SCANNING ELECTRON MICROSCOPICAL STUDIES ON THE SPORES OF PTERIDOPHYTES.

VIII. THE TREE FERN FAMILY (CYATHEACEAE) AND ITS ALLIED SPECIES FOUND IN TAIWAN.[1,2]

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Abstract: The spores of seven species of Cyatheaceae found in Taiwan are studied and analyzed. Incipient heterospory is found in two species of *Alsophila* having spinulose spores (*A. metteniana* and *A. podophylla*). Spinulose type of spores are also found in *Sphaeropteris lepifera*. Most other *Alsophilas* have striated spores (*A. denticulata*, *A. fenicis*, *A. loheri*, and *A. spinulosa*). The general evolutionary sequence of sculptine morphology in the Cyatheaceae are discussed in terms of traditional systems of classification and the phylogeny proposed recently by Tryon. The psilate and striated spores of *Cibotium cumingii* and *C. barometz* (Dicksoniaceae), respectively, are also studied and their possible phylogenetic relationship to the Cyatheaceae evaluated.

INTRODUCTION

There are about 800 species in the tree fern family (Cyatheaceae), nearly equally distributed between the paleotropics and the neotropics. They are found throughout the wetter parts of the tropical and subtropical rain forests and some even grow in temperate regions, especially in the southern hemisphere (e. g. New Zealand).

Despite the longevity of these tree ferns and repeated attempts to solve the basic problems of systematics and evolution in this group of ferns, an unsatisfactory classification has persisted in the Cyatheaceae for a longer time than in any other of the large groups of ferns. There are uncertainties concerning the taxonomy of the two basic groups of genera, namely, the *Cyathea* group and the *Dicksonia* group with allied genera. There have been differences of opinions regarding infra-familial classification within the Cyatheaceae (Brown, 1810; Copeland, 1909, 1947; Domin, 1930; Holttum, 1963; Tryon, 1970).

The different systems of classification proposed for the tree fern family do not satisfy all those who were concerned. Indusial characters emphasized by previous workers are, to use an old adage "unfortunately for the science, upon the sorus there's no reliance". Any attempt to suggest any clearly definable morphological characters in the Cyatheaceae were futile (Holttum, 1957). However, in modern classification systems of the Cyatheaceae (Holttum, 1963; Tryon, 1970) scale characters are regarded as more important than the indusial characters (DeWolf, 1953). We still have very broad morphological terms for which we have no precise understanding. Many more potentially useful characters need to be explored. The spore character is one among them.

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The literature on descriptions of the spore morphology of Cyatheaceae have generally been imprecise or evasive and far from dependable (Harris, 1955; Erdtman, 1957, 1971; Nayar, 1964; Kremp & Kawasaki, 1972). Partly because of their illusive, complicate or confusing sculptine patterns seen under ordinary light microscope (see Plate I) little use has thus been made of these spore characteristics in classification and identification.

Because previous studies on the sculptine morphology of many fern spores have indicated that they offer both reliable and stable morphological characteristics which may be employed as dependable criteria in the identification of genera and species (Brown, 1960; Hires, 1965; Nayar & Devi, 1968; Wagner, 1974; Liew, 1976a), as well as in the tracing of possible affinities and trend of evolution between the genera and higher systematic categories (Wilce, 1972; Liew, 1976b), it seems highly probable that spore morphology may become a useful character in solving the basic problems of systematics and evolution of tree ferns.

The present investigation is thus undertaken to resolve the differences in proposed systems of classification of the tree fern family, and to provide additional data on the characters used for the assessment of phylogenetic relationship and taxa demarcation. This communication reports the results of our study on the spores of Formosan tree ferns as revealed by light and scanning electron microscopes, and discusses the evolution of the spores of tree ferns in general. For purpose of comparison, members of the Dicksoniaceae found in Taiwan (*Cibotium* species) were also included.

