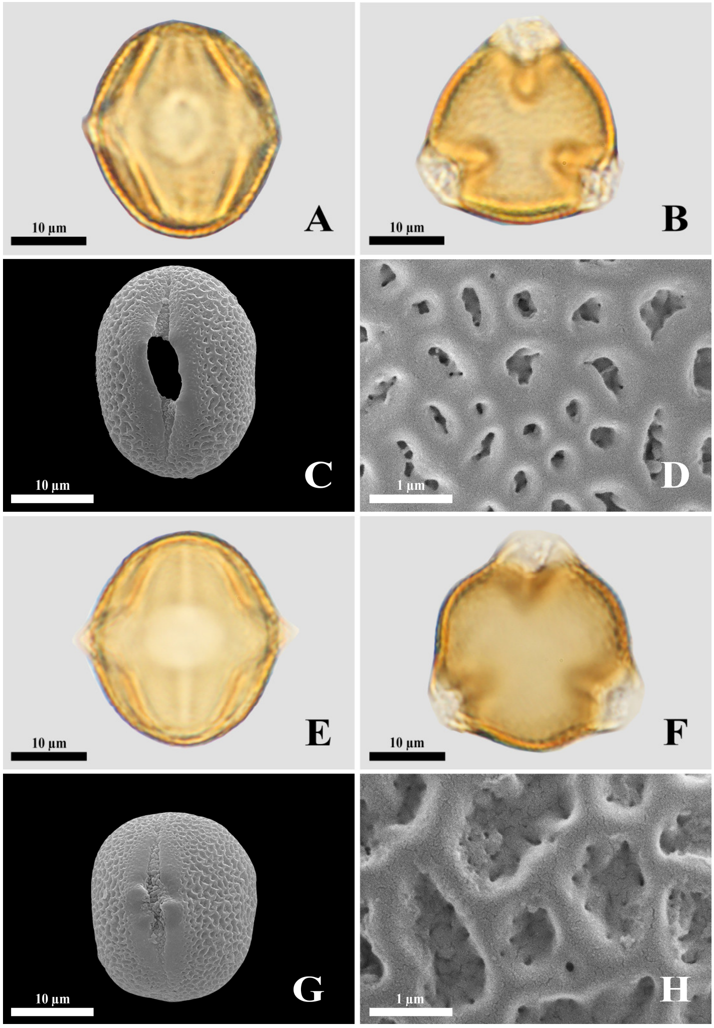

FIGURE 3. Pollen morphology of Thai *Campylotropis*: A-D, *C. decora*; E-H, *C. harmsii*; A & E, equatorial view; B & F, polar view; C & G, SEM overview of grains; D & H, SEM showing the ornamentation

margin declined, 0.5–1.1 µm wide, muri 0.2–0.5 µm wide.

Voucher specimen.— *Satthaphorn and Leeratiwong 90* (**PSU**).

Note.— Pollen grains of the species exhibit the declined margin of lumina which is similar to pollen grains of *C. decora*. However, this character is different from the vertical margin of lumina in the other species.

3. ***Campylotropis decora*** (Figs. 3A–3D)

Description.— Length of polar diameter 22.5–32.5 µm; length of equatorial diameter 19.6–27.5 µm; margo perforate, colpi 20.6–25.6 µm long; endoaperture 8.0–10.4 µm long, 9.7–10.6 µm wide; exine 1.1–1.8 µm thick, microreticulate; lumina margin declined, 0.2–0.9 µm wide, muri 0.4–0.6 µm wide.

