

Leaf Epidermal Morphology and Its Systematic Implications in Taiwan Pteridaceae

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ABSTRACT: Forty-nine species of Taiwan Pteridaceae were examined for their leaf epidermal features. Some of these features are stable characters without location variation, and are very good in differentiating taxa, especially at generic level. All genera except *Cheilanthes* were supported by the present study data. Taiwan *Cheilanthes* may be better divided into four genera. Leaf epidermal features are also provide some clues of systematic relationships among several genera. *Coniogramme* and *Pteris* may be more close to each other than previously thought.

KEY WORDS: Taiwan, Pteridaceae, Leaf epidermal morphology, Scanning electron microscopy.

INTRODUCTION

As in many families of pteridophytes, the family Pteridaceae has been variously delimited. The most recent worldwide treatment (Tryon *et al.*, 1990) included 6 subfamilies and 34 genera. The relationships among subfamilies, genera and infrageneric taxa were not clear in most cases (Tryon *et al.*, 1990). The family number recognized for these plants in the past ranged from one to ten (Tryon *et al.*, 1990) might be related to these unclear relationships. In Taiwan, the classification of these plants was either one family system (Kuo, 1985, 1997) or three families, Adiantaceae, Parkeriaceae, and Pteridaceae (Huang *et al.*, 1994). Chinese Flora (Ching and Shing, 1990) classified these Taiwan plants into six families: Acrostichaceae, Adiantaceae, Hemionitidaceae, Parkeriaceae, Pteridaceae, and Sinopteridaceae.

Recently, studies using molecular (Gastony and Rollo, 1995, 1998; Hasebe *et al.*, 1995; Wollenweber and Schneider, 2000) and micromorphological data (Chen and Huang, 1974; Lin and DeVol, 1977, 1978; Lee and Oh, 1988; Lee *et al.*, 1990; Yu *et al.*, 2001; Zhang and Li, 1999) have been attempted to give a better understanding of these plants. Among them, leaf epidermal morphology was well known for its great taxonomic and practical value in the past (Stace, 1984; Thurston, 1969), and its systematic implications in vascular plant were numerous (Royal Botanic Gardens, 2000 provided a convenient gateway of finding these examples). The leaf epidermis studies involved some Pteridaceae genera in China (Zhang and Li, 1999) and Korea (Lee and Oh, 1988) showed their usefulness in intrafamilial and species delimitation in the taxa they surveyed. In addition, the correlations between some epidermal features and chemical constituents in this family (Wollenweber and Schneider, 2000) may further point to the greater systematic implication of leaf epidermis. The present study, then, was to extend the study of leaf epidermis morphology to Taiwan Pteridaceae genera in which few or no species had been examined in the past. It is hoped that the results would highlight some relationship among subfamilies, genera and species of Taiwan taxa.

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MATERIALS AND METHODS

Forty-nine species (Table 1) were examined in this study. The classification and generic names followed Tryon *et al.* (1990). However, the name *Paraceterach* (F. v. Muller) Copel. was not used. There is only one species, *P. vestita* found in Taiwan. This species was for the most part placed in *Gymnopteris*. However, the type species of *Gymnopteris*, *G. rufa* (L.) Underw. was hybridizing with the type species of *Hemionitis*, and two type species also showed high degree of morphological similarity; therefore, these two genera were combined and the Old World elements were moved to *Paraceterach* (Tryon and Tryon, 1982; Tryon, 1987). However, there are at least two elements existed in *Paraceterach*, and later Shing (1994) established *Paragymnopteris* to house *P. vestita* and its close relatives. Species names mostly followed Huang *et al.* (1994) except the following (names within parentheses were those used by Huang *et al.* 1994): *Adiantum taiwanianum* Tagawa [*Adiantum roborowskii* Maxim. var. *taiwanianum* (Tagawa) W. C. Shieh], *Cheilanthes concolor* (Langsd. & Fisch.) R. M. Tryon & A. F. Tryon [*Doryopteris concolor* (Langsd. & Fisch.) Kuhn], *Cheilanthes formosana* Hayata [*Cheilanthes farinosa* (Forssk.) Kaulf., *p. p.*], *Cheilanthes nitidula* Hook. [*Mildella henryi* (H. Christ) C. C. Hall & Lellinger], *Cheilanthes nudiuscula* (R. Br.) T. Moore [*Cheilanthes hirsuta* (Poir.) Mett.], *Cheilanthes subargentea* (Ching) C. M. Kuo [*Cheilanthes farinosa* (Forssk.) Kaulf., *p. p.*], *Onychium lucidum* (D. Don) Spreng. [*Onychium contiguum* Hope], *Paragymnopteris vestita* (Hook.) K. H. Shing [*Gymnopteris vestita* (Hook.) Underw.], *Pteris dimidiata* Willd. [*Pteris semipinnata* L.], and *Pteris semipinnata* L. [*Pteris dispar* Kunze].

