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Micromorphological analysis of spores on various species of pteridophytes: Implications for species identifications

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Abstract. *Mildawati, Hanafi SPS, Putri E, Aziz MA, Ivani S, Nurhasna, Solfiyeni. 2025. Micromorphological analysis of spores on various species of pteridophytes: Implications for species identifications. Biodiversitas 26: 2332-2338.* Pteridophytes, a group of vascular plants, play a critical role in ecosystem balance. However, taxonomic challenges persist in identifying and classifying their species. Spore micromorphological characters, unique to each species, offer a potential solution to these issues. This study aimed to examine the spore micromorphology of several pteridophyte species growing on the Universitas Andalas campus, Padang, Indonesia. The species examined included *Antrophyum callifolium*, *Asplenium nidus*, *Davallia denticulata*, *Pteris vittata*, *Pyrrosia adnascens*, *P. longifolia*, and *P. piloselloides*. Spore samples were observed using a binocular light microscope with a magnification 40x objective lens and documented with the OptiLabView4 application. The results revealed that most pteridophytes spores studied exhibited a monolete laesura type with an ellipsoid shape, except for *A. callifolium* and *P. vittata*, which showed a trilete laesura type with a tetrahedral shape. Exospore ornamentation was varied: verrucate in *A. callifolium*, *A. nidus*, *D. denticulata*, and *P. vittata*; reticulate in *P. adnascens* and *P. longifolia*; and echinate in *P. piloselloides*. Spore sizes were categorized as medium (25-50 μm) for *A. callifolium*, *A. nidus*, *D. denticulata*, and *P. vittata*.; and large (60 μm) for *P. adnascens*, *P. longifolia*, and *P. piloselloides.* Spore micromorphology of pteridophytes on the Universitas Andalas campus, revealing significant diversity in size, shape, and ornamentation.

Keywords: Micromorphology, monolete, pteridophyte, spore, taxonomic

INTRODUCTION

Pteridophytes, a diverse group of vascular plants, are abundant in tropical regions such as Indonesia, where they play crucial roles in forest ecosystems. These roles include preventing soil erosion, regulating water levels, supporting nutrient cycling, and aiding the decomposition of forest litter (Ulfa 2017). Beyond their ecological functions, pteridophytes are important indicators of forest health and biodiversity. Globally, they are classified into approximately 11,916 species, distributed across 337 genera, 51 families, 14 orders, and two classes (PPG I 2016). In Indonesia alone, more than 1,300 species have been documented, with Sumatra being one of the richest regions in terms of pteridophyte diversity. For instance, Mildawati et al. (2020) reported 69 species across 36 genera and 20 families, with the Polypodiaceae family showing notable diversity in Siberut National Park, West Sumatra, Indonesia.

Phylogenetic studies suggest that pteridophytes, considered among the most primitive vascular plants, evolved as early as the Devonian period, more than 360 million years ago. Despite their ancient origins, they have undergone significant diversification and adaptation, making them a valuable group for taxonomic, ecological, and evolutionary research (Mildawati et al. 2023). Among the key diagnostic tools for studying pteridophytes is spore morphology, which offers critical features for species identification and phylogenetic analysis (Giacosa 2014). Pteridophyte spores exhibit remarkable variation in size, shape, surface ornamentation, wall layering, and aperture types. Sizes range widely from 15 μm to 130 μm, with genera like *Ceratopteris* producing exceptionally large spores (Makgomol 2006; Adeonipekun et al. 2021).

Spore shapes may be ellipsoidal, tetrahedral, or spherical, typically displaying either monolete or trilete apertures. These apertural types along with more complex patterns such as colpate, porate, or colporate provide key information about dispersal strategies and germination ecology (Albert et al. 2018). Surface ornamentation including cristate, granulate, reticulate, tuberculate, verrucate, and others is highly species-specific and helps delineate taxonomic boundaries (Makgomol 2006; Szkudlarz et al. 2024). However, the diagnostic value of spore features can vary among families. For example, while spore microsculpture may aid in species recognition in some Aspleniaceae, in other cases it reflects broader group-level traits (Szkudlarz et al. 2024).

