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Morphology of the Gametophytes and Young Sporophytes of Cyatheaceae Native to Taiwan[1]

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ABSTRACT: Seven species of Cyatheaceae are native to Taiwan. *Sphaeropteris lepifera, Alsophila denticulata, A. metteniana*, and *A. podophylla* produced 64 spores per sporangium, whereas *A. loheri, A. spinulosa*, and *A. fenicis* produced 16 spores per sporangium. Spore germination was Cyathea-type, except in *A. denticulata* and *A. metteniana*. In these two species, the rhizoid formation was delayed. Gametophytes of all seven species usually underwent Drynaria-type development, but a few gametophytes of all seven species exhibited Adiantum-type development. Multicellular, scale-like hairs on the dorsal and ventral surfaces of the midrib cushion increased in size and changed shape with age. These scale-like hairs distinguish Cyatheaceae gametophytes from the gametophytes of other fern families. The first three or four fronds of young sporophytes lacked midribs. Uniseriate to multiseriate and club-shaped pluricellular hairs were intermingled on the fronds of juvenile sporophytes of all six species of *Alsophila*. The lacking of club-shaped pluricellular hairs on Juvenile sporophytes of *S. lepifera* supports the taxonomic separation of *Sphaeropteris* from *Alsophila*. The presence of 16- and 64-spored sporangia suggests two evolutionary events within *Alsophila*.

KEY WORDS: Cyatheaceae, *Alsophila*, *Sphaeropteris*, Gametophyte, Sporophyte.

INTRODUCTION

The Cyatheaceae is a large family (6 genera, about 900 species) of arborescent ferns (Zhang *et al.*, 1990) that predominantly grow in montane areas of the neotropics and paleotropics (Tryon and Lugardon, 1990). Seven species of Cyatheaceae are native to Taiwan. *Sphaeropteris lepifera* (Hook.) Tryon, *Alsophila metteniana* Hance, *A. podophylla* Hook., and *A. spinulosa* (Hook.) Tryon grow at low and middle elevations throughout Taiwan. *Alsophila denticulata* Bak. is restricted to northern Taiwan, *A. loheri* (Christ) Tryon only grows in Chinshuiying in southern Taiwan, and *A. fenicis* (Copel.) C. Chr. is found only on Lanyu (Shieh, 1994). There are different opinions regarding the division within the Cyatheaceae. Holttum (1963) proposed a single genus *Cyathea* for the Flora Malesiana region. He also found that indusium type varied widely and thus not a good generic character. According to Holttum's criteria, some botanists (e.g., Kuo, 1985; Shieh, 1994) placed all Cyatheaceae species of Taiwan in one genus *Cyathea*. However, on the base of Tryon's (1970) classification which divided the Cyatheaceae into six genera, some other botanists placed the Taiwanese Cyatheaceae into two genera, *Sphaeropteris* and *Alsophila* (e.g., DeVol, 1975; Wang, 1976).

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Genera or species often can be distinguished by characteristics of their pteridophyte spores (Lellinger and Taylor, 1997). External characters of taxonomic value are spore size, number of spores per sporangium (Goswami and Khandelwal, 1980; Sen, 1964; Gastony, 1974), and the pattern of spore sculpturing (Kurita, 1981; Burrows, 1997). In Taiwan, the ornamentation and size of Cyathaceae spores were examined by light microscopy (Huang, 1981) and a key to native species was constructed on the basis of spore characters visible with a scanning electron microscope (Wang, 1976; Liew and Wang, 1976). However, the number of spores per sporangium was not documented.

