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Cover: A digital art of water birds of Noyyal River and its wetlands in Coimbatore District by Megha A. Kashyap.



## Pollen morphology of Annonaceae from the Bicol Region, Philippines

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**Abstract:** Annonaceae is one of the most prominent families with diverse pollen morphology. The present study aimed to investigate and describe the pollen morphology of 12 species of Annonaceae from the Bicol Region, Philippines. The pollen grains were subjected to acetolysis and described using a scanning electron microscope, and the hierarchical cluster analysis was done to cluster the pollen grains with similar characters. The 12 Annonaceae species share characters such as monads, inaperturate, and isopolarity, but they formed three distinct clusters based on pollen size. Their polar axis (PA) and equatorial diameter (ED) are statistically significant due to their variability, with PA ranging  $36.41 \pm 15.86 \mu\text{m}$  and ED  $28.27 \pm 14.27 \mu\text{m}$ . The polar length-to-equatorial diameter (PA/ED) ratio is 1.32, with mostly sub-prolate shape. Exine ornamentations showed significant variability among the 12 Annonaceae species with echinate, rugulate, scabrate, psilate, and verrucate. The pollen morphology of the two endemic species, namely *Friesodielsia lanceolata* (Merr.) Steenis and *Goniothalamus elmeri* Merr. is first reported here. Collections of more endemic Philippine Annonaceae species are deemed necessary to comprehensively analyze their pollen characters, which are helpful for infrageneric relationships within the family.

**Keywords:** Acetolysis, endemic species, equatorial diameter, exine ornamentation, palynology, polar axis, pollen size, pollen shape, pollination, SEM.

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**Author contributions:** AORD—contributed to the field collections, data analysis, discussion of results, and conclusion of the manuscript. GJDA—led the discussion, editing, and paper review for the manuscript.

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## INTRODUCTION

Annonaceae is a pantropical family comprising 110 genera and approximately 2,500 species (Chatrou et al. 2012; Xue et al. 2021). The family members are characterized by exstipulate, distichous leaves, trimerous perianth of two whorls of petals, numerous stamens, and free carpels (van Heusden 1992; Chatrou et al. 2012; Couvreur et al. 2012). Moreover, the family has the greatest basal angiosperm diversity at both macromorphological and pollen morphological levels (Doyle & Le Thomas 2012). Annonaceae provide forest and ecosystem services, such as provisioning, regulating, cultural, and supporting services (Handayani & Yuzammi 2021; Erkens et al. 2023). They are widely distributed in Asia-Pacific regions such as Thailand, Malaysia, Borneo, and the Philippines (Turner 2011; Johnson et al. 2021).

The palynology of Annonaceae has gained interest because it is a significant source of evidence for systematics and phylogenetic analysis (Doyle & Le Thomas 1997; Xue et al. 2011; Ragho 2020). The minute pollen grains contain a remarkable degree of information in their highly resistant sporopollenin wall (Davey et al. 2015), which provides additional plant identification and classification characters to solve differences in problematic groups (Okechukwu et al. 2021); solve complicated taxonomic interrelationships (Saunders et al. 2018).

Several studies on pollen morphology, such as *Neo-uvaria* Airy Shaw, showed inaperturate, monads with scabrate or micro-echinate exine ornamentations (Chaowasku et al. 2011); the pollen grains of some Thai *Artabotrys* R.Br. were described as monad pollen, inaperturate, apolar, and medium to large grains. The pollen shapes were divided into two groups, subprolate & euprolate, and different exine ornamentations with rugulate & perforate-fossulate exine sculptures (Eiadhong & Insura 2014); species from China have small, medium-sized, and large to very large pollen grains, elliptic, subspherical in monads for *Artabotrys*, *Fissistigma* (Merr.) Steenis, *Miliusa* Lesch. ex A.DC., *Trivalvaria* (Miq.) Miq., *Uvaria* L., and *Polyalthia* Blume, and tetrads for *Annona* L., *Goniothalamus* Hook.f. & Thomson, *Mitrephora* Hook.f. & Thomson, and *Polyalthia rumphii* (Blume ex Hensch.) Chaowasku (Gan et al. 2015); three species of *Annona* L. have been studied, namely *Annona squamosa* L. and *Annona senegalensis* L. were tetragonal with a globose shape, rugulate exine ornamentation, inner structure, and *Annona muricata* L. was rhomboidal with an ellipsoidal shape, reticulate exine ornamentation (Okechukwu et al. 2021). The pollen morphology studies

reaffirm the great diversity among and within genera in Annonaceae (Shao & Xu 2017).

While pollen morphology of Annonaceae species from America and Africa has been studied well (Couvreur et al. 2008; Turner 2011; Azeez & Folorunso 2014; Shao & Xu 2018), research in the Philippines remains limited. The Philippines has 33 genera and 147 species recognized, and 97 are endemic (Pelser et al. 2011 onwards). For the diversity of Annonaceae species, floral inventories and collections are deemed necessary to study their pollen morphology, which would supplement the identification and classification of the Annonaceae. Pollen studies of the Philippine Annonaceae need to be investigated well, especially among the endemic species. The present study was the first attempt to study pollen morphology on the 12 species of Annonaceae collected from the Bicol Region, Philippines, utilizing a scanning electron microscope (SEM); thus, it is important to provide detailed descriptions and present a better understanding of pollen diversity.

## MATERIALS AND METHODS

### Plant collection

The flowers of Annonaceae were collected during the explorational surveys for Annonaceae in the four protected areas (PAs) in the Bicol Region, Philippines, during the flowering month of July in 2019 and 2021. The PAs include Abasig-Matogdon-Mananap Natural Biotic Area (AMMNBA) covering Mt. Mananap in San Vicente, Mt. Matogdon in San Lorenzo Ruiz, and Labo, Camarines Norte; Bulusan Volcano Natural Park (BVNP), Sorsogon; Mt. Isarog Natural Park (MINP) in Panicuason, Naga City, Camarines Sur, and Mt. Mayon Volcano Natural Park (MMVNP) in Barangay Mayon, Albay (Image 1). Gratuitous Permits were secured from the Department of Environment and Natural Resources (DENR) Region V.