Spore micromorphology also offers insights into evolutionary processes, such as synapomorphic traits shared within lineages for example, the oblate-spheroidal shape found in certain clades (Adeonipekun et al. 2021). Comparative studies from India, China, and Nigeria have demonstrated the global significance of spore traits in resolving taxonomic ambiguities and supporting phylogenetic hypotheses (Chao and Huang 2018; Adeonipekun et al. 2021; Li et al. 2021; Morajkar et al. 2021). In the Dryopteridaceae, for instance, detailed examination of ornamentation and perispore ultrastructure has proven crucial for distinguishing morphologically similar species (Shah et al. 2021).

In addition, spore morphology is increasingly employed to test and refine taxonomic concepts in complex genera like *Asplenium*, *Cyathea*, and *Pteris* (Braggins and Large 1990; Shah et al. 2021). Advanced microscopy techniques such as Light Microscopy (LM) and Scanning Electron Microscopy (SEM) enable detailed observation of spore ultrastructure across pteridophyte families, contributing to more robust taxonomic frameworks (Adeonipekun et al. 2021; Shah et al. 2021). Multivariate statistical approaches further validate the significance of these traits at the species level. Recent phylogenetic reconstructions using spore morphological characters have elucidated relationships within and between families, highlighting the evolutionary patterns shaping the diversity of this group (Vaganov 2022).

Despite these advancements, comprehensive studies on pteridophyte spore micromorphology remain limited in Indonesia, particularly in biodiverse but underexplored regions. Therefore, this study aimed to examine the spore characteristics of pteridophytes found on the campus of Universitas Andalas. By documenting micromorphological traits, the research seeks to enhance species identification, refine regional taxonomic classifications, and contribute to a broader understanding of the evolutionary relationships among Indonesia's rich pteridophyte flora.

MATERIALS AND METHODS

Study area

This research was conducted in the Universitas Andalas campus in Limau Manis, Padang, West Sumatra, Indonesia, characterized by its diverse tropical ecosystem in May 2024. The area supports a rich biodiversity, including 160 bird species from 44 families, with several protected and threatened species (Janra 2019). The campus also hosts a variety of Odonata, with 32 species of dragonflies and damselflies identified across 9 families (Janra and Herwina 2020). This diversity extends to other insect groups, such as termites, with 12 species from 2 families recorded in the forested areas of the campus (Mairawita et al. 2022). The university's environment encompasses various habitats, including ponds, rivers, green spaces, and both secondary and primary forests, providing suitable conditions for this wide range of flora and fauna (Janra 2019). The vicinity of Universitas Andalas gate, the Department of Biology, and the Biological forest make it an ideal location for taxonomic exploration, particularly of pteridophytes (Figure 1). The tropical environment of the study site provides significant opportunities to examine the diversity of pteridophyte spores, which is expected to contribute to a deeper understanding of morphological variation and taxonomic potential of pteridophytes in this region.