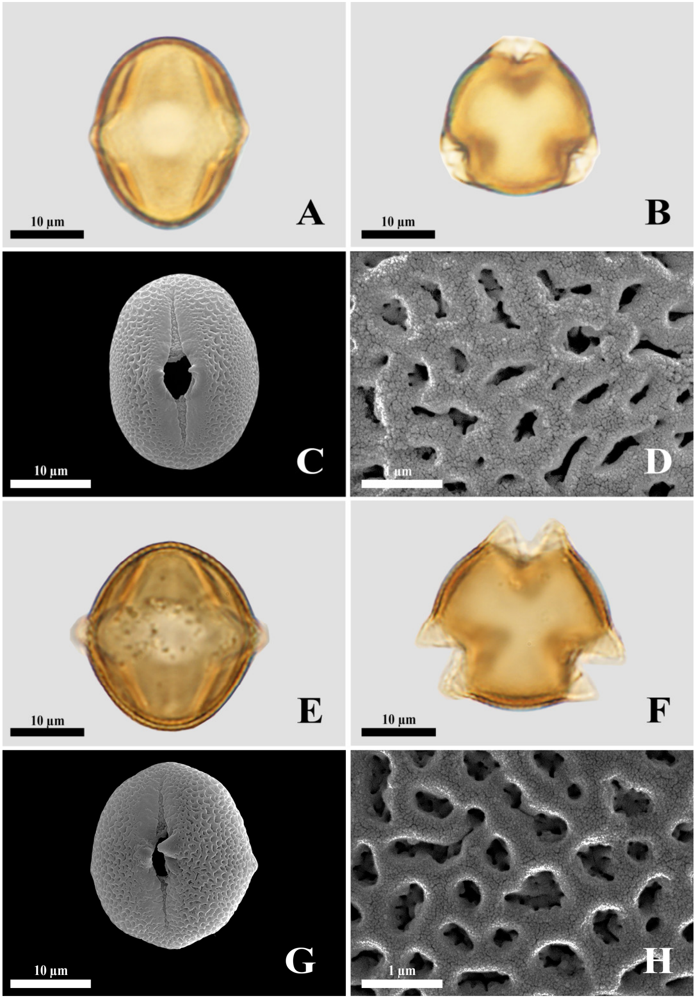

FIGURE 4. Pollen morphology of Thai *Campylotropis*: A-D, *C. parviflora*; E-H, *C. pinetorum*; A & E, equatorial view; B & F, polar view; C & G, SEM overview of grains; D & H, SEM showing the ornamentation

Voucher specimen.— *Satthaphorn and Leeratiwong 91* (**PSU**).

4. ***Campylotropis harmsii*** (Figs. 3E–3H)
Description.— Length of polar diameter 25.4–40.0 µm; length of equatorial diameter 20.7–37.0 µm; margo perforate, colpi 22.8–24.5 µm long; endoaperture 5.4–9.0 µm long, 7.6–9.0 µm wide; exine 1.0–1.2 µm thick, microreticulate to reticulate; lumina margin vertical, 0.8–2.0 µm wide, muri 0.3–0.5 µm wide.
Voucher specimen.— *Satthaphorn and Leeratiwong 88* (**PSU**).

5. ***Campylotropis parviflora*** (Figs. 4A–4D)
Description.— Length of polar diameter 25.0–30.0 µm; length of equatorial diameter 18.4–23.8 µm; margo perforate, colpi 20.9–22.9 µm long; endoaperture 6.6–7.9 µm

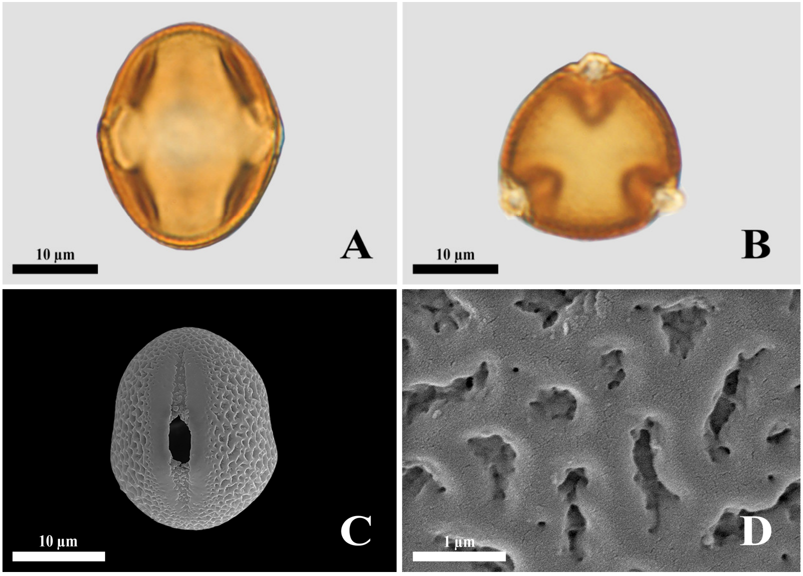

FIGURE 5. Pollen morphology of Thai *Campylotropis*: A-D, *C. sulcata*; A, equatorial view; B, polar view; C, SEM overview of grains; D, SEM showing the ornamentation

long, 7.4–8.9 µm wide; exine 0.9–1.3 µm thick, microreticulate; lumina margin vertical, 0.3–0.9 µm wide, muri 0.3–0.6 µm wide.
Voucher specimen.— *Satthaphorn and Leeratiwong 92* (**PSU**).