Gametophyte morphology, including types of spore germination and early development, mature form, trichomes, and gametangia, has been used to characterize fern taxa (Atkinson and Stokey, 1964; Nayar and Kaur, 1971; Atkinson, 1973). These characteristics are also important in studies of fern phylogeny and reproductive biology (Chiou and Farrar, 1997; Chiou *et al.*, 1998; Masuyama, 1975a, b, 1979). Stokey (1918, 1930) observed the gametophyte morphology of some species of Cyathaceae. Momose (1967), Wang (1976), and Wang *et al.* (1977) gave a brief account of the gametophytes of Taiwanese species. Huang *et al.* (2000) described the life history of *S. lepifera* gametophytes and Lee *et al.* (1999) described the morphology of *A. podophylla* gametophytes. However, gametophytes of the other species in Taiwan were not described in detail.

We studied the number of spores per sporangium, the type of spore germination and gametophyte development, gametangial structure, and the morphology of the gametophyte and young sporophyte of each species of Cyathaceae in Taiwan. These findings should advance understanding of the taxonomy, phylogeny, and reproduction of the Cyatheaceae of Taiwan.

MATERALS AND METHODS

Spores collected from Cyatheaceae sporophytes growing in Taiwan (Table 1) were stored in the refrigerator at 4℃. Voucher specimens were deposited in the Herbarium of Taiwan Forestry Research Institute. To determine the number of spores per sporangium, for each species, the spores in 10 sporangia randomly selected from each of 5 sori on two sporophytes, were counted under a light microscopes.

Spores were sown in the laboratory. Culture media and conditions are the same as the description in Huang *et al.* (2000) and Chiou *et al.* (2000). Morphological characters were observed with microscopes (Leica, Wild M8; Leitz, Dialux 20) and a drawing tube was used to make illustrations.

RESULTS

Alsophila fenicis, A. loheri, and *A. spinulosa* sporangia contained 16 spores each, whereas each sporangium of the other four species contained 64 spores (Table 1).

Spores of *S. lepifera* germinated one week after they were sown, but the spores of the other six species took two weeks to germinate. In five species, not including *A. metteniana* and *A. denticulata*, the first rhizoid was formed by the first cell division parallel to the spore axis (Fig. 1), and a uniseriate filament was formed by a series of transverse divisions (Figs. 2 and 3). In *A. denticulata* and *A. metteniana*, the first rhizoid did not appear until the filament

Table 1. Spore sources, spore number and voucher specimens for the seven species of Cyatheaceae native to Taiwan.