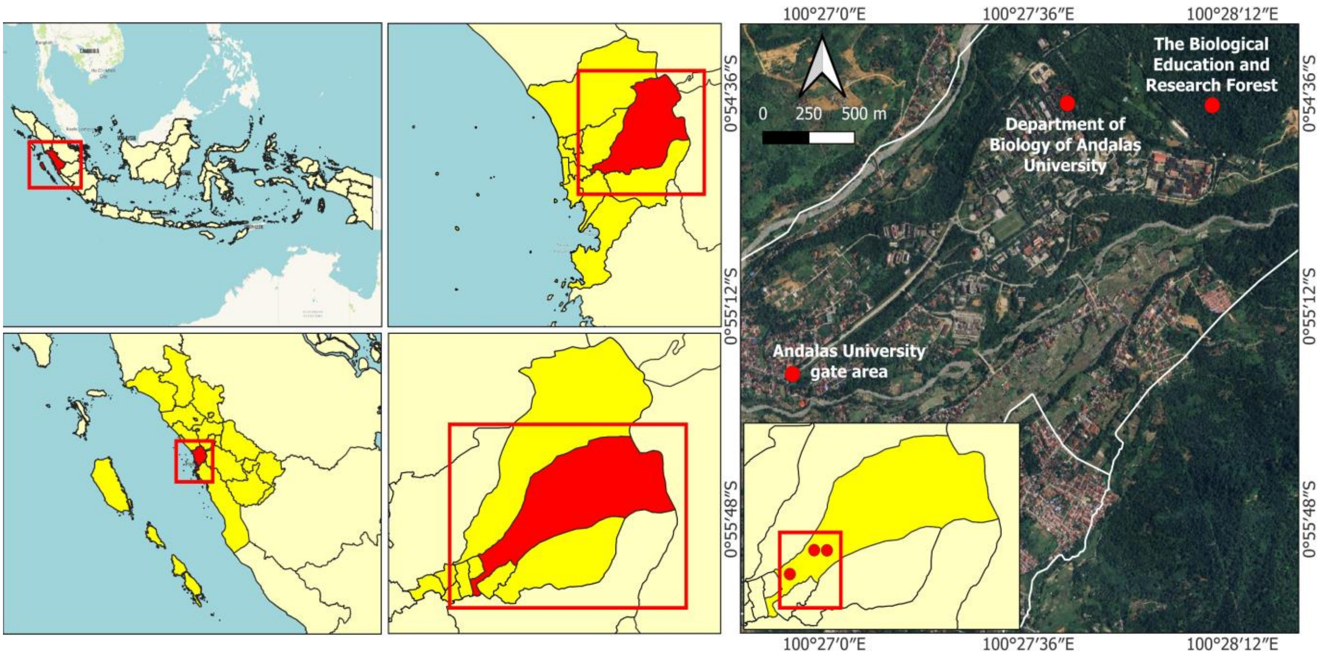

Figure 1. Location of sample collection in Universitas Andalas, Padang, West Sumatra, Indonesia

Procedures

Specimens were collected from three distinct locations around Universitas Andalas, Padang, i.e.: the university gate, the Biology Department garden, and the biological forest (Figure 1). These sites yielded several species, including *Antrophyum callifolium* Blume, *Asplenium nidus* L., *Davallia denticulata* (Burm.fil.) Mett., *Pteris vittata* L., *Pyrrosia adnascens* (Sw.) Ching, *Pyrrosia longifolia* (Burm.fil.) C.V.Morton, and *Pyrrosia piloselloides* (L.) M.G.Price. Only specimens with spores were collected, and identification was carried out using official resources such as A revised Flora of Malaya, Vol II Ferns of Malaya (Holttum 1966; Nooteboom 1998) and Pteridophytes of Solomon (Chen et al. 2017) and internet search using Global online sites Biodiversity Information Facility (GBIF) (https: //www.gbif.org/) and Plants of the World Online (POWO) (https://powo.science.kew.org/).

Spore observations were performed at the Teaching IV Laboratory of the Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Andalas. Spores were examined using an OptiLab Iris 4 binocular light microscope, with images captured via a Sigma microscope camera connected to the OptiLabView 4 application. For observation, a small portion of the sorus, containing approximately five sporangia, was carefully extracted from the underside of the sporophyll using a needle. The sporangia were gently tapped and broken to release their contents, which were subsequently examined under the microscope at various magnifications. After observation, the prepared slides were discarded. The spores analyzed in this study were utilized exclusively during the observation period and were not preserved in the palynological bank. Each spore was examined for key micromorphological characteristics, including laesura type, ornamentation, color, size, and shape. Spore sizes vary widely, ranging from very small (<10 μm), small (10-25 μm), medium (25-50 μm), large (50-100 μm), very large (100-200 μm), and gigantic (>200 μm) (Erdtman 1957; Lashin 2012; Wei and Dong 2012).

Data analysis

The data obtained from the spore observations were subjected to both descriptive and qualitative analysis. This approach aimed to provide a comprehensive and detailed characterization of the spores from each Pteridophyte species, focusing on their morphological features, including size, shape, surface ornamentation, and aperture types. Through this process, the spore traits were categorized and compared across species to identify distinguishing characteristics and contribute to the taxonomic understanding of the pteridophytes studied.

