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Seed micromorphology of tribe Desmodieae (subfamily Papilionoideae, family Leguminosae) from Thailand with its taxonomic implications

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Abstract. *Saisorn W, Suddee S. 2023. Seed micromorphology of tribe Desmodieae (subfamily Papilionoideae, family Leguminosae) from Thailand with its taxonomic implications. Biodiversitas 24: 5572-5585.* The seed micromorphology of 21 genera and 58 species of the tribe Desmodieae in Thailand was studied. The result showed that the shape of the seed can be ellipsoid or transversely ellipsoid, irregular, oblongoid, quadrangular, rectangular, reniform, rhomboid, subcircular, and triangular. An oblongoid shape is restricted to the genus *Sohmaea*; the seeds' length, width, and thickness are 0.94-5.93 mm, 0.78-3.65 mm, and 0.39-1.92 mm, respectively. The testa color can be light green to green, yellow, light to dark brown, or black. Testa patterns can be classified into nine types: colliculate, colliculate-rugulate, fissured, pitted, reticulate, reticulate-reticulate, reticulate-rugulate, rugulate, and smooth. The rim-arillate aril can be thin, thick, or well-developed. This tribe is classified into three groups based on aril types. Group I: a thin rim-arillate type is restricted to *Akschindlium godefroyanum*. Group II: a thick rim-arillate type is found on the seeds of the most studied plants. Group III: a well-developed rim-arillate type is a taxonomic characteristic of *Codariocalyx*. The overall shape of the rim-arillate aril is subcircular, circular, subcircular-elliptic, elliptic, elliptic-oblong, and oblong. An oblong shape of the rim-arillate aril is a unique character for *Grona heterophylla* compared to other species within *Grona.*

Keywords: *Desmodium*, Fabaceae, *Grona*, Papilionoideae, plant taxonomy

INTRODUCTION

Tribe Desmodieae belongs to the family Leguminosae (Fabaceae) and subfamily Papilionoideae. The tribe was first described by Hutchinson (1964) and previously classified into three subtribes: Bryinae, Desmodiinae and Lespedezinae (Ohashi et al. 1981). At least two studies have shown that subtribe Bryinae was not in an appropriate placement (Bailey et al. 1997; Doyle et al. 2000), and it was then moved to tribe Phaseoleae (Ohashi 2005). Recently, the classification systems at generic and specific ranks of the tribe were proposed following either DNA sequences or morphological characters in a series of research articles (e.g., Jabbour et al. 2018; Ohashi and Ohashi 2018a, 2018b, 2018c; Ohashi et al. 2018a, 2018b; Ohashi et al. 2019). Desmodieae consists of two subtribes, 44 genera, and ca. 530 species worldwide. They are mostly distributed in tropical and subtropical regions of all continents except Europe or rarely found in temperate regions. There are 24 genera and ca. 84 species recorded in Thailand. The species of this tribe are mostly characterized by their articulate pods. They are prostrate, climbing, or erect herb to shrub with an odd number of leaflets up to 7. The inflorescences are fascicle, raceme, pseudoraceme, and compound raceme or pseudoraceme. Flowers are papilionaceous with white to purple or yellow petals, monadelphous or diadelphous stamens and a 1-carpellate ovary. Pods are dehiscent or indehiscent with one to several articles as well as one to several seeds. Seeds are reniform, rectangular, or quadrangular (e.g., Ohashi 1973, 1982, 2004a, 2004b; Niyomdham 1994; Pedley 1999; Saisorn and Chantaranothai 2013, 2015, 2018, 2019 and 2020; Lima et al. 2014; Leeratiwong et al. 2017; Satthaphorn et al. 2018; Tokaew et al. 2020).

The results of several studies have revealed that seed characters are useful for plant classification or identification in various families and genera. For example, seed ornamentation of 117 *Impatiens* species (Balsaminaceae) was divided into 3 main types, including reticulate, protrusive, and appendicular. Each type was further classified into 3, 3, and 4 subtypes, respectively (Song et al. 2022); the character of the testa periclinal cell wall can be used to distinguish between *Evolvulus alsinoides* (L.) L. and *Evolvulus nummularius* (L.) L. (Convolvulaceae) (Ketjarun et al. 2016); other characteristics, the ornamentation on ridges and cell rows between ridges were used to identify *Xyris* species (Xyridaceae) (Nardi et al. 2016). Several authors reported taxonomic characteristics of seeds in Fabaceae. Kirkbride et al. (2003a and 2003b) studied the fruits and seeds of 435 genera in the subfamily Faboideae (or Papilionoideae in the recent system). The keys to those genera were provided. The key was based on several seed characters: size, shape, testa pattern, raphe, and hilum. The 22 genera and 194 species of tribe Desmodieae were also included viz *Alysicarpus*, *Aphyllodium*, *Arthroclianthus*, *Campylotropis*, *Christia*, *Codariocalyx*, *Dendrolobium*, *Desmodiastrum*, *Desmodium*, *Droogmansia*, *Eleiotis*, *Kummerowia*, *Leptodesmia*, *Lespedeza*, *Mecopus*, *Melliniella*, *Phyllodium*, *Pseudarthria*, *Pycnospora*, *Tadehagi*, *Trifidacanthus*, and *Uraria*. Gandhi et al. (2011) studied the seed morphology of *Crotalaria*, *Alysicarpus*, and *Indigofera.* Seeds of *Crotalaria* have a kidney (reniform)

shape, while seeds of *Alysicarpus* and *Indigofera* can be oblong, ovoid, ellipsoid, orbicular, rounded, spherical, or rectangular. Al-Ghamdi (2011) studied the seed morphology of 18 species of *Indigofera*. Several characters, such as shape, testa pattern, hilum and seed color, were used for species identification. De Queiroz et al. (2012) studied the seed morphology of 13 species of *Tephrosia* from South America. The seed characters were examined: size, shape, testa pattern and color, hilum position, and aril. The two testa patterns, crested and simple-reticulate were commonly found in the genus. The new characteristics of testa patterns were also revealed including foveolate, multifoveolate and subgrooved patterns. Ninkaew et al. (2019) studied the seed morphology of 19 *Crotalaria* species in Thailand. They were divided into 5 species groups based on size, shape, testa pattern, and aril of seeds. This work aims to examine the seed morphology of Desmodieae in Thailand and to search for taxonomic characteristics for plant classification and identification.

MATERIALS AND METHODS

Seeds of 21 genera and 58 species were taken from herbarium specimens kept at BKF and KKU and from field surveys for morphological studies (Table 2). The length, width, and thickness of 10-20 seeds for each collection were measured using a digital vernier caliper. Shape, testa color and pattern, hilum, and aril were also examined. The testa pattern was investigated under a scanning electron microscope (SEM). For the study under SEM, seeds were attached to the specimen stub with carbon tape. The seed samples were then coated with gold-palladium alloy under vacuum and examined under Leo 1450 VP SEM. The terminology for seed descriptions is mainly followed by Kirkbride et al. (2003a, 2003b) and Lersten (1981).

RESULTS AND DISCUSSION

Seed micromorphology

The seed micromorphology of the tribe Desmodieae in Thailand can be summarized as follows (Table 1). Seed shapes can be ellipsoid, irregular, oblongoid, quadrangular, rectangular, reniform, rhomboid, subcircular, transversely elliptic, and triangular (Figures 1-6). The length, width, and thickness are 0.94-5.93 mm, 0.78-3.65 mm, and 0.39-1.92 mm, respectively. There are various testa colors: light green to green, yellow, light to dark brown, and black. There are nine types of testa patterns: colliculate, colliculate-rugulate, fissured, pitted, reticulate, reticulate-reticulate, reticulate-rugulate, regulate, and smooth (Figures 8-10). Seeds of all species have a rim-arillate aril which can be thin, thick, or well-developed (Figure 7). Rim-arillate aril is located around the hilum and their shape can be subcircular, circular, subcircular-elliptic, elliptic, elliptic-oblong, or oblong (Figure 7). The hilum position of all species is located at the center. The seed morphology of each genus can be described in the following paragraphs.

Seed description

Akschindlium *H.Ohashi (Figures 1.A-B)*

Seed shape is reniform with an average length, width, and thickness of 4.80±0.33 mm, 3.09±0.28 mm, and 1.62±0.12 mm, respectively. Testa is light brown with reticulate-rugulate (Figures 10.A-B) and regulate patterns. Rim-arillate aril is a thin type with a circular shape (Figure 7.A).

Alysicarpus *Neck. ex Desv. (Figures 1.C-H)*

Seed shape is elliptic, oblongoid, rhomboid, and transversely ellipsoid with an average length, width, and thickness of 1.62±0.59 mm, 0.92±0.12 mm, and 1.34±0.08 mm, respectively. Testa is light green and light to dark brown with colliculate, reticulate-rugulate, and rugulate patterns. Rim-arillate aril is a thick type with a circular shape.

Aphyllodium *Gagnep. (Figures 1.I-J)*

Seed shape is reniform with an average length, width, and thickness of 3.03±0.31 mm, 2.00±0.14 mm, and 1.07±0.12 mm, respectively. Testa is light to dark brown with colliculate, reticulate-rugulate, and regulate patterns. Rim-arillate aril is a thick type with a circular shape.

Campylotropis *Bunge (Figures 1.K-T)*

Seed shape is reniform with an average length, width, and thickness of 3.86±0.81 mm, 2.36±0.62 mm, and 1.09±0.18 mm, respectively. Testa is green, brown, and dark brown to black with colliculate, colliculate-rugulate, fissured (Figures 8.E-F), reticulate-rugulate, and rugulate (Figures 10.C-D) patterns. Rim-arillate aril is a thick type with a circular shape (Figure 7.B).

