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Fern Diversity in the Mid-Cretaceous Amber Forests Revealed by Exceptionally Preserved Sporangium Types

Chunxiang Li[1*], Xile Zhou[2], Yiran Wang[1,3]

[1]Department of Cenozoic Biological Evolution and Environment, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China
[2]Xiangxi Tujia and Miao Autonomous Prefecture Forest Resources Monitoring Center, Jishou, China
[3]School of Resources and Earth Sciences, China University of Mining and Technology, Xuzhou, China
Email: *cxli@nigpas.ac.cn

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Abstract

The amber deposits from the Albian-Cenomanian in Myanmar have emerged as a pivotal source for exceptionally abundant fossil insect fauna since their initial discovery. Recent studies have increasingly focused on elucidating the fern inventory and examining newly available fossils from Myanmar amber, suggesting a diverse fern flora that once thrived in Cretaceous forests. Through investigations of amber collections, with particular emphasis on sporangium structures—especially the annulus types preserved in amber inclusions—this study revealed additional novelties within the Cyatheales and Schizaeales in mid-Cretaceous Myanmar amber forests. The described specimens and newly discovered fossils provide compelling evidence that Polypodiales were not only diverse and abundant but also that other fern lineages, such as Cyatheales and Schizaeales, coexisted in these ancient forest ecosystems. This study reveals the high diversity of ferns in the mid-Cretaceous Myanmar area, while also implying the paleoecological and paleogeographical significance of the Mesozoic Burmese amber forests.

Keywords

Mid-Cretaceous, Myanmar Amber, Polypodiales, Cyatheales, Schizaeales, Sporangium

1. Introduction

Ferns, along with lycophytes, have traditionally been grouped under collective terms such as “pteridophytes” or “ferns and allied plants”, as delineated by [1]

[2]. These plants are characterized by their lack of flowers and seeds, relying instead on spore production for reproduction. They occupy diverse ecological niches across various vertical strata within forest canopies. Serving as a vital component of ground vegetation in numerous forest ecosystems, with approximately one-third of fern species colonizing tree trunks and branches, ferns play a fundamental role in shaping the structure and dynamics of epiphytic plant communities [3]. The mid-Cretaceous (Albian-Cenomanian) amber deposits from Myanmar provide an unparalleled window into the ecosystems of that era, particularly for understanding the diversity of ferns within the amber forests of the mid-Cretaceous. The site has yielded a multitude of exquisitely preserved fossils, encompassing new species, genera, and families of plants and invertebrates [4]. Despite the identification of 65 orders and 540 families of arthropods from this locality [4], botanical discoveries, particularly pertaining to ferns, have been relatively scarce in comparison. To date, the Myanmar amber has revealed fern inclusions representing only eight families (Cystodiaceae, Dennstaedtiaceae, Dryopteridaceae, Hymenophyllaceae, Lindsaeaceae, Marsileaceae, Pteridaceae, Thyrsopteridaceae) across four orders (Cyatheales, Hymenophyllales, Polypodiales, Salviniales) (**Table 1**).

Table 1. Ferns described from Myanmar Amber inclusions.

Taxon	Family	Order	Reference
Cladarastega burmanica	Dennstaedtiaceae	Polypodiales	Poinar [5]
Cretacifilix fungiformis	Dryopteridaceae	Polypodiales	Poinar and Buckley [6]; Regalado *et al.* [7]
Cystodium parasorbifolium	Cystodiaceae	Polypodiales	Li *et al.* [8]
Cystodium sorbifolioides	Cystodiaceae	Polypodiales	Regalado *et al.* [9]
Heinrichsia cheilanthoides	Pteridaceae	Polypodiales	Regalado *et al.* [10]
Holttumopteris burmensis	Thelypteridaceae*	Polypodiales	Regalado *et al.* [11]
Krameropteris resinatus	Dennstaedtiaceae	Polypodiales	Schneider *et al.* [12]
Microlepia burmasia	Dennstaedtiaceae	Polypodiales	Long *et al.* [13]
Proodontosoria myanmarensis	Lindsaeaceae	Polypodiales	Li *et al.* [14]
Prosperiflix sepeliogladius	Dryopteridaceae	Polypodiales	Long *et al.* [15]
Unnamed	Lindsaeaceae	Polypodiales	Regalado *et al.* [16]
Thyrsopteris cretacea	Thyrsopteridaceae	Cyatheales	Li *et al.* [17]
Thyrsopteris cyathindusia	Thyrsopteridaceae	Cyatheales	Zhang *et al.* [18]
Marsileaceaephyllum ciliatum	Marsileaceae	Salviniales	Wang *et al.* [19]
Hymenophyllites angustus	Hymenophyllaceae	Hymenophyllales	Li *et al.* [20]
Hymenophyllites kachinensis	Hymenophyllaceae	Hymenophyllales	Li *et al.* [20]
Hymenophyllites setosus	Hymenophyllaceae	Hymenophyllales	Li *et al.* [20]