RESULTS AND DISCUSSION

General micromorphological characteristics of spores

The results revealed the morphological (Figure 2) and micromorphological characteristics of spores (Figure 3) from several pteridophyte species collected around the Universitas Andalas campus, which are summarized in Table 1. Two types of laesura on spores were identified: trilete and monolete. Trilete laesura type was found in *A. callifolium* and *P. vittata*, while monolete laesura was found in *A. nidus, D. denticulata, P. adnascens, P. longifolia,* and *P. piloselloides.* These studies demonstrate that spore morphology, including features like the laesura, cingulum, and ornamentation patterns, provides valuable information for pteridophytes taxonomy across various families and genera within Pteridophyta.

Species micromorphological description

Asplenium nidus *L.*

Asplenium nidus produces ellipsoidal spores with dimensions averaging 23.34 × 41.02 μm, which places them in the medium-size category. The spores exhibit distinct verrucate ornamentation, characterized by small wart-like projections on the surface, contributing to their unique micromorphology. The laesura type is monolete, a defining feature of the species within its ecological niche. These morphological traits align with its adaptive strategies as an epiphytic fern, optimizing spore dispersal in forest canopies.

Davallia denticulata *(Burm.fil.) Mett.*

This species is characterized by ellipsoidal spores measuring approximately 27.27 × 37.83 μm, also falling within the medium-size range. The spore surface is verrucate, with raised, irregular structures that enhance adherence to substrates during dispersal. The monolete laesura type signifies a common morphological adaptation among epiphytic ferns, aiding in efficient reproduction within its habitat.

Table 1. Micromorphology spore of some pteridophyte species

Species	Family	Laesura type	Shape	Ornamentation type	Size (μm)	
Asplenium nidus L.	Aspleniaceae	Monolete	Ellipsoidal	Verrucate	23.34 × 41.02	medium
Davallia denticulata (Burm.fil.) Mett.	Polypodiaceae	Monolete	Ellipsoidal	Verrucate	27.27 × 37.83	medium
Pyrrosia adnascens (Sw.) Ching	Polypodiaceae	Monolete	Ellipsoidal	Reticulate	39.13 × 54.50	large
Pyrrosia longifolia (Burm.fil.) C.V.Morton	Polypodiaceae	Monolete	Ellipsoidal	Reticulate	40.33 × 61.13	large
Pyrrosia piloselloides (L.) M.G.Price	Polypodiaceae	Monolete	Ellipsoidal	Echinete	41.62 × 59.71	large
Antrophyum callifolium Blume	Pteridaceae	Trilete	Tetrahedral	Verrucate	45.91 × 49.71	medium
Pteris vittata L.	Pteridaceae	Trilete	Tetrahedral	Verrucate	51.58 × 53.18	medium