Christia *Moench (Figures 2.A-D)*

Seed shape is reniform with an average length, width, and thickness of 2.00±0.17 mm, 1.57±0.1.5 mm, and 0.81±0.09 mm, respectively. Testa is yellow to brown with colliculate and colliculate-rugulate patterns. Rim-arillate aril is a thick type with a circular shape.

Codariocalyx *Hassk. (Figures 2.E-J)*

Seed shape is reniform with an average length, width, and thickness of 3.07±0.46 mm, 2.13±0.36 mm, and 0.97±0.20 mm, respectively. Testa is dark brown to black with colliculate, colliculate-rugulate (Figures 8.C-D), pitted (Figures 2.E-F and Figures 9.A-B), and rugulate patterns. Rim-arillate aril is a well-developed type (Figure 7.C) with elliptic and elliptic-oblong shapes.

Dendrolobium *(Wight & Arn.) Benth. (Figures 2.K-T and Figures 3.A-B)*

Seed shape is quadrangular, rectangular, reniform, and subcircular with an average length, width, and thickness of 3.44±0.73 mm, 2.53±0.53 mm, and 1.25±0.26 mm, respectively. Testa is yellow, light to dark brown, and black with colliculate, reticulate, reticulate-reticulate, rugulate, and smooth (Figures 10.E-F) patterns. Rim-arillate aril is a thick type with a circular shape.

Table 1. Seed morphological characters of tribe Desmodieae in Thailand

Taxon	Seed shape (side view)	Testa color	Size (mm)		Rim-arillate aril		Testa pattern
			Length ($\bar{x}$±S.D.)	Width ($\bar{x}$±S.D.)	Type	Shape	
Akschindlium godefroyanum	Reniform	Light brown	4.43-5.42 (4.80±0.33)	2.75-3.62 (3.09±0.28)	Thin	Circular	Reticulate-rugulate, rugulate
Alysicarpus bupleurifolius	Rhomboid	Brown	1.27-1.48 (1.38±0.15)	1.29-1.34 (1.32±0.04)	Thick	Circular	Colliculate, rugulate
A. rugosus	Transversely ellipsoid	Light green, Light to dark brown	0.94-1.17 (1.06±0.08)	1.24-1.46 (1.35±0.08)	Thick	Circular	Colliculate, rugulate
A. vaginalis	Ellipsoid, oblongoid	Light to dark brown	1.83-2.50 (2.23±0.19)	1.20-1.49 (1.33±0.10)	Thick	Circular	Colliculate, reticulate-rugulate
Aphyllodium biarticulatum	Reniform	Light to dark brown	2.71-3.74 (3.03±0.31)	1.83-2.30 (2.00±0.14)	Thick	Circular	Reticulate-rugulate, rugulate, colliculate
Campylotropis capillipes	Reniform	Brown	4.12-5.05 (4.71±0.28)	2.64-3.24 (2.97±0.18)	Thick	Circular	Colliculate, rugulate
C. decora	Reniform	Brown	4.57-5.16 (4.88±0.30)	3.07-3.42 (3.20±0.19)	Thick	Circular	Fissured, rugulate
C. parviflora	Reniform	Dark brown to black	3.71-3.87 (3.79±0.06)	2.22-2.44 (2.38±0.07)	Thick	Circular	Reticulate-rugulate, rugulate
C. pinetorum	Reniform	Green, brown	2.31-3.12 (2.84±0.25)	1.30-1.66 (1.53±0.11)	Thick	Circular	Rugulate
C. sulcata	Reniform	Brown	3.21-3.40 (3.29±0.10)	1.78-1.93 (1.88±0.09)	Thick	Circular	Colliculate-rugulate, rugulate
Christia obcordata	Reniform	Brown	1.75-1.97 (1.87±0.07)	1.29-1.56 (1.45±0.08)	Thick	Circular	Colliculate
C. vespertilionis	Reniform	Yellow to light brown	1.98-2.31 (2.17±0.11)	1.62-1.83 (1.71±0.08)	Thick	Circular	Colliculate, colliculate-rugulate
Codariocalyx gyroides	Reniform	Dark brown to black	3.13-3.39 (3.26±0.10)	2.01-2.42 (2.21±0.13)	Well-developed	Elliptic	Colliculate, pitted
C. microphyllus	Reniform	Brown to black	2.06-2.95 (2.50±0.27)	1.29-1.92 (1.67±0.20)	Well-developed	Elliptic	Colliculate-rugulate, rugulate
C. motorius	Reniform	Brown to black	2.85-3.96 (3.35±0.27)	2.12-2.70 (2.39±0.16)	Well-developed	Elliptic-oblong	Colliculate-rugulate, rugulate
Dendrolobium baccatum	Reniform	Brown	2.53-3.62 (3.17±0.37)	1.95-2.63 (2.31±0.27)	Thick	Circular	Rugulate
D. lanceolatum	Reniform	Yellow to light brown	4.02-4.26 (4.14±0.09)	2.05-2.43 (2.26±0.11)	Thick	Circular	Rugulate
D. olivaceum	Reniform, rectangular	Dark brown to black	2.30-3.21 (2.69±0.33)	2.26-2.75 (2.49±0.20)	Thick	Circular	Rugulate, smooth
D. thorelii	Reniform, rectangular, subcircular	Brown to dark brown	3.21-3.60 (3.44±0.14)	3.02-3.48 (3.24±0.15)	Thick	Circular	-
D. triangulare	Reniform, quadrangular	Brown to dark brown	2.21-2.81 (2.52±0.17)	1.71-1.89 (1.80±0.06)	Thick	Circular	Colliculate, rugulate
D. umbellatum	Reniform	Dark brown to black	3.99-4.68 (4.34±0.20)	2.82-3.06 (2.97±0.09)	Thick	Circular	Rugulate
Desmodium craibii	Reniform	Brown to dark brown	2.93-3.44 (3.16±0.16)	2.45-2.76 (2.60±0.12)	Thick	Circular	Reticulate, reticulate-reticulate
D. scorpiurus	Ellipsoid	Light brown to brown	2.35-2.89 (2.64±0.21)	0.90-1.12 (1.01±0.08)	Thick	Circular	Rugulate
D. uncinatum	Triangular	Brown	2.76-3.22 (3.08±0.15)	1.76-2.12 (1.98±0.14)	Thick	Circular	Colliculate, colliculate-rugulate, rugulate
Grona auricoma	Reniform	Light to dark brown	1.68-2.12 (1.91±0.16)	1.20-1.54 (1.38±0.13)	Thick	Circular	Colliculate-rugulate, rugulate
G. brevipedicellata	Reniform	Light to dark brown	1.29-1.83 (1.49±0.15)	0.96-1.41 (1.13±0.12)	Thick	Circular	Colliculate-rugulate, rugulate
G. griffithiana	Reniform	Dark brown	2.06-2.36 (2.23±0.10)	1.50-1.72 (1.64±0.06)	Thick	Circular	Colliculate, reticulate-rugulate
G. heterocarpa	Reniform	Light to dark brown	1.71-1.99 (1.87±0.09)	1.34-1.58 (1.46±0.07)	Thick	Circular	Colliculate-reticulate, rugulate
G. heterophylla	Reniform	Light to dark brown	2.45-3.12 (2.80±0.19)	1.84-2.28 (2.07±0.16)	Thick	Oblong	Colliculate-reticulate, rugulate
G. strigillosa	Reniform	Light green to dark brown	1.83-2.23 (2.01±0.11)	1.18-1.53 (1.36±0.14)	Thick	Circular	Rugulate
G. styracifolia	Reniform	Brown	2.05-2.29 (2.15±0.09)	1.51-1.62 (1.56±0.05)	Thick	Circular	Colliculate, reticulate-reticulate
Hegnera obcordata	Reniform	Dark brown to black	3.60-3.84 (3.74±0.08)	2.34-2.62 (2.56±0.08)	Thick	Subcircular	Reticulate