MATERIALS AND METHODS

Spores of Formosan species of Cyatheaceae were taken directly from fresh materials collected in the fields by the authors. A few of them were taken from specimens deposited in the herbarium of the Department of Botany, National Taiwan University. Materials used for scanning electron and optical microscopical observations were listed in Table I.

Table I. A list of the Formosan taxa of tree ferns (Cyatheaceae and Dicksoniaceae) used in our scanning electron (SEM) and light microscopical (LM) studies. All specimens are deposited in TAI.

Taxon	Locality, Collection Number, LM or SEM	
1. *Alsophila denticulata* Baker	Taipei: Yangmingshan Taipei: Ta-dong-shan	Liew 1054 (SEM), Wang 17 (LM) Liew 2154 (SEM)
2. *A. fenicis* (Copel.) C. Chr.	Orchid Isl.: Wang-nan-fung Orchid Isl.: Hung-tou-shan	Liew 9043 (LM, SEM) Liew 9068 (SEM)
3. *A. loheri* (Christ) Tryon	Pingtung: Chin-shui-yin	Liew 8033 (LM, SEM)
4. *A. metteniana* Hance	Keelung: Luan-luan Taipei: Pii-hu	Liew 1244 (SEM), Wang 27 (LM) Liew 2239 (SEM)
5. *A. podophylla* Hooker	Taipei: Ta-dong-shan Nantou: Sun Moon Lake	Liew 2183 (SEM) Liew 6032 (LM, SEM)
6. *A. spinulosa* (Hook.)	Taipei: Yangmingshan Taipei: Nui-shuan-chi Taipei: Wulai	Wang 11 (LM) Liew 1096 (SEM) Liew 2142 (SEM)
7. *Sphaeropteris lepifera* (Hook.) Tryon	Taipei: Yangmingshan Taipei: Ta-dong-shan Orchid Isl.: Chung Sing Farm	Liew 1071 (SEM) Liew 2160 (LM) Liew 90195b (SEM)
8. *Cibotium barometz* (L.) J. Sm.	Taichung: Nan-shih Nantou: Sun Moon Lake	Liew 5037 (SEM) Kuo 1827 (SEM)
9. *C. cumingii* Kunze	Taipei: Chuk-tze-shan Taipei: Yangmingshan	Wang 100 (SEM) Moo & Hsu 1221 (SEM)

For light microscopy, spores were dispersed in a drop or two of Hoyer solution and observed . Detail of methods of preparation and observation on scanning electron microscope were as described before (Liew, 1975). Briefly, spores of individual taxon were dusted or carefully transferred from the sporangia to a piece of clean paper with uncontaminated tooth pick and mounted in a drop of Hoyer solution for preliminary observation under light microscope. After justifying the proper identity of the spores concerned, some of the materials were used directly for scanning electron microscopy. The spores were adhered to a double sided scotch tape attached onto a metalic stub and coated first with carbon, and then with a thin layer of gold inside a manual or automatic rotatory vacuum evaporator. It was then observed with a scanning electron microscope (Joel JSM U3) operating at accelerating voltages ranging from 5 to 15 kv and under magnification from 100X to 10,000X.

RESULTS

The spinulose spores of both *Alsophila metteniana* and *A. podophylla* have two different sizes within one sporangium, one smaller than the other. For ten measurements, the larger spores measure about 30-35 $\mu \times$ 35-41 μ (polar $\times$ equatorial diameters), and the smaller ones 23-27 $\mu \times$ 28-31 μ. Incipient heterospory is thus suspected.

The two genera of Cyatheaceae found in Taiwan, *Alsophila* and *Sphaeropteris*, are characterized by trilete, tetrahedral spores, with triangular amb commonly having straight or concave sides, and prominent or rather inconspicuous laesural arms, with a size of about 23-35 $\mu\times$ 28-41μ for ten readings. (Plates I to IV)

The results of our study indicate that two major classes of sculpture patterns may be distinguished within Formosan Cyatheaceae. The sculptine morphology of one group of the spores is striated, the ridges of which sometimes crack and peel off as small flakes (Plate II). It includes four species of *Alsophila* found in Taiwan. They are *A. denticulata*, *A. fenicis*, *A. loheri*, and *A. spinulosa*. The other group of tree ferns is found to have spinulose type of spore sculpture (Plate III), and it includes *Alsophila metteniana*, *A. podophylla* and *Sphaeropteris lepifera*.