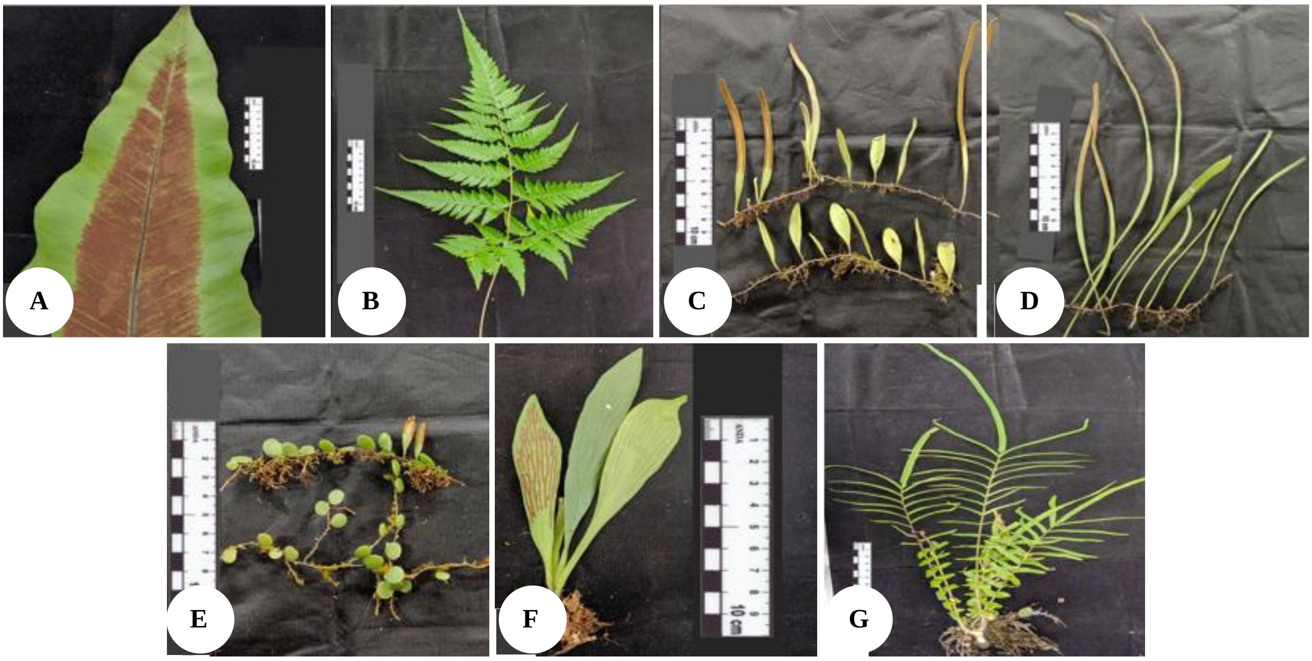

Figure 2. Morphological characteristics pteridophytes species of: A. *Asplenium nidus*; B. *Davallia denticulata*; C. *Pyrrosia adnascens*; D. *Pyrrosia longifolia*; E. *Pyrrosia piloselloides*; F. *Antrophyum callifolium*; and G. *Pteris vittata*