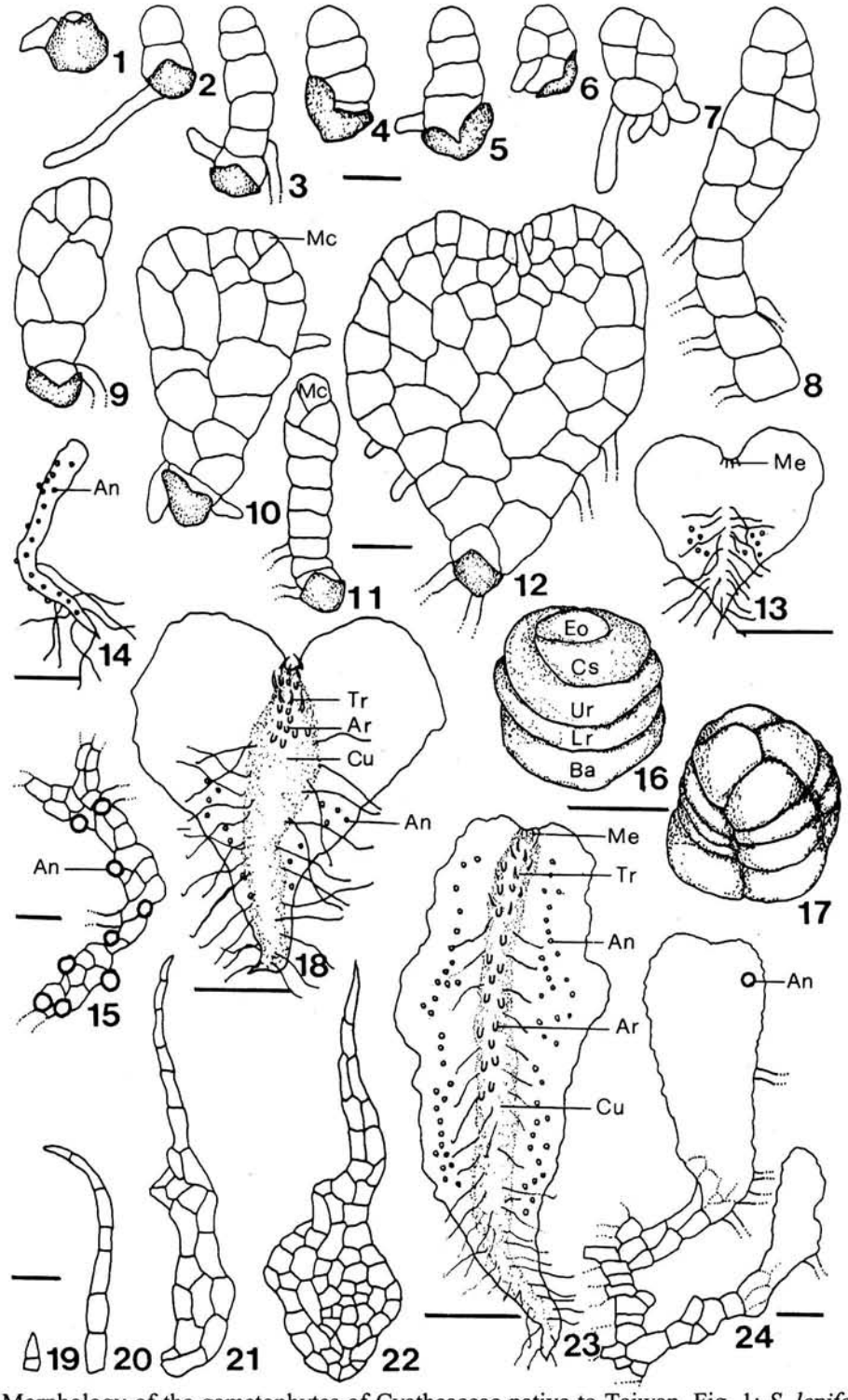
Species	Locations	Voucher specimens[1]	No of spores/sporangium
Alsophila fenicis	Lanyu, Taitung	*Chen 9767* [2]	16
	Lanyu, Taitung	*Lee 292*	16
A. loheri	Chinshuiying, Pintung	*Chen 9719* [2]	16
	Tahanshan, Pingtung	*Chiou 14958*	16
A. spinulosa	Shanlinhsi, Nantou	*Huang s. n.*[2]	16
	Shamaoshan, Taipei	*Lee 4*	16
A. denticulata	Chihsingshan, Taipei	*Lee 125* [2]	64
	Wulai, Taipei	*Chiou 14517*	64
A. metteniana	Pinghsi, Taipei	*Lee s. n.* [2]	64
	Wulai, Taipei	*Chiou 14843* [2]	64
A. podophylla	Lienhuachih, Nantou	*Chiou 14842* [2]	64
	Pichiashan, Taipei	*Chiou 14622* [2]	64
Sphaeropteris lepifera	Yangmingshan, Taipei	*Huang s. n.* [2]	64
	Wulai, Taipei	*Huang 26* [2]	64

1. Materials used to determine sporangium capacity.
2. Materials used to observe gametophyte and young sporophyte morphology.

was 3 to 4 cells long (Figs. 4 and 5). Sometimes, the first rhizoid of *A. denticulata* formed on the second protenema cell instead of the basal cell (Fig. 6) or 2 to 3 rhizoids grew from one cell (Fig. 7). In all species, when the filament was 3 to 8 cells long, the subapical (Figs. 6 and 8) or apical cell (Fig. 7) divided in the second dimension. Next, a spathulate plate formed (Fig. 9). Usually, a wedge-shaped, meristematic cell formed in the apical region when gametophytes were 3 to 5 cells wide (Fig. 10), but an apical meristematic cell sometimes formed during the filament stage (Fig. 11). The apical meristematic cell underwent repeated oblique divisions until it was replaced by a pluricellular meristem, whose activity formed an apical notch (Fig. 12). When the gametophyte was about 1 mm wide, a midrib formed behind the meristem. The wings of the gametophyte were one cell thick and were usually flat, but became more curved and ruffled with age. Most rhizoids formed on the ventral surface of the midrib, but a few appeared on the wing and the dorsal surface of the midrib.