6. ***Campylotropis pinetorum*** (Figs. 4E–4H)
Description.— Length of polar diameter 23.8–29.5 µm; length of equatorial diameter 19.5–25.0 µm; margo absent, colpi 19.5–21.6 µm long; endoaperture 8.0–8.6 µm long, 7.5–8.9 µm wide; exine 0.8–1.3 µm thick, microreticulate; lumina margin vertical, 0.4–0.9 µm wide, muri 0.2–0.3 µm wide.
Voucher specimen.— *Satthaphorn and Leeratiwong 84* (**PSU**).
Note.— Pollen grains of *C. pinetorum* were apparently distinguished from other species by the absence of margo along the colpi.

7. ***Campylotropis sulcata*** (Figs. 5A–5D)
Description.— Length of polar diameter 22.4–28.5 µm; length of equatorial diameter 17.9–24.5 µm; margo psilate, colpi 18.9–22.0 µm long; endoaperture 6.7–7.9 µm long, 6.7–8.0 µm wide; exine 0.8–1.5 µm thick, microreticulate to reticulate; lumina margin vertical, 0.3–1.3 µm wide, muri 0.4–0.6 µm wide.
Voucher specimen.— *Satthaphorn 75* (**PSU**).

DISCUSSION AND CONCLUSIONS

Pollen grains of the genus *Campylotropis* in this study are monad, prolate, isopolar, radially symmetric and tricolporate with lalongate endoaperture. This pollen morphology is congruent with palynological studies of Guinet (1981) and Ferguson and Skvarla (1981) that the basic type of pollen grains in the family Leguminosae is tectate-reticulate single grains with tricolporate aperture. This pollen type is recognized as an advance character in Angiosperms. Interestingly, flowers in the subfamily Papilionoideae have highly evolved with an explosive pollination mechanism which required pollinators such as insects, birds and bats, to stimulate pollen grains releasing (Aluri and Reddi, 1995; Miguel-Peñaloza et al., 2019). Ferguson and Skvarla (1982) revealed that entomophilous pollination species in the subfamily Papilionoideae contain simple reticulate or perforate surface sculpturing pollen grains, while bird-pollinated and bats-pollinated species illustrate coarsely rugulate or verrucate pollen grains and stickier than those entomophilous pollen grains. Because the *Campylotropis* flowers are not showy and easily breaking, the pollinators of the genus are predominant by insect groups especially bees rather than those huge and solid papilionaceous flowers, for instance, *Erythina* or *Mucuna* species which require birds or bats (Graham and Tomb, 1977; Arrayo, 1981).

The findings of this study uncovered characteristics that can assist investigation of some *Campylotropis* pollen grains at interspecific level. These characteristics included presence and type of margo (psilate, perforate and absent, Figs. 1A-1C), type of exine ornamentation (microreticulate vs microreticulate to reticulate) and type of lumina margin (vertical vs declined, Figs. 1D-1E). Even though the presence of protrusion seemed to be observed as a distinct feature in *C. harmsii*, *C. parviflora* and *C. pinetorum* (Figs. 3G, 4C, 4G), the study of Kuang et al. (2012) pointed out that the presence or absence of this character depends on anther stage and acetolysis technique. This character should be excluded from taxonomic structures. Although pollen morphology of *C. capillipes* subsp. *prainii*, *C. decora*, *C. parviflora* and *C. sulcata* were described in previous studies (Ohashi, 1971; Mitra and Mondal, 1982; Perveen and Qaiser, 1998; Iokawa and Ohashi, 2002), this study presented the first diagnoses of the pollen morphology of *C. bonii*, *C. harmsii* and *C. pinetorum*.