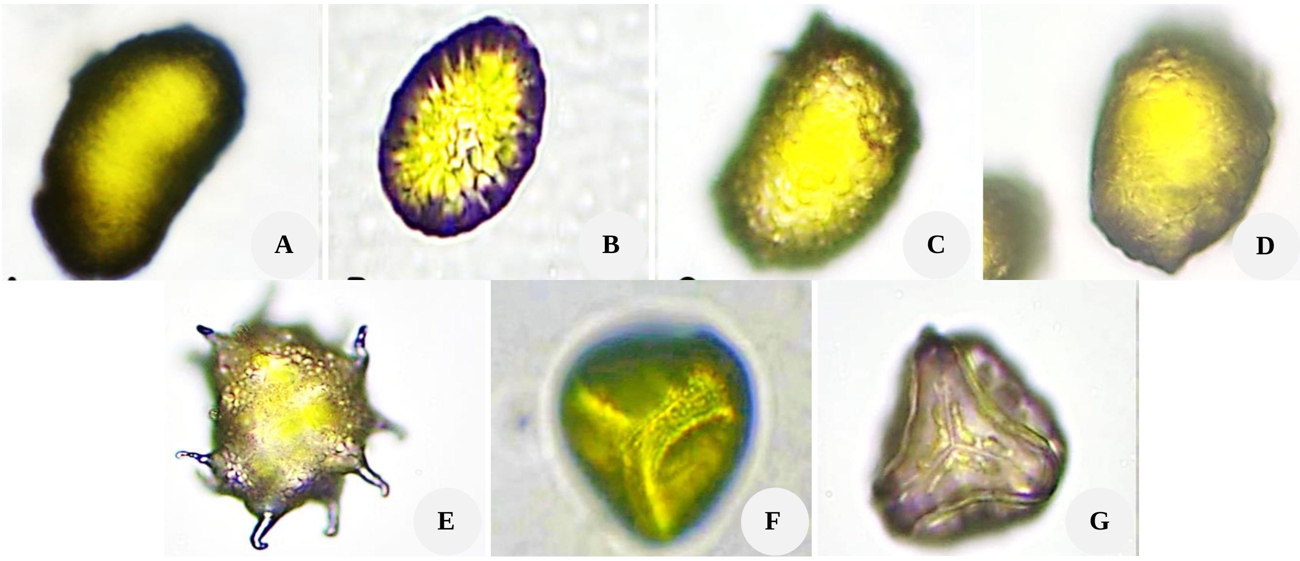

Figure 3. Micromorphological characteristics pteridophytes species of: A. *Asplenium nidus*; B. *Davallia denticulata*; C. *Pyrrosia adnascens*; D. *Pyrrosia longifolia*; E. *Pyrrosia piloselloides*; F. *Antrophyum callifolium*; and G. *Pteris vittata*

Pyrrosia *spp.*

The genus *Pyrrosia* demonstrates notable diversity in spore ornamentation, reflecting its adaptive differentiation: (i) *P. adnascens* and *P. longifolia* exhibit reticulate ornamentation, with a net-like surface pattern facilitating optimal attachment and moisture retention, (ii) *P. piloselloides*, in contrast, features echinate ornamentation, with spiny projections likely enhancing spore protection and dispersal efficiency.

The spore size within this genus is relatively large, ranging from 39.15 × 54.50 µm (*P. adnascens*) to 40.33 × 61.13 µm (*P. longifolia*), reflecting the evolutionary investment in robust reproductive units for habitat resilience.

Antrophyum callifolium *Blume*

Tetrahedral in shape, the spores of *A. callifolium* measure approximately 45.91 × 49.71 µm, representing medium-sized spores. Their verrucate ornamentation is marked by dense, wart-like projections, indicative of adaptations for specific environmental challenges. The trilete laesura is a key diagnostic feature, suggesting its placement within terrestrial habitats with dynamic environmental interactions.

Pteris vittata *L.*

The spores of *P. vittata* are tetrahedral, with a size of 51.58 × 53.18 µm, which also falls under the medium-size category. The verrucate surface pattern is similar to that of *A. callifolium*, indicating potential convergent adaptations in ornamentation for ecological functionality. The trilete laesura type reinforces its classification among terrestrial ferns, as this structure supports effective dispersal mechanisms across varied environmental conditions.

Identification key of selected pteridophyte species

1a. Monolete laesura.. 2
1b. Trilete laesura 6
2a. Reticulate ornamentation 3
2b. Non-reticulate ornamentation 4
3a. Medium size .... *Pyrrosia adnascens*
3b. Large size .... *Pyrrosia longifolia*
4a. Echinate ornamentation .... *Pyrrosia piloselloides*
4b. Verrucate ornamentation 5
5a. Size 23.34 × 41.02 µm .... *Asplenium nidus*
5b. Size 27.27 × 37.83 µm .... *Davallia denticulata*
6a. Tetrahedral shape, size 45.91 × 49.71 µm... *A. callifolium*
6b. Tetrahedral shape, size 51.58 × 53.18 µm....... *P. vittata*

Discussion

Palynology, which includes the study of pollen, spores, and other organic-walled microfossils, has provided valuable insights into past climates and ecosystems, as evidenced by reconstructions of the last glacial maximum and holocene climate optimum (Grant 2018; Kar and Quamar 2019). Beyond paleoclimatic reconstructions, palynology plays an integral role in understanding the paleo-environments of ancient regions, such as the Sergipe-Alagoas Basin, by revealing vegetation shifts and marine influences through pollen assemblages (Garcia 2016). Today, palynology's interdisciplinary applications, particularly in ecological and evolutionary contexts, have proven invaluable for sustainable landscape management and biodiversity conservation (Jiménez-Zamora et al. 2023).