Gametophytes first produced antheridia during late spathulate or primary heart-shaped stages, when they were about 0.5mm wide. Typically, antheridia appeared on the ventral surface of the wings of heart-shaped gametophytes (Fig. 13). However, if the apical notch had not formed or the midrib was weakly developed, antheridia were distributed over most of the ventral surface, or along the margin, especially on filamentous gametophytes only 1 to 2 cells wide (Figs. 14 and 15). The antheridium wall was composed of a basal cell, a lower ring cell, an upper ring cell, a crescent-shaped cell, and an elliptical opercular cell (Fig. 16). When mature antheridia were watered, the opercular cell was shed, releasing the spermatozoids. Archegonia formed on the ventral surface of the midrib, but did not appear until gametophytes were about 2 mm wide. Hermaphroditic gametophytes were found in all species, but only *A. fenicis*, A. *denticulata* and *A. metteniana* had gametophytes that were strictly female. The neck of the archegonium was composed of 4 tiers of cells, with 4 to 5 cells per tiers (Fig. 17). Antheridia and archegonia were produced throughout the hermaphroditic phase.

After archegonia had formed, chloroplast-containing trichomes appeared on dorsal and ventral surfaces of the midrib (Fig. 18). Trichomes began as uniseriate, needle-like structures, and grew by intercalary divisions into bi- or tri-seriate, lanceolate structures. Over time, some became multiseriate or broadened into scale-like structures with a uniseriate tip (Figs. 19-22).



Figs. 1-24. Morphology of the gametophytes of Cyatheaceae native to Taiwan. Fig. 1: *S. lepifera*. Figs. 2-3: *A. spinulosa*. Figs. 4-5: *A. metteniana*. Figs. 6-7: *A. denticulata*. Fig. 8: *A. spinulosa*. Figs. 9-11: *A. fenicis*. Fig. 12-13: *A. denticulata*. Fig. 14: *A. podophylla*. Fig. 15: *S. lepifera*. Fig. 16: Antheridium of *S. lepifera*. Fig. 17: Archegonium of *S. lepifera*. Fig. 18: Bisexual heart-shaped gametophyte of *A. loheri*. Figs. 19-22: Scale-like hairs on the gametophyte of *A. loheri*. Fig. 23: An elongated bisexual gametophyte of *A. loheri*. Fig. 24: A gametophyte with a regenerated branch of *S. lepifera*. Bar = 20 μm for figs. 16-17; 50 μm for figs 1-12; 100 μm for figs 15, 19-22, 24; 500 μm for fig. 14; 1mm for figs. 13, 18, 23. An = antheridium. Ar = archegonium. Ba = basal cell. Cs = crescent-shaped cell. Cu = cushion. Eo = opercular cell. Lr = lower cell. Mc = meristematic cell. Me = meristem. Tr = trichome. Ur = upper cell.