Our results indicated that pollen grains of each species of Thai *Campylotropis* showed non-significant variations of P-axis and E-axis values which might be correlated to stability at species level. Mitra and Mondal (1982) reported average values of P-axis and E-axis lengths of *C. capillipes* subsp. *prainii* and *C. parviflora* were slightly longer than those in the present study. Likewise, Iokawa and Ohashi (2002) illustrated longer values of measurements in *C. sulcata* except those of *C. parviflora* and *C. decora* were shorter than our measurements. These differences might be connected to diverse meiotic abnormalities, ploidy or geographical variation (Aguilar-García et al., 2012; Storme et al., 2013). According to Satthaphorn et al. (2018), this palynological information can be also used in taxonomic implication in some morphological-related species in Thailand. For instance, *C. parviflora* and *C. pinetorum* exhibit pinkish-white to creamy-white corolla color with green blotches on the standard while other species display dark blue or light to dark violet color. However, their pollen morphology is different by having perforate margo in *C. parviflora* but absence in *C. pinetorum*. Another example is that *C. capillipes* subsp. *prainii* and *C. bonii* similarly pose appressed hairs on their peduncles while their pollen grains have distinct characters to discriminate: psilate margo and vertical margin of lumina in *C. bonii*, whereas perforate margo and declined margin of lumina in *C. capillipes* subsp. *prainii*.

The pollen grains of *Campylotropis* were also morphologically similar to those of most taxa in the tribe Desmodieae, such as pollen from genera *Alysicarpus*, *Dendrolobium*, *Desmodium*, *Lespedeza*, *Kummerowia*, *Ohwia* and *Phyllodium* (Ferguson and Skvarla, 1981; Chen and Huang, 1993; Perveen and Qaiser, 1998; Iokawa and Ohashi, 2002; Xu et al., 2011; Ohashi et al., 2013; Saisorn and Chantaranothai, 2015). Chen and Huang (1993) indicated that pollen grains of the genus *Dendrolobium* of the subtribe Desmodiinae were closely related to pollen of the subtribe Lespedezinae (*Campylotropis*, *Lespedeza* and *Kummerowia*) due to having coarse reticulate tectum. Moreover, this type of tectum was later observed in the genera *Phyllodium* and *Ohwia* (Ye et al., 2011; Ohashi et al., 2013). The close relation deduced from the similarity in pollen sculpture was recently supported by molecular evidence which suggested that the subtribe Lespedezinae is phylogenetically sister to subtribe the Desmodiinae (Jabbour et al., 2018). However, brief details of exine sculpturing may not be taken into account when examining pollen morphology at infratribal level because of the occurrence of convergent and divergent characters among angiosperm pollen grains (Chen and Huang, 1993; Halbritter and Hesse, 1995).

In addition to palynological characteristics shared within the tribe Desmodieae, the coarsely reticulate tectum and lalongate endoaperture of *Campylotropis* were also found in pollen grains of *Lespedeza* and *Kummerowia* in previous investigations (Ferguson and Skvarla, 1981; Ohashi et al., 1981; Chen and Huang, 1993). These findings might indicate a close relationship within the subtribe Lespedezinae. The similarities of pollen grains were also consistent with phylogenetic molecular studies that suggested *Campylotropis* is sister to *Lespedeza* with nested *Kummerowia* (Han et al., 2010; Nemoto et al., 2010; Jabbour et al., 2018). Because of the close relationship between the three genera, the delimitation of *Campylotropis* from the other two by pollen morphology is obscure, particularly from the genus *Lespedeza*. Notwithstanding, *Kummerowia* can be distinguished by its additional funiform structure on the exine sculpturing concealing lumina, while absent in *Campylotropis* and *Lespedeza* pollen grains (Xu et al., 2011). Generic recognition might also contradict intergeneric classification based on studies of macromorphology. It should be noted that the macromorphological studies compared flowers (two flowers per subtended bract in *Lespedeza* and *Kummerowia* with one flower per subtended bract in *Campylotropis*) and habits (shrubby in *Campylotropis* and *Lespedeza* vs herbaceous in *Kummerowia*) clearly distinguished between these three genera (Iokawa and Ohashi, 2002; Lewis et al., 2005; Puhua et al., 2010).

In conclusion, this palynological investigation provided information of pollen morphology, description and identification key to species based on palynological evidence for Thai *Campylotropis*. Information of pollen morphology of *C. bonii*, *C. harmsii* and *C. pinetorum* are firstly reported in the present study. The implications of pollen morphology can be used to solve taxonomic aspects for distinguishing some morphological-related species in the genus. Clarification of the relationship within and between the genus *Campylotropis* and its related genera requires more samples and more evidence, such as anatomical and molecular studies from wider floristic regions or monographic scale.

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