All material were collected in fresh condition and examined under light microscope. The leaf with sorus and maximum vein number which is mature in all aspects (Tsuyuzaki, 2000) was selected for the scanning electron microscope study. Voucher specimens were made and deposited in the herbarium at the Department of Biological Sciences, National Sun Yat-Sen University (SYSU). Several species studied were with more than one collections (Table 1) which collected from different geographical areas, and each of these collections was with at least three samples. These collections were examined to see the possible effects of geographical and ecological differences on leaf epidermal features. To minimize the possible epidermal feature change, the material was fixed by 3% glutaraldehyde in 0.1 M phosphate buffer, pH = 7 and dehydrated with acetone series at the temperature 4°C (Reed, 1982). Hitachi HCP-2 with liquid CO₂ was used in critical point drying, and Hitachi E101 was used for coating 10-15 nm gold. The coated materials were then examined in a Hitachi S-2400 SEM at 12-15 kV, 23 mm working distance and a consistent spot size. The results were recorded on Kodak Tmax 100 films and screen-catched computer images. Magnification was verified by Hitachi magnification calibration standard at the same instrument setting used for viewing leaf epidermis samples.

RESULTS AND DISCUSSION

Among many characters with variable states, stomata types, sunken stomata, long-axis direction of epidermal cells, epidermal cell long-side incision pattern, epidermal cell surface striation, and vestiture were determined to be useful in differentiating Taiwan Pteridaceae taxa (Table 1). Stomata size and frequency were used to distinguished Korean Dennstaedtiaceae and Pteridaceae generic groups (Lee and Oh, 1988), but were found to be more or less variable among different geographical regions in the same Taiwan taxon.

Table 1. Species of Taiwan Pteridaceae for which leaf epidermis were examined in this study.

