

## The Distribution and Habitats of the *Pteris fauriei* Complex in Taiwan

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**ABSTRACT:** Polyploidization is a significant mode of speciation in plants. Polyploids often occupy habitats different from those of their diploid parents. In Taiwan, two varieties of *Pteris fauriei*, one diploid and one triploid, have been identified. The number of spores per sporangium and the size of spores are reliable indicators of ploidy. Diploid *P. fauriei* have 64-spore sporangia and the spores are significantly smaller than spores of triploid plants, which have 32-spore sporangia. Based on these findings, the distribution and habitats of the two cytotypes in Taiwan are characterized from both living plants and herbarium specimens. Altogether, 516 live plants from 32 locations and 76 herbarium specimens were analyzed. In general, diploid plants occur in warmer habitats than triploid plants. Diploid plants are widely distributed in Taiwan and nearby islands, but do not occur in central Taiwan nor in the Matsu islands. In contrast, triploid plants are not found in southern tip of Taiwan nor on islands west of central Taiwan. In northern Taiwan and on the west-central islands, diploids grow most often in exposed sites and grasslands. However, in southern Taiwan and islands Lanyu and Lutao, diploids also occur in woodlands. Triploids are restricted to grassland and woodland habitats in Taiwan, but grow in exposed sites, grassland and woodland habitats in Matsu islands. In general, triploids grow at higher elevations than the diploids.

**KEY WORDS:** Diploid, cytotype, distribution, habitat, Pteridaceae, *Pteris fauriei*, triploid, Taiwan.

### INTRODUCTION

Polyploids, which contain more than two sets of chromosomes per cell, have been important in plant evolution (Stebbins, 1971; Lewis, 1980). The proportion of angiosperm species that are polyploid is estimated at 50% (Stebbins, 1971; Grant, 1981), with estimates ranging from 30-80% (Stebbins, 1971; Goldblatt, 1980; Leitch and Bennett, 1997). Up to 95% of pteridophytes may be polyploid (Grant, 1981) and recent polyploids may comprise 45% of extant homosporous ferns (Vida, 1976; Haufler and Soltis, 1986). Polyploidy may lead to significant reproductive isolation (Ramsey and Schemske, 1998), and changes in gene expression (Adams et al., 2003) and ecological interactions (Segraves et al., 1999). Despite its importance in plant evolution, many aspects of polyploid speciation remain poorly understood.

Distributional data are important to answering many questions about polyploid speciation (Baack, 2004). Usually, an increase in ploidy level is associated with the origin of novel adaptations (Levin, 2002). Polyploids often occupy habitats different from those of their diploid parents (Soltis and Soltis, 2000).

Plants with different ploidy levels may be adapted to different temperature regimes (Levin, 2002). In some flowering plants, e.g. *Chamerion angustifolium* (Mosquin, 1967), *C. latifolium* (Small, 1968), *Anthoxanthum odoratum* (Hedberg, 1969), *Fraxinus americana* (Schaefer and Miksche, 1977), *Claytonia cordifolia* (Lewis, 1967) and *Centaurea jacea* (Hardy et al., 2000), diploids occurred in colder climates than their polyploid counterparts. In other species, e.g. *Hedyotis caerulea* (Lewis and Terrell, 1962), and *Suaeda maritima* (Sharma and Dey, 1967), polyploids are more cold tolerant than their diploid counterparts.

Although data are available for fern floras from different parts of the world, there is not a simple relationship between ploidy level and habitat (reviewed by Walker, 1979). Some studies have

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found that lower-ploids occur in warmer habitats than higher-ploids (e.g. *Lepisorous thunbergianus* (diploid vs. tetraploid) (Mitui et al., 1987), *Woodwardia orientalis* (diploid vs. tetraploid) (Mitui, 1968), *Dryopteris erythrosora* (diploid vs. triploid) (Hirabayashi, 1974), *Pteris dispar* (diploid vs. tetraploid) (Nakato, 1981), and *Diplazium nipponicum* (triploid vs. tetraploid) (Takamiya et al., 2000). However, in many parts of Europe all three cytotypes (2x, 4x, 6x) of the *Polypodium vulgare* complex were found in close proximity (Shivas, 1961). In addition, Matsumoto (2003) did not find a significant relationship between latitude and ploidy level in the *Cyrtomium falcatum* complex. However, there was an association between ploidy level and habitat: diploids grew on sea cliffs or in dry forests, triploids grew at forest edges, and tetraploids grew in wet forests.

Previous studies have found distinct correlations between reproductive mode and habitat (Holbrook-Walker and Lloyd, 1973; Lloyd, 1974). Sexual reproduction is most frequent in moist habitats, whereas apomictic reproduction is more common in ferns growing in xeric habitats (Tryon, 1968). However, some apomictic species do not live in xeric habitats (e.g. some Japanese *Diplazium*, *Diplazium maonense*, and *Cornopteris christenseniana*) (Takamiya et al., 1999; Moore et al., 2002; Park and Kato, 2003).

*Pteris fauriei* Hieron is ideal for studies of the relationships between ploidy level, habitat gradient, and reproductive mode. This fern is distributed in Japan, China, the Ryukyu Islands, Taiwan and Vietnam (Shieh, 1975, 1994). In Taiwan it is a widely distributed terrestrial fern that occurs in a variety of habitats ranging from exposed sites to shady forest on Taiwan and nearby islands. Two varieties, triploid *P. fauriei* var. *fauriei* and diploid *P. fauriei* var. *minor*, have been documented (Hieronymus, 1914). *Pteris fauriei* var. *minor* produces sporophytes by sexual mode, whereas *P. fauriei* var. *fauriei* produces sporophytes by apogamy (Huang et al., 2006). In this study, we documented differences in the distributions and habitats of the *P. fauriei* infraspecific cytotypes.