### SEM preparation of pollen grains

The flowers of the Annonaceae species collected from the Bicol Region (Dioneda & Alejandro 2022, 2023) and pollen grains were placed in microtubes with labels and stored in the refrigerator at 50 °C. The present study used the acetolysis procedure by Halbritter et al. (2018a). The pollen grains were placed in a small test tube with a mixture of nine parts acetic anhydride and one part concentrated sulfuric acid and heated for four minutes at 100 °C. The acetolyzed mixtures were placed in a water bath while heating. After heating, the liquid was decanted, and the residues were washed with acetic

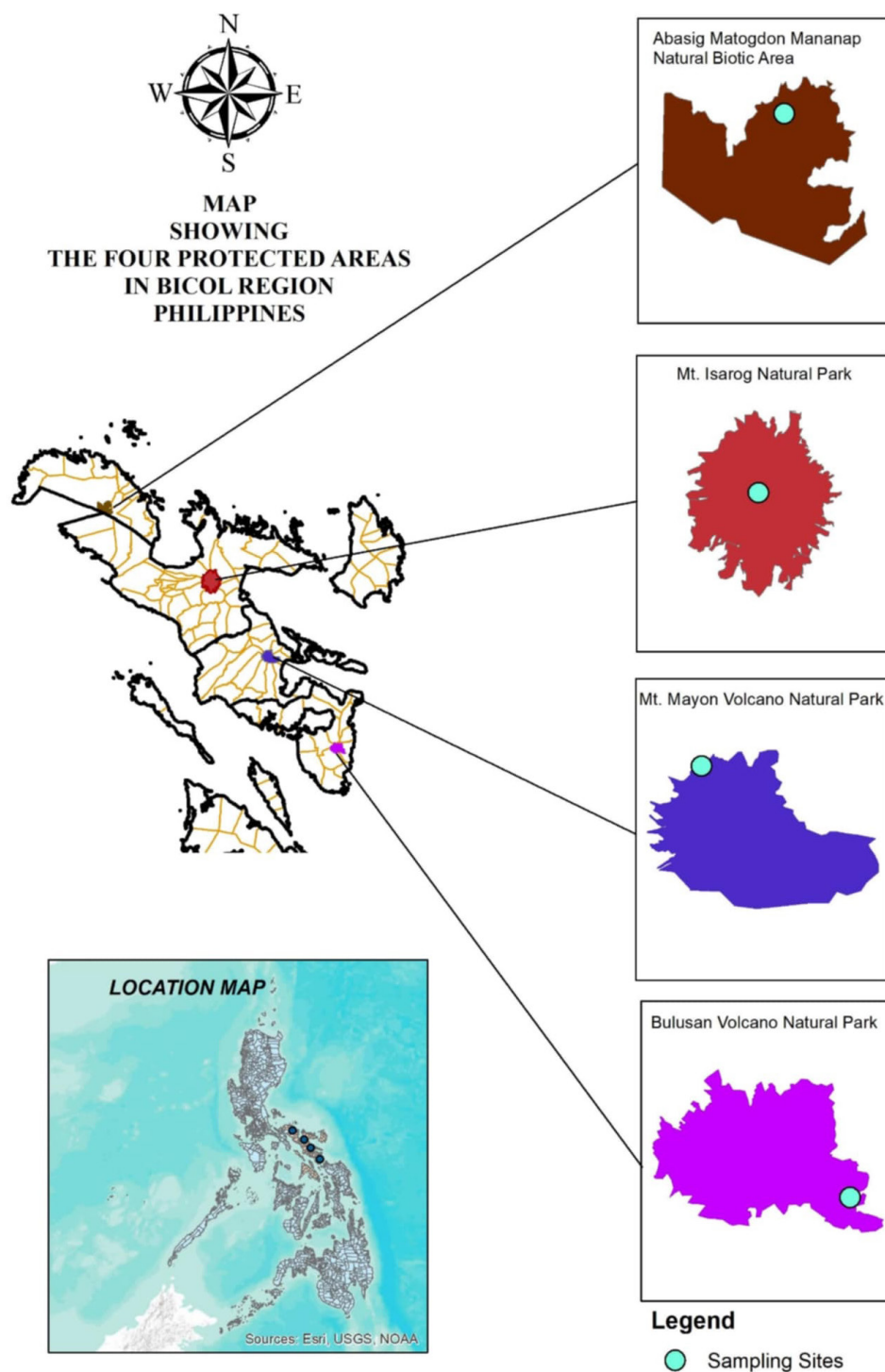


Image 1. The map shows the study site, the Bicol Region, and the four PAs. The collection sites were marked in green circles inside the PAs of AMMNBA (brown), MINP (red), MMVNP (blue), and BVNP (purple). The map was prepared using ARC-GIS (DENR-Region V 2023).

acid three times. Then, more water was added to wash further. The mixture was filtered, and the pollen grains were air-dried. The air-dried pollens were placed on the stub with carbon tape and inside the SEM chamber (HITACHI TM 3000). For each species, 20 pollen grains

were measured, and intricate images of pollen were observed using the higher resolution of SEM (2000–3000 magnification or more). The SEM observation was held at the Analytical Services Laboratory, Research Center for the Natural and Applied Sciences (RCNAS), University

**Table 1. Pollen shape classes and suggested relationships between polar axis (PA) and equatorial diameter (ED) (Erdtman 1952).**

Pollen shape classes	PA / ED	100 x PA / ED
Peroblate	<4/8	< 50
Oblate	4/–6/8	50–75
Suboblate	6/8–7/8	75–88
Oblate spheroidal	7/8–8/8	88–100
Prolate spheroidal	8/8–8/7	100–114
Subprolate	8/7–8/6	114–133
Prolate	8/6–8/4	133–200
Perprolate	>8/4	>200

of Santo Tomas, España, Manila. Photomicrographs of the examined pollen grains were taken for further identification.