Species	Voucher	Character					
		A	B	C	D	E	F
<i>Acrostichum aureum</i> L.	Chuang 493	0	0	2	0	0	-
<i>Adiantum capillus-veneris</i> L.	Chuang 299, 371, 498	0	1	0	1	0	1
<i>Adiantum caudatum</i> L.	Chuang 310, 318	0	0	3	1	0	1
<i>Adiantum diaphanum</i> Blume	Chuang 412	0	1	3	0	2	-
<i>Adiantum edgeworthii</i> Hook.	Chuang 364	0	1	0	1	0	1
<i>Adiantum flabellulatum</i> L.	Chuang 376, 432	0	1	0	1	0	1
<i>Adiantum formosanum</i> Tagawa	Chuang 365	0	1	0	0	2	-
<i>Adiantum hispidulum</i> Sw.	Chuang 386	0	0	3	0	2	-
<i>Adiantum malesianum</i> Ghatak	Chuang 488, 500	0	1	3	1	0	1
<i>Adiantum myriosorum</i> Baker	Chuang 475	0	1	0	1	0	1
<i>Adiantum phillippense</i> L.	Chuang 309, 327	0	1	0	1	0	1
<i>Adiantum taiwanianum</i> Tagawa	Chuang 336, 470	0	1	0	1	0	1
<i>Anogramma leptophylla</i> (L.) Link	Chuang 335	0	0	0	1	0	1
<i>Ceratopteris thalictroides</i> (L.) Brongn	Chuang 497	1	0	0	0	1	-
<i>Cheilanthes argentea</i> (Gmel.) Kunze	Chuang 464	0	0	1	0	0	2
<i>Cheilanthes chusana</i> Hook.	Chuang 315, 441, 487	0	0	2	1	0	0
<i>Cheilanthes concolor</i> (Langsd. & Fisch) R. & A. Tryon	Chuang 460, 486	0	0	2	0	0	0
<i>Cheilanthes formosana</i> Hayata	Chuang 384, 461, 490	0	0	1	0	1	2
<i>Cheilanthes nitidula</i> Hook.	Chuang 494	0	0	0	1	0	1
<i>Cheilanthes nudiuscula</i> (R. Br.) T. Moore	Chuang 316	0	0	4	1	0	0
<i>Cheilanthes subargentea</i> (Ching) C. M. Kuo	Chuang s. n.	0	0	1	0	1	2
<i>Coniogramme fraxinea</i> (Don) Diels	Leong s. n.	2	0	0	0	2	-
<i>Coniogramme intermedia</i> Hieron.	Chuang 344, 361	2	0	2	0	2	-
<i>Coniogramme japonica</i> (Thunb.) Diels	Chuang 405	2	0	2	0	2	-
<i>Cryptogramma brunoniana</i> Wall. ex Hook. & Grev.	Chuang 337	0	0	2	0	1	1
<i>Onychium japonicum</i> (Thunb.) Kunze	Chuang 377, 387, 484	0	0	2	1	1	-
<i>Onychium lucidum</i> (Don) Sprengel	Chuang 353, 476	0	0	2	1	1	-
<i>Paragymnopteris vestita</i> (Hook.) K. H. Shing	Chuang 495	0	0	4	0	0	0
<i>Pityrogramma calomelanos</i> (L.) Link	Chuang 317, 449, 489	0	0	1	1	0	1
<i>Pteris bella</i> Tagawa	Liou s. n.	2	0	2	0	2	-
<i>Pteris biaurita</i> L.	Chuang 302, 311, 389	2	0	2	0	2	-
<i>Pteris cadieri</i> H. Christ	Liou s. n.	2	0	2	0	2	-
<i>Pteris cretica</i> L. var. <i>cretica</i>	Chuang 346, 479	2	0	2	0	2	-
<i>Pteris dactylina</i> Hook.	Chuang 413, 471	2	0	2	0	2	-
<i>Pteris dimidiata</i> Willd.	Chuang 434, 492	2	0	2	0	2	-
<i>Pteris ensiformis</i> Burm.	Chuang 373, 485	2	0	2	0	2	-
<i>Pteris excelsa</i> Guadich.	Chuang 478	2	0	2	0	2	-
<i>Pteris fauriei</i> Hieron.	Chuang 437, 445	2	0	2	0	2	-
<i>Pteris formosana</i> Baker	Liou 2567	2	0	2	0	2	-
<i>Pteris grevilleana</i> Wall. ex J. Agardh	Chuang 320	2	0	2	0	2	-
<i>Pteris linearis</i> Poir.	Chuang 385	2	0	2	0	2	-
<i>Pteris longipes</i> Don	Chuang 308, 390	2	0	2	0	2	-
<i>Pteris longipinna</i> Hayata	Chuang 368	2	0	2	0	2	-
<i>Pteris scabristipes</i> Tagawa	Chuang 360	2	0	2	0	2	-
<i>Pteris semipinnata</i> L.	Chuang 379, 446	2	0	2	0	2	-
<i>Pteris setuloso-costulata</i> Hayata	Chuang 496	2	0	2	0	2	-
<i>Pteris tokioi</i> Masamune	Ko s. n.	2	0	2	0	2	-
<i>Pteris vittata</i> L.	Chuang 409, 448	2	0	2	0	2	-
<i>Pteris wallichiana</i> J. Agardh	Chuang 428, 458	2	0	2	0	2	-

Character A (stomata type): 0 = anomocytic, 1 = polycytic, 2 = anomocytic and polycytic; B (stomata sunken): 0 = no, 1 = yes; C (vestiture): 0 = glabrous, 1 = glandular, 2 = clavellate, 3 = cylindrical, 4 = woolly; D (epidermal cell long-axes parallel with veins): 0 = no, 1 = yes; E (epidermal cell axes): 0 = more or less straight; 1 = more or less straight, but branched at end or sideways, 2 = curved; F (epidermal cell long-side incision): 0 = regular, 1 = irregular, 2 = regular and irregular, - = not applicable.

Stomata, especially stomata types were used extensively in previous studies (Lee and Oh, 1988; Zhang and Li, 1999). There are at least two different classification systems on fern stomata types. Cotthem (1970) classified mature leaf stomata into twelve types. Sen and De (1992) indicated that the same stomata type defined by Cotthem (1970) might arise from different development processes, so they classified fern stomata into twenty-four development types. However, some collections used in this study did not have all necessary development stages to assess Sen and De's system (1992) and the Cotthem's (1970) system still provides some meaningful taxonomic information (Tryon *et al.*, 1990). Therefore, Cotthem's (1970) system was used in the present study for practical reason. In addition, since several stomata development types in a single developing leaf might be found, thus the determination of stomata types in this paper was based on the mature leaf only. Only two stomatal types were found in Taiwan Pteridaceae. Anomocytic stomata type only was found in *Acrostichum*, *Adiantum*, *Anogramma*, *Cheilanthes*, *Cryptogramma*, *Onychium*, *Paragymnopteris*, and *Pityrogramma*. Polycytic stomata type only was found in *Ceratopteris*. The mixed type with both anomocytic and polycytic stomata types in the same leaf was found in *Coniogramme* and *Pteris* species. In addition, sunken stomata were only found in nine *Adiantum* species.