The micromorphological characteristics of pteridophyte spores, such as size, shape, ornamentation, and laesura type, offer critical insights into taxonomy, ecology, and species identification. Identification key by micromorphological data present in this study. Micromorphological study of *A. nidus*, the spores are predominantly ellipsoidal with an average size of 23.34 × 41.02 µm and a verrucate ornamentation pattern. The monolete laesura is a distinguishing feature, corroborated by Shah et al. (2020), who reported elliptical spores with dimensions ranging from 28.3 × 50.2 µm to 27.6 × 45.8 µm. Additional studies by Wei and Dong (2012) revealed a broader size range of 35.7-50.1 × 24.1-32.4 µm, highlighting variability that may be linked to environmental conditions. During germination, the chlorophyllous filaments and heart-shaped gametophytes further underline the ecological adaptability of this species.

Comparative analyses across fern families emphasize substantial differences in spore morphology. For instance, the monolete, ellipsoidal spores of *D. denticulata* display verrucate ornamentation, with perispore papillae serving as diagnostic traits for *Davallia* species (Makgomol 2006). Sofiyanti et al. (2020) reported medium-sized spores averaging 35.23±5.75 µm, Sofiyanti and Harahap (2019) described significantly larger spores (78.30±24.70 µm), which might reflect environmental influences such as temperature, humidity, and altitude. Similarly, size variation in *Pyrrosia* species is evident; *P. adnascens* and *P. longifolia* possess reticulate ornamentation, whereas *P. piloselloides* exhibits echinate patterns. The tetrahedral spores of *A. callifolium,* characterized by a trilete laesura and verrucate ornamentation, measure approximately 45.91 × 49.71 µm. The unique spore structure, including rodlet-shaped papillae and a mildly wavy exospore, underscores the taxonomic importance of micromorphological traits (Campbell and Reece 2005; Tryon and Lugardon 2012). Likewise, *P. vittata* demonstrates a tetrahedral shape with a trilete laesura and verrucate perispore, measuring 51.34±1.83 µm (Palacios-Rios et al. 2017; Chao and Huang 2018; Sofiyanti et al. 2019; Irfan et al. 2021; Li et al. 2021). The pronounced cingulum and intricate surface features, such as rugae and verrucae, further support its medium-size classification and unique morphological adaptations.

Our research focused on seven fern species spanning five genera, namely *Antrophyum, Asplenium*, *Davallia*, *Pteris,* and *Pyrrosia.* The laesura type observed in these species was predominantly monolete with ellipsoidal ornamentation, except in *A. callifolium* and *P. vittata*. Findings revealed notable diversity in spore shape, size, and ornamentation, with forms ranging from tetrahedral to oblate and sizes from 22 µm to 60 µm (Morajkar et al. 2021; Setyati et al. 2021). In this study, the smallest spores were observed in *A. nidus* (23.34 × 41.02 µm), while the largest occurred in *P. longifolia* (40.33 × 61.13 µm). These patterns align with ancestral traits within the subfamily Microsoroideae, where Goniophlebieae and Lecanoptereae show verrucate ornamentation, Microsoreae are globular, and Lepisoreae exhibit rugulate structures (Chen et al. 2021). The morphological diversity of spores reflects broader taxonomic and evolutionary relationships within pteridophytes, as differences in ornamentation provide essential markers for species differentiation and classification (Morajkar et al. 2021). These findings reinforce the role of spore palynology in not only taxonomic work but also in advancing our understanding of biodiversity and ecosystem dynamics. This morphological diversity in spores parallels the phenotypic variation observed in sporophytes, highlighting the significance of sporophyte-spore relationships in pteridophyta evolution and ecology.

Pteridophytes spore morphology is a valuable tool for species identification and taxonomic studies (Vaganov 2022). Spore sizes vary significantly, ranging from medium (25-50 µm) to very large (100-200 µm) across different species (Adeonipekun et al. 2021; Wang and Dobritsa 2018; Setyati et al. 2021; Morajkar et al. 2021). Spore size strongly correlates with genome size and ploidy level, with tetraploids having larger spores than diploids (Barrington et al. 2020). The variability in spore ultrastructure and perispore ornamentation reflects morphological differences in sporophytes and has significant taxonomic value. Light microscopy and scanning electron microscopy are essential tools for studying pteridophytes spore morphology and its taxonomic implications (Adeonipekun et al. 2021). It was found that the observed spores fell into two size categories, namely medium and large (Table 1). Monolete spores are kidney-shaped, while trilete spores have a triangular shape in polar view (Giacosa 2014). The spore wall consists of an exospore and perispore, both typically two-layered. Surface ornamentation is diverse, with 11 different types identified, including psilate and gammate patterns (Morajkar et al. 2021). Abnormal spores may occur, displaying variations in size, aperture type, and ornamentation. Pteridophyte spores are typically found as monads but can also occur in dyads, triads, and tetrads (Giacosa 2014; Sofiyanti et al. 2019).