### Pollen descriptions and measurements

The pollen characters used to describe the pollen grains were pollen shapes, sizes, exine sculpture or ornamentations, distribution, and apertures (El-Amier 2015; Halbritter et al. 2018b). Punt et al. (2007) and Halbritter et al. (2018c) were used for pollen descriptions and terminology. Pollen shape and size terminology followed Erdtman (1952).

The polar axis (PA) and equatorial diameter (ED) were measured. The equatorial measurement of the pollen grains was done by measuring the grain from one side of the equator to the opposite side. Polar measurement was done by measuring one pole to the other to indicate pollen shape accurately. The mean value of both axes was computed. The shape of the pollen was determined by the ratio of PA/ED (Table 1). The PA and ED were subjected to statistical analysis using IBM SPSS software v. 3, and Hierarchical cluster analysis was used to cluster Annonaceae species with similar characters and generate the dendrogram to visually represent the relationships between characters.

## RESULTS AND DISCUSSION

### General description of pollen grains of Annonaceae species from the Bicol Region

The pollen morphology of Annonaceae from the Bicol Region was notably varied. Mostly, the pollen grains were monads, a few were dyads, and tetrads. The pollen sizes ranged from small (10–30  $\mu\text{m}$ ), medium-sized (30–50  $\mu\text{m}$ ), and large to very large (50–100  $\mu\text{m}$ ). The polar axis (PA) value ranges  $36.86 \pm 15.86 \mu\text{m}$ , and the equatorial

diameter (ED) value ranges  $28.27 \pm 14.27 \mu\text{m}$ . The total mean value of the polar axis is  $35.27 \mu\text{m}$ , the total mean value of the equatorial axis is  $27.22 \mu\text{m}$ , and the total mean PA/ED ratio is 1.32, with a generally sub-prolate shape. The exine ornamentations also varied in echinate, rugulate, scabrate, psilate with micro-perforations, and verrucate. Detailed morphometry is presented in Tables 2 & 3.

### Species-level pollen descriptions

#### Tribe Miliuseae

*Meiogyne cylindrocarpa* (Burck) Heusden, 1994 (Image 2)

Pollen unit: monad, pollen size: small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: sub-prolate, aperture: inaperturate, PA mean value:  $30.94 \pm 4.20 \mu\text{m}$  with ED mean value  $25.37 \pm 3.38 \mu\text{m}$ , PA/ED ratio: 1.22, ornamentation: rugulate.

*Monoon grandifolium* (Elmer) B.Xue & R.M.K.Saunders, 2012 (Images 2 & 3)

Pollen unit: monad, small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: sub-prolate, aperture: inaperturate, PA mean value  $35.47 \pm 9.33 \mu\text{m}$ , ED mean value  $28.27 \pm 6.73 \mu\text{m}$ , PA/ED ratio 1.32, ornamentation: granular-rugulate.

*Phaeanthus ophthalmicus* (Roxb. ex G.Don) J. Sinclair, 1955 (Images 2&3)

Pollen unit: monad, pollen size: small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: prolate, aperture: inaperturate, PA mean value  $34.71 \pm 8.57 \mu\text{m}$ , ED mean value  $24.64 \pm 5.43 \mu\text{m}$ , PA/ED ratio 1.41, ornamentation: scabrate.

*Polyalthia obliqua* Hook.f. & Thomson, 1855 (Images 2&3)

Pollen unit: monad, pollen size: small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: prolate, aperture: inaperturate, PA mean value  $27.46 \pm 5.92 \mu\text{m}$ , ED mean value:  $20.41 \pm 6.11 \mu\text{m}$ , PA/ED ratio 1.39, ornamentation: verrucate.

*Popowia pisocarpa* (Blume) Endl. ex. Walp., 1842 (Image 2)

Pollen unit: monad, pollen size: small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: sub-prolate, PA mean value  $31.85 \pm 10.58 \mu\text{m}$ , ED mean value  $27.17 \pm 12.41 \mu\text{m}$ , PA/ED ratio 1.17, ornamentation: scabrate.

#### Tribe Uvarieae

*Fissistigma latifolium* (Dunal) Merr., 1919 (Image 2)