Epidermal cell morphology provided many important characters. Long axes of the ordinary epidermal cell provided two diagnostic characters. Although cell margins are slightly indented to deeply lobed and branched, long axes were more or less recognizable. Some species have these cell long-axes more or less straight and other species are distinctly curved. Because the width of the cell margin incision is generally as large as the cell width in the curved cell, the cell axis direction of these cells is approximate. If cells are more or less straight, then the long-axis is either parallel with veins or irregular in directions. The direction of curved cells, when recognized, is generally not correlated with vein direction. Cells with straight long-axes may be branched at cell end or at sideways. If branching is at only one side and at cell end, occasionally few cells may be curved-looking but still are distinguishable based on the whole leaf morphology. The incisions on cell margin are regular, irregular, or both. However, the determination of curved cell incision regularity is difficult because the unprecise identity of cell axis. The third character is cell surface. When most species are with smooth surface, striation was constantly found in two *Cheilanthes* species, *C. chusana* Hook. and *C. nudiuscula* (R. Br.) T. Moore. Three *Adiantum* species were found to have very light striations occasionally in one or two sample leaves, but the extent and the frequency of these features need a further study.

For vestiture, there were five character states can be used to divide Taiwan Pteridaceae. Except eleven glabrous species, most species are with trichomes. Trichomes are either with an expanded glandular head (Fig. 17) or ungladular. Ungladular trichomes are either wooly (Fig. 20) or short straight. The short straight hairs are either cylindrical (Figs. 4, 6, 7) or clavellate (Figs. 11, 13, 14). The clavellate trichomes in many species are only slightly narrower toward their bases, and the cylindrical trichomes are always with a distinct dilated base.

Although leaf surface features may be affected by different geographical or ecological conditions (Stace, 1984), all leaf epidermal characters chosen in this study were constant in the same species at different locations except *Adiantum* species epidermal cell surface striations. It was also found that the leaf epidermis characters were taxonomically useful at different categorical levels. For convenience, the leaf epidermal features of each genus are described below, and their taxonomic implications are discussed. In addition, intergeneric relationships inferred from the leaf epidermal data are also discussed wherever appropriate.

Acrostichum

Fig. 1

Stomata anomocytic, not sunken; trichomes clavellate; epidermal cells more or less straight, without definite long axis direction, margins lobed, rarely branched.

Tryon and Tryon (1982) regarded *Acrostichum* as a distinct and morphological isolated genus. The leaf epidermal features of *Acrostichum* are unique, but may be seen as a combination of *Pteris* and *Cheilanthes* features and incline to the features of *Cheilanthes*. The leaf epidermal features of these three genera are different. Ching (1978) treated *Pteris* and *Cheilanthes* in different families and separated *Acrostichum* into a monotypic family Acrostichaceae, the leaf epidermal data were consistent with this arrangement. However, if a broader classification is needed, a single family with three genera in it (e. g. Copeland, 1947; Holttum, 1947; Tryon *et al.*, 1990) is probably better. The treatment with *Pteris* and *Cheilanthes* in one family and *Acrostichum* in another (e. g. Huang *et al.*, 1994) is not preferred.

Adiantum

Figs. 2-7

Stomata anomocytic, sunken or not sunken; glabrous or with cylindrical trichomes; epidermal cells varied in shapes and margins, surfaces smooth but occasionally with few light striations. Two species groups can be recognized. The epidermal cells in the first group of species are straight and parallel with veins, and with more or less regular indentate margins. The epidermal cells in the second group of species are variable in shapes, margins, and long axis directions.