Huangtcia oblata	Reniform	Brown	3.05-3.77 (3.32±0.21)	2.16-2.59 (2.26±0.13)	Thick	Circular	Colliculate-rugulate, rugulate, reticulate-rugulate
H. renifolia	Reniform	Brown	3.42-3.82 (3.59±0.11)	2.01-2.28 (2.14±0.07)	Thick	Circular	Colliculate-rugulate
Mecopus nidulans	Reniform	Brown	1.40-1.98 (1.75±0.20)	1.08-1.46 (1.31±0.14)	Thick	Circular	Colliculate-rugulate, rugulate
Ototropis amethystina	Reniform, ellipsoid	Brown	2.21-2.64 (2.43±0.15)	1.73-2.10 (1.97±0.11)	Thick	Circular	Reticulate-rugulate, rugulate
O. hayatae	Reniform	Brown	3.16-3.77 (3.47±0.23)	2.42-2.75 (2.59±0.12)	Thick	Circular	Colliculate-rugulate, reticulate
O. kingiana	Subcircular	Dark brown	1.93-2.47 (2.26±0.20)	1.92-2.32 (2.13±0.17)	Thick	Circular	Rugulate
O. megaphylla	Reniform	Brown to black	2.81-3.66 (3.28±0.21)	2.22-2.68 (2.44±0.13)	Thick	Circular	Reticulate, reticulate-rugulate
O. multiflora	Reniform	Brown to dark brown	2.51-3.04 (2.79±0.16)	1.62-2.07 (1.86±0.11)	Thick	Circular	Reticulate-rugulate, rugulate
Phyllodium elegans	Reniform	Light to dark brown	2.60-3.03 (2.77±0.12)	1.91-2.23 (2.03±0.09)	Thick	Circular	Colliculate-rugulate, rugulate
P. kurzianum	Reniform, rectangular, subcircular	Light brown to black	3.02-3.88 (3.48±0.30)	2.56-3.18 (2.87±0.24)	Thick	Circular	Colliculate-rugulate, rugulate
P. longipes	Reniform, rectangular	Light to dark brown	2.50-3.71 (3.12±0.33)	2.11-2.92 (2.52±0.25)	Thick	Circular	Colliculate-rugulate, rugulate
P. pulchellum	Reniform	Light to dark brown	2.27-2.70 (2.58±0.16)	1.84-2.10 (1.96±0.09)	Thick	Circular	Colliculate-rugulate, rugulate
P. vestitum	Reniform	Brown	3.76-4.25 (3.98±0.15)	2.54-3.00 (2.76±0.14)	Thick	Circular	Reticulate, reticulate-reticulate
Pleurolobus gangeticus	Reniform	Light brown to brown	1.94-2.37 (2.17±0.12)	1.40-1.81 (1.67±0.09)	Thick	Circular	Colliculate, reticulate, reticulate-reticulate
Polhillides velutina	Reniform	Light brown to black	2.23-2.42 (2.33±0.07)	1.69-1.83 (1.75±0.05)	Thick	Circular	Reticulate, rugulate, smooth
Pycnospora lutescens	Reniform	Light green to dark brown	2.23-2.47 (2.30±0.09)	1.40-1.58 (1.47±0.06)	Thick	Circular	Rugulate
Sohmaea hispida	Oblongoid	Dark brown	1.99-2.35 (2.16±0.11)	1.18-1.36 (1.28±0.06)	Thick	Circular	Rugulate
S. laxiflora ssp. *laxiflora*	Oblongoid	Brown	2.24-2.63 (2.44±0.10)	0.94-1.07 (1.01±0.04)	Thick	Circular	Recticulate-rugulate
S. teres	Oblongoid	Brown	3.31-4.45 (3.89±0.40)	0.78-1.15 (0.95±0.11)	Thick	Circular	Colliculate-rugulate
Tadehagi rodgeri	Reniform	Light to dark brown	5.49-5.93 (5.65±0.12)	3.34-3.65 (3.49±0.09)	Thick	Subcircular-elliptic	Rugulate
T. triquetrum	Reniform	Brown	2.58-3.08 (2.84±0.16)	1.86-2.22 (2.13±0.11)	Thick	Subcircular	Rugulate
Tateishia concinna	Reniform	Dark brown	2.48-2.79 (2.61±0.10)	1.51-1.80 (1.65±0.08)	Thick	Circular	Rugulate
Uraria acuminata	Reniform, irregular	Light to dark brown	1.91-2.40 (2.25±0.14)	1.65-1.94 (1.77±0.09)	Thick	Circular	Colliculate-rugulate
U. crinita	Reniform	Brown	2.41-2.79 (2.62±0.13)	1.94-2.24 (2.07±0.08)	Thick	Circular	Reticulate, rugulate
U. lagopodioides	Reniform	Brown	2.23-2.69 (2.41±0.12)	1.48-1.72 (1.59±0.08)	Thick	Circular	Colliculate-rugulate, reticulate-rugulate
U. oblonga	Reniform	Brown	2.64-3.02 (2.88±0.13)	1.98-2.24 (2.09±0.10)	Thick	Circular	Colliculate-rugulate, reticulate-rugulate

Table 2. List of voucher specimens of tribe Desmodieae included in this study

Taxon	Voucher specimen	Locality
Akschindlium godefroyanum (Kuntze) H.Ohashi	Saisorn 476 (KKU)	Northeastern Thailand
Alysicarpus bupleurifolius (L.) DC.	van Beusekom et al. 4014 (BKF)	Kanchanaburi
A. rugosus (Willd.) DC.	Smitinand 4894 (BKF)	Loei: Wang Saphung
A. vaginalis (L.) DC.	Saisorn et al. 293 (KKU)	Saraburi: Phra Phutthabat
Aphyllodium biarticulatum (L.) Gagnep.	Saisorn et al. 277 (KKU)	Phetchaburi: Cha-am
Campylotropis capillipes (Franch.) Schindl.	Koyama et al. T-33268 (BKF)	Chiang Mai: Chiang Dao
C. decora (Kurz) Schindl.	van de Bult 1161 (BKF)	Chiang Rai: Mae Sai
C. parviflora (Kurz) Schindl.	Maxwell 88-321 (BKF)	Chiang Mai: Doi Suthep
C. pinetorum (Kurz) Schindl.	Chayamarit & Phathanacharoen 701 (BKF)	Chiang Mai: Doi Pui
C. sulcata Schindl.	Srisanga 1834 (BKF)	Nan: Doi Phu Wae
Christia obcordata (Poir.) Bakh.f.	Maxwell 94-1161 (BKF)	Lamphun: Doi Khun Tan National Park
C. vespertilionis (L.f.) Bakh.f.	S.N. 261 (BKF)	Chaiyaphum: Phu Khiao
Codariocalyx gyroides (Roxb. ex Link) X.Y.Zhu	Saisorn 372 (KKU)	Phetchabun: Nam Nao National Park
C. microphyllus (Thunb.) H.Ohashi	Saisorn 262 (KKU)	Sakon Nakhon: Phu Phan National Park
	Saisorn 339 (KKU)	Chiang Mai: Chiang Dao
	Saisorn 370 (KKU)	Phetchabun: Nam Nao National Park
C. motorius (Houtt.) H.Ohashi	Saisorn 260 (KKU)	Sakon Nakhon: Phu Phan National Park
	Saisorn 334 (KKU) & 338 (KKU)	Chiang Mai: Chiang Dao
Dendrolobium baccatum (Schindl.) Schindl.	Puudjaa & Hemrat 1522 (BKF)	Ubon Ratchathani: Mueang Ubon Ratchathai
D. lanceolatum (Dunn) Schindl.	Saisorn 375 (KKU)	Khon Kaen: Phu Wiang National Park
D. olivaceum (Prain) Schindl.	Chaloenphol 404 (BKF)	Lampang
D. thorelii (Schindl.) Schindl.	Saisorn 475 (KKU)	Phetchabun: Nam Nao National Park
D. triangulare (Retz.) Schindl.	Smitinand s.n. (BKF SN044100)	Chiang Rai: Doi Tung
D. umbellatum (L.) Benth.	Pooma et al. 6454 (BKF)	Surat Thani: Don Sak
Desmodium craibii H.Ohashi	Pooma 1354 (BKF)	Uttaradit: Ban Kok
D. scorpiurus (Sw.) Desv.	Saisorn & Pisuttimarn 450 (KKU)	Loei: Chiang Khan
D. uncinatum (Jacq.) DC.	Saisorn 341 (KKU)	Chiang Mai: Chiang Dao
Grona auricoma (Graham ex Benth.) H.Ohashi & K.Ohashi	Saisorn 426 (KKU) & 429 (KKU)	Sakon Nakhon: Phu Phan National Park
G. brevipedicellata (W.Saisorn, Chantar. & Balslev) H.Ohashi & K.Ohashi	Saisorn 425 (KKU)	Sakon Nakhon: Phu Phan National Park
G. griffithiana (Benth.) H.Ohashi & K.Ohashi	Tagawa et al. T-1534 (BKF)	Loei: Phu Luang
G. heterocarpa (L.) H.Ohashi & K.Ohashi	Saisorn 230 (KKU)	Yasothon: Na Wiang
G. heterophylla (Willd.) H.Ohashi & K.Ohashi	Saisorn 259 (KKU)	Sakon Nakhon: Phu Phan National Park
G. strigillosa (Schindl.) H.Ohashi & K.Ohashi	Mattapha 2011-I (KKU)	Nong Bua Lamphu: Phu Phan Noi
	Saisorn 415 (KKU)	Surin: Kap Choeng
G. styracifolia (Osbeck) H.Ohashi & K.Ohashi	Pooma et al. 2145 (BKF)	Surin: Huai Thabthan
Hegnera obcordata (Miq.) Schindl.	Put 62 (BKF)	Sa Kaeo: Aranyaprathet
Huangtcia oblata (Baker ex Kurz) H.Ohashi & K.Ohashi	Maxwell 97-249 (BKF)	Lampang: Wang Nuea
H. renifolia (L.) H.Ohashi & K.Ohashi	Saisorn et al. 298 (KKU)	Khon Kaen: Phu Wiang National Park
Mecopus nidulans Benn.	Charoenphol et al. 4903 (BKF)	Loei: Na Noi
Ototropis amethystina (Dunn) H.Ohashi & K.Ohashi	Saisorn 337 (KKU)	Chiang Mai: Chiang Dao
O. hayatae (H.Ohashi) H.Ohashi & K.Ohashi	Saisorn 336 (KKU)	Chiang Mai: Chiang Dao
O. kingiana (Prain) H.Ohashi & K.Ohashi	Maxwell 93-1442 (BKF)	Lampang: Mae Mo
O. megaphylla (Zoll. & Moritzi) H.Ohashi & K.Ohashi	Saisorn 432 (KKU)	Loei: Phu Kradueng
	Saisorn 335 (KKU)	Chiang Mai: Chiang Dao
O. multiflora (DC.) H.Ohashi & K.Ohashi	Saisorn 430 (KKU)	Loei: Phu Kradueng
Phyllodium elegans (Lour.) Desv.	Saisorn 478 (KKU)	Northeastern Thailand
P. kurzianum (Kuntze) H.Ohashi	Saisorn 479 (KKU)	Northeastern Thailand
P. longipes (Craib) Schindl.	Saisorn 474 (KKU)	Chiang Rai: Mae Fah Luang University
	Saisorn 477 (KKU)	Northeastern Thailand
P. pulchellum (L.) Desv.	Saisorn 480 (KKU)	Northeastern Thailand
P. vestitum Benth.	Gardner & Sidisunthorn ST2537 (BKF)	Satun: La-ngu
Pleurolobus gangeticus (L.) J.St.-Hil.	Saisorn et al. 330 (KKU)	Nakhon Ratchasima: Wang Nam Khiao
	Saisorn et al. 286 (KKU)	Ratchaburi: Pak Tho
Polhillides velutina (Willd.) H.Ohashi & K.Ohashi	Saisorn 368 (KKU)	Phetchabun: Nam Nao National Park
Pycnospora lutescens (Poir.) Schindl.	Ninkaew 380-1 (KKU)	Sakon Nakhon: Phu Phan National Park
Sohmaea hispida (Franch.) H.Ohashi & K.Ohashi	Saisorn 343 (KKU)	Chiang Mai: Chiang Dao
S. laxiflora (DC.) H.Ohashi & K.Ohashi ssp. *laxiflora*	Saisorn 345 (KKU)	Chiang Mai: Chiang Dao
	Saisorn 353 (KKU)	Chiang Mai: Doi Pha Hom Pok National Park
S. teres (Wall. ex Benth.) H.Ohashi & K.Ohashi	Saisorn 352 (KKU)	Chiang Mai: Doi Pha Hom Pok National Park
	Saisorn 376 (KKU)	Khon Kaen: Phu Wiang National Park
Tadehagi rodgeri (Schindl.) H.Ohashi	Saisorn 112 (KKU)	Phetchabun: Nam Nao National Park
T. triquetrum (L.) H.Ohashi	Koyama et al. T-32914 (BKF)	Kanchanaburi: Thong Pha Phum
Tateishia concinna (DC.) H.Ohashi & K.Ohashi	Hanmontri 10 (KKU)	Loei: Phu Ruea National Park
Uraria acuminata Kurz	Murata et al. T-16574 (BKF)	Nakhon Sawan: northwest of Nakhon Sawan
U. crinita (L.) Desv. ex DC.	Maxwell 94-1177 (BKF)	Rayong: Klaeng
U. lagopodioides (L.) DC.	Maxwell 93-838 (BKF)	Chon Buri: Si Racha
U. oblonga (Wall. ex Benth.) H.Ohashi & K.Ohashi	Saisorn 340 (KKU)	Chiang Mai: Chiang Dao