*The systematic placement is based on ancestral character state reconstruction [11].

In this study, we contribute to our understanding of fern diversity in the mid-Cretaceous amber forests by examining the exceptionally preserved types of sporangia found within the amber inclusions. By utilizing a fern phylogeny as our phylogenetic framework, we systematically map the distribution of three distinct sporangium types across the major fern lineages, corresponding to their respective orders. Our data offers novel insights into the diversity of ferns during the mid-Cretaceous within the amber forests of Myanmar and information on the evolutionary history of these ancient plant lineages.

2. Mapping Sporangium Types on Fern Phylogeny

2.1. Fern Phylogeny—A Phylogenetic Frame

Over the past three decades, similar to other branches of the tree of life, the taxonomic system of lycophytes and ferns has undergone significant changes due to the accumulation of vast amounts of new information, particularly molecular data. In 2016, these phylogenetic hypotheses were synthesized and presented in a community-derived classification for extant lycophytes and ferns, known as the system of the Pteridophyte Phylogeny Group I (PPG I, **Figure 1**) [2]. This classification categorizes ferns and lycophytes into 14 orders and two classes: Lycopodiopsida (lycophytes) and Polypodiopsida (ferns). Globally, with an estimated 10,578 extant species, ferns (Polypodiopsida) alone constitute the second most diverse group of vascular plants, spanning 12 orders: Equisetales, Psilotales, Ophioglossales, Marattiales, Cyatheales, Gleicheniales, Osmundales, Salviniales, Polypodiales, Hymenophyllales, and Schizaeales (**Figure 1**) [2]. Here, we took this fern phylogeny as the phylogenetic frame to see the distributions of three exceptionally preserved sporangium types among the main lineages of ferns corresponding to orders to indicate the fern diversity in the mid-Cretaceous amber forests.

2.2. The Sporangium Types of Ferns—An Indication of Fern Diversity of Orders

Historically, fern taxonomy has primarily relied on the morphology of sorus, and associated structures continue to play a crucial role in classifying higher hierarchical levels (such as order classifications) for ferns [12] [24]. Special emphasis has been placed on sporangia exhibiting the morphologically unique catapult mechanism, representing the apomorphy of polypod ferns [12] [25]. This distinctive sporangium type (the sporangium with a vertical annulus interrupted by a stalk (**Figure 1(A)**) is present in over 95% of Polypodiales but absent in other ferns. Consequently, the presence of such sporangia serves as compelling evidence for the occurrence of polypod ferns in mid-Cretaceous amber forests, as demonstrated by all polypod ferns identified thus far from mid-Cretaceous Myanmar amber [5]-[16].

The sporangium annulus refers to a row or patch of partially or entirely thickened, usually darkened cells of the capsule that contract or break, allowing the capsule to open and discharge its spores (**Figures 1(A)-(C)**). In addition to the vertical annulus characteristic of Polypodiales, there are two other distinct