Adiantum is a very large genus with about 150 species, and three infrageneric classifications were published. Shieh (1973) divided all species into two sections; Ching and Lin (Lin, 1980) proposed a seven-series classification; and Tryon and Tryon (1982) classified species into eight informal species groups. The present study indicated that there are two leaf epidermal species groups. Although two groups, the leaf epidermal species groups did not match Shieh's (1973) sections, with the species in section *Pedatoadiantum* belonged to the first leaf epidermal species group, and with the species in section *Adiantum* belonged to both leaf epidermal species groups. Five out of seven series in Ching and Lin (Lin, 1980) system were studied here. There are three series belonged to the first leaf epidermal species group, and another two series belonged to both leaf epidermal species groups. Four out of eight species groups in Tryon and Tryon (1982) are found in this study, with two species groups belonged to the first leaf epidermal species group, and another two species groups belonged to the second leaf epidermal species groups. Therefore, the groups proposed by Tryon and Tryon (1982) are at least homogeneous within their own group, and the groups proposed by other two systems are paraphyletic in at least one of their proposed groups.

Anogramma

Fig. 8

Stomata anomocytic, not sunken; glabrous; epidermal cells straight, parallel with veins, cell margin indentations slightly irregular, and with surface smooth.

Ceratopteris

Fig. 9

Stomata polycytic, not sunken; glabrous; epidermal cells without definite long axis direction, and with margins cleft to branched at both cell-ends. The stomata distribution, density, and size are more or less even on both surfaces, which is unique in this family and possibly due to the adaptive consequence of the aquatic habit.

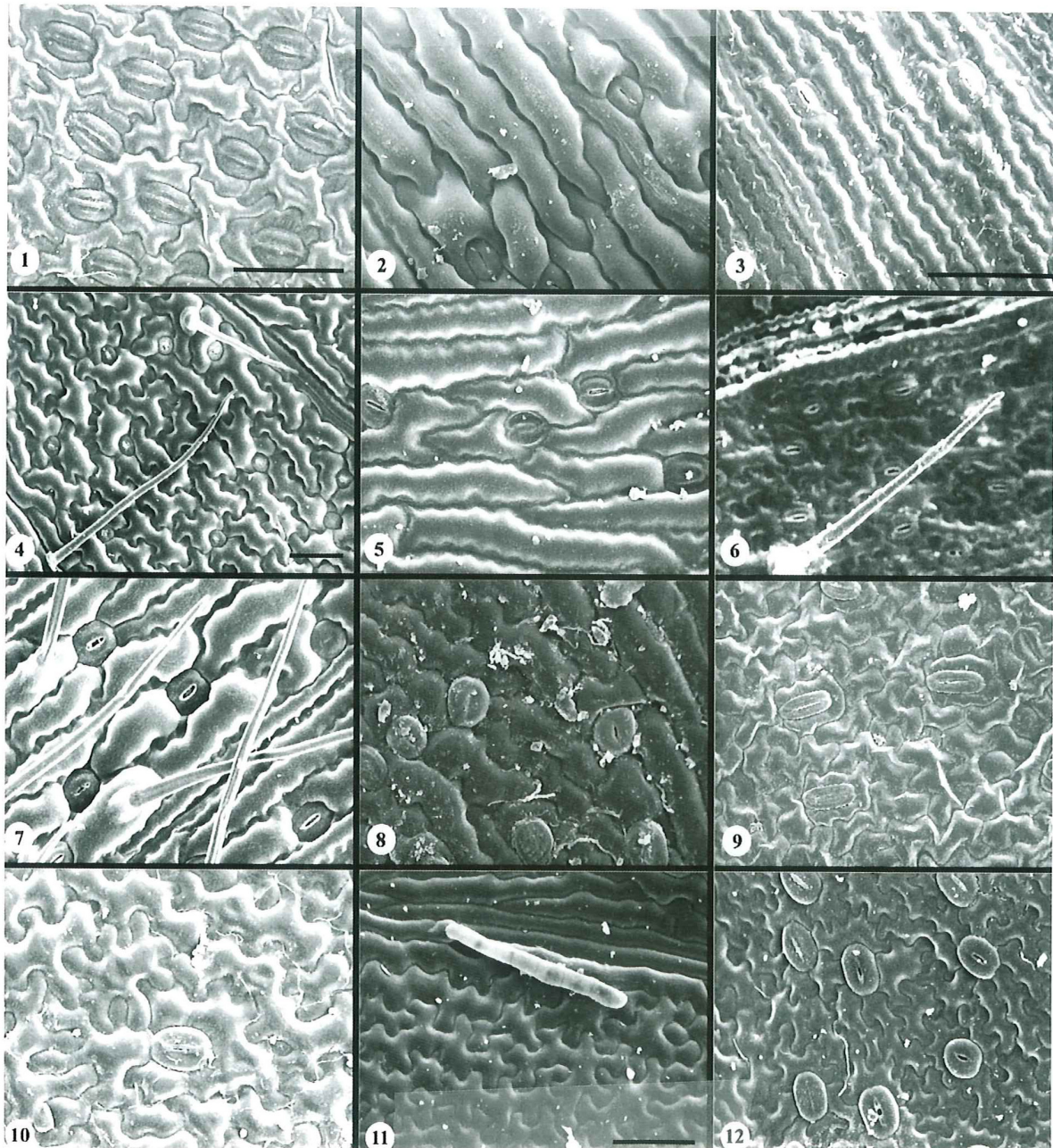
Due to its unique leaf epidermal features were not found in any other taxon, the relation of this genus to any other ferns is unclear. A monotypic subfamily (Ceratopteridoideae) or family (Parkeriaceae) is justified.