There are differences in the density, distribution, kinds and degree of pointedness of the spines in the spinulose spores. Such is also the case for the flakes or ridges of the striated spores. By using sculptine characteristics species identification and delimitation is possible within the seven species of Formosan tree ferns. A key to the several taxa of tree ferns found in Taiwan are given as below. Detailed descriptions of these spores will be the subject of a latter communication.

A KEY TO THE FORMOSAN SPECIES OF TREE FERNS BASED ON PALYNOLOGICAL CHARACTERISTICS

1. Spores striated, forming flakes or thin and high ridges
   2. Spores with larger and more irregular flakes
      3. Flakes high and thin, up to 4 μ tall, edge spiny .... *Alsophila denticulata*
      3. Flakes lower, up to 2 μ tall, edge irregular .... *A. fenicis*
   2. Spores with lower and straight, more or less parallel flakes
      4. Flakes small and low, about 1 μ tall, regularly distributed. .... *A. loheri*
      4. Flakes higher, about 3 μ, distribution irregular .... *A. spinulosa*
1. Spores spinulose, spines acicular or with broad base
   5. Spines in blocks, numerous, closely associated; spores of two sizes
      6. Larger spores larger, about 35 $\mu\times$41 μ, sculptine easily ablate .... *A. metteniana*

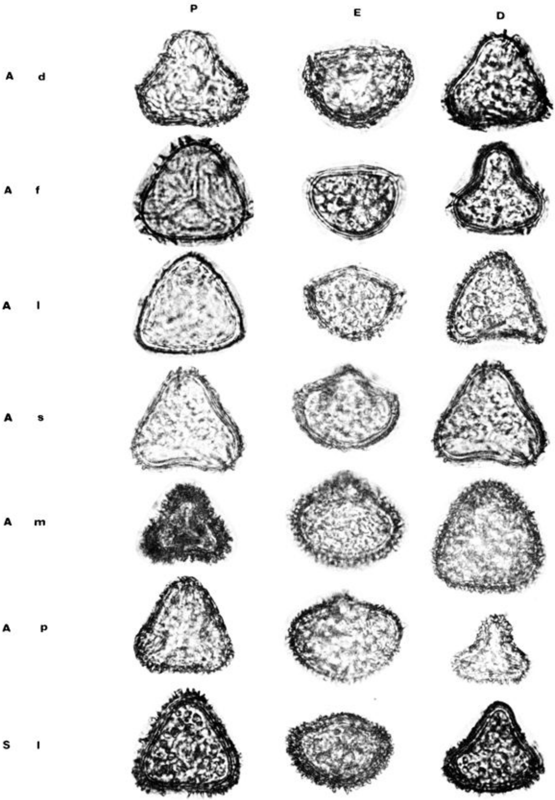
P
E
D
A d
A f
A l
A s
A m
A p
S l

Plate I. Untreated spores of seven species of Formosan Cyatheaceae as seen under the light microscope. For each species three faces of the spore were examined. From left to right, column P for proximal view, E for equatorial view, and D for distal view. Each row represents three spores of one species. From top to bottom, they are: row *A. d.* for ***Alsophila denticulata;*** *A. f.* for *A. fenicis; A. l.* for *A. loheri; A. s.* for *A. spinulosa; A. m.* for *A. metteniana*; *A. p.* for *A. podophylla;* and *S. l.* for *Sphaeropteris lepifera.* All micrographs are of the same magnification of 450 times, or one centimeter equals approximately 19 μ.