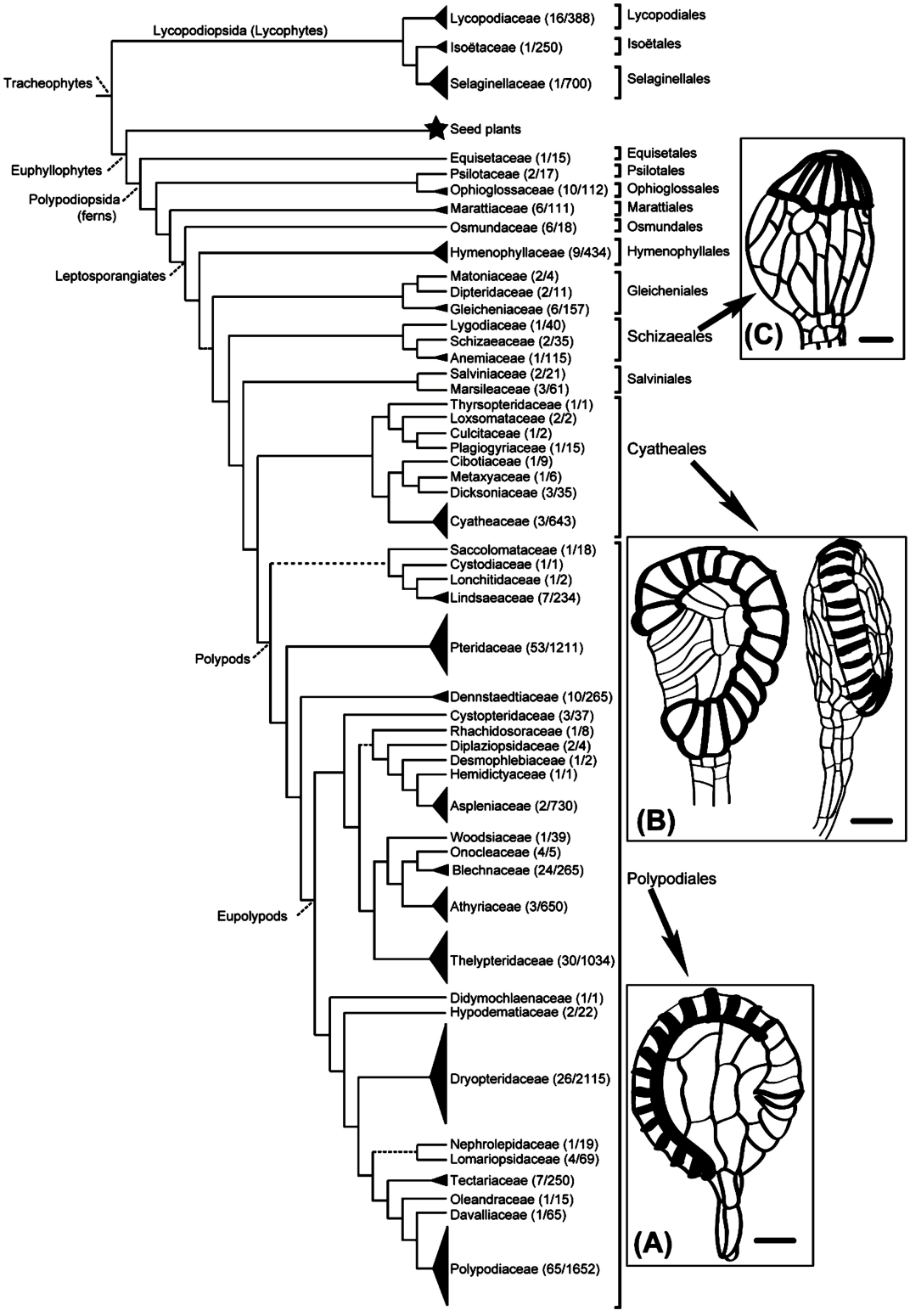

Figure 1. Phylogenetic relationships among families and orders of lycophtes and ferns, highlighting three fern orders characterized by distinctive sporangial annuli patterns. (A) Illustration of a sporangium featuring a vertical annulus interrupted by a stalk, adapted from Figure 24 of [21]; (B) Depictions of sporangia viewed from two angles, showcasing oblique annuli that bypass the stalk, based on Figure 28B of [22]; (C) Representation of a sporangium with an apical annulus, following Figure 8D of [23]. Phylogeny follows [2]. Scale bars = 50 μm ((A)-(C)).

types of annuli corresponding to Cyatheales and Schizaeales. In Cyatheales, the annuli are oblique and complete, bypassing the sporangium stalk (**Figure 1(B)**), whereas in Schizaeales, the annuli are apical or subapical, representing a synapomorphy for Schizaeales (**Figure 1(C)**) [24] [26] [27].