Cheilanthes

Figs. 13-17

Stomata anomocytic, not sunken; other characters varied.

Among seven species studied, four groups were recognized based on leaf epidermal features. The first group consists of *Cheilanthes argentea* (Gmel.) Kunze, *Cheilanthes formosana* Hayata and *Cheilanthes subargentea* (Ching) C. M. Kuo (Fig. 17); the leaf abaxial



Figs. 1-12. Scanning electron micrographs of selected leaf epidermis of Taiwan Pteridaceae. Scale bar in Fig. 1 = 100 μm and applies to all other figures except figures 3, 4 and 11 where individual scale bar is also = 100 μm . 1. *Acrostichum aureum*. 2. *Adiantum capillus-veneris*. 3. *Adiantum caudatum*. 4. *Adiantum diaphanum*. 5. *Adiantum formosanum*. 6. *Adiantum hispidulum*. 7. *Adiantum malesianum*. 8. *Anogramma leptophylla*. 9. *Ceratopteris thalictroides*. 10. *Coniogramme fraxinea*. 11. *Coniogramme intermedia*. 12. *Cryptogramma brunoniana*.

surfaces are densely glandular; the leaf epidermal cells are without definite long axis direction and without striation, but with cell margin incisions regular to irregular, sometimes deeply cut. The second group consists of *Cheilanthes chusana* Hook. (Fig. 13) and *Cheilanthes nudiuscula* (R. Br.) T. Moore (Fig. 16); trichomes are woolly in the latter species and clavellate in the former species; the leaf epidermal cells are with long-axis direction parallel with veins, with surfaces stratified, and with margin incisions regular. The third group, *Cheilanthes nitidula* Hook. (Fig. 15) has its leaf epidermal cell more or less straight, long axes parallel with veins, cell margin incisions irregular and lobes occasionally branched; and has its epidermis cell surfaces glabrous and without striation. The fourth group, *Cheilanthes concolor* (Langsd. & Fisch) R. & A. Tryon (Fig. 14) has its leaf epidermal cells straight, but no definite long-axis direction and no striation on surfaces, cell margins are regularly indented; and has clavellate trichomes. These four groups corresponded well with Shieh's (1973) three genera and two sections classification, and with Ching's (1978) four genera arrangement. The polyphyletic origin of the genus have been hinted (Tryon *et al.*, 1990) and supported by recent molecular studies (Gastony and Rollo, 1995, 1998). Since no Taiwan species were included in the molecular studies and the four genera classification reflected the leaf epidermal characters better, further morphological and molecular studies in detail are needed to confirm Ching's (1978) classification hypothesis. A recent molecular and morphological study on *Cheilanthes dealbata* D. Don, treated here as *C. formosana* Hayata, and its close relative in Taiwan (Weng, 2000) may be a good beginning of this task.

Coniogramme

Figs. 10-11

Stomata anomocytic and polycytic, not sunken; glabrous or trichomes clavellate; leaf epidermal cells smooth, curved and without definite long axis orientation; cell margins lobed and lobes branched, branch-end often dilated.

The leaf epidermal morphology of *Coniogramme* is almost identical with *Pteris* except one species, *C. fraxinea* (Don) Diels having glabrous leaf surfaces. Copeland (1947) indicated this genus might evolve from *Pteris*, but many authors (e. g. Ching, 1978; Tryon *et al.*, 1990) placed them in different subfamilies or families. The true relationships between these two genera probably need a further examination.