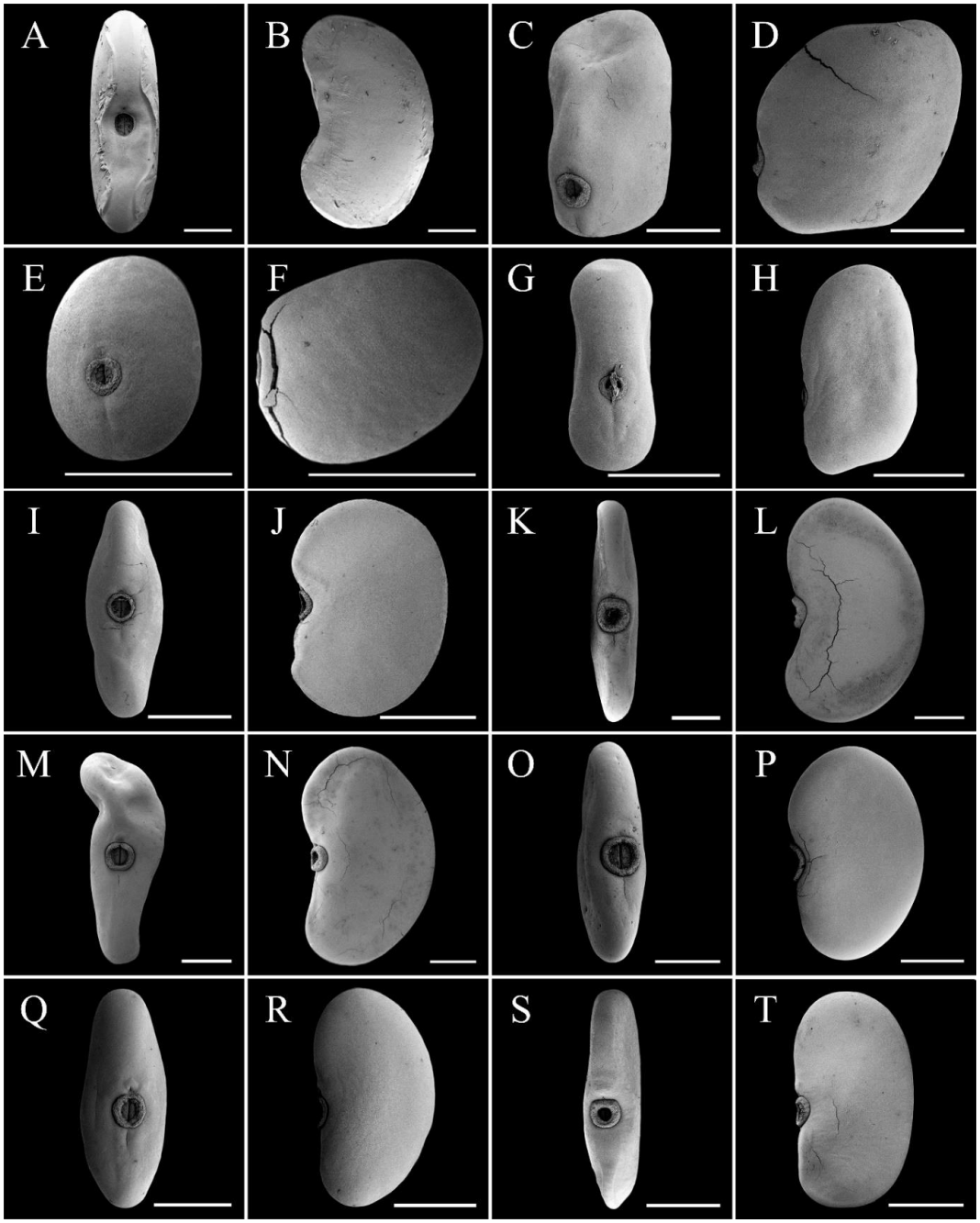

Figure 1. Seed morphology. A-B. *Akschindlium godefroyanum*. C-D. *Alysicarpus bupleurifolius*. E-F. *A. rugosus*. G-H. *A. vaginalis*. I-J. *Aphyllodium biarticulatum*. K-L. *Campylotropis capillipes*. M-N. *C. decora*. O-P. *C. parviflora*. Q-R. *C. pinetorum*. S-T. *C. sulcata*. Scale bars 1 mm

Desmodium *Desv. (Figures 3.C-H)*

Seed shape is elliptic, reniform, and triangular with an average length, width, and thickness of 3.01±0.26 mm, 1.96±0.64 mm, and 0.94±0.19 mm, respectively. Testa is light to dark brown with colliculate, colliculate-rugulate, reticulate, reticulate-reticulate, and rugulate patterns. Rim-arillate aril is a thick type with a circular shape.

Grona *Lour. (Figures 3.I-T and Figures 4.A-B)*

Seed shape is reniform with an average length, width, and thickness of 2.06±0.38 mm, 1.49±0.29 mm, and 0.74±0.20 mm, respectively. Testa is light green and light to dark brown with colliculate (Figures 8.A-B), colliculate-reticulate, colliculate-rugulate, reticulate-reticulate, reticulate-rugulate, and rugulate patterns. Rim-arillate aril is a thick type with circular and oblong (Figure 7.D) shapes.

Hegnera *Schindl. (Figures 4.C-D)*

Seed shape is reniform with an average length, width, and thickness of 3.74±0.08 mm, 2.56±0.08 mm, and 1.01±0.07 mm, respectively. Testa is dark brown to black with a reticulate pattern. Rim-arillate aril is a thick type with a subcircular shape.