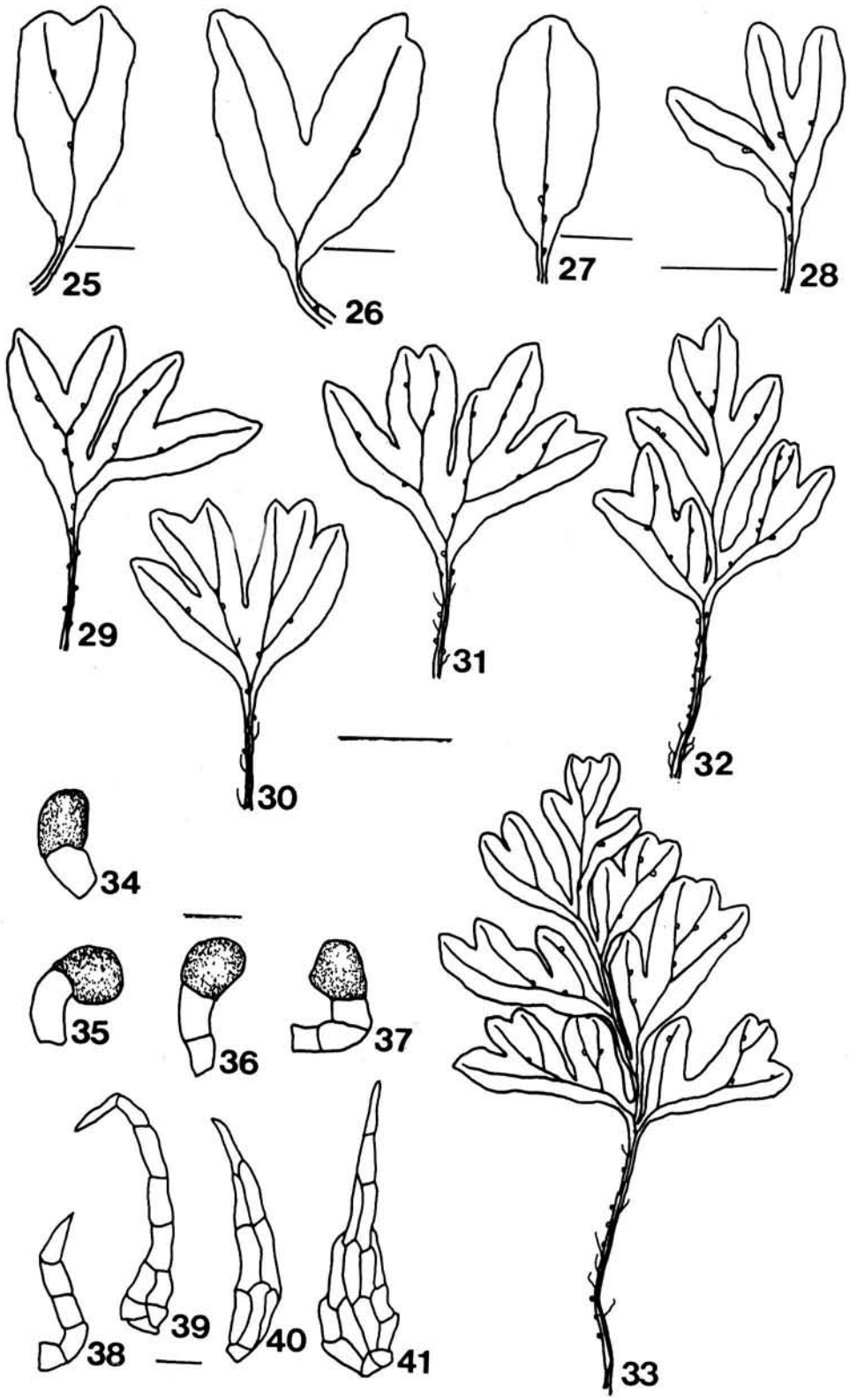
Some gametophytes of all species became elongate and elliptical as they aged (Fig. 23). Older gametophytes became pale, even necrotic, posteriorly but kept growing anteriorly. Those gametophytes could produce daughter gametophytes, derived from one or a few cells on the dorsal or ventral surfaces, or on the margin (Fig. 24). Each of the daughter gametophytes eventually developed a pluricellular meristem, midrib and gametangia. As daughter gametophytes grew, their parent's gametophyte died gradually from posterior to anterior part, and the daughter gametophytes became independent. Sometimes the parent gametophytes did not die and a large clone (ca. 3 cm in diameter for 3-year-culture) formed eventually.