## MATERIALS AND METHODS

Altogether, 516 live plants were collected from 32 locations in Taiwan and nearby islands. Up to 30 live plants were sampled at each location. The number of plants sampled varied with population size. For populations of <10, 11-50, 51-100, or >100

plants, all, 10, 20 or 30 plants were sampled, respectively. The latitude, elevation and habitat type of each plant were recorded (Table 1). Exposed sites lacked vegetation tall enough to shade sampled plants, grassland had some surrounding vegetation higher than the sampled plants, and woodland was mostly shaded. Five sporangia from each plant were randomly sampled to count the number of spores per sporangium. Plants with 64-spore sporangia were considered diploid, and those with 32-spore sporangia were considered triploid (Huang et al., 2006). Principle component analysis (PCA) was used as a pattern recognition method, and to determine the correlation between ploidy levels and environmental factors. PCA was performed with the statistical software package PC-ORD (McCune and Mefford, 1999).

In addition, we examined 76 specimens deposited in the four main herbaria in Taiwan: the Herbarium of Academia Sinica, Taipei (HAST), the Herbarium of National Taiwan University (TAI), the Herbarium of Taiwan Forestry Research Institute (TAIF), and the Herbarium of the National Museum of Natural Science (TNM). Twenty spores from each herbarium specimen were randomly sampled and the diameter of each was measured under a light microscope (Leitz, Dialux 20). Spores of diploid and triploid *P. fauriei* differ significantly in size (Huang et al., 2006). Using this information, herbarium specimens were classified as diploid or triploid.

## RESULTS

Of the 516 live plants, 193 plants from 14 locations had 64-spore sporangia and were considered diploid, and 323 living plants from 22 locations had 32-spore sporangia and were considered triploid (Table 1). Among the herbarium specimens, 34 plants had small spores ranging from  $33.1 \pm 1.6$  to  $38.6 \pm 3.0$   $\mu\text{m}$  in diameter, and 42 plants had large spores ranging from  $46.1 \pm 3.7$  to  $53.3 \pm 5.0$   $\mu\text{m}$  in diameter (Fig. 1; Appendix 1). Plants with smaller spores were considered diploid and those with larger spores triploid (Huang et al., 2006).

Diploid plants were distributed from 25°37'N to 21°57'N, and ranged from northern Taiwan (Keelung City, Taipei, Ilan, and Hsinchu Counties), to eastern Taiwan (Hualien County), southern Taiwan (Pingtung and Kaohsiung Counties), and the southeastern islands of Lanyu and Lutaο. Most islands had diploid plants and only diploid plants were found on the islands of Pengchiayu, Penghu, Lutaο and Lanyu (Fig. 2). No diploid plants were found in central Taiwan nor in Matsu islands.

Table 1. Ploidy level, latitude and elevation of live plants in the *Pteris fauriei* complex in Taiwan and nearby islands. Locations arranged from high to low latitudes.

Location Region, County/City	Sample No.		Latitude (N), elevation (m) <sup>(1)</sup>	Habitat type <sup>(2)</sup>	
	Diploid	Triploid		Diploid	Triploid
Beigang, Matsu		30	26°13', 50		1,2,3
Nangang, Matsu		30	26°09', 120		3
Pengchiayu, Keelung	20		25°37', 100	1,2	
Yehliu, Taipei	15	15	25°13', 5 <sup>D</sup> 10 <sup>T</sup>	1,2	3
Keelungtao, Keelung	25	5	25°11', 5 <sup>D</sup> 150 <sup>T</sup>	1,2	3
Hopintao, Keelung	7	23	25°09', 3 <sup>D</sup> 15 <sup>T</sup>	1	2,3
Pali, Taipei		1	25°08', 6		3
Yangmingshan, Taipei		20	25°08', 380		3
Shuanghsi, Taipei		5	25°08', 480		3
Patoutzu, Keelung		20	25°08', 30		3
Chinkuashin, Taipei		1	25°05', 400		3
Elephant Mt., Taipei		30	25°01', 90		3
Chingtung, Taipei		30	25°01', 350		3
Sanhsia, Taipei		7	24°56', 440		3
Wulai, Taipei		30	24°52', 500		3
Kueishan Island, Ilan	5	25	24°50', 2 <sup>D</sup> 120 <sup>T</sup>	1	3
Fushan, Taipei		30	24°45', 610		2,3
Chutung, Hsinchu	2		24°44', 20	2	
Nanfangao, Ilan		6	24°34', 15		2,3
Peipu, Hualien		3	24°02', 50		3
Wushe, Nantou		3	24°01', 1150		3
Lienhuachih, Nantou		2	23°54', 650		3
Huching Islet, Penghu	20		23°29', 30	1	
Stiping, Hualien	3		23°29', 5	1	
Sanhsientai, Taitung		5	23°08', 4		3
Tengchih, Kaohsiung	2		23°04', 1500	3	
Chiweishan, Kaohsiung	1		22°56', 250	3	
Tulanshan, Taitung		2	22°53', 440		3
Lutao, Taitung	30		22°41', 15	1,2,3	
Lanyu, Taitung	30		22°04', 10	1,2,3	
Jialeshuei, Pingtung	30		21°59', 8	1,2,3	
Oluanpi, Pingtung	3		21°57', 20	3	
<b>Total</b>	<b>193</b>	<b>323</b>			