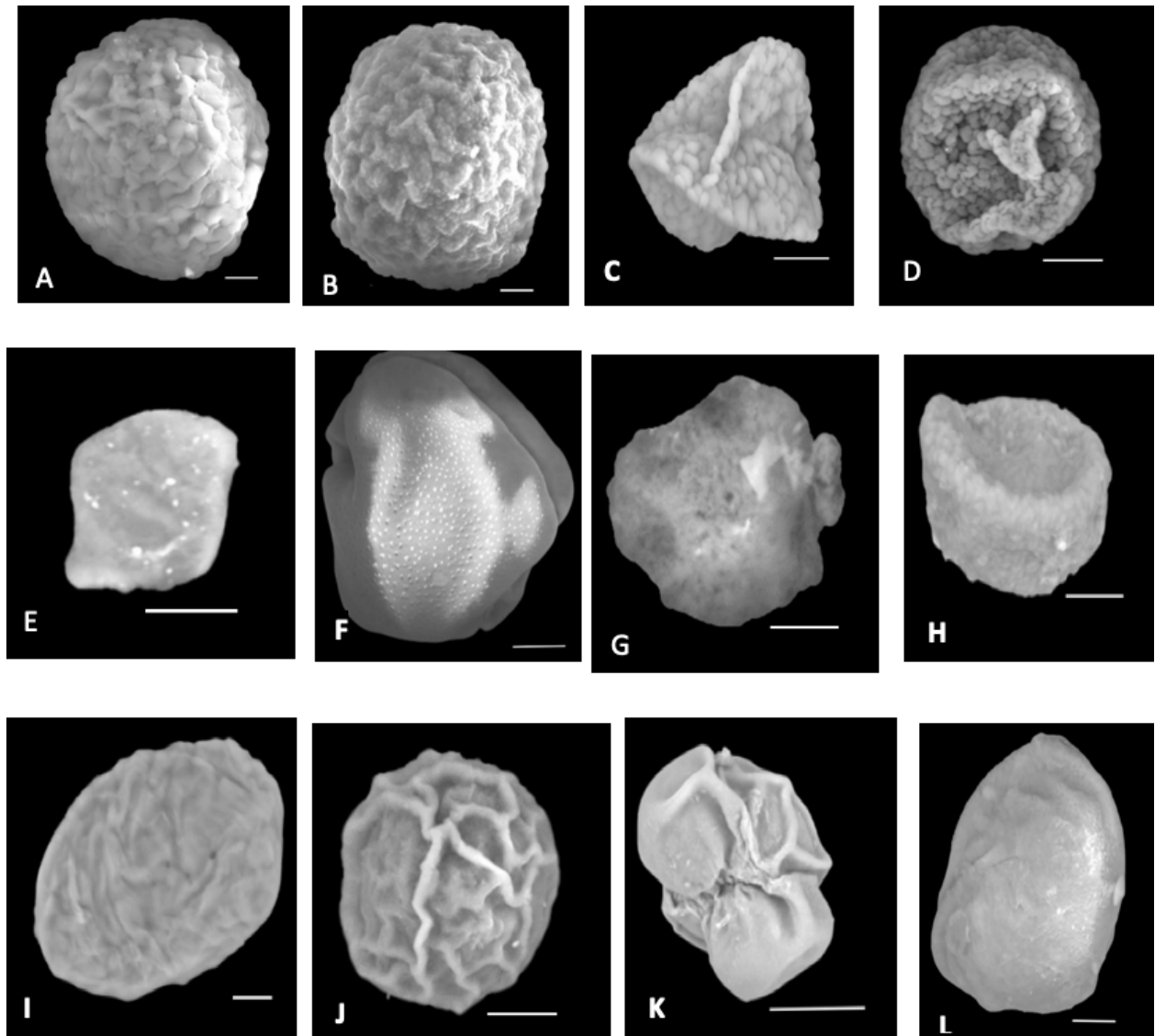


Image 2. SEM views of twelve pollen grains: A—*Meiogyne cylindrocarpa* | B—*Monoon grandifolium* | C—*Phaeanthus ophthalmicus* | D—*Polyalthia obliqua* | E—*Popowia pisocarpa* | F—*Cananga odorata* | G—*Drepananthus acuminatus* | H—*Fissistigma latifolium* | I—*Friesodielsia lanceolata* | J—*Uvaria monticola* | K—*Goniothalamus elmeri* | L—*Artabotrys suaveolens*. © Retuerma-Dioneda. Scale bar: K 100  $\mu\text{m}$ ; F 50  $\mu\text{m}$ ; C, D, E, G, H, I, J, L 30  $\mu\text{m}$ ; A, B 20  $\mu\text{m}$ .

Pollen unit: monad, pollen size: small to medium-sized (10–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: prolate; aperture: inaperturate, PA mean value  $24.47 \pm 5.39$   $\mu\text{m}$ , ED mean value  $18.15 \pm 5.10$   $\mu\text{m}$ , PA/ED ratio 1.35, ornamentation: verrucate.

*Friesodielsia lanceolata* (Merr.) Steenis, 1964 (Image 2)

Pollen unit: monad, pollen size: small to medium-sized (20–30  $\mu\text{m}$ ), polarity: isopolar, pollen shape: prolate, aperture: inaperturate, PA mean value  $33.55 \pm 7.70$   $\mu\text{m}$ , ED mean value  $24.10 \pm 7.82$   $\mu\text{m}$ , PA/ED ratio 1.39, ornamentation: echinate.

*Uvaria monticola* Miq., 1865 (Images 2 & 3)

Pollen unit: monad, pollen size: medium to large (30–50  $\mu\text{m}$ ), polarity: isopolar, pollen shape: prolate, aperture: inaperturate, PA mean value  $32.20 \pm 2.46$   $\mu\text{m}$ , ED mean value  $28.81 \pm 2.51$   $\mu\text{m}$ , PA/ED mean value 1.12, ornamentation: coarsely rugulate.

**Tribe Canangeae**

*Cananga odorata* (Lam.) Hook.f. & Thomson, 1855 (Images 2)

Pollen unit: dyad, pollen size: large to very large-sized (50–100  $\mu\text{m}$ ), polarity: isopolar, pollen shape: sub-prolate, apertures: inaperturate; PA value  $73.14 \pm 14.91$

**Table 2. SEM pollen morphometry of the 12 Annonaceae species from the Bicol Region, Philippines (Erdtman 1952).**

Name of species	PA value	ED value	PA/ED ratio
<b>Tribe Miliusae</b>			
<i>Meiogyne cylindrocarpa</i> (Burck) Heusden	30.94 ± 4.20	25.37 ± 3.38	1.22
<i>Monoon grandifolium</i> (Elmer) B.Xue & R.M.K.Saunders	35.47 ± 9.33*	26.84 ± 6.73*	1.32
<i>Phaeanthus ophthalmicus</i> (Roxb. ex G.Don) J.Sinclair	34.71 ± 8.57*	24.64 ± 5.43*	1.41
<i>Polyalthia obliqua</i> Hook.f. & Thomson	27.46 ± 5.92	20.40 ± 6.11	1.35
<i>Popowia pisocarpa</i> (Blume) Endl. ex. Walp.	31.85 ± 10.58*	27.17 ± 12.41*	1.17
<b>Tribe Uvarieae</b>			
<i>Fissistigma latifolium</i> (Dunal) Merr.	24.47 ± 5.33	18.15 ± 5.10	1.35
<i>Friesodielsia lanceolata</i> (Merr.) Steenis	35.55 ± 7.70	24.1 ± 7.82	1.39
<i>Uvaria monticola</i> Miq.	32.20 ± 2.46	28.81 ± 2.51	1.12
<b>Tribe Canangeae</b>			
<i>Cananga odorata</i> (Lam.) Hook.f. & Thomson	73.14 ± 14.91*	61.05 ± 15.75*	1.20
<i>Drepananthus acuminatus</i> (C.B.Rob.) Survesw & R.M.K.Saunders	29.40 ± 8.72*	19.31 ± 6.27*	1.52
<b>Tribe Annoneae</b>			
<i>Goniothalamus elmeri</i> Merr.	33.62 ± 10.95*	24.28 ± 7.51*	1.38
<b>Tribe Xylopieae</b>			
<i>Artabotrys suaveolens</i> (Blume) Blume	34.71 ± 8.57*	23.43 ± 8.27*	1.48
<b>Mean values</b>	<b>36.41 ± 15.86*</b>	<b>28.27 ± 14.27*</b>	<b>1.32**</b>

\*—significant | \*\*—not significant.