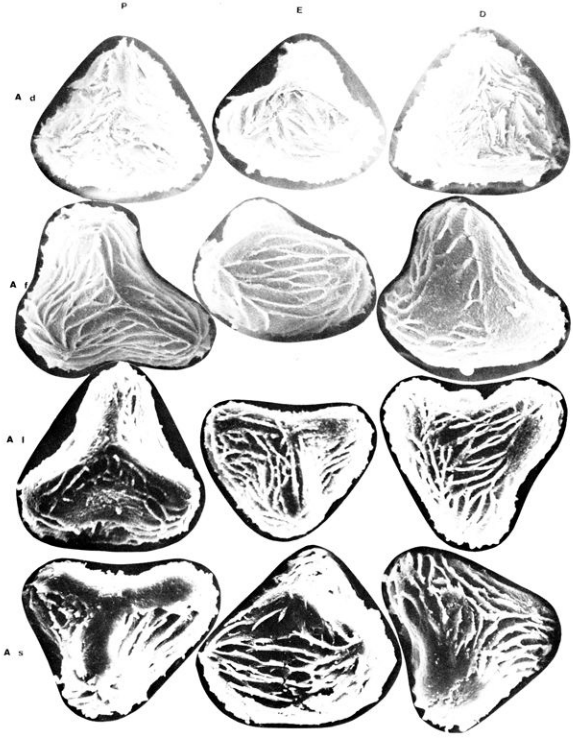
P
E
D
A d
A f
A l
A s

Plate II. Scanning electron micrographs of the striated spores of Formosan Cyatheaceae. Legends are as in Plate I. From top to bottom the species are: row ***A. d.*** for ***A. denticulata;*** *A. f.* for *A. fenicis;* *A. l.* for ***A. loheri;*** and *A. s.* for ***A. spinulosa.*** All micrographs are magnified 1,000×, or one centimeter equals to 10 μ. The magnification for the equatorial view of the spore of ***A. denticulata*** is exceptional. It is magnified 1,250×.

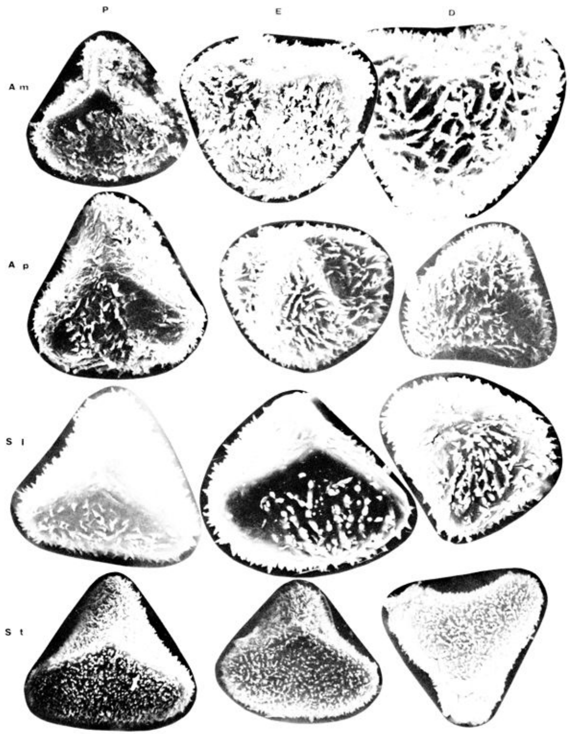
P
E
D
A m
A p
S l
S t

Plate III. Scanning electron micrographs of the spinulose spores of Cyatheaceae. Legends are as in Plate I. From top to bottom the species are: row *A. m.* for *A. metteniana; A. p.* for *A. podophylla; S. l.* for *Sphaeropteris lepifera;* and *S. t.* for the Philippine species of *S. tripinnata.* All micrographs are magnified 1,000×, or one centimeter equals to 10 μ. The magnification for the distal view of *A. metteniana* is exceptional. It is magnified 1,250×.