(1) D: diploid; T: triploid

(2) 1: exposed site; 2: grassland; 3: woodland

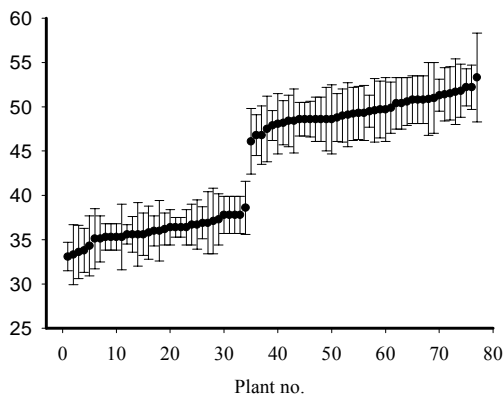


Fig. 1. Spore sizes of herbarium specimens in the *Pteris fauriei* complex. Smaller spores in the group on the left represent diploid plants; spores in the right group represent triploid plants. Detailed information about each plant, listed by number, is provided in Appendix 1.

Triploid plants were distributed from 26°13'N to 22°53'N, somewhat more northerly than the diploids. In Taiwan, triploids grew in the northern and eastern regions, and in the central mountains but did not occur on the southern tip, the Henchung Peninsula. Diploid and triploid plants co-occurred on islands in the north, Keelungtao (Keelung City), Hopintao (Keelung City), and Kueishan island (Ilan County), but only triploids were found in Matsu islands. No triploids were found in islands Lutao and Lanyu (Taitung County) or western-central (Huching islet, Penghu County) regions (Fig. 2).

Except for two plants in Tengchih (Kaohsiung County, 1500 m) and one plant in Chiweishan (Kaohsiung County, 250 m) in southern Taiwan, all other diploid plants (98.4%) grew below 100 m elevation. In contrast, 58.5% (190/323) of triploid plants grew above 100 m elevation and were found as

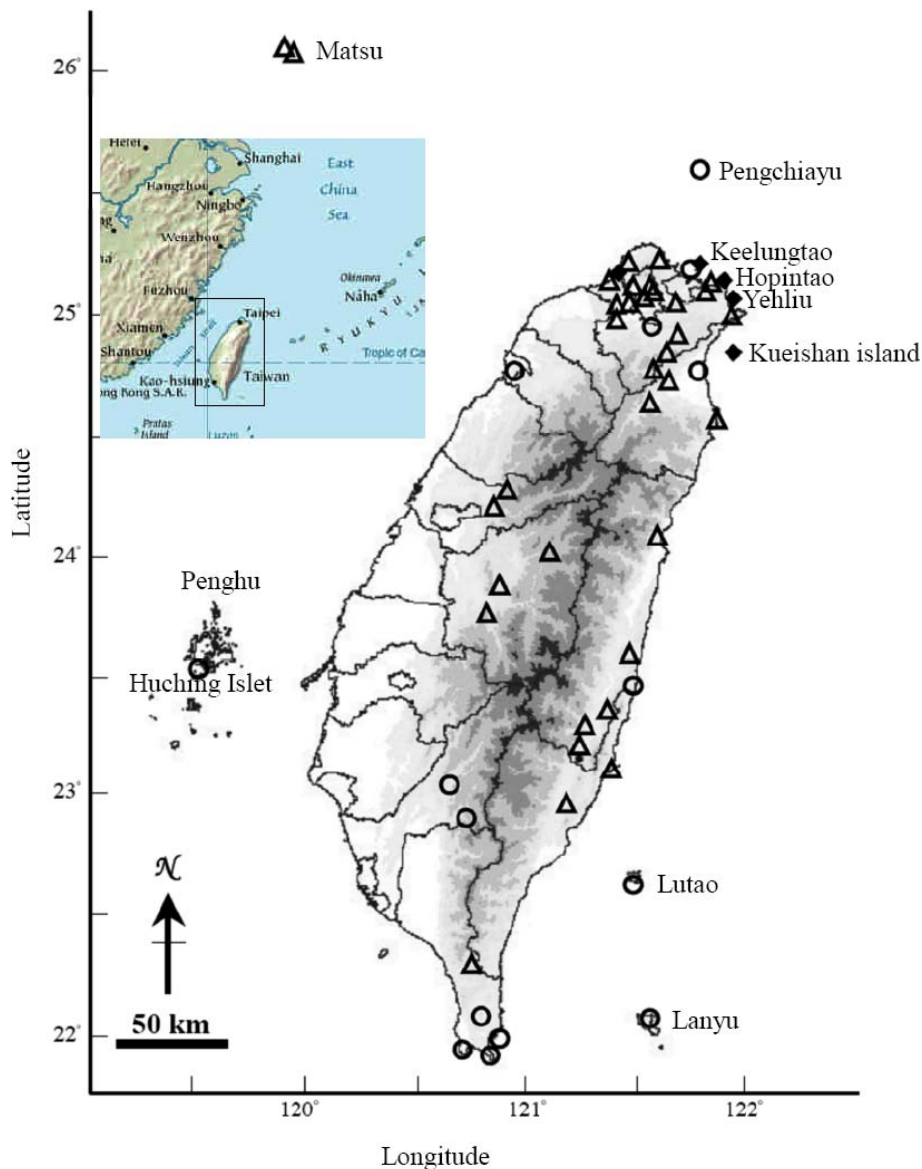


Fig. 2. Distributional map of *Pteris fauriei* complex cytotypes on Taiwan and nearby islands based on the survey of living plants and herbarium specimens. ○: diploids; △: triploids; ◆: diploids mixed with triploids.

high as 1150 m in central Taiwan. Among those triploid plants growing below 100 m elevation, most (95.8%, 182/190) grew in northern or northeastern Taiwan and the others grew in woodlands along the east-central coast (Table 1).