µm, ED mean value 61.05 ± 15.75 µm, PA/ED ratio 1.20, ornamentation: psilate with microperforations.

*Drepananthus acuminatus* (C.B.Rob.) Survesw. & R.M.K. Saunders, 2010 (Image 2)

Pollen unit: monad, pollen size: small to medium-sized (20–30 µm), polarity: isopolar, pollen shape: prolate, aperture: aperturate; PA mean value 29.40±8.72 µm, ED mean value 19.31±6.27 µm, P/E ratio 1.52, ornamentation: scabrate

#### Tribe Annoneae

*Goniothalamus elmeri* Merr., 1912 (Image 2)

Pollen unit: tetrad, pollen size: small to medium-sized (20–100 µm), polarity: isopolar, pollen shape: prolate, aperture: inaperturate, PA mean value 33.62 ± 10.95 µm, ED mean value 24.28 ± 7.51 µm, PA/ED ratio 1.38, ornamentation: coarsely rugulate.

#### Tribe Xylopieae

*Artabotrys suaveolens* (Blume) Blume, 1830 (Image 2)

Pollen unit: monad, size (pollen unit): small to medium-sized (20–30 µm), polarity: isopolar, pollen shape: prolate, apertures: inaperturate; PA mean value 34.71 ± 8.57 µm, ED mean value 23.43 ± 8.27 µm, PA/ED

ratio 1.48, ornamentations rugulate.

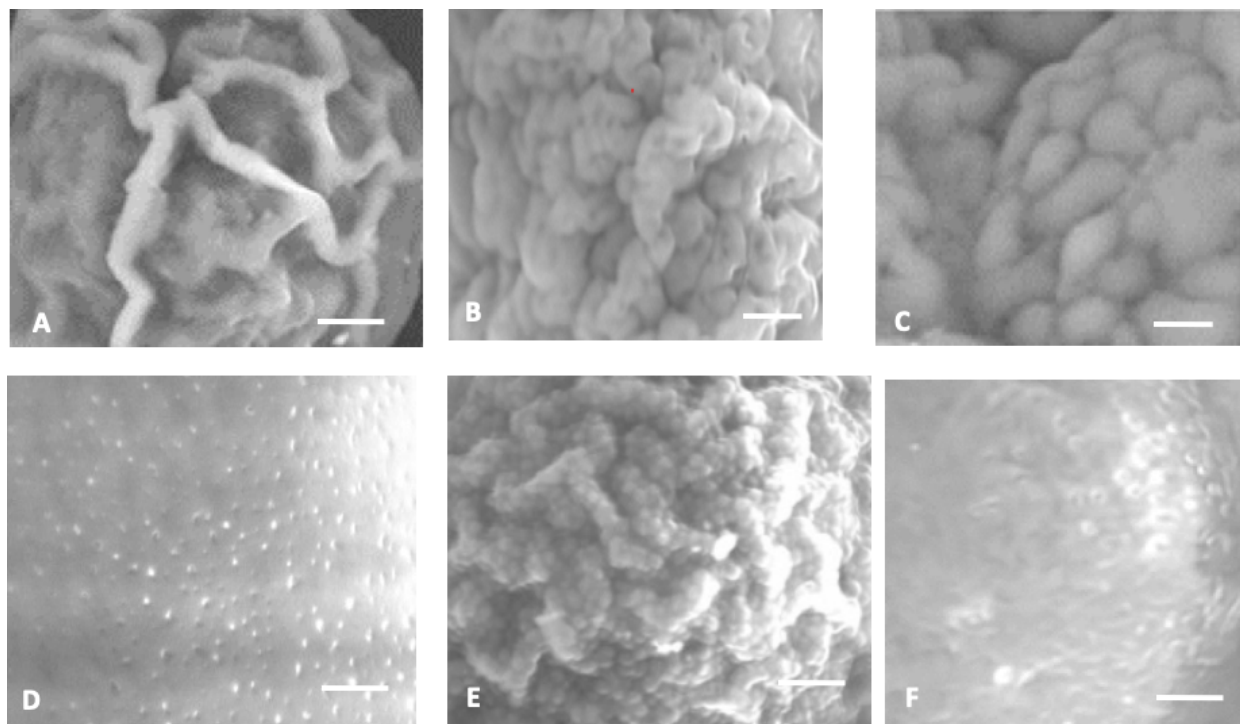
## DISCUSSION

The pollen morphology of basal angiosperms like the Annonaceae is highly diverse (Lu et al. 2015). This diversity of pollen types gained interest because it provides insights into the evolutionary history. Annonaceae, one of the most prominent primitive families, produces a variety of pollen types, including monads, dyads, tetrads, and polyads composed of eight, 16, or 32 grains (Walker 1971). The variety of pollen grains in Annonaceae in terms of size, aperture number, shape, and exine ornamentations was observed in many studies (Eiadthong & Insura 2014; Shao & Xu 2018). According to Lora et al. (2014), pollen production in monads is plesiomorphic in angiosperms, but the aggregation into tetrads has arisen independently at different times during the evolution of flowering plants. Aggregated forms offer advantages in situations involving infrequent pollinators, short pollen viability, pollen transfer periods, and protection from desiccation. Furthermore, aggregated pollen is considered an advanced character in Annonaceae, surpassing the traditional monad form



**Table 3.** Pollen morphology of the 12 species of Annonaceae pollen grains from Bicol Region, Philippines (Punt et al. 2007; Halbritter et al. 2018b).