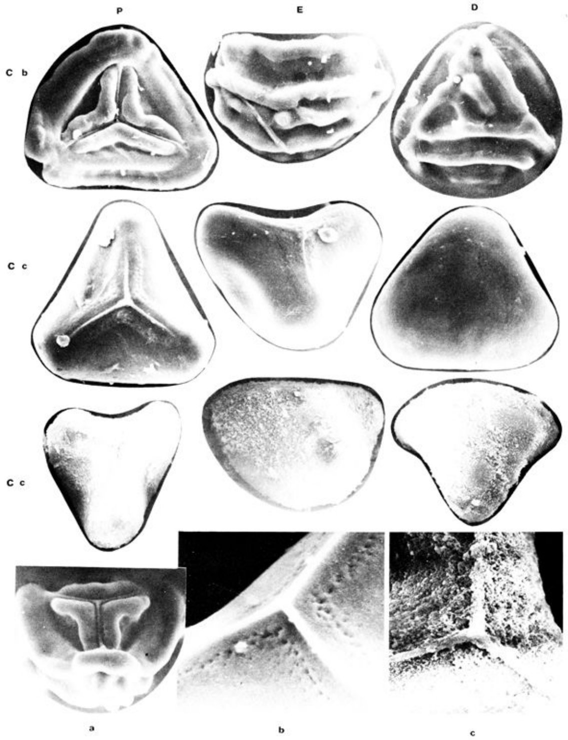
P
E
D
C b
C c
C c
a
b
c

Plate IV. Scanning electron micrographs of the spores of *Cibotiums* found in Taiwan. Legends are as in Plate I, except the last row. From top to bottom the species are: row *C. b.* for *Cibotium barometz;* second row *C. c.* for *C. cumingii* (*Moo & Hsu 1221*, Yangming-shan); third row *C. c.* for the same species, but from different collection and locality (*Wang 100,* Chuk-tze-shan). Three close-up views of the spores of *Cibotium* are given in the last row. Small holes distributed near laesural ridges are clearly shown in figs. a and b, and the covering layer in fig. c. All micrographs are of the same magnification of 750×, or one centimeter equals to 13.4 μ. The magnification of the proximal- and distal- views of the third row *C. c.* (500×, 1 cm=20 μ), and last row figs. b and c (1,500×, 1 cm=6.7 μ) are exceptional.

6. Larger spores smaller, about $30\mu\times35\mu$, sculptine more resistant .... *A. podophylla*
5. Spines mostly isolated, or at most a few spines jointed together, small and lower; spores of similar size .... *Sphaeropteris lepifera*

Spores of *Cibotium* are very differently sculptured (see Plate IV). For *C. barometz*, the tetrahedral trilete spore has thick, raised, long plane or circumfluent field-distal ridges on the distal surface, annulate equatorial ridges on the equator, and with three either short or long plane field-laesural ridges along the margo of the laesural arm in the proximal face. *C. cumingii* is found to have similar laesural margo, with or without inconspicuous narrow band-laesural ridges. But both of the proximal and distal surfaces are psilate or smooth. Both species of *Cibotiums* are unique in having a row of small holes (fovea) distributed on each laesural ridge (Plate IV). Spores of *Cibotium* are larger than the tree ferns *Alsophila* and *Sphaeropteris*, averaging $36\mu\times47\mu$ in polar and equatorial diameters respectively.

The actual identity of the spores of *Cibotium* species found in Taiwan is not fully established. Spores of *C. barometz* found in Taiwan (e.g. *Kuo 1827*) and other areas (e.g. *Carricic 634* of Malaya, in KLU) are distinctive in having laesural- equtorial- and distal- ridges. However, some Malesian taxa of *Cibotium cumingii* studied by the present authors are also found to have spores of similar structures, for example, in the Philippine taxa, *Elmer 22023* (Luzon, in SING) and *Quisumbing 2221* (Luzon, in SING), and in the Malaysian taxa, *Clemens 29672* (Borneo, in SING) and *Chew, Corner & Stainton 998* (Mt. Kinabalu, in SING). Moreover, in Taiwan, *C. cumingii* are found to have two types of spores (see Plate IV). One with a thin layer of amorphous coverings on their surfaces (e.g. *Wang 100*, third row *C. c.* in Plate IV, presumably spores are fully mature) while the others are psilate (e.g. *Moo & Hsu 1221*, second row *C. c.* in Plate IV, spores may be younger, but they are the most common spores found in this species.)