Cryptogramma

Fig. 12

Stomata anomocytic, not sunken; trichomes clavellate; leaf epidermal cells curved and few-branched, without definite long-axis orientation; cell surfaces smooth.

The leaf epidermal morphology of this genus is similar to that of *Onychium* and intermediate between *Cheilanthes* and *Coniogramme*. However, spore morphology of this genus is quite distinct (Yu *et al.*, 2001) and different from all other genera in the subfamily Cheilanthoideae or in the family Sinopteridaceae where it was placed by different authors. The true systematic position of this genus still needs further investigation.

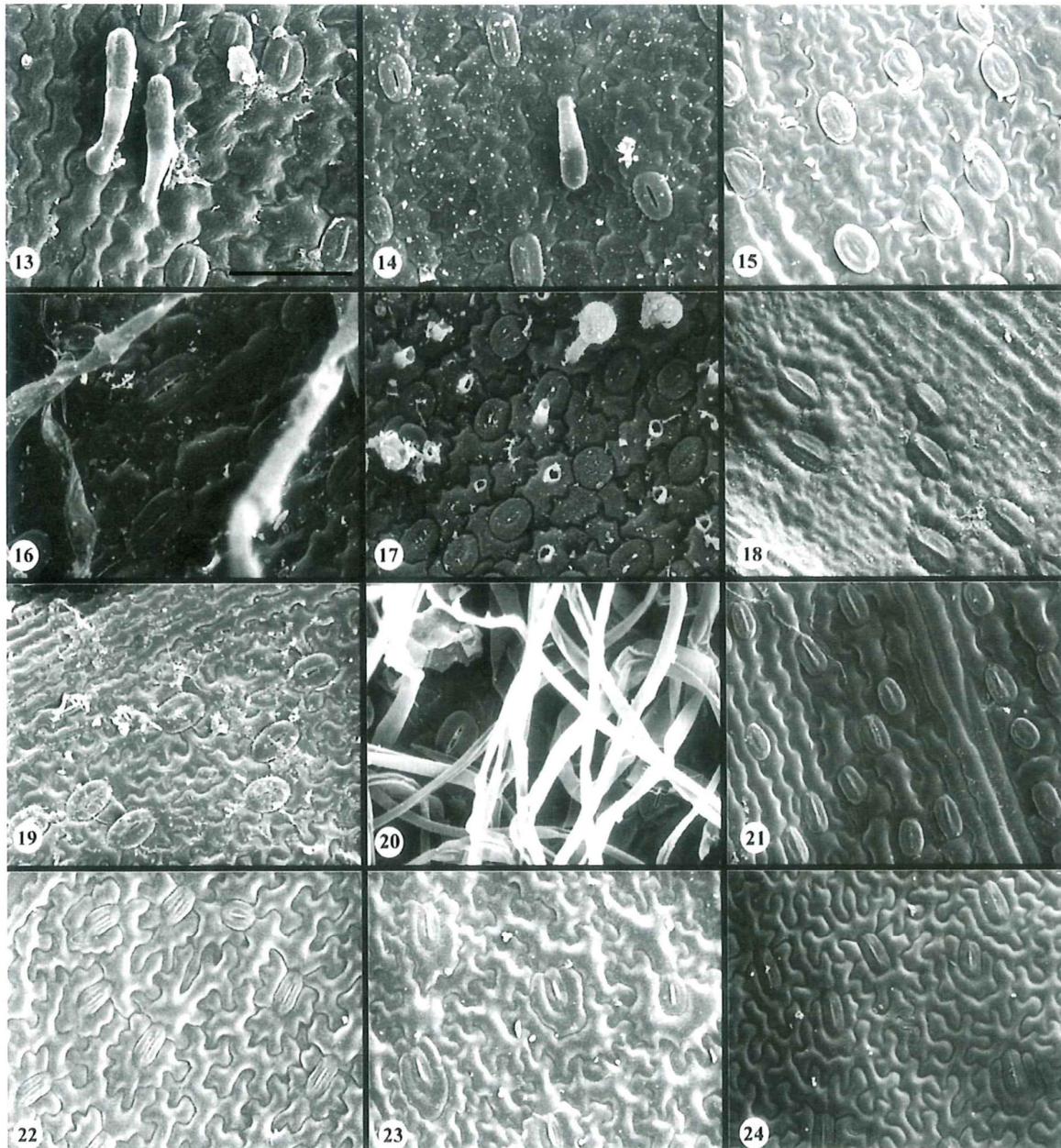
Onychium

Figs. 18-19

Stomata anomocytic, not sunken; trichomes few, clavellate, with cell boundary indistinct; leaf epidermal cells straight, with margins irregularly indented and lobes sometimes branched, and with cell long axes parallel with veins; cell surfaces smooth.