Name of species	Pollen size (μm)	Pollen size	Pollen shape	Pollen unit	Pollen aperture	Exine ornamentation
<b>Tribe Miliusae</b>						
<i>Meiogyne cylindrocarpa</i> (Burck) Heusden	20–30	Small–medium	Sub-prolate	Monad	Inaperturate	Rugulate
<i>Monoon grandifolium</i> (Elmer) B.Xue & R.M.K.Saunders	20–30	Small–medium	Sub-prolate	Monad	Inaperturate	Rugulate
<i>Phaeanthus ophthalmicus</i> (Roxb. ex G.Don) J. Sinclair	20–30	Small–medium	Prolate	Monad	Inaperturate	Scabrate
<i>Polyalthia obliqua</i> Hook.f. & Thomson	20–30	Small–medium	Prolate	Monad	Inaperturate	Verrucate
<i>Popowia pisocarpa</i> (Blume) Endl. ex Walp	20–30	Small–medium	Sub-Prolate	Monad	Inaperturate	Scabrate
<b>Tribe Uvarieae</b>						
<i>Fissistigma latifolium</i> (Dunal) Merr.	10–30	Small–medium	Prolate	Monad	Inaperturate	Verrucate
<i>Friesodielsia lanceolata</i> (Merr.) Steenis	20–30	Small–medium	Prolate	Monad	Inaperturate	Echinate
<i>Uvaria monticola</i> Miq.	30–50	Medium–large	Prolate-Spheroidal	Monad	Inaperturate	Rugulate
<b>Tribe Canangeae</b>						
<i>Cananga odorata</i> (Lam.) Hook.f. & Thomson	50–100	Medium–very large	Sub-Prolate	Dyad	Aperturate	Psilate-microperforation
<i>Drepananthus acuminatus</i> (C.B. Rob.) Survesw & R.M.K.Saunders	20–30	Small–medium	Prolate	Monad	Aperturate	Scabrate
<b>Tribe Annoneae</b>						
<i>Goniothalamus elmeri</i> Merr.	20–100	Medium–very large	Prolate	Tetrad	Inaperturate	Rugulate
<b>Tribe Xylopieae</b>						
<i>Artabotrys suaveolens</i> (Blume) Blume	20–30	Small–medium	Prolate	Monad	Inaperturate	Rugulate



**Image 3.** The exine ornamentation: A—*Uvaria monticola*, rugulate | B—*Polyalthia obliqua*, verrucate | C—*Phaeanthus ophthalmicus*, scabrate | D—*Cananga odorata*, psilate- microperforations | E—*Monoon grandifolium*, granular rugulate | F—*Friesodielsia lanceolata*, echinate. © Retuerma-Dioneda. Scale bar: 6 μm.

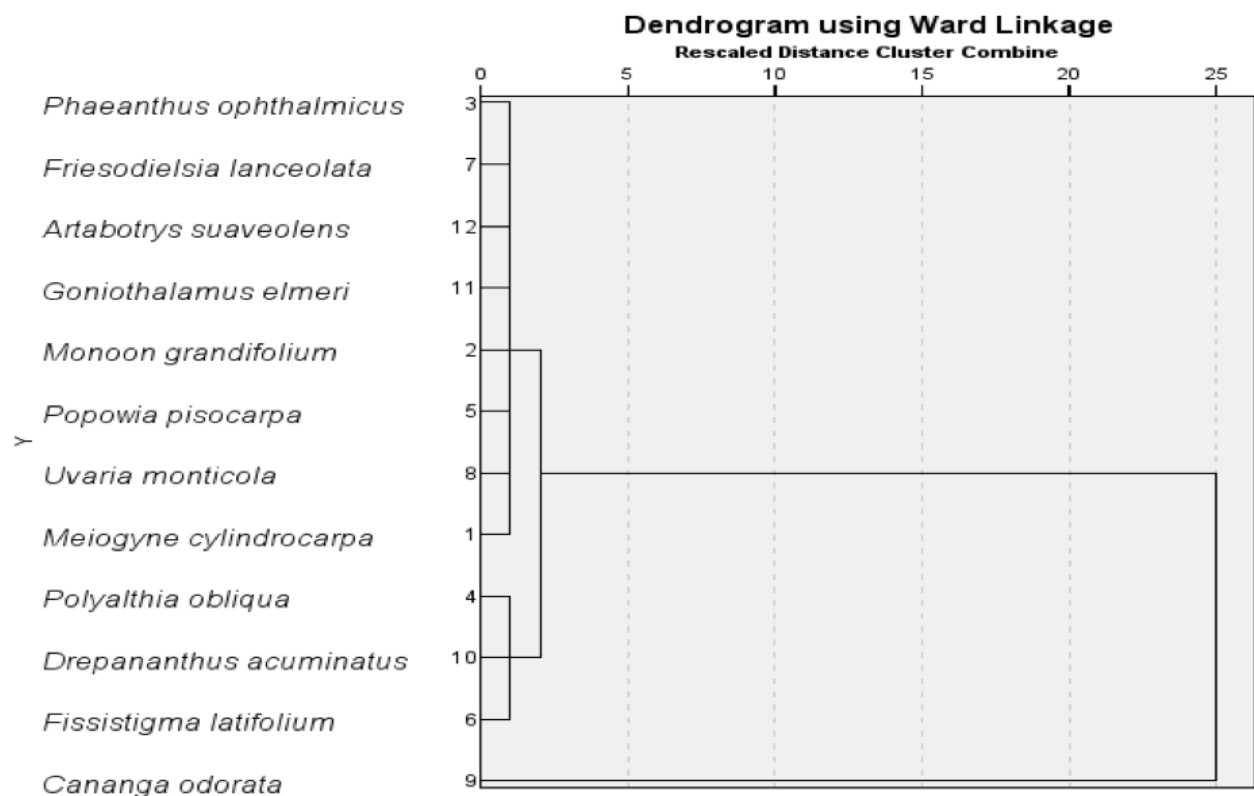


Figure 1. Dendrogram derived from hierarchical clustering of the pollen samples using Ward's method.

(Azeez & Folorunso 2014).