2.3. Paleogeographical Setting and Investigated Specimens

The amber specimens investigated in this study were from Hukawng Valley in Tanai Township, Myitkyina District of Kachin State, Myanmar, and were collected in 2016 (**Table 2**). Previous research by [28] estimated the Burmese

Table 2. Myanmar Amber inclusions investigated in this study.

Collection	Illustration	Sporangium Description
NPA-PB-201602	**Figure 2(A)**	One isolated empty sporangium with a vertical annulus (ca. 19 annulus cells), well visible stomium, and the annulus is interrupted by the remnant stalk at the base of the sporangium.
NPA-PB-201603	**Figure 2(B)**	One isolated sporangium with a vertical annulus (ca. 15 annulus cells), well visible stomium, and the annulus is interrupted by the remnant stalk at the base of the sporangium.
NPA-PB-201727	**Figure 2(C)**	One isolated empty sporangium with a vertical annulus (ca. 13 annulus cells), well visible stomium, and the annulus is interrupted by a remnant stalk (three rows) at the base of the sporangium.
NPA-PB-XFY01	**Figure 2(D)**	One isolated empty sporangium with a vertical annulus (ca. 13 annulus cells), well visible stomium, and the annulus is interrupted by a remnant stalk (two rows) at the base of the sporangium.
NPA-PB-XFY04	**Figure 2(E)**	One isolated empty sporangium with a vertical annulus (ca. 13 annulus cells), well visible stomium, and the annulus is interrupted by a remnant stalk (two rows) at the base of the the sporangium
NPA-PB-XFY05	**Figure 2(F)**	One isolated sporangium with two visible spores, vertical annulus (ca. 14 annulus cells), well visible stomium, a few acicular hairs projecting from the sporangium wall, and the annulus is interrupted by a remnant stalk (two rows) at the base of the sporangium.
NPA-PB-201719	**Figure 3(A)** and **Figure 3(B)**	Two isolated sporangia with oblique annuli (ca. 21 - 24 annulus cells) and well visible stomium.
NPA-PB-201813	**Figure 3(C)** and **Figure 3(D)** and **Figure 3(E)**	Three isolated sporangia with oblique annuli from exindusiate sori, and vaguely visible spores.
NPA-PB-201712	**Figure 3(F)** and **Figure 3(G)**	Two isolated sporangia with oblique annuli (ca. 20 indurated cells) and vaguely visible stomium.
NPA-PB-YN17	**Figure 3(H)**	One isolated sporangium with oblique and complete annulus, and the annulus is passing its stalk.
NPA-PB-201738	**Figure 4(A)** and **Figure 4(B)** **Figure 4(C)**	Modified laminas with two rows of naked and dehisced sporangia, the sporangia with complete apical annuli containing trilete spores which show some reticulate ridges.
NPA-PB-201814	**Figure 4(D)**	Naked sporangia with complete subapical annuli borne on strongly modified lamina.
NPA-PB-201718	**Figure 4(E)**	Naked and dehisced sporangia with complete apical annuli borne on modified lamina.

Kachin amber to be about the Cenomanian–Turonian based on the stratigraphic distributions of Cretaceous insect families. Furthermore, Cruickshank and Ko [29] reported an ammonite *Mortoniceras* of Middle or Upper Albian age. More precise dating was provided by [30], who assigned an earliest Cenomanian age (98.79 ± 0.62 Ma) based on U–Pb zircon dating to the sedimentary matrix of the amber-bearing beds. More recently, this dating was further refined by [31], who, using biostratigraphic and radioisotope data, constrained the age of the Burmese Kachin amber to approximately the Upper Albian to Lower Cenomanian period. The amber specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. For examination, the specimens were prepared by trimming it with a water-fed saw and grinding and polishing with a lap to expose the inclusions. Photographic documentation of the fossil inclusions was performed using a Zeiss Stereo Discovery V18 microscope system. To capture the details of these inclusions, both incident and transmitted lighting techniques were employed. The resultant images were then compiled, arranged, and annotated using Adobe Photoshop Pro DC for presentation and analysis.