*Pteris fauriei* grew in three types of habitats; exposed sites, grasslands, and woodlands. In northern Taiwan and on nearby islands, such as Keelungtao, Hopintao and Kueishan, diploids grew only in exposed sites and grasslands. In southern Taiwan and islands, such as Lutaο and Lanyu, diploid plants grew in all three habitat types. In contrast, in Matsu islands, the most northern location in this study, triploids grew in all three habitat-types, but in the south triploids were restricted to grasslands and woodlands.

PCA analysis of ploidy levels and environmental factors determined that the first PCA axis accounted for 45.6% of the variation, the second for 33.1%, and the third for 21.2%. Two factors significantly contributed to the loading of the first axis, habitat (coefficient = 0.70) and elevation (0.69). Only latitude coefficient (0.98) was significant for the second axis (coefficient = 0.98). Triploids were found more in the upper and right parts of the plot whereas diploids were more in the lower and left parts (Fig. 3). This PCA ordination showed that triploids tended to occur in woodlands, at higher elevations, and in the northern regions, whereas diploids tended to occur in exposed habitats, at lower elevation, and in the southern regions.

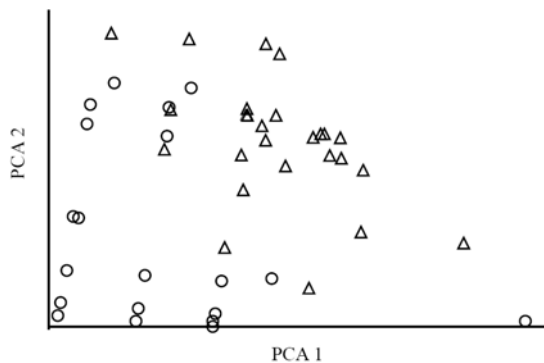


Fig. 3. PCA ordination of *Pteris fauriei* complex based on elevation, latitude, and habitat variables. The first axis mainly represents habitat (coefficient = 0.70) and elevation (coefficient = 0.69) and reflects a gradient from lower elevation with exposed habitat (left) to higher elevation with woodland habitat (right). The secondary axis mainly represents latitude (coefficient = 0.98). Low latitude is in the low part of the plot. Circle: diploids; Triangle: triploids.

## DISCUSSION

Compared to diploids, polyploids are thought to have several advantages due to the greater diversity in their genome (Grant, 1981; Soltis and Soltis, 1993). They may be more tolerant to low nutrient availability, drought stress, cold, pests, and pathogens (Levin, 1983), and better at colonizing disturbed habitats (Stebbins, 1950, 1971; Ehrendorfer, 1980). In many polyploid complexes, the polyploids have spread over a wide range of geographical regions and ecological conditions, whereas their counterpart diploids are restricted to smaller areas (e.g. Stebbins, 1950, 1971).

Among pteridophytes, most studies comparing the geographical distributions of diploids and their polyploid counterparts have focused on diploids vs. even polyploids, such as *Asplenium ceterach* (diploid vs. tetraploid vs. hexaploid) (Trewick et al., 2002), *Lepisorus thunbergianus* (diploid vs. tetraploid) (Mitui et al., 1987). Only a few studies have compared the distribution of diploids and triploids, which usually have different reproductive modes. In Japan, the sexual diploid *Cyrtomium falcatum* was distributed over nearly the same latitude range as apogamous triploids (Matsumoto, 2003). However, a cytogeographical survey of the *Dryopteris erythroosora* complex in Japan found that diploids occurred in southern regions and triploids in northern regions, with little overlap in their distributions (Hirabayashi, 1974).

In Taiwan, the latitudinal distributions of diploid and triploid *Pteris fauriei* overlapped greatly.

However, only triploid *P. fauriei* occurred in the northernmost site (Matsu islands) and only diploids were found in the southernmost sites. In addition, triploid plants grew at higher elevations than diploid plants.

In many ferns, reproductive barriers are likely to exist between polyploids and their ancestors. This increases the potential for the development of their spatial segregation (Vogel et al., 1999). Many examples demonstrate that microenvironment (habitat) selection is partially responsible for maintaining the separation of different cytotypes in ferns and flowering plants (Lumaret et al., 1987; Ohta and Takamiya, 1999; Johnson et al., 2003; Matsumoto, 2003). In *P. fauriei*, crossing diploid and triploid plants was unsuccessful (unpublished data). Although the geographic distribution of the diploids and triploids overlap, at a given location their habitats somewhat differed. Both triploid and diploid *P. fauriei* grew in exposed, grassland, and woodland habitats, but occurrence in a specific habitat varied with latitude and elevation.

In exposed habitats, the lower elevation, and more southerly sites have warmer conditions, and diploid plants predominate. Thus, diploid *P. fauriei* seems to be adapted to warmer habitats than triploids. Other ferns with diploid and triploid plants exhibit similar adaptations (reviewed by Walker, 1979).