The 12 species of Annonaceae have shared pollen characteristics like single pollen grains, monads, and inaperturate pollen, except dyads for *Cananga odorata* and tetrad for *Goniothalamus elmeri*. The present study confirms that the genus *Cananga* is often observed as a dyad; although some authors reported that some pollen grains of *Cananga* were possibly in tetrads, the links between pollen pairs might have been loose within the tetrad and resulted in dyad pollen grains (Walker 1971; Xu & de Craene 2012; Li et al. 2023). On the other hand, pollen grains of *Goniothalamus elmeri* were tetrahedral tetrads, and different types were seen as tetragonal in *G. sawtehii* C.E.C.Fisch, *G. tamirensis* Pierre ex Finet & Gagnep., and *G. undulatus* Ridl. at the same time, *G. wynadensis* (Bedd.) Bedd. has two types of decussate and tetragonal tetrads (Jayan & Sreekala 2023).

In terms of the hierarchical cluster analysis, the pollen grains from the Bicol Region formed three clusters (Figure 1). The species *Cananga odorata* belongs to cluster I; it has dyad pollen grains, with the most significant variation in the PA and ED, pollen size of 50–100  $\mu\text{m}$ , and psilate with micro-perforation exine ornamentations. In cluster II, eight species share characters of pollen

grains as monads, with sizes ranging from small to medium (20–30  $\mu\text{m}$ ), namely, *Artabotrys suaveolens* (Blume) Blume, *Friesodielsia lanceolata* (Merr.) Steenis, *Goniothalamus elmeri* Merr., *Phaeanthus ophthalmicus* (Roxb. ex G.Don) J. Sinclair, *Meiogyne cylindrocarpa* (Burck) Heusden, *Monoon grandifolium* (Elmer) B.Xue & R.M.K.Saunders, *Popowia pisocarpa* (Blume) Endl. Ex Walp., and *Uvaria monticola* Miq. The species *Goniothalamus elmeri* was found nearer the cluster's centre with prolate shapes, while the *Uvaria monticola* was found farther from the cluster centre with prolate-spheroidal shapes. On the other hand, in cluster III, three species, namely *Drepananthus acuminatus* (C.B.Rob.) Survesw. & R.M.K.Saunders, *Fissistigma latifolium* (Dunal) Merr., and *Polyalthia obliqua* Hook.f. & Thomson shares pollen characters of monads, inaperturate, and prolate, but differs in the sizes of the PA, ED, and exine ornamentations.

Pollen sizes greatly vary among the species, from small to very large grains. The PA and ED are statistically significant due to a wide range of variability (Table 2). The species *Fissistigma latifolium* has smaller pollen sizes from small to medium (10–20  $\mu\text{m}$ ) and medium to large (30–50  $\mu\text{m}$ ) in *Uvaria monticola* and *Cananga*

*odorata*, while very large as tetrahedral-type tetrad (100  $\mu\text{m}$ ) but as monads (20  $\mu\text{m}$ ) for *Goniothalamus elmeri*. The variability in pollen size of Annonaceae is highly homoplastic and influenced by the preparation method, which appears to be shrunken using SEM rather than in the light microscope (Halbritter et al. 2018b). Although grain size seems unstable, it plays a role in the systematics (Lee 1984). According to Ejsmond et al. (2011), the desiccation intensity of pollen grains may decrease the pollen sizes due to climatic factors such as temperature, potential evapotranspiration, and altitude, which may significantly affect pollen grains' sizes. Environmental stresses like heat, drought, cold, and humidity affect pollen production & viability. During anthesis, the pollen grains of some plants enter a metabolically "inactive state" to support survival during pollen dispersal. The pollen grains lose water and reach a state of complete or partial desiccation tolerance, depending on environmental conditions (Pacini & Dolferus 2019). Furthermore, pollen size is also affected by the mineral content of the soil, shoot defoliation, and climate change. Higher concentrations of soil nitrogen and phosphorus have been reported to increase pollen grains' size, yield, and germinability (Lau & Stephenson 1994).

The prominent pollen shapes were prolate, sub-prolate, and prolate-spheroidal (Table 3). The prolate shape (1.34–1.99) was observed in the six species, namely *Artabotrys suaveolens*, *Drepananthus acuminatus*, *Fissistigma latifolium*, *Friesodielsia lanceolata*, *Goniothalamus elmeri*, *Phaeanthus ophthalmicus*, and *Polyalthia obliqua*, while sub-prolate shape (1.15–1.33) was observed in *Cananga odorata*, *Meiogyne cylindrocarpa*, *Monoon grandifolium*, *Popowia pisocarpa*, and prolate-spheroidal shape (1.01–1.14) was found only in *Uvaria monticola*. *Friesodielsia desmoides* (Craib) Steenis has spheroidal shape compared to *F. lanceolata* with prolate, and *Artabotrys hexapetalus* (L.f.) Bhandari has perprolate shape compared to *Artabotrys suaveolens* with a prolate shape. The PA/ED ratio was not statistically significant because it showed no variability among the species. Moreover, most of the 12 pollen grains are isopolar, with identical proximal and distal poles. Most species are inaperturate with no visible aperture or indication of a pole, except for *Drepananthus acuminatus*, which has a small opening (Image 2). This small opening is a disulcate aperture, as confirmed by Xu & de Craene (2012). Hence, pollen aperture is a significant criterion for identifying and describing pollen (Waha & Merawetz 1988). Nevertheless, recognizing apertures' position, shape, and nature is often problematic. The pollen grain is surrounded by a resistant wall called exine;

certain regions of the pollen surface receive little or no exine deposition, leaving an aperture that serves as a site for pollen tube exit (Sarwar & Takahashi 2012; Zhang et al. 2017).