3. Results and Discussion

3.1. Sporangia of Polypodiales in the Mid-Cretaceous of Myanmar Amber Forest

The Polypodiales, comprising approximately 80% of extant fern species, is strongly supported as monophyletic by molecular studies [24] [32]-[38]. Within this order, two distinct morphological synapomorphies characterize the sporangium: a three-rowed stalk (**Figure 1(A)**, **Figure 2(C)**) and a vertically interrupted annulus at the stalk (**Figure 1(A)**, **Figure 2**) [1] [12] [25]. Despite some exceptions such as the Lindsaeaceae [39] and Athyriaceae [40], most families within Polypodiales lack a well-documented fossil record traceable to the Mesozoic from stratigraphic deposits [41] [42] [43] until the discovery of the first polypod fern fossil in mid-Cretaceous Myanmar amber [12]. One challenge stems from the scarcity of diagnostic characteristics, particularly the sporangium's vertical annulus and distinct stomium, which are often lost in fossilized material.

To date, the majority of ferns identified from mid-Cretaceous Myanmar amber belong to Polypodiales, particularly to its basal families, including Dennstaedtiaceae [5] [12] [13], Lindsaeaceae [14] [16], Cystodiaceae [8] [9], and Pteridaceae [10]. For the more divergent lineage Eupolypods within Polypodiales, only two compelling fossils, *Holttumopteris burmensis* [11] and *Cretacifilix fungiformis* [6] [7], have been discovered. Additionally, some dispersed polypod sporangia have been reported [12] [28]. In addition to these published findings, new dispersed sporangia exhibiting characteristic features of Polypodiales (**Table 2**, **Figure 2**) have been uncovered in mid-Cretaceous Myanmar amber, including one specimen potentially affiliated with Eupolypods (NPA-PB-XFY05 of **Table 2**, **Figure 2(F)**). This affiliation is supported by two spores with a lophate perine within the sporangium and a few acicular hairs protruding from the sporangium, both characteristic features indicative of a connection to Eupolypods [11]