In general, apogamous plants tend to be better adapted to xeric habitats than their sexually reproducing counterparts (Klekowski, 1969), though there are exceptions (Takamiya et al., 1999; 2000). For ferns growing in xeric habitats, fertilization would be severely limited. In Taiwan, many diploids of *P. fauriei* grew in sunny exposed habitat along the seashore. Exposed sites may be dry relative to woodlands, but they receive more than 1500 mm rain annually (except for Penghu only 950 mm) (Central Weather Bureau, 2006). They are not really xeric and sexual reproduction may not be constrained by a lack of moisture. Many spores may remain viable in the soil for years after dispersal (Lindsay and Dyer, 1990; Dyer and Lindsay, 1992; Dyer, 1994). Thus, dispersed spores of diploid *P. fauriei* may germinate immediately and develop, with fertilization occurring when it is wet enough, or spores may wait in the soil spore bank until conditions are favorable.

In this study, the habitats, latitude, and elevation of *P. fauriei* cytotypes were recorded. These parameters are related to temperature. In general, triploid plants grow in cooler sites than diploid plants. Testing the cold-hardiness of diploids and triploids, and how it affects their distributions, requires additional study and experimentation.

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## LITERATURE CITED

- Adams, K. L., R. Cronn, R. Percifield and J. F. Wendel. 2003. Genes duplicated by polyploidy show unequal contributions to the transcriptome and organ-specific reciprocal silencing. *Proc. Natl. Acad. Sci.* **100**: 4649-4654.
- Baack, E. J. 2004. Cytotype segregation on regional and microgeographic scales in snow buttercups (*Ranunculus adoneus*: Ranunculaceae). *Amer. J. Bot.* **91**: 1783-1788.
- Central Weather Bureau. 2006. Monthly mean climate data for Taiwan: Precipitation (1971-2000 years). <http://www.cwb.gov.tw/V5e/index.htm>
- Dyer, A. F. 1994. Natural soil spore bank – can they be used to retrieve lost ferns? *Biod. Cons.* **3**: 160-175.
- Dyer, A. F. and S. Lindsay. 1992. Soil spore banks of temperate ferns. *Amer. Fern J.* **82**: 89-122.
- Ehrendorfer, F. 1980. Polyploidy and distribution. In: Lewis, W. H. (ed.), *Polyploidy: Biological Relevance*. Plenum Press, NY, USA. pp. 45-60.
- Goldblatt, P. 1980. Polyploidy in angiosperms. In: Lewis, W. H. (ed.), *Polyploidy: Biological Relevance*. Plenum Press, NY, USA. pp. 219-239.
- Grant, V. 1981. *Plant Speciation* (2nd ed.). Columbia Univ. Press, USA. 563pp.
- Hardy, O. J., S. Vanderhoeven, M. De Loose and P. Meerts. 2000. Ecological, morphological, and allozymic differentiation between diploid and tetraploid knapweeds (*Centaurea jacea*) from a contact zone in the Belgian Ardennes. *New Phytol.* **146**: 281-290.
- Haufler, C. H. and D. E. Soltis. 1986. Genetic evidence suggests that homosporous ferns with high chromosome numbers are diploid. *Proc. Natl. Acad. Sci.* **83**: 4389-4393.
- Hedberg, I. 1969. Cytotaxonomic studies on *Anthoxanthum odoratum* L. s. lat. III. Investigations of Swiss and Austrian population samples. *Sv. Bot. Tidskr.* **63**: 233-250.
- Hieronymus, V. G. 1914. Beiträge zur Kenntnis der Gattung *Pteris*. II. Über *Pteris quadriaurita* Retz und einige asiatische, malesische und polynesische *Pteris* – Arten aus der Gruppe und Verwandtschaft dieser Art. *Hedwigia*, **55**: 325-375.
- Hirabayashi, H. 1974. Cytogeographic Studies on *Dryopteris* of Japan. Harashobo, Tokyo, Japan. 176pp.
- Holbrook-Walker, S. and R. M. Lloyd. 1973. Reproductive biology and gametophyte morphology of the Hawaiian fern genus *Sadleria* (Blechnaceae) relative to habitat diversity and propensity for colonization. *Bot. J. Linn. Soc.* **67**: 157-174.
- Huang Y.-M., H.-M. Chou, T.-H. Hsieh, J.-C. Wang and W.-L. Chiou. 2006. Cryptic characteristics distinguish diploid and triploid varieties of *Pteris fauriei* (Pteridaceae). *Can. J. Bot.* **84**: 261-268.
- Johnson M. T. J., B. C. Husband and T. L. Burton. 2003. Habitat differentiation between diploid and tetraploid *Galax urceolata* (Diapensiaceae). *Int. J. Plant Sci.* **164**: 703-710.
- Klekowski, E. J. Jr. 1969. Reproductive biology of the Pteridophyta. II. Theoretical considerations. *Bot. J. Linn. Soc.* **62**: 347-359.
- Leitch, I. J. and M. D. Bennett. 1997. Polyploidy in angiosperms. *Trends Plant Sci.* **2**: 470-476.
- Levin, D. A. 1983. Polyploidy and novelty in flowering plants. *Amer. Naturalist* **122**: 1-25.
- Levin, D. A. 2002. *The Role of Chromosomal Change in Plant Evolution*. Oxford Univ. Press, Oxford, UK. 240pp.
- Lewis, W. H. 1967. Cytocatalytic evolution in plants. *Bot. Rev.* **33**: 105-115.
- Lewis, W. H. 1980. Polyploidy in species populations. In: Lewis, W. H. (ed.), *Polyploidy: Biological Relevance*. Plenum Press, NY, USA. pp. 103-144.
- Lewis, W. H. and E. E. Terrell. 1962. Chromosomal races in eastern North American species of *Hedyotis* (*Houstonia*). *Rhodora* **64**: 313-323.
- Lindsay, S. and A. F. Dyer, 1990. Fern spore banks: implications for gametophyte establishment. In: Rita, J. (ed.), *Taxonomía, Biogeografía y Conservación de Pteridófitos*. Societat d'Historia Natural de les Illes Balears – Institut Menorquí d'Estudis, Palma de Mallorca, Spain. pp. 243-253.
- Lloyd, R. M. 1974. Mating systems and genetic load in pioneer and non-pioneer Hawaiian Pteridophyta. *Bot. J. Linn. Soc.* **69**: 23-35.
- Lumaret, R., J. L. Guillermin, J. Delay, A. A. L. Loutfi, J. Izco and M. Jay. 1987. Polyploidy and habitat