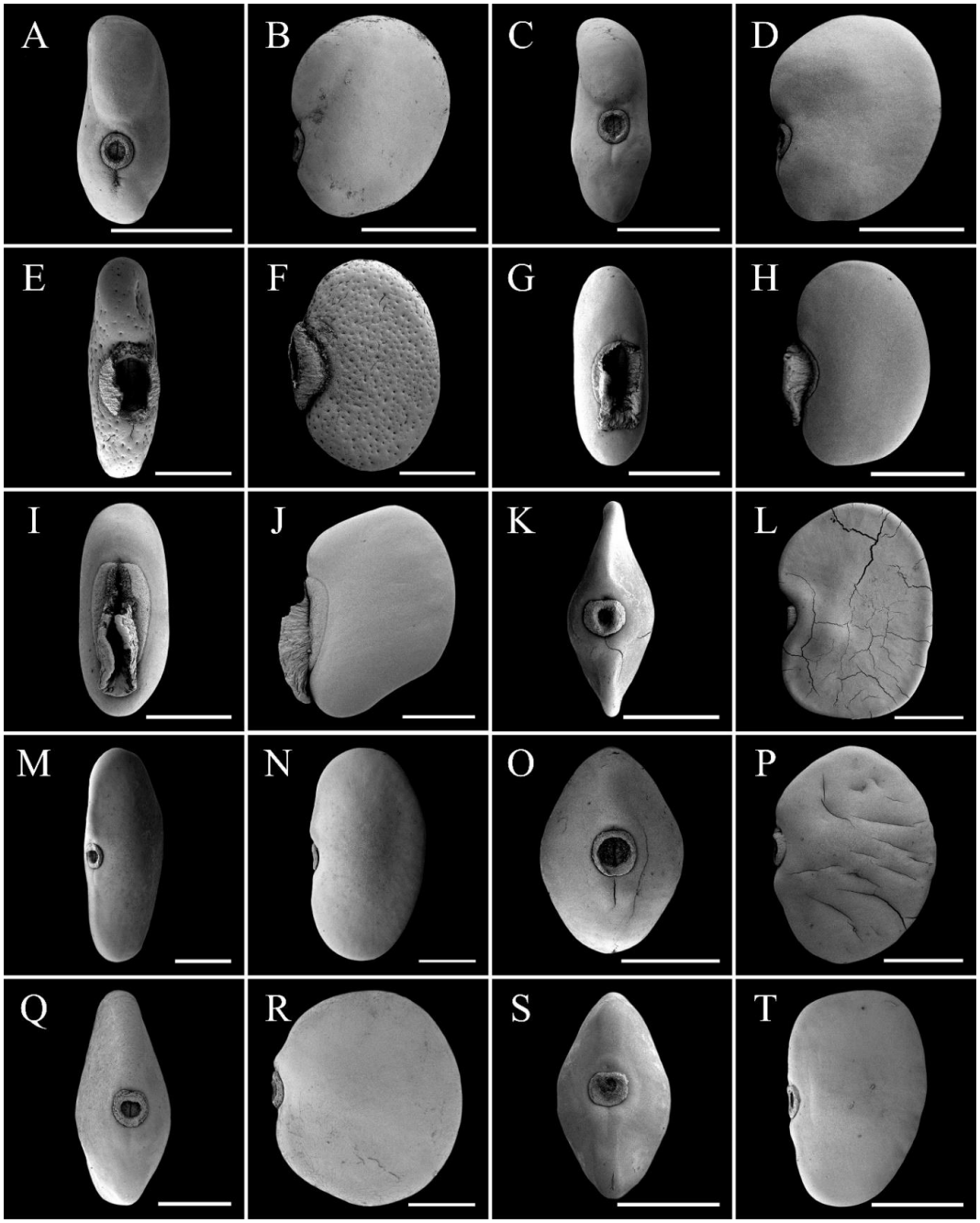

Figure 2. Seed morphology. A-B. *Christia obcordata*. C-D. *C. vespertilionis*. E-F. *Codariocalyx gyroides*. G-H. *C. microphyllus*. I-J. *Codariocalyx motorius*. K-L. *Dendrolobium baccatum*. M-N. *D. lanceolatum*. O-P. *D. olivaceum*. Q-R. *D. thorelii*. S-T. *D. triangulare*. Scale bars 1 mm

Huangtcia *H.Ohashi & K.Ohashi (Figures 4.E-H)*

Seed shape is reniform with an average length, width, and thickness of 3.46±0.21 mm, 2.20±0.12 mm, and 0.84±0.10 mm, respectively. Testa is brown with colliculate-rugulate, reticulate-rugulate, and rugulate patterns. Rim-arillate aril is a thick type with a circular shape.

Mecopus *Benn. (Figures 4.I-J)*

Seed shape is reniform with an average length, width, and thickness of 1.75±0.20 mm, 1.31±0.14 mm, and 0.63±0.08 mm, respectively. Testa is brown with colliculate-rugulate and rugulate patterns. Rim-arillate aril is a thick type with circular shape.

Ototropis *Nees (Figures 4.K-T)*

Seed shape is ellipsoid, reniform, and subcircular with an average length, width, and thickness of 2.92±0.47 mm, 2.21±0.30 mm, and 1.17±0.24 mm, respectively. Testa is light to dark brown and black with reticulate-rugulate, rugulate, colliculate-rugulate, and reticulate patterns. Rim-arillate aril is a thick type with circular shape.

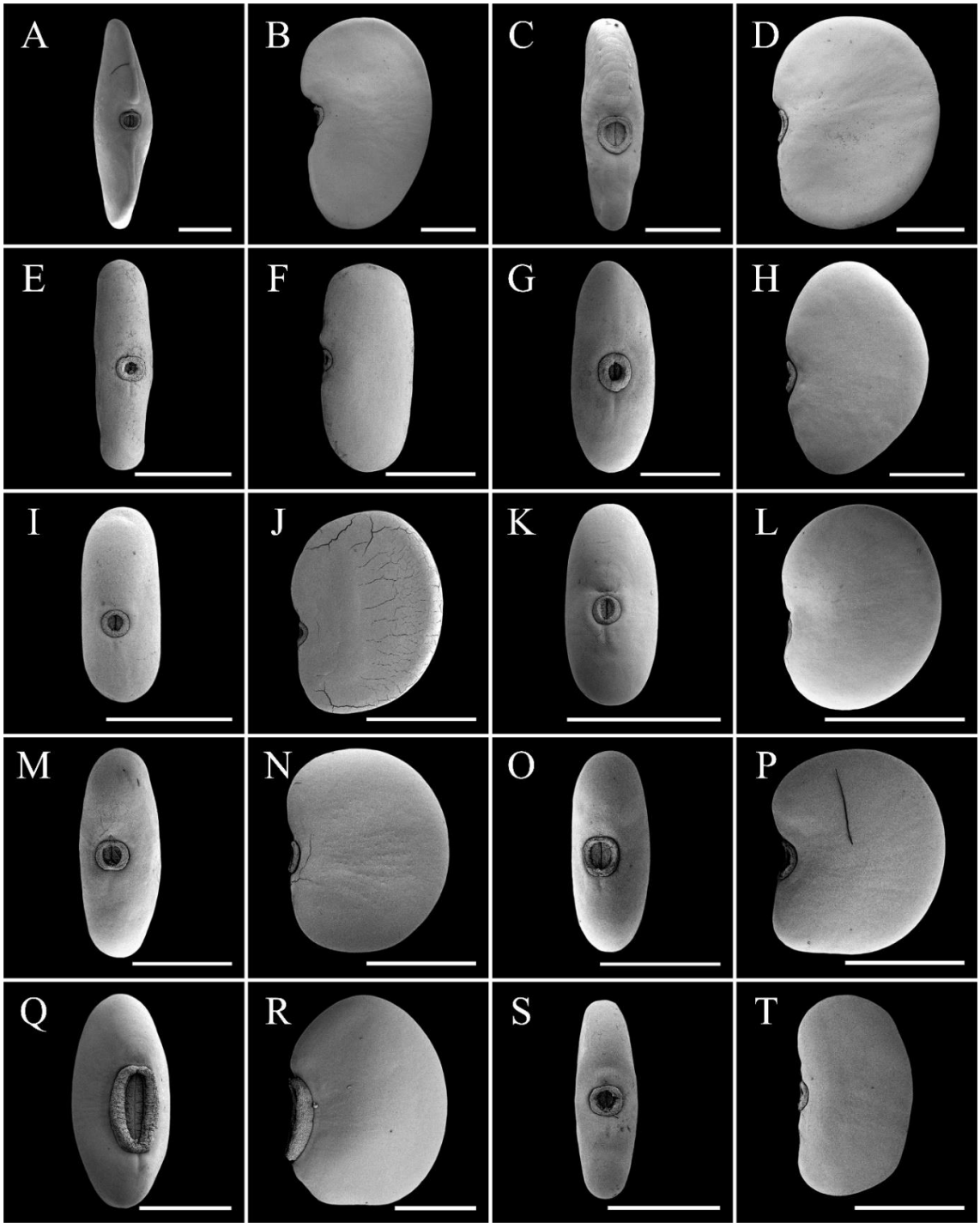

Figure 3. Seed morphology. A-B. *Dendrolobium umbellatum*. C-D. *Desmodium craibii*. E-F. *D. scorpiurus*. G-H. *D. uncinatum*. I-J. *Grona auricoma*. K-L. *G. brevipedicellata*. M-N. *G. griffithiana*. O-P. *G. heterocarpa*. Q-R. *G. heterophylla*. S-T. *G. strigillosa*. Scale bars 1 mm

Phyllodium *Desv. (Figures 5.A-J)*

Seed shape is rectangular, reniform, and subcircular with an average length, width, and thickness of 3.17±0.52 mm, 2.44±0.39 mm, and 1.06±0.17 mm, respectively. Testa is light to dark brown and black with colliculate-rugulate, reticulate, reticulate-reticulate (Figures 9.E-F), and rugulate patterns. Rim-arillate aril is a thick type with circular shape.

Pleurolobus *J.St.-Hil. (Figures 5.K-L)*

Seed shape is reniform with an average length, width, and thickness of 2.17±0.12 mm, 1.67±0.09 mm, and 0.72±0.05 mm, respectively. Testa is light brown to brown with colliculate, reticulate, and reticulate-rugulate patterns. Rim-arillate aril is a thick type with circular shape.