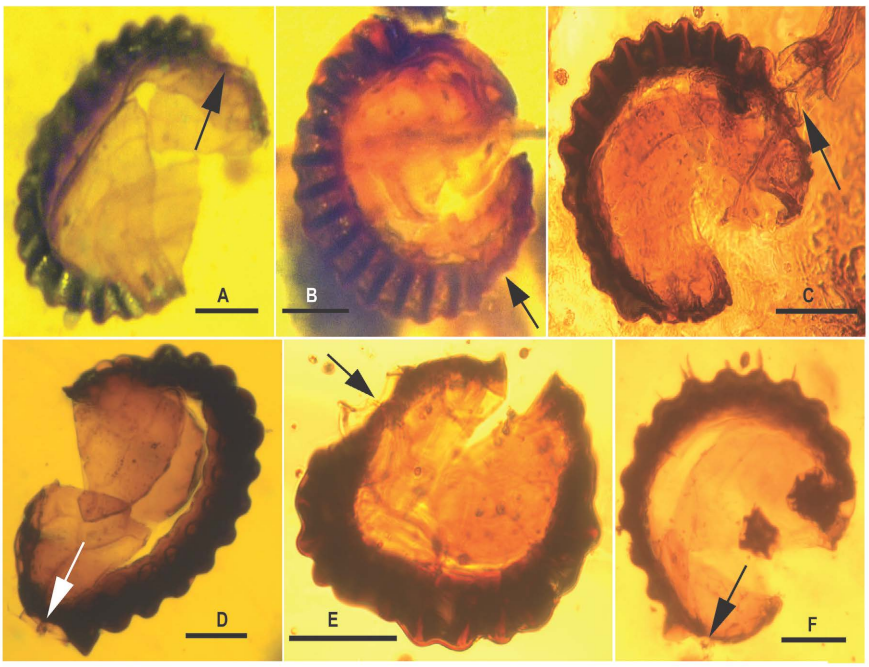

Figure 2. Morphological diversity of dispersed sporangia featuring vertical annuli in Cretaceous Myanmar amber forests. (A) An empty sporangium displaying a clearly visible stomium and a partial stalk interrupted by the annulus (Specimen NPA-PB-201602); (B) An empty sporangium with well visible stomium, and with a remnant stalk interrupted at the annulus (NPA-PB-201603); (C) An empty sporangium showcasing a clearly visible stomium and a stalk characterized by three rows of cells, interrupted at the annulus (Specimen NPA-PB-201727); (D) An empty sporangium with a pronounced stomium and a fragmentary stalk interrupted at the annulus (Specimen NPA-PB-XFY01); (E) An empty sporangium displaying a visible stomium and a residual stalk interrupted at the annulus (Specimen NPA-PB-XFY04); (F) A sporangium with a clearly visible stomium, containing two spores with a lophate perine and four acicular hairs emanating from the sporangium wall, accompanied by a partial stalk interrupted at the annulus (Specimen NPA-PB-XFY05). Arrows indicate the sporangium base where the stalk is attached. Scale bars = 50 μm for all images ((A)-(F)).

[12]. These recent findings contribute further evidence to support the notion that the Cretaceous amber forests of Myanmar boasted a diverse fern flora, likely dominated by polypods based on current data [11] [12].

3.2. Sporangia of Tree Ferns (Cyatheales) in the Mid-Cretaceous of Myanmar

Traditionally, Cyatheales known as "tree ferns" was confined to the families Cyatheaceae, Dicksoniaceae, Lophosoriaceae, and Metaxyaceae [22] [44]. Recent phylogenetic studies have significantly expanded this understanding, revealing that these families form a coherent clade with the Loxomataceae and Plagiogyriaceae. Such relationships were previously unanticipated and underscore the power of molecular data in revealing evolutionary linkages [33] [45]. Additionally, these analyses have led to the placement of Lophosoriaceae into Dicksoniaceae and Hymenophyllopsidaceae, endemic to the tepui region of southern Ve-

nezuela, into *Cyathea* [46]. Apart from the conspicuous feature of the rhizome, tree ferns exhibit two distinct common characteristics in their sporangia, in contrast to the Polypodiales, the Cyatheales exhibit a unique sporangial morphology, characterized by a greater number of stalk cells and complete, ring-like annuli that bypass (not interrupted by) the sporangium stalk (**Figure 1(B)**, **Figure 3**). These features facilitated the identification of a tree fern inclusion within Myanmar amber as *Thyrsopteris Cretacea* of the Thyrsopteridaceae, marking the first record of the order from this locale [17]. More dispersed sporangia with oblique annuli from the mid-Cretaceous Myanmar amber were recognized in this study (**Table 2**, **Figure 3**). Annulus cells of these sporangia are usually more than that in Polypodiales (**Table 2**), as observed in extant Polypodiales and Cyatheales [47].