- differentiation in *Dactylis glomerata* L. from Galicia (Spain). *Oecologia* **73**: 436-446.
- Matsumoto, S. 2003. Species ecological study on reproductive systems and speciation of *Cyrtomium falcatum* complex (Dryopteridaceae) in Japanese Archipelago. *Ann. Tsukuba Bot. Gard.* **22**: 1-141.
- McCune, B. and M. J. Mefford. 1999. PC-ORD. Multivariate analysis of ecological data, vers. 4. Glenden Beach, OR, MjM Software Design. 237pp.
- Mitui, K. 1968. Chromosome and speciation in ferns. *Sci. Rep. Tokyo Edu. Univ., Sec. B*, **203**: 285-333.
- Mitui, K., N. Nakato and S. Masuyama. 1987. Studies on intraspecific polyploids of the fern *Lepisorus thunbergianus* (2) Cytogeography of main cytotypes. *J. Jap. Bot.* **62**: 311-319.
- Moore, S.-J., T.-H. Hsieh, Y.-M. Huang and W.-L. Chiou. 2002. *Diplazium maonense* Ching, a poorly known species of the Athyriaceae (Pteridophyta) in Taiwan. *Taiwan J. For. Sci.* **17**: 113-118.
- Mosquin, T. 1967. Evidence for autopolyploidy in *Epilobium angustifolium* (Onagraceae). *Evolution* **21**: 713-719.
- Nakato, N. 1981. Notes on chromosomes of Japanese pteridophytes (1). *J. Jap. Bot.* **56**: 200-205.
- Ohta, N. and M. Takamiya. 1999. Taxonomic studies of the *Diplazium mettenianum* complex (Woodsiaceae: Pteridophyta) in Japan: morphology, cytology and taxonomy of plants with normal-shaped spores. *J. Plant. Res.* **112**: 67-86.
- Park, C. H. and M. Kato. 2003. Apomixis in the interspecific triploid hybrid fern *Cornopteris christenseniana* (Woodsiaceae). *J. Plant Res.* **116**: 93-103.
- Ramsey, J. and D. W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Ann. Rev. Ecol. Syst.* **29**: 467-501.
- Schaefer, V. G. and J. P. Miksche. 1977. Microspectrophotometric determination of DNA per cell and polyploidy in *Fraxinus americana* L. *Silvae Genet.* **26**: 184-192.
- Segraves, K. A., J. N. Thompson, P. S. Soltis and D. E. Soltis. 1999. Multiple origins of polyploidy and the geographic structure of *Heuchera grossularifolia*. *Mol. Ecol.* **8**: 253-262.
- Sharma, A. K. and D. Dey. 1967. A comprehensive cytotoxic study on the family Chenopodiaceae. *J. Cytol. Genet.* **2**: 114-127.
- Shieh, W.-C. 1975. Pteridaceae. In: Li, H.-L. et al. (eds.), *Flora of Taiwan*, 1st ed. **1**: 281-301, Epoch, Taipei, Taiwan.
- Shieh, W.-C. 1994. Pteridaceae. In: Huang, T.-C. et al. (eds.), *Flora of Taiwan*, 2nd ed. **1**: 206-233. Editorial Committee, Dept. Bot., NTU, Taipei, Taiwan.
- Shivas, M. G. 1961. Contributions to the cytology and taxonomy of species of *Polypodium* in Europe and America: I. Cytology. *J. Linn. Soc. (Bot.)* **58**: 13-25.
- Small, E. 1968. The systematics of autopolyploidy in *Epilobium latifolium* (Onagraceae). *Brittonia* **20**: 169-181.
- Soltis, D. E. and P. S. Soltis. 1993. Molecular data and dynamic nature of polyploidy. *Crit. Rev. Pl. Sci.* **12**: 243-273.
- Soltis, P. S. and D. E. Soltis. 2000. The role of genetic and genomic attributes in the success of polyploids. *Proc. Natl. Acad. Sci.* **97**: 7051-7057.
- Stebbins, G. L. 1950. Variation and evolution in plants. Columbia Univ. Press, NY, USA. 643pp.
- Stebbins, G. L. 1971. Chromosomal Evolution in Higher Plants. Addison-Wesley, MA, USA. 216pp.
- Takamiya, M., C. Takaoka and N. Ohta. 1999. Cytological and reproductive studies on Japanese *Diplazium* (Woodsiaceae: Pteridophyta): apomictic reproduction in *Diplazium* with evergreen bi- to tripinnate leaves. *J. Plant Res.* **112**: 419-436.
- Takamiya, M., N. Ohta, C. Fujimaru-Takaoka and K. Uki. 2000. Cytological and reproductive studies of Japanese *Diplazium* (Woodsiaceae: Pteridophyta). II. Polyploidy and hybridity in the species group with summer-green bi- to tripinnate leaves. *J. Plant Res.* **113**: 203-215.
- Trewick, S. A., M. Morgan-Richardds, S. J. Russell, S. Henderson, F. J. Rumsey, I. Pintér, J. A. Barrett, M. Gibby and J. C. Vogel. 2002. Polyploidy, phylogeography and Pleistocene refugia of the rockfern *Asplenium ceterach*: evidence from chloroplast DNA. *Mol. Ecol.* **11**: 2003-2012.
- Tryon, A. F. 1968. Comparisons of sexual and apogamous races in the ferns genus *Pellaea*. *Rhodora* **70**: 1-24.
- Vida, G. 1976. The role of polyploidy in evolution. In: Novak V. J. A. and B. Pacltova (eds.), *Evolutionary Biology*. Czechoslovak Acad. Sci., Prague, Crechoslovak. pp. 267-294.
- Vogel, J. C., F. J. Rumsey, J. J. Schneller, J. Barrett and M. Gibby. 1999. Where are the glacial refugia in Europe ? Evidence from pteridophytes. *Biol. J. Linn. Soc.* **66**: 23-37.
- Walker, T. G. 1979. The cytogenetics of ferns. In: Dyer, A. F. (ed.), *The Experimental Biology of Ferns*. Acad. Press, London, UK. pp. 87-132.