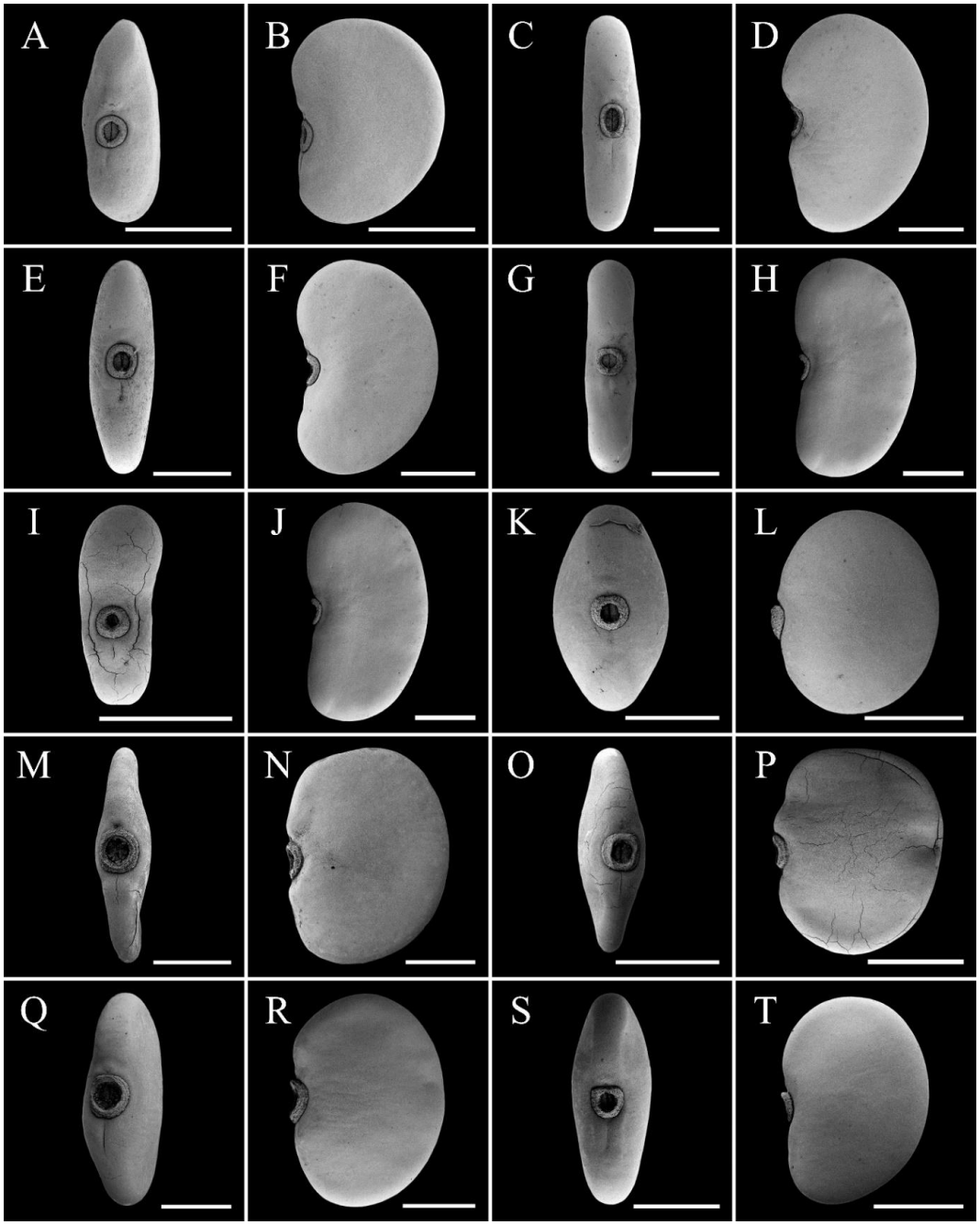

Figure 4. Seed morphology. A-B. *Grona styracifolia*. C-D. *Hegnera obcordata*. E-F. *Huangtcia oblata*. G-H. *H. renifolia*. I-J. *Mecopus nidulans*. K-L. *Ototropis amethystina*. M-N. *O. hayatae*. O-P. *O. kingiana*. Q-R. *O. megaphylla*. S-T. *O. multiflora*. Scale bars 1 mm

Polhillides *H.Ohashi & K.Ohashi (Figures 5.M-N)*

Seed shape is reniform with an average length, width, and thickness of 2.33±0.07 mm, 1.75±0.05 mm, and 1.01±0.07 mm, respectively. Testa is light brown to black with reticulate, rugulate and smooth patterns. Rim-arillate aril is a thick type with circular shape.

Pycnospora *R.Br. ex Wight & Arn. (Figures 5.O-P)*

Seed shape is reniform with an average length, width, and thickness of 2.30±0.09 mm, 1.47±0.06 mm, and 0.76±0.05 mm, respectively. Testa is light green to dark brown with rugulate pattern. Rim-arillate aril is a thick type with circular shape.

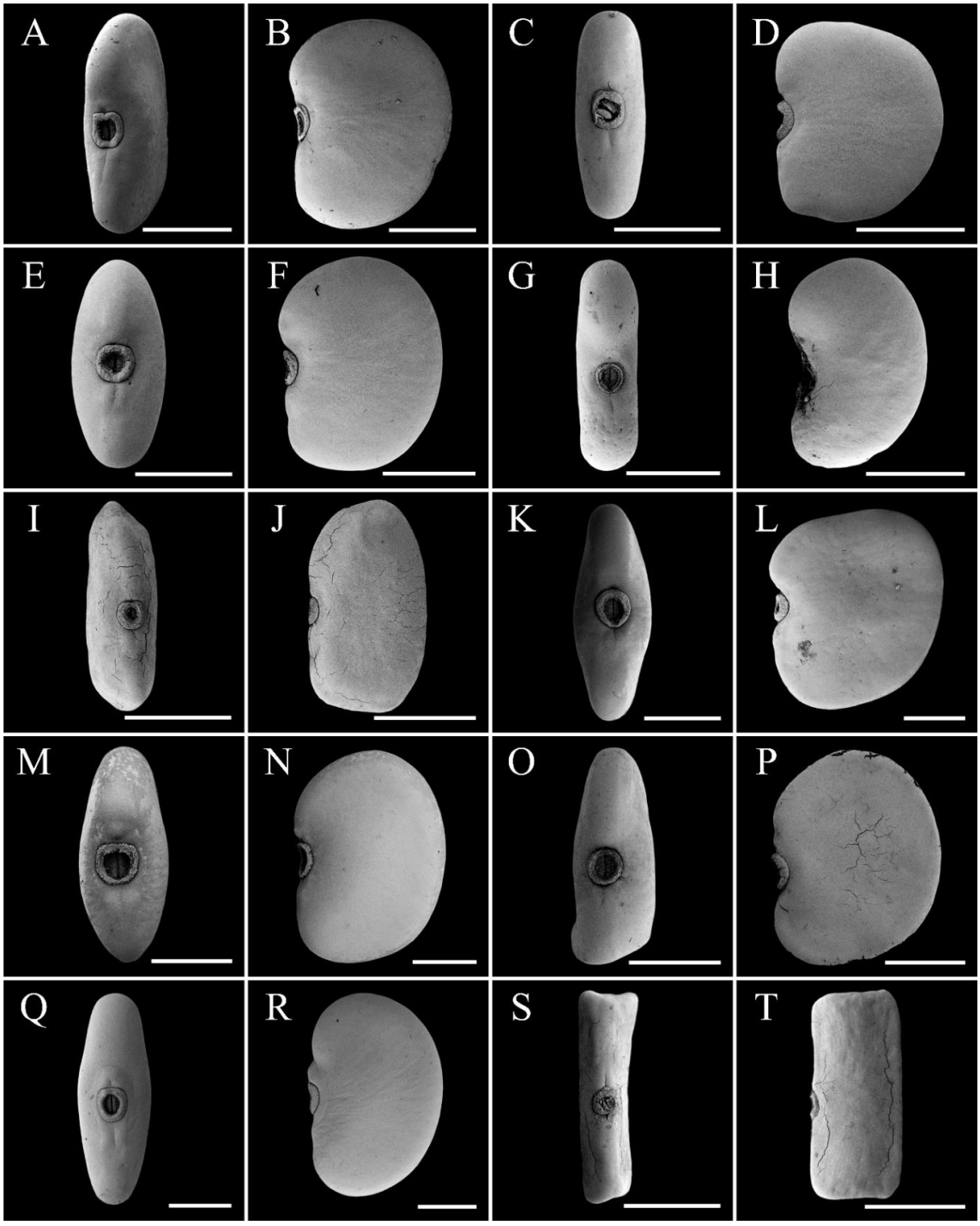

Figure 5. Seed morphology. A-B. *Phyllodium elegans*. C-D. *P. kurzianum*. E-F. *P. longipes*. G-H. *P. pulchellum*. I-J. *P. vestitum*. K-L. *Pleurolobus gangeticus*. M-N. *Polhillides velutina*. O-P. *Pycnospora lutescens*. Q-R. *Sohmaea hispida*. S-T. *S. laxiflora* ssp. *laxiflora*. Scale bars 1 mm

Sohmaea *H.Ohashi & K.Ohashi (Figures 5.Q-T and Figures 6.A-B)*

Seed shape is oblongoid with an average length, width, and thickness of 2.96±0.82 mm, 1.04±0.14 mm, and 0.66±0.12 mm, respectively. Testa is brown to dark brown with colliculate-rugulate, reticulate-rugulate, and rugulate patterns. Rim-arillate aril is a thick type with circular shape.