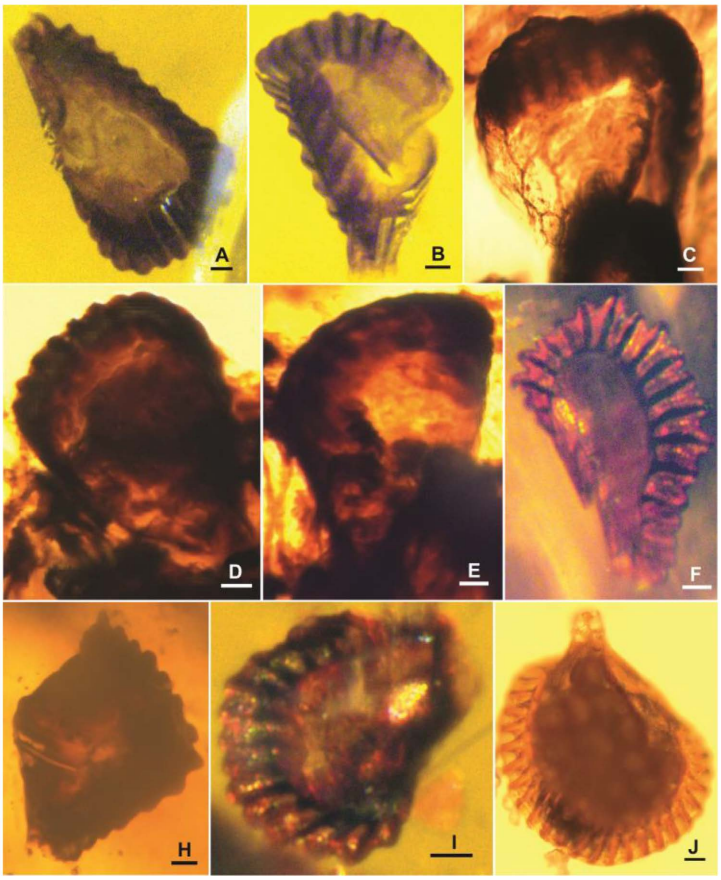

Figure 3. Comparative analysis of dispersed sporangia featuring oblique annuli in Cretaceous Myanmar amber forests and the extant *Cibotium barometz* (Cibotiaceae, Cyatheales). ((A) and (B)) Detailed views of sporangia with clearly visible stomium from specimen NPA-PB-201719; ((C)-(E)) Sporangia from amber piece NPA-PB-201813, illustrating morphological details; ((F) and (G)) Sporangia obtained from amber piece NPA-PB-201712, showcasing their unique features; (H) A close-up of a sporangium from specimen NPA-PB-201712, highlighting the annulus passing through its stalk; (I) A representative sample of the extant *Cibotium barometz* (Cibotiaceae, specimen NPA-FJ41), for comparative purposes. Scale bars = 25 μm for all images ((A)-(I)), facilitating detailed morphological comparisons.

The current investigation extends the knowledge of Cyatheales-type sporangia in the mid-Cretaceous Myanmar amber, introducing additional sporangial types and thereby highlighting the complexity and diversity of the fern flora within these ancient forests. These findings indicate that the mid-Cretaceous forests of Myanmar were not only rich in polypods, as previously documented but also harbored a significant diversity of tree ferns, pointing towards a more complex ecosystem than currently recognized. Furthermore, the extant tree ferns frequently constitute a locally dominant component of the wet southern temperate rainforests across Australasia, southern Africa, and regions adjacent to the tropics in South America. Historically, most fossil records of Cyatheales have been discovered in the Southern Hemisphere, leading to the widely accepted view that they are of Gondwanan origin [44] [45] [46]. However, this current investigation has identified Cyatheales-type sporangia within the mid-Cretaceous amber forests of Myanmar, a region part of Laurasia, thereby broadening our understanding of the historical biogeography of tree ferns. Previously considered to be predominantly Gondwanan, these findings suggest that the distribution of Cyatheales was more extensive than currently recognized, indicating that they once thrived in Laurasia as well.

3.3. Sporangia of Schizaeales in the Mid-Cretaceous of Myanmar

The Schizaeales, a monophyletic group encompassing the families Lygodiaceae, Schizaeaceae, and Anemiaceae, primarily distributed in warm, moist environments near water sources such as riverbanks, represent a fascinating case study in the field of plant phylogenetics [32] [33] [48] [49] [50]. The Schizaeales are distinguished by their unique sporangial characteristics, notably the complete apical or subapical annulus [22] [51]. Based on the sporangium characters, three amber pieces (NPA-201738, NPA-201914, and NPA-201918 of **Table 2**) from our collections could be put into Schizaeales (**Table 2**, **Figure 4**). With naked sporangia and trilete spores, specimens in amber piece of NPA-201738 (**Table 2**) could be considered as affinity with Anemiaceae; similarly, with naked sporangia and a bigger distal plate (with more than one cell) on the apical end of the sporangia, specimen in an amber piece of NPA-201914 (**Table 2**), could be considered as affinity with Anemiaceae too. These investigations have revealed the presence of diverse schizaeoid ferns within the rich fern flora of mid-Cretaceous Myanmar amber forests. Additionally, the ecological preferences of Schizaeales, which favor warm, humid environments close to water sources, are consistent with the inferred depositional environment of the Myanmar amber forests. This suggests a proximity to a nearshore marine setting, such as a bay or estuary [28] [29] [30] [52], or alternatively, a dynamic coastal forest environment for the mid-Cretaceous Myanmar amber forests [31]. This alignment between the ecological characteristics of Schizaeales and the depositional context of the amber indicates a complex ecosystem where these ferns thrived.