Appendix 1. Collection location, spore size and ploidy level of herbarium specimens in the *Pteris fauriei* complex from Taiwan and nearby islands.

No.	Location (Region, County/City)	Spore size ( $\mu\text{m}$ )	Ploidy	Vouchers
1	Lanyu, Taitung	33.1 $\pm$ 1.6	2	TAIF 164673
2	Keelung, Keelung	33.3 $\pm$ 3.4	2	TAIF 21603
3	Kenting, Pingtung	33.6 $\pm$ 3.0	2	TNM 1959
4	Lanyu, Taitung	33.8 $\pm$ 2.5	2	TAIF 115238
5	Kueishan Island, Ilan	34.3 $\pm$ 3.4	2	TNM 10281
6	Lanyu, Taitung	35.1 $\pm$ 3.4	2	TAIF 148053
7	Lutao, Taitung	35.1 $\pm$ 2.6	2	HAST 94393
8	Pengchiayu, Keelung	35.3 $\pm$ 1.5	2	TAI 223462
9	Lanyu, Taitung	35.3 $\pm$ 1.5	2	TAIF 92319
10	Lanyu, Taitung	35.3 $\pm$ 1.5	2	TAIF 115239
11	Lanyu, Taitung	35.3 $\pm$ 3.7	2	TAI 224845
12	Jialeshuei, Pingtung	35.6 $\pm$ 1.1	2	TAIF 164672
13	Keelung, Keelung	35.6 $\pm$ 2.0	2	TAIF 102444
14	Lanyu, Taitung	35.6 $\pm$ 3.6	2	TAIF 115240
15	Keelungtao, Keelung	35.6 $\pm$ 2.4	2	TNM 9902
16	Chialeshuei, Pingtung	35.8 $\pm$ 3.0	2	HAST 38336
17	Lanyu, Taitung	36.0 $\pm$ 1.7	2	TAIF 164842
18	Lanyu, Taitung	36.0 $\pm$ 3.4	2	TAI 183297
19	Lanyu, Taitung	36.2 $\pm$ 1.8	2	HAST 38346
20	Lanyu, Taitung	36.4 $\pm$ 2.0	2	HAST 38345
21	Lanyu, Taitung	36.4 $\pm$ 1.1	2	TAI 246064
22	Lanyu, Taitung	36.4 $\pm$ 1.1	2	TAIF 142980
23	Lanyu, Taitung	36.4 $\pm$ 2.0	2	TAI 187942
24	Keelungtao, Keelung	36.7 $\pm$ 2.3	2	TAI 8343
25	Lanyu, Taitung	36.7 $\pm$ 2.8	2	TAI 187906
26	Lutao, Taitung	36.9 $\pm$ 1.8	2	TAIF 150556
27	Chiaochi, Ilan	36.9 $\pm$ 3.5	2	HAST 38355
28	Muchishan, Taipei	37.1 $\pm$ 3.7	2	HAST 40244
29	Juifang, Taipei	37.3 $\pm$ 2.9	2	HAST 70470
30	Kenting, Pingtung	37.8 $\pm$ 2.1	2	TAI 245430
31	Kenting, Pingtung	37.8 $\pm$ 2.1	2	TAI 245776
32	Nanjenshan, Pingtung	37.8 $\pm$ 2.1	2	TAI 246062
33	Lutao, Taitung	37.8 $\pm$ 2.1	2	TAIF 150557
34	Kua-yin Shan, Taipei	38.6 $\pm$ 3.0	2	TAI 8313
35	Tatung, Ilan	46.1 $\pm$ 3.7	3	HAST 38358
36	Hoping, Taichung	46.8 $\pm$ 2.3	3	TNM 9263
37	Wulai, Taipei	46.8 $\pm$ 3.3	3	TNM 2210
38	Taisan, Taipei	47.5 $\pm$ 3.7	3	TAIF 112398
39	Tanshui, Taipei	47.9 $\pm$ 1.7	3	TAIF 85065
40	Shihtsokou, Hualien	48.1 $\pm$ 3.4	3	HAST 38359
41	Neihu, Taipei	48.2 $\pm$ 2.5	3	TAIF 152777
42	Wulai, Taipei	48.4 $\pm$ 2.9	3	TNM 2220
43	Shihtsokou, Hualien	48.4 $\pm$ 3.6	3	HAST 38360
44	Kua-yin Shan, Taipei	48.6 $\pm$ 1.9	3	TAI 8321
45	Chuyuanshan, Taichung	48.6 $\pm$ 1.9	3	TAI 132413
46	Chiapuanshan, Pingtung	48.6 $\pm$ 2.0	3	TAIF 165202
47	Yangmingshan, Taipei	48.6 $\pm$ 2.5	3	TAI 246061
48	Yuntungssu, Taipei	48.6 $\pm$ 2.5	3	TAIF 115740
49	Erworishan, Taipei	48.6 $\pm$ 3.6	3	TAIF 88619
50	Tulanshan, Taitung	48.6 $\pm$ 3.9	3	TAIF 165989
51	Wulai, Taipei	48.8 $\pm$ 2.7	3	HAST 38156
52	N. Cross Highway, Ilan	49.0 $\pm$ 3.0	3	TAIF 166683
53	Wulai, Taipei	49.1 $\pm$ 3.6	3	TNM 2292
54	Chinshan, Taipei	49.2 $\pm$ 3.0	3	TNM 9904
55	Keelung, Keelung	49.3 $\pm$ 3.0	3	TAI 245415
56	Yuli, Hualien	49.3 $\pm$ 3.1	3	HAST 38347
57	Neihu, Taipei	49.5 $\pm$ 1.8	3	TAIF 152782