Tadehagi *(Schindl.) H.Ohashi (Figures 6.C-F)*

Seed shape is reniform with an average length, width, and thickness of 4.25±1.45 mm, 2.81±0.70 mm, and 1.25±0.25 mm, respectively. Testa is light to dark brown with rugulate pattern. Rim-arillate aril is a thick type with subcircular and subcircular-elliptic shapes.

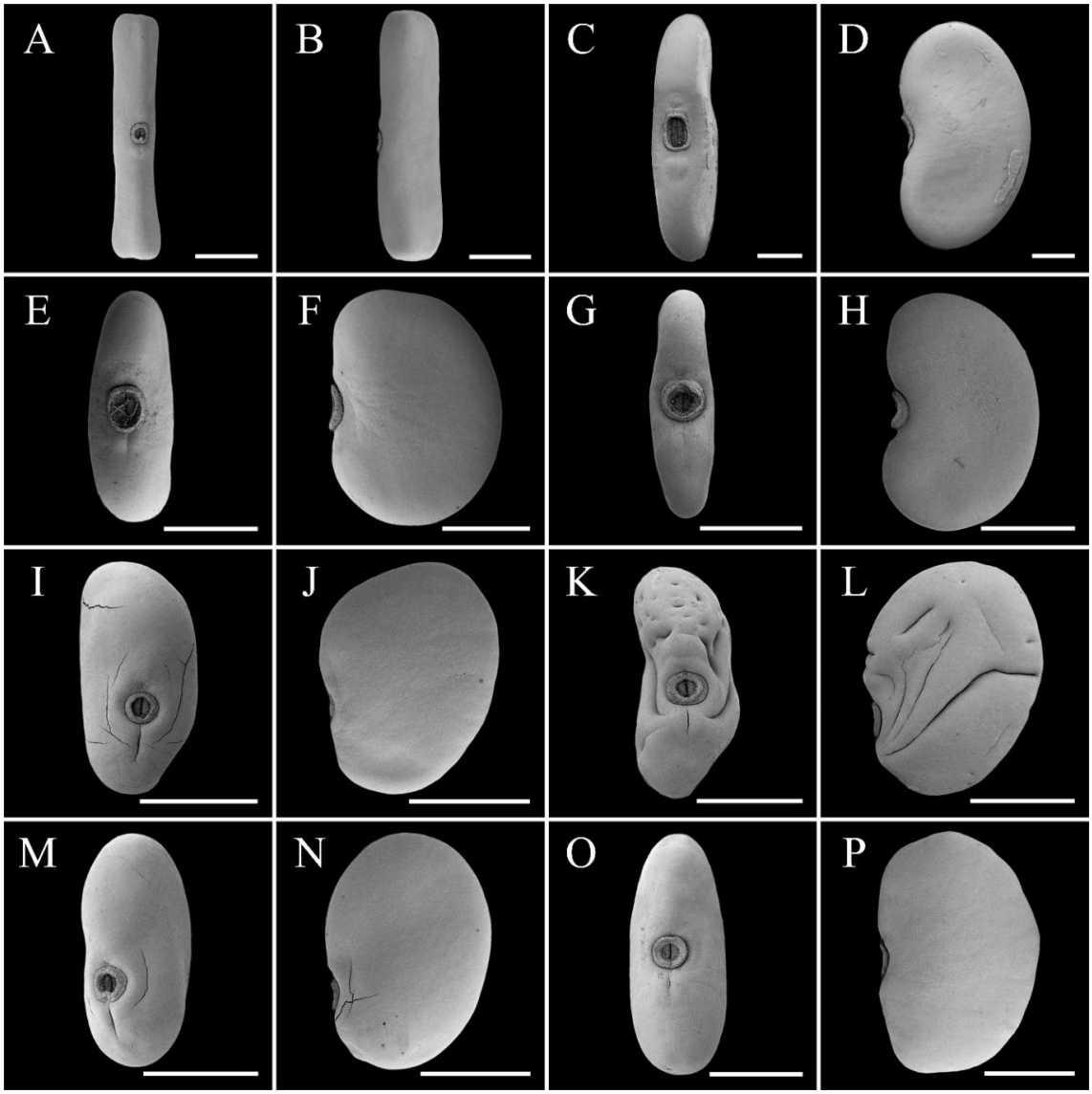

Figure 6. Seed morphology. A-B. *Sohmaea teres*. C-D. *Tadehagi rodgeri*. E-F. *T. triquetrum*. G-H. *Tateishia concinna*. I-J. *Uraria acuminata*. K-L. *U. crinita*. M-N. *U. lagopodioides*. O-P. *U. oblonga*. Scale bars 1 mm

Tateishia *H.Ohashi & K.Ohashi (Figures 6.G-H)*

Seed shape is reniform with an average length, width, and thickness of 2.61±0.10 mm, 1.65±0.08 mm, and 0.70±0.03 mm, respectively. Testa is dark brown with rugulate pattern. Rim-arillate aril is a thick type with circular shape.

Uraria *Desv. (Figures 6.I-P)*

Seed shape is irregular and reniform with an average length, width, and thickness of 2.50±0.26 mm, 1.86±0.23 mm, and 1.08±0.09 mm, respectively. Testa is light to dark brown with colliculate-rugulate, reticulate (Figures 9.C-D), reticulate-rugulate, and rugulate patterns. Rim-arillate aril is a thick type with circular shape.

Classification of tribe Desmodieae

The result of the current study reveals that the tribe Desmodieae in Thailand can be classified into three groups based on aril types. Group I has a thin rim-arillate type and *Akschindlium* belongs to this group. Group II has a thick rim-arillate type and consists of 19 genera viz., *Alysicarpus*, *Aphyllodium*, *Campylotropis*, *Christia*, *Dendrolobium*, *Desmodium*, *Grona*, *Hegnera*, *Huangtcia*, *Mecopus*, *Ototropis*, *Phyllodium*, *Pleurolobus*, *Polhillides*, *Pycnospora*, *Sohmaea*, *Tadehagi*, *Tateishia*, and *Uraria*. Group III has a well-developed rim-arillate type, which is found in *Codariocalyx*. This classification differs from previous classification systems as the tribe was previously classified into two subtribes and three groups based on other morphological characters and molecular data by Ohashi (2005).

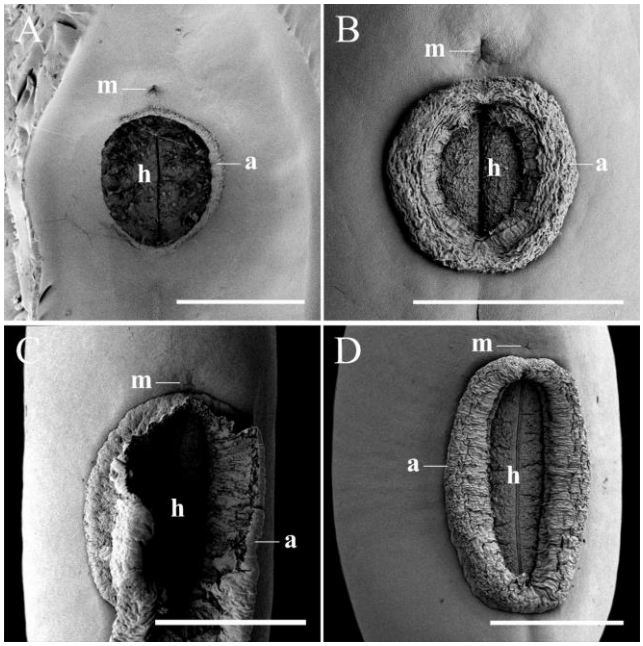

Figure 7. Photographs show types of rim-arillate aril. A. A thin type of *Akschindlium godefroyanum*. B. A thick type and circular shape of *Campylotropis pinetorum*. C. A well-developed type of *Codariocalyx microphyllus*. D. A thick type and oblong shape of *Grona heterophylla*. a: aril; h: hilum; m: micropyle. Scale bars 0.5 mm

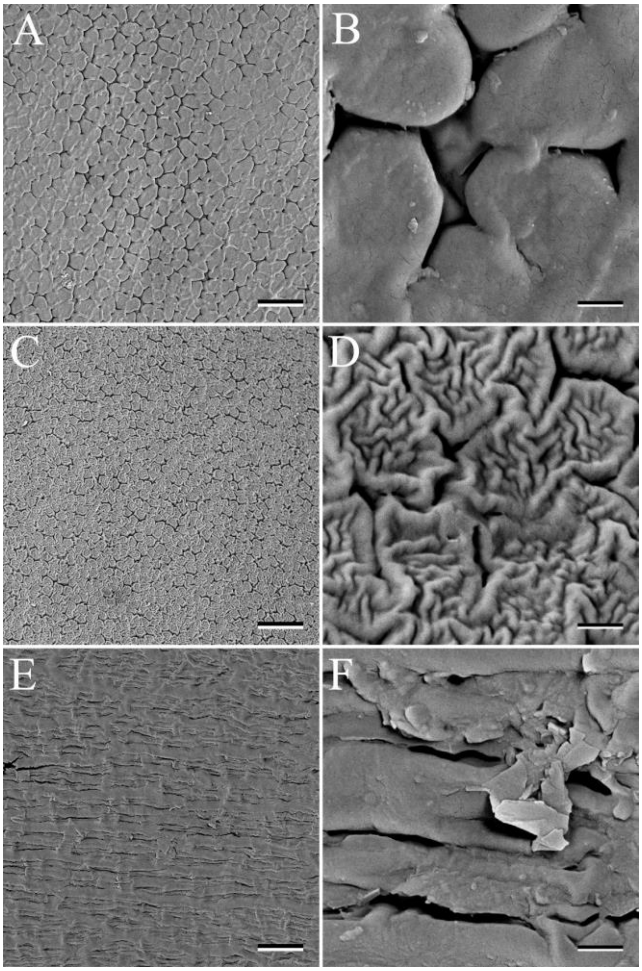

Figure 8. A, C, E. Seed testa patterns were examined under SEM with 1,000x; and B, D, F. 10,000x magnification. A-B. Colliculate pattern of *Grona styracifolia*. C-D. Colliculate-rugulate pattern of *Codariocalyx microphyllus*. E-F. Fissured pattern of *Campylotropis decora*. Scale bars 10 μm for A, C, E and 1 μm for B, D, F