DISCUSSION

1. Incipient Heterospory

The prescence of two sizes of spores within a sporangium is a new finding in tree ferns not reported before. Such a situation is common in both *Alsophila metteniana* and *A. podophylla* found in Taiwan. This is not due to artificial shrinkage because we did not acetolyze the spores, and the possibility of differences in developmental stage is also ruled out because they are found within the same sporangium. It is not hybrid abnormality either because the spores are perfectly normal except the difference in sizes. It might be another case of incipient heterospory in ferns (Tryon, 1964).

2. Cyatheaceae

We have studied the spores of all the seven species of Formosan Cyatheaceae, and found that their sculptine patterns are either spinulose or striated (see Plate I to IV). We have also checked the spores of several other Cyatheaceae taxa found in neighbouring Malesian region. For example, in *Sphaeropteris*, *S. tripinnata* (Copel.) Tryon of the Philippines (Mindano, San Ravior; *E. B. Copeland, s. n.*, 1907) and *S. glauca* (Bl.) Tryon of Malaya (Selangor, Ulu Gombak Road; *E. E. Khoo, s. n.*, May 26, 1970) are found to have spinulose spores. In *Alsophila*, both Malayan species of *A. commutata* Mett. (Pahang, Gunong Ulu Kali Road (4.1 mi.), 3,650 ft.; *E. A. Turnau 1,187*, Jan. 16, 1968) and *A. glabra* (Bl.) Hook. (Pahang, Gunong Ulu Kali Road (4 mi.), 3,550 ft.; *E. A. Turnau 1,184*, Nov. 1, 1967) are also found to have spinulose spores.

Attempts to select and accommodate our present finding on spore morphology with both old and new schemes of classification of the tree fern family (Smith, 1793; Brown, 1810; Copeland, 1909, 1947; Holttum, 1963; Tryon, 1970) were met with difficulties of explanation (Table II). The scheme recently proposed by Tryon (1970) appears to best explain our results. In his phyletic arrangement of the squamate genera of the Cyatheaceae that have dorsal sori Tryon derived two independent family branches for the scaly tree ferns from ancestors at the evolutionary level of the genus *Sphaeropteris*. One branch consists of *Alsophila* and *Nephelea* with apically setate, structurally marginate petiole scales, the other consists of *Trichipteris, Cyathea*, and *Cnemidaria* with apically non-setate and structurally flabelloid petiole scales.

Table II. The sculptine patterns of the spores of the tree fern family found in Taiwan and its relationship to the different systems of classification proposed.(1)

Chief Diagnostic Character				
Sorus	Indusium	Indusium & Scale	Scale	Spore
Smith, 1793	Brown, 1810	Holttum, 1963, 1974	Tryon, 1970	Liew & Wang, 1976
I. *Cyathea* (Sori dorsal)	I. *Cyathea* (Indusium complete)	*Cyathea* I. Subgenus *Alsophila* (Stipe scale flabelloid) a. Section *Alsophila* (Sori indusiate)	I. *Alsophila* (Stipe scale marginate)	I. *Alsophila* (?) (Spore striated or spinulose)
1. *C. fenicis*	*C. f.*	*C. f.*	*A. f.*	*A. f.* (striated)
2. *C. loheri*	*C. l.*	*C. l.*	*A. l.*	*A. l.* (striated)
3. *C. spinulosa*	*C. s.*	*C. s.*	*A. s.*	*A. s.* (striated)
	II. *Alsophila* (Indusium reduced or absent)	b. Section *Gymnosphaera* (Sori exindusiate)		
4. *C. denticulata*	*A. d.*	*C. d.*	*A. d.*	*A. d.* (striated)
5. *C. metteniana*	*A. m.*	*C. m.*	*A. m.*	*A. m.* (spinulose)
6. *C. podophylla*	*A. p.*	*C. p.*	*A. p.*	*A. p.* (spinulose)
		II. Subgenus *Sphaeropteris* (Stipe scale setiferous) a. Section *Sphaeropteris* (Costules not widely spaced)	II. *Sphaeropteris* (Stipe scale conform)	II. *Sphaeropteris* (?) (Spore spinulose)
7. *C. lepifera*	*A. l.*	*C. l.*	*S. l.*	*S. l.* (spinulose)
		b. Section *Schizocaena* (Costules widely spaced)		