Onychium, *Anogramma*, and *Pityrogramma* are in the subfamily Taenitidoideae.

However, *Onychium* is quite different from the other two genera. Ching (1978) placed the latter two genera into Hemionitidaceae, and classified *Onychium* into Sinopteridaceae. The epidermal cell morphology of *Onychium* is very close to *Cryptogramma*, but spore data suggested *Onychium* has some affinities with *Pteris* (Yu *et al.*, 2001).



Figs. 13-24. Scanning electron micrographs of selected leaf epidermis of Taiwan Pteridaceae. Scale bar in Fig. 13 = 100 μ m and applies to all other figures. 13. *Cheilanthes chusana*. 14. *Cheilanthes concolor*. 15. *Cheilanthes nitidula*. 16. *Cheilanthes nudiuscula*. 17. *Cheilanthes subargentea*. 18. *Onychium japonicum*. 19. *Onychium lucidum*. 20. *Paragymnopteris vestita*. 21. *Pityrogramma calomelanos*. 22. *Pteris biaurita*. 23. *Pteris dispar*. 24. *Pteris longipes*.

Paragymnopteris

Fig. 20

Stomata anomocytic, not sunken; trichomes woolly; leaf epidermal cells straight, with regular margin indentations, but without definite long-axis orientation; cell surfaces smooth.

This genus shares almost the same leaf epidermal characters with *Cheilanthes nudiuscula*, which indicated a close link between these two taxa. Ching (1978) placed this genus into Hemionitidaceae but placed *Cheilanthes* in Sinopteridaceae, but he also indicated this genus is very similar to *Notholaena* (under *Cheilanthes* in Tryon *et al.*, 1990) which he placed in Sinopteridaceae.

Pityrogramma

Fig. 21

Stomata anomocytic, not sunken; densely glandular on abaxial surface; leaf epidermal cells straight with long axes parallel with veins, but with margin indentations slightly irregular; cell surfaces smooth.

The leaf epidermal features of this genus and *Anogramma* are very similar to each other and to *Cheilanthes nitidula*. Ching (1978) placed this genus and *Anogramma* into Hemionitidaceae but placed *Cheilanthes* in Sinopteridaceae, however, he also indicated this genus and *Anogramma* were very similar to *Notholaena* which he placed in Sinopteridaceae.

Pteris

Figs. 22-24

Stomata anomocytic and polycytic, not sunken; trichomes clavellate and usually along veins; leaf epidermal cells smooth, curved without definite long-axis orientation, branched along the long-axis, some species with branch-end dilated.

The genus is quite uniform in the leaf epidermal morphology. The width of leaf epidermal cells of most species is more or less the same along the long-axes except *Pteris ensiformis* Burm. and *Pteris semipinnata* L. whose cells may be dilated at some points.

In summary, some of Taiwan Pteridaceae leaf epidermal features are stable taxonomic characters, and are very good in differentiating taxa, especially at generic level. All genera except *Cheilanthes* were supported by the present study data. Taiwan *Cheilanthes* may be better divided into four genera. Other systematic implications of leaf epidermal features are: *Ceratopteris* was unique and a monotypic subfamily or family classification for it was justified; *Acrostichum* was isolated as indicated by its uncommon leaf epidermal features; *Anogramma* and *Pityrogramma* are very close genera and near to *Cheilanthes* and *Paragymnopteris*; *Onychium* is close to *Cryptogramma* and different from most genera. In addition, the relationship between *Coniogramme* and *Pteris* revealed by this study demands a close look.

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臺灣鳳尾蕨科葉表皮形態及其系統分類之應用

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摘 要

以 49 種臺灣鳳尾蕨科為材料進行其葉表皮形態之觀察。部分特徵為穩定之形態，不隨地點不同而有所變化；這些特徵在不同之分類階層上都有其用處，用於探討屬間之區別及關係尤佳。除碎米蕨屬外，其他屬皆有其一定之葉表皮特徵；臺灣之碎米蕨屬最好分為四屬。鳳了蕨屬與鳳尾蕨屬可能有非常接近之關係。

關鍵詞：臺灣、鳳尾蕨科、葉表皮形態、掃描式電子顯微鏡技術。

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