## Appendix 1 Continued.

No.	Location (Region, County/City)	Spore size ( $\mu\text{m}$ )	Ploidy	Vouchers
58	Kungliao, Taipei	49.6 $\pm$ 3.6	3	TNM 9103
59	Wulai, Taipei	49.7 $\pm$ 3.2	3	TNM 2331
60	Pali, Taipei	49.7 $\pm$ 3.6	3	TAI 177046
61	Wulai, Taipei	49.9 $\pm$ 2.9	3	HAST 35608
62	N. Cross Highway, Ilan	50.4 $\pm$ 2.9	3	TAIF 164677
63	Chiapuanshan, Pingtung	50.4 $\pm$ 2.9	3	TAIF 165201
64	Wulai, Taipei	50.6 $\pm$ 2.7	3	HAST 40982
65	Kua-yin Shan, Taipei	50.8 $\pm$ 2.7	3	TAI 8319
66	Wulai, Taipei	50.8 $\pm$ 2.7	3	TAI 245431
67	Yangmingshan, Taipei	50.8 $\pm$ 2.7	3	TAI 246063
68	Mientianshan, Taipei	51.0 $\pm$ 4.0	3	TAI 184813
69	Yunhsienleyuan, Taipei	51.3 $\pm$ 1.8	3	TAIF 152797
70	Chohsi, Hualien	51.4 $\pm$ 3.0	3	TNM 6800
71	Chiapuanshan, Pingtung	51.5 $\pm$ 3.0	3	TAIF 165200
72	Keelung, Keelung	51.7 $\pm$ 3.7	3	HAST 26064
73	Tanshui, Taipei	51.8 $\pm$ 3.0	3	TAIF 103097
74	Taibalangshan, Hualien	52.2 $\pm$ 2.1	3	TAIF 156666
75	Keelung, Keelung	52.2 $\pm$ 2.5	3	TAI 8339
76	Chichi, Nantou	53.3 $\pm$ 5.0	3	TAI 193512

## 臺灣地區傅氏鳳尾蕨複合群之分布及棲地

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### 摘 要

多倍體化為植物種化之重要模式之一，多倍體棲地類型通常與它們的二倍體親本有所不同。在臺灣，傅氏鳳尾蕨 (*Pteris fauriei*) 已被證實具有二倍體及三倍體兩個變種，而孢子囊內孢子數及孢子大小為判斷倍體數的可信依據，二倍體植株孢子囊內孢子數 64 且孢子顯著小於三倍體植株，而三倍體植株孢子囊內孢子數則為 32；基於這些發現，藉由新鮮植株及標本館標本，檢視臺灣地區此二核型的分布及棲地分布。從 32 族群的 516 株新鮮植株及 76 份標本館標本資料顯示，二倍體植株通常較三倍體植株生存在較溫暖的棲地，二倍體植株廣泛分布於臺灣本島及鄰近島嶼，但未出現在臺灣本島中部地區或臺灣北方的馬祖島嶼，相對地，三倍體植株則未在臺灣南端或臺灣中部的西側島嶼被發現。臺灣本島北部及中西側島嶼，二倍體植株最常生長在開闊地及草生地，然而，臺灣本島南部及東南側的島嶼，二倍體植株也在林地出現；臺灣本島三倍體植株侷限分布於草生地及林地，但在馬祖島嶼的開闊地、草生地及林地均可發現其蹤跡。除此之外，三倍體植株一般較二倍體植株具有較高的海拔分布。

關鍵詞：二倍體、細胞型、分布、棲地、鳳尾蕨科、傅氏鳳尾蕨、三倍體、臺灣。

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