A gametophyte usually produced one sporophyte if fertilization was successful. However, in *A. denticulata, A. podophylla, A. spinulosa* and *S. lepifera,* a few daughter gametophytes might produce sporophytes no matter if their mother gametophyte produced the sporophyte. Usually, the first sporophyte frond was cuneate, with a short petiole, a single vein that forked into two veins of equal size, and a shallowly or deeply notched apex (Figs. 25 and 26). *Alsophila metteniana*, *A. spinulosa*, and *S. lepifera,* occasionally had simple fronds with one vein (Fig. 27). The second frond had a broad lamina with a distinct apical notch, and its vein forked twice (Figs. 28 and 29). The lamina of the third frond was broader still, and the vein had more forks (Figs. 30 and 31). The fourth frond elongated and became trilobed (Fig. 32). Subsequent juvenile fronds were pinnately divided (Fig. 33). Juvenile fronds, except those of *S. lepifera*, were covered with club-shaped hairs. Each hair had a swollen apical cell with dense cytoplasm and a slender, uniseriate stalk, one to several cells long (Figs. 34-37). In addition, uniseriate to multiseriate, pluricellular hairs, resembling those on gametophytes, were present on the juvenile fronds of all seven species (Figs. 38-41).

DISCUSSION

Most *Alsophila* (*sensu* Tryon, 1970) native to America sporangia contained 16 spores each (Gastony 1974). However, there were 64 spores in each sporangium of *A. decurrens, A. podophylla, A. cicatricosa, A. rigens, A. gigantea, A. atropurpurea,* and *A. rebeccae*, species native to the Old World. *Alsophila salvinia*, from Mexico and Central America, and *A. capensis*, which grows in southern Africa and southeastern Brazil, also have 64 spores in each sporangium (Gastony and Tryon, 1976). Among Taiwanese Cyatheaceae, *Alsophila fenicis, A. loheri,* and *A. spinulosa* contained 16 spores per sporangium, whereas each sporangium of *A.denticulata*, *A. metteniana,*and *A. podophylla* contained 64 spores. However, the species with 64-spored sporangia do not form a single, closely related group (Gastony and Tryon, 1976), but belong to two different sections, *Cyathea* and *Gymnosphaera* (*sensu* Holttum, 1963). *Alsophila* includes species with 16-spored sporangia, and species with 64-spored sporangia, which may indicate at least two evolutionary events. *Sphaeropteris lepifera* has 64-spored sporangia, being the same as which of other species of *Sphaeropteris* counted by Gastony (1974).

Nayar and Kaur (1971) defined several types of spore germination and gametophyte development. Except for *A. denticulata* and *A. metteniana*, species of Taiwanese Cyathaceae exhibited "Cyathea-type" spore germination, in which the filament grows along the polar axis and the first rhizoid protrudes from the equatorial plane. This character is typical characteristic of Cyatheaceae (Nayar and Kaur, 1971). In *A. denticulata* and *A. metteniana*, however, formation of the first rhizoid did not occur until the filaments were 3 to 4 cells long.



Figs. 25-33. A series of juvenile fronds of Cyatheaceae sporophytes. Figs. 25-26: *A. metteniana*. Fig. 27: *A. spinulosa*. Figs. 28-33: *A. fenicis*. Figs. 34-37: Club-shaped hairs on the juvenile fronds of *A. metteniana*. Figs. 38-41: Scale-like trichomes on the juvenile fronds of *A. metteniana*. Bar = 50 μm for figs 34-37; 100 μm for figs. 38-41; 1 mm for figs 25, 27; 2 mm for fig. 26; 5 mm for figs. 28-33.

In *A. denticulata*, the first rhizoid did not form on the basal cell. This delayed-formation of rhizoids was also found in some *Elaphoglossum* (Chiou *et al.* 1998). On the other hand, gametophytes of all seven species usually underwent Drynaria-type development, but Adiantum-type development occurred on a few gametophytes of all of these species.