(1) Some additional Malesian species of *Alsophila* and *Sphaeropteris* were examined. The following taxa were found to have spinulose spores: (1) *A. commutata* (Malaya), (2) *A. glabra* (Malaya), (3) *S. glauca* (Malaya), and *S. tripinnata* (The Philippines).

In terms of spore evolution it seems probable that, in one branch, while evolving from conform (*Sphaeropteris*) to setate and marginate petiole scales (*Alsophila* and *Nephelea*) the spore has evolved in the direction of changing from spinulose (*Sphaeropteris*) to striated spore sculptine (*Nephelea*), with the intermediate genus (*Alsophila*) comprising mixed spore sculptine of both types. In the other branch, concomittant with the evolution from setiferous (*Sphaerop-*

teris) to non-setate and flabelloid petiole scales (*Trichipteris, Cyathea*, and *Cnemidaria*) the general form of sculptine evolution has changed from spinulose sculptine (*Sphaeropteris, Trichipteris*) to having small apertures or depressions arranged at random or in vague patterns along the surface (*Cyathea*), to the reduction of spores devoid of perine and having one large pore located near the center of each side, on or near the equator (*Cnemidaria*).

Under such an evolutionary scheme *Alsophila* could be conceived of as a genus of mosaic characters, containing species with both primitive or generalized (spinulose) and specialized (striated) spore characteristics. Such would also be the case for the transitional genera *Trichipteris* and *Cyathea* in the other branch of the evolutionary line.

Despite the fact that some feel that Tryon has not really justified the recognition of his groups as independent genera (Morton, 1971; Holttum, 1974), his seemingly "one-character" classification system does provide us with a working framework, and the full range of many studies can be assessed. In addition to taxonomic reviews (Tryon, 1971; Gastony, 1973; Barrington, 1974; Conant, 1974; Tryon, 1974; Windisch, 1974; Stoltz, 1974) recent research on many aspects of the Cyatheaceae do, in general, support his phyletic scheme.

Based on a broad anatomical study of the Cyatheaceae Lucansky concluded that "the squamate genera in the Cyatheaceae shows striking similarities in both anatomical and morphological characters, and constitutes a natural grouping" (Lucansky, 1974b), and that "data from nodal and vascular anatomy basically support Tryon's phyletic scheme for the family" (Lucansky & White, 1974). However, substantially dissimilar results obtained after extensive and critical investigations made on Formosan materials of *Alsophila* and *Sphaeropteris* species compelled us to accept their observations and conclusions with reservation (Wang, 1976).

In terms of sporangial capacity types the distribution is in accordance with the generic phyletic scheme proposed by Tryon (Gastony, 1974). The 64-spores sporangia found in *Sphaeropteris* are shown to be carried over into the *Trichipteris-Cyathea-Cnemidaria* branch whereas the *Alsophila-Nephelea* branch is associated with the reduced spore number of 16. Hairy genera of the tree ferns (*Lophosoria* and *Metaxya*) also have 64 spores per sporangium. The distribution of the perine is also, in general, congruous with the scheme proposed by Tryon (Gastony, 1974). It is found that in one branch, perine is either present or absent in intermediate genera (*Trichipteris* and *Cyathea*), and becoming completely lost in *Cnemidaria*. On the other hand, perine is present from *Sphaeropteris* to *Alsophila* and *Nephelea*. The two genera of hairy tree ferns are also perinous.