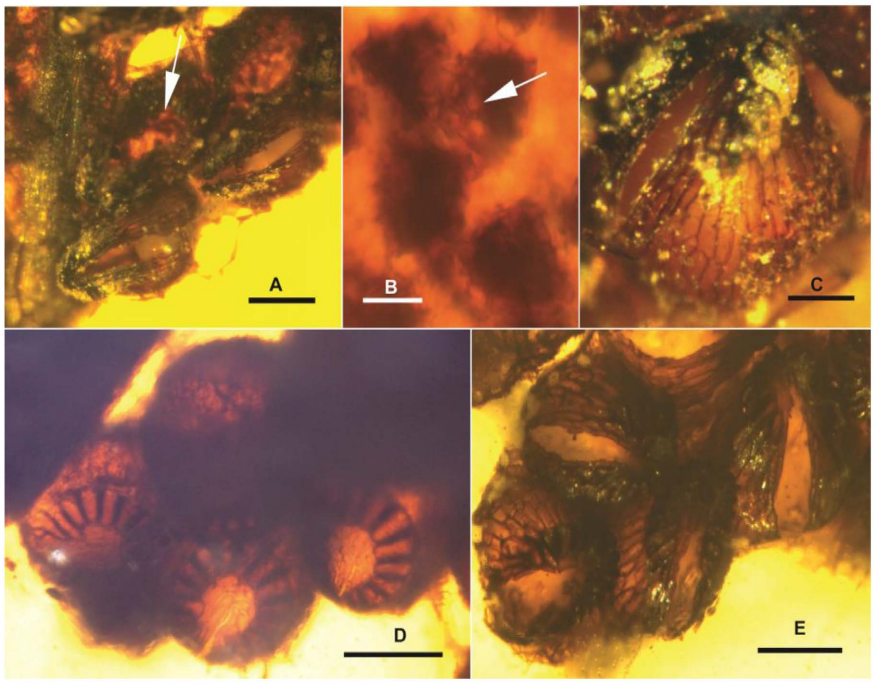

Figure 4. Illustration of pinnae fragment inclusions with sporangia featuring apical annuli in Myanmar amber, highlighting the diversity of fern flora, including Schizaeales. (A) A fragment of a pinna showcasing two rows of exposed and dehisced sporangia with intact apical annuli. Visible spores are indicated by an arrow, with a detailed view provided in (B) (Specimen NPA-PB-201712). (B) Close-up of four trilete spores within a sporangium from the amber piece depicted in (A), displaying reticulate ridges (indicated by an arrow). (C) A single sporangium with an apical annulus and clearly visible stomium (Specimen NPA-PB-201712). (D) Four exposed sporangia with complete subapical annuli (the distal plate of the annuli showing an increased number of cells) attached to significantly altered laminae (Specimen NPA-PB-201914). (E) Four exposed sporangia with complete apical annuli attached to significantly altered laminae (Specimen NPA-PB-201918). Scale bars = 0.2 mm ((A), (D), (E)), and 0.1 mm ((B) and (C)).

4. Concluding Remark

Phylogenetic investigations have greatly enhanced our comprehension of fern systematics and evolutionary history. Notably, they have resolved ferns as the sister group of seed plants, incorporated Psilotaceae and Equisetaceae within ferns [32] [33] and elucidated a significant radiation of polypod ferns concurrent with the rise of angiosperms [34] [35]. However, these studies face challenges due to limited information on extinct ferns and restricted taxon sampling, particularly restricted to extant species. The paleontological record of ferns remains incomplete, leaving gaps in our understanding of extinct taxa. Thus, there is a risk associated with phylogenetic analyses focusing solely on extant taxa [53].

Cretaceous fossils of derived leptosporangiate ferns are crucial for understanding terrestrial vegetation during the Cretaceous-Terrestrial Revolution. Molecular dating methods heavily depend on fossil records for age calibration [54]. Therefore, the documentation and assessment of new fern fossils, particularly from pivotal periods in fern lineage establishment and radiation, are im-

perative. In this study, in addition to providing further evidence for the presence of polypod ferns, our investigations confirm the existence of additional fern fossils belonging to Cyatheales and Schizaeale in the mid-Cretaceous Myanmar amber forests, based on extensive analyses of isolated sporangium structures, notably their annulus type. Incorporating the new fossil evidence within a phylogenetic framework lends support to the hypothesis that the Cretaceous forests of Myanmar harbored a diverse fern flora.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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