Relationship between *Akschindlium* and *Tadehagi*

Akschindlium is a monotypic genus distributed in Thailand, Laos, Cambodia, and Vietnam. A species of this genus was previously treated under *Tadehagi* (an Asian-Australian genus) due to the similarity in some characteristics, such as flowers, pods, petioles, and pollen grains. It is also similar to *Droogmansia* (an endemic genus of Africa) in the stamens, calyx, seeds, and bracteoles. A common characteristic among these three genera is a uni-foliolate leaf with a winged petiole. The best evidence that can be used to delimit the generic rank of those three genera, is their distributional range (Ohashi 1973, 2003; Saisorn and Chantaranothai 2013). The current work results show that the seed of *Akschindlium godefroyanum* has a thin rim-arillate aril, which is different from the two species of *Tadehagi* that have a thick rim-arillate aril. This probably confirms the difference between *Akschindlium* and *Tadehagi*.

Taxonomic characteristics of *Codariocalyx*

Three species belong to *Codariocalyx* viz., *C. gyroides*, *C. motorius*, and *C. microphyllus*. The first two species have long been treated under this genus. The last one, a former member of *Desmodium*, was added to *Codariocalyx* due to the presence of a well-developed rim-arillate aril as in the first two species (Ohashi 2004a). Previous reports showed that the seed of *Codariocalyx* has a well-developed rim-arillate aril (Ohashi 1973; Kirkbride et al. 2003b; Saisorn and Chantaranothai 2019).

The current study agrees with those reports; this characteristic can be used to identify the genera. Recently, some studies on the phylogenetic relationship of the tribe Desmodieae suggested that *C. microphyllus* formed a clade with *Leptodesmia*, a genus with the same type of aril as *Codariocalyx*. This species was transferred to *Leptodesmia* (Ohashi et al. 2018a); there is little evidence to delimit both genera. More data is needed for classification; therefore the delimitation of these two genera for this current work still follows the Ohashi system (2004a).

Taxonomic characteristics of *Sohmaea*

Sohmaea has been proposed as a new genus based on morphological and molecular data (Ohashi et al. 2018b). It has a linear pod with oblong to elliptic pod articles; this would be a characteristic of the genus. Additionally, previous molecular studies revealed that the genus is quite distinct from other genera of the tribe Desmodieae and is closely related to *Alysicarpus* and *Bouffordia* (Ohashi and Ohashi 2018b; Ohashi et al. 2018a; Ohashi et al. 2019).

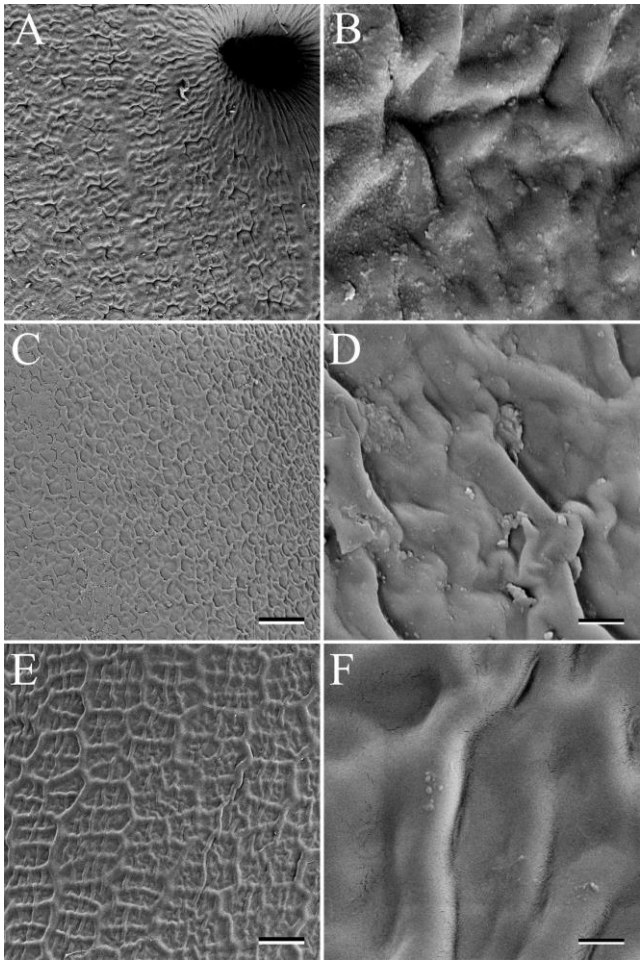

Figure 9. A, C, E. Seed testa patterns were examined under SEM with 1,000x; and B, D, F. 10,000x magnification. A-B. Pitted pattern of *Codariocalyx gyroides*; C-D. Reticulate of *Uraria crinita*; E-F. Reticulate-reticulate of *Phyllodium vestitum*. Scale bars 10 μm for A, C, E and 1 μm for B, D, F

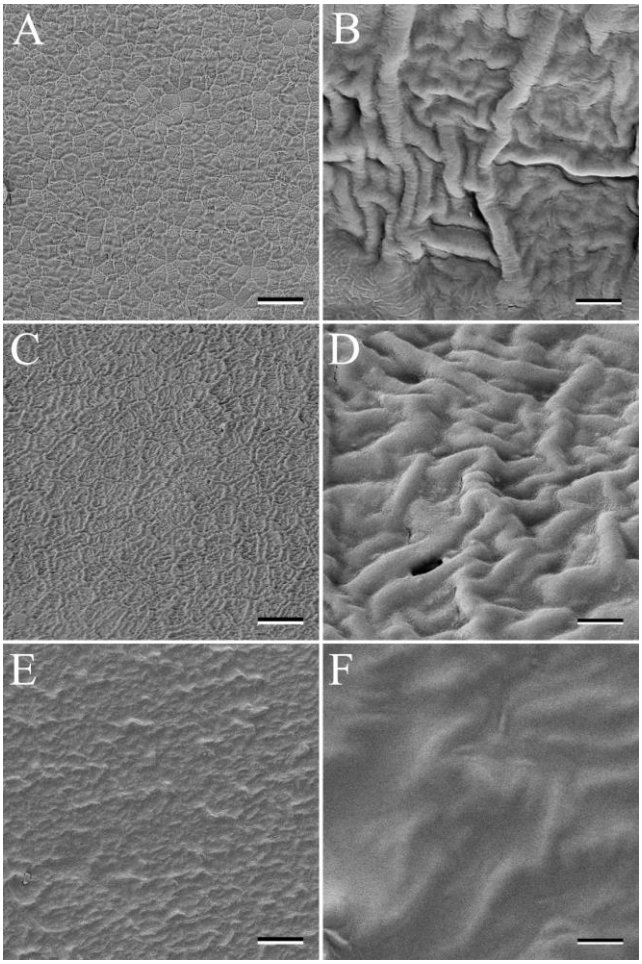

Figure 10. A, C, E. Seed testa patterns were examined under SEM with 1,000x; and B, D, F. 10,000x magnification. A-B. reticulate-rugulate of *Akschindlium godefroyanum*. C-D. rugulate of *Campylotropis decora*; E-F. smooth of *Dendrolobium olivaceum*. Scale bars 10 μm for A, C, E and 1 μm for B, D, F

The result of the current study reveals that the seed characteristic of *Sohmaea* is an oblongoid shape; this character is not found in any other species except *Alysicarpus vaginalis*. This evidence confirms that the genus is distinct from other genera, as reported in previous studies. The seed shape of *Alysicarpus vaginalis* can be ellipsoid or oblongoid. This result agrees well with a previous study (Gandhi et al. 2011). The phylogenetic relationship between *Sohmaea* and *Alysicarpus* probably supports it.

A unique character of *Grona heterophylla*

Grona heterophylla is similar to other species of *Grona* in terms of morphological characters, including *G. auricoma* and *G. brevipedicellata*. (Ohashi and Ohashi 2018a; Ohashi et al. 2018b). The result of this work reveals that the characteristic of *G. heterophylla* is a thick type and an oblong shape of the rim-arillate aril. While other species of *Grona* included in this study, have a thick type and a circular shape of the rim-arillate aril. This characteristic can probably be used to identify this species. However, three species of Thai *Grona* have not been included in this study (*G. adscendens*, *G. rubra*, and *G. triflora*). Therefore, the species identification of *Grona*, based on seed characters should, be carefully examined.In conclusion, this work has provided the most complete seed morphologies for the tribe Desmodieae from Thailand. The character of aril is used to clarify the taxonomic confusion between *Akschindlium* and *Tadehagi*. Three species of *Codariocalyx*, including *C. gyroides*, *C. motorius*, and *C. microphyllus* share common characteristics as they have a well-developed rim-arillate aril. The oblongoid shape of seeds is restricted to *Sohmaea*. Distinct characteristics of arils, including thick type and oblong shape, are specific to one species, *Grona heterophylla*. Lastly, tribal classification is proposed in this work based on aril characters.

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