These studies and our finding on the sculptine pattern of Formosan species of *Alsophila* and *Sphaeropteris* would not fit in any of the classical classification system, such as the three genera system (*Cyathea, Hemitelia* and *Alsophila*) of Brown (1810), the system that recognized only the comprehensive genus *Cyathea* (Copeland, 1947; Holttum, 1963), or the one that considered only *Cnemidaria* as generically distinct from *Cyathea* among the scaly tree ferns (Holttum & Sen, 1961).

However, Tryon's system is not the only final resolution for the tree fern family. Many characters sorely needed for the tree ferns were not studied and many aspects of basic and botanically significant research has not been done. For example, the chemical and serological relationship of these plants have scarcely been touched upon (Lin & Lin, 1965). Detail studies on the morphological, developmental and structural variabilities in Cyatheaceous sculptine are also badly needed. They may help to resolve some of the basic problems of systematics and phylogeny of tree ferns. Results of our investigation in this direction will be reported later when data become sufficiently available for analysis. A better natural system for the tree ferns which will accomodate all the data acquired should continually be sought.

3. Cyatheaceae-Dicksoniaceae Relationship

In his revised classification of the family Cyatheaceae, Tryon (1970) left the taxonomic aligment of the Dicksonoid genera in abeyance. He did indicated that some evidence suggested that hairy Cyatheaceae might be closer to the Dicksoniaceae than to the scaly Cyatheaceous genera.

These tree ferns have undergone many taxonomic changes at the family level, and systems of classification for them have periodically been revised. In the early days when the position and the structure of sori were the overriding criteria in classification, *Cyathea* (sori superficial, with or without true indusia) and *Dicksonia* (sori marginal, with or without outer indusia) were placed in distinct tribes (Brown, 1810). Latter, the two basic groups of genera and their allied genera were then placed in the single family Cyatheaceae (Mettenius, 1856; Diels, 1902; Christensen, 1905; Maxon, 1911). Placing major emphasis on soral position Bower (1926) created three families for the group (Protocyatheaceae, Cyatheaceae, and Dicksoniaceae). Following Bower, most botanists reverted to the earlier view and separated the *Cyathea* and *Dicksonia* allies into two distinct families, the Cyatheaceae and Dicksoniaceae (Christensen, 1938; Copeland, 1947, 1958).

Based upon morphological, developmental, and anatomical characters Holttum and Sen (1961) again incorporated *Metaxya* and *Lophosoria* and the Dicksonioid genera into a single family, the Cyatheaceae (Holttum, 1963). Earlier reports dealing with the anatomy of paleotropical species of tree ferns indicated similar results (Gwynne-Vaughan, 1903; Stephenson, 1908; Ogura, 1927, 1972; Sen, 1964). Recent comparative studies on nodal and vascular anatomy in neotropical Cyatheaceae also pointed out that hairy genera (*Lophosoria* and *Metaxya*) show, in some respects, an affinity to members of the Dicksoniaceae (Lucansky, 1974a; Lucansky & White, 1974).

The present investigation on the sculptine morphology of the spores of Formosan tree ferns indicates that possible relationship between Dicksoniaceae (*Cibotium barometz* and *C. cumingii*) and the scaly Cyatheaceae (*Alsophila* and *Sphaeropteris* species) are quite remote and distant, although not totally unconnected. Hairy genera with striated spores (Erdtman, 1957; Holttum & Sen, 1961; Gastony, 1974) belonging to an independent position at the base of the Cyatheoid line may be closer to the Dicksoniaceae than to the scaly Cyatheaceae. However, more information is needed before the evolutionary line in the Dicksonioid-Cyatheoid alliance can clearly be traced, and the family or families can be recognized with assurance.

Since our results were based on observations of the species of genera of Cyatheaceae found only in Taiwan and a small number of other Cyatheaceous members of the Malesian region, our preliminary inference reached must not be considered or accepted as the final conclusion. It will undoubtedly be corrected and amplified by further investigation of this group.

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