The pollen wall structure, exine, is one of the characteristics used for identification (Sari et al. 2015). Rugulate ornamentation was observed in the pollen grains of *Artabotrys suaveolens*, *Goniothalamus elmeri*, *Meiogyne cylindrocarpa*, *Monoon grandifolium*, and *Uvaria monticola*. The scabrate ornamentations were seen in *Phaeanthus ophthalmicus*, *Popowia pisocarpa*, and *Drepananthus acuminatus*. In addition, verrucate was observed in *Polyalthia obliqua* and *Fissistigma latifolium*, and the psilate with micro-perforation was found only in *Cananga odorata*. In the study of Shao & Xu (2017), *Goniothalamus laoticus* (Finet & Gagnap.) Bân has psilate ornamentations and *Polyalthia bullata* King rugulate with different exine ornamentations; *Artabotrys hexapetalus* has microrugulate and coarsely rugulate in *Fissistigma oldhamii* (Hemsl.) Merr. exine ornamentations (Xu & de Craene (2012) (Table 4). The above results corroborate the diverse exine ornamentations in Annonaceae species. Some studies also reaffirm the variety of exine ornamentations in some species such as the Asian genus of *Friesodielsia* which were heterogeneous (Walker 1971) with echinate-perforate with well-developed spines but differs from the African genus with coarsely verrucate pollen ornamentations, *Uvaria* with coarsely rugulate observed in *Uvaria grandiflora* (Lesch. Ex DC) and scabrate in *Uvaria macrocarpa* (Dunal)Vahl (Xu & de Craene 2012) and some species in the tribe Xylopieae with coarsely fossulate-perforate ornamentations (Shao & Xu 2017). Despite the differences among species, exine ornamentation patterns are one of the important characteristics of pollen, which is significant in the study of genetic evolution and systematic taxonomy. The ornamentation exine of pollen grains is highly conserved and genetically stable (Xu & de Craene 2012; Shao & Xu 2017).

Interestingly, the surface ornamentation of pollen grains correlates with pollination types by interacting with pollinators and how the pollen can efficiently be transferred from one flower to another (Sannier et al. 2009). The pollen ornamentation, such as spines and rough surfaces, can make pollen more sticky and less likely to fall off on the pollinator's body, allowing it to better adhere to the pollinators like insects or animals, increasing the number of flowers it can reach (Hasegawa et al. 2021). The identified exine ornamentations with complex patterns in the present study include some pollen grains with echinate, rugulate, scabrate, and



Table 4. Comparison of pollen characters of pollen grains from Bicol Region, Philippines with the pollen grains from Thailand (Xu &amp; de Craene 2012; Shao &amp; Xu 2017).

Pollen types	<i>Friesodielsia lanceolata</i> *	<i>Friesodielsia desmoldes</i>	<i>Goniothalamus elmeri</i> *	<i>Goniothalamus laoticus</i>	<i>Polyalthia obliqua</i> *	<i>Polyalthia bullata</i>	<i>Artabotrys suaveolens</i> *	<i>Artabotrys hexapetalus</i>	<i>Fissistigma latifolium</i> *	<i>Fissistigma oldhamii</i>
Pollen unit	monad	monad	tetrad	tetrad	monad	monad	monad	Monad with single furrow	monad	Monad
Pollen shape	prolate	spheroidal	Tetrahedral	tetrahedral	prolate	prolate	prolate	Perprolate	prolate	Prolate spheroidal
Pollen aperture	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate	Inaperturate
Pollen ornamentation	Microechinate	Echinate-perforate with spines	rugulate	psilate	verrucate	rugulate	rugulate	Microrugulate	verrucate	Coarsely rugulate
Polar axis (µm)	35.55	29	100	105	27.46	48	34.71	56	24.47	35

Legend: \* present study

verrucate ornamentations, indicating that animals have been pollinating flowers of Annonaceae. The plants pollinated by animals develop complex patterns with various decorations on their pollen surface. The various spines, ridges, and papilla on their exine surface may help pollen grains attach to animal pollinators, influencing how pollen grains are dispersed and interact with the pollinators. This finding corroborates that the majority of pollinators of the family Annonaceae are beetles included in the family of Nitidulidae, Staphylinidae, Chrysomelidae, and Curculionidae and other insect groups like thrips, flies, bees, and cockroaches have also been identified as pollinators in some Annonaceae species such as *Popowia pisocarpa* and *Xylopia aromatica* (Lam.) Mart. (Gottsberger 1999; Momose et al. 2006; Lau et al. 2016).

Furthermore, the exine ornamentations can deter pollen consumption by flower visitors than the target pollinators (Lynn et al. 2020). In addition, the exine ornamentations facilitate the pollen-stigma interaction, pollen hydration, and release of pollen tubes for fertilization (Mach 2012). In contrast, the psilate with micro-perforations in *Cananga odorata* indicates that it was pollinated by wind or water, and a smooth surface may improve the aerodynamics of pollen. Hence, water is not a common method of pollination in Annonaceae (Lau et al. 2016).

Two endemic species were included in the study, namely, *Friesodielsia lanceolata* and *Goniothalamus elmeri*, and they were compared with the study of Xu & de Craene (2012) and Shao & Xu (2017) (Table 4). The species *Friesodielsia lanceolata* pollen grains are prolate monads, echinate, PA of 35.55 µm, and differ from *F. desmoldes* pollen grains are spheroidal monads with no visible aperture, and echinate-perforate with well-developed spines and a mean PA of 29 µm, while *Goniothalamus elmeri* shares characteristics with *G. laoticus* of tetrahedral tetrad pollen, inaperturate and PA of ±100; however, they differ in exine ornamentations of rugulate and psilate, respectively. Although these species have the same genus, pollen sizes, shapes, and exine ornamentations differ.

## CONCLUSION

The pollen morphology of the 12 Annonaceae studied exhibited high diversity, and they shared characters such as monad, inaperturate, and isopolar characters, but formed three clusters based on pollen size. Most have sub-prolate pollen shapes. They varied significantly

in PA & ED axis and size from small to very large, and exine ornamentations include echinate, rugulate, psilate with micro-perforations, scabrate, and verrucate. The present study was the first attempt to investigate 12 species of Annonaceae collected from the Bicol Region, Philippines. Pollen morphology of two endemic species is first reported here. Therefore, increasing the collection of endemic Philippine Annonaceae is recommended to search for new pollen characters that generate a comprehensive analysis of infrageneric relationships and family classifications.

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