This study has effectively elucidated the morphological characteristics of pteridophyte spores through comprehensive palynological analysis, highlighting several taxonomically significant features that aid in species classification and identification. Key findings reveal that while most pteridophyte spores possess a monolete laesura and ellipsoidal shape, notable exceptions such as *A. callifolium* and *P. vittata* exhibit trilete laesurae and tetrahedral shapes. Additionally, exine ornamentation patterns varied across species, with verrucate patterns observed in *A. callifolium*, *A. nidus*, *D. denticulata*, and *P. vittata*; reticulate patterns in *P. adnascens* and *P. longifolia*; and echinate patterns in *P. piloselloides*. Variations in spore size were also noted, with medium-sized spores in *A. callifolium*, *A. nidus*, *D. denticulata*, and *P. vittata*, contrasting with the larger spores of *P. adnascens*, *P. longifolia*, and *P. piloselloides*.

As spore producers, sporophytes are essential in determining the morphological characteristics of various pteridophytes species and gametophytes. Therefore, evaluating and reviewing the kinship relationships among pteridophyte species is essential. Spore morphological characters-including aperture, exine level, exine ornamentation, size, and shape, have significant value in plant taxonomy and evolution (Nair 1991). In addition, these characteristics are significant in species identification and clarification, as they can effectively distinguish markers between species in the same genus.

Studies across different regions have revealed significant diversity in spore characteristics. These characteristics vary among species, even within the same genus, as observed in *Asplenium* (Pranita et al. 2017). The diversity in spore morphology reflects differences in sporophyte morphology and has significant value in pteridophytes systematics, species identification, and paleopalynological studies (Adeonipekun et al. 2021; Morajkar et al. 2021). The novelty of this study lies in the identification of previously overlooked exine ornamentation patterns and significant interspecies variations in spore size, providing a crucial contribution to the taxonomic understanding of pteridophytes. This study presents an in-depth investigation of pteridophyte spore micromorphology, emphasizing its significance in species identification and taxonomic refinement. The analysis reveals considerable morphological variation among species, with distinctive ornamentation patterns and size differences offering valuable taxonomic markers. By providing detailed regional data, this study contributes to the broader understanding of pteridophyte diversity and enhances global palynological records. The findings highlight how spore traits reflect evolutionary divergence and ecological adaptation, facilitating more accurate classification and differentiation of closely related taxa. Moreover, this research underscores the role of palynological studies in supporting biodiversity documentation and promoting strategies for the conservation and sustainable management of Indonesia's unique pteridophyte. The variability observed in spore size, shape, and ornamentation across taxa highlights their significance in taxonomy and ecology. Scanning Electron Microscopy (SEM) has proven invaluable for elucidating detailed surface features, including tubercules, cristate sculptures, and verrucate patterns (Shah et al. 2024). These traits not only facilitate species identification but also reflect ecological adaptations, offering a broader understanding of fern diversity and evolution. Future research focusing on environmental factors influencing spore morphology, such as light intensity and geospatial variation, will enhance our knowledge of fern adaptation and speciation and the correlation with species conservation (Shah et al. 2021; Solfiyeni et al. 2024).

In conclusion, spore micromorphology can be an important parameter in distinguishing fern species and families. The laesura type and spore shape are consistently related to the family classification, where monolete-ellipsoidal is common in Aspleniaceae and Polypodiaceae, while trilete-tetrahedral is typical in Pteridaceae. In addition, variations in spore ornamentation and size add diagnostic value in taxonomic identification. Thus, spore micromorphological characters have great potential in supporting taxonomic and systematic studies of ferns.

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