In the Cyatheaceae, the antheridial wall is usually composed of 5 cells (Stokey, 1930; Atkinson and Stokey, 1964). The antheridium of all species in this study was composed of one basal cell, two ring cells, a crescent-shaped cell and an elliptical opercular cell that was shed at antheridial dehiscence. The neck of the archegonium was composed of four tiers of four to five cells each. The neck of the archegonium of seven species of Cyatheaceae native in Japan had the same structure (Momose 1967). However, the archegonial neck of some species of Cyatheaceae is 6 to 8 cells long (Nayar and Kaur 1971). The significance of this variation is unclear.

The multicellular trichomes on the gametophyte cushion are characteristic of Cyatheaceae gametophytes (Stokey, 1930). Similar, multicellular trichomes also occur on gametophytes in the family Loxomataceae (Stokey, 1930; Atkinson and Stokey, 1964). The result may indicate their relationship (c.f., Kramer, 1990).

The gametophytes of some Cyatheaceae species, and species in many other fern families, have the potential to produce large clones by vegetative growth, especially when fertilization fails (Stokey, 1930; Atkinson and Stokey, 1964; Chiou and Farrar, 1997). Clone formation may increase the probability of intergametophytic mating has been issued in *Alsophila podophylla* (Chiou *et al.*, 2000) and other families (eg., Chiou *et al.* 1998). More studies are needed to recognize the reproductive function of gametophyte clones of other Cyatheaceae species.

The young, sporophyte fronds of all species of Cyathaceae in Taiwan were dichotomously branched and of the midribless-blade type (Wagner, 1952). Although the first frond of a few sporophytes had a 1-vein lamina, they were considered weak individuals (Wagner, 1952). The absence of club-shaped hairs in *S. lepifera* supports the taxonomic separation of *Sphaeropteris* from *Alsophila.* However, more species from a variety of locations need to be studied to determine whether the club-shaped hair is a useful characteristic for separating *Sphaeropteris* from *Alsophila.*

The Drynaria- and Adiantum-types of gametophyte development are typical of ferns in many families and also occur in all species of Cyatheaceae native to Taiwan. However, Cyathea-type spore germination, a 5-cell antheridium wall, and multicellular, scale-like trichomes are unique to the Cyatheaceae. Spore germination type of *A. metteniana* and *A. denticulata* is unique and was, until now, undocumented in Cyatheaceae. Sporangium capacity (16 or 64 spores) and the different types of trichomes on young sporophytes may be useful for characterizing, and determining the evolutionary history of, different genera or sections in the Cyatheaceae.

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台灣產桫欏科植物配子体與幼孢子体的形態

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摘　　要

台灣產七種桫欏科植物中，筆筒樹、韓氏桫欏、台灣樹蕨、與鬼桫欏之每個孢子囊有 64 顆孢子，而南洋桫欏、台灣桫欏及蘭嶼筆筒樹則有 16 顆孢子。除了韓氏桫欏與台灣樹蕨外，孢子發芽都屬「桫欏型」；韓氏桫欏與台灣樹蕨之孢子發芽時，假根形成較延遲。七種植物之配子体發育型式均為「槲蕨型」，但每種均有少數以「鐵線蕨型」發育。多細胞之鱗片狀毛發生在中肋的腹背兩面，並隨年齡增長而加大体型，此種多細胞之鱗片狀毛為桫欏科植物所特有。第一至第三或四片幼孢子葉無中肋，單列至多列及棍棒狀多細胞毛混生於桫欏屬之幼孢子葉上，但筆筒樹之幼孢子葉則缺棍棒狀多細胞毛，此或可為系統發生上分離之一證據。此外，孢子囊內具 16 或 64 顆孢子之特徵也反應桫欏屬植物在演化上的兩個事件。

關鍵詞：桫欏科，桫欏屬，筆筒樹屬，配子体，孢子体。

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