

## Review Article

# Polyploidy and Speciation in *Pteris* (Pteridaceae)

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The highest frequency of polyploidy among plants is considered to occur in the Pteridophytes. In this study, we focused on polyploidy displayed by a specific fern taxon, the genus *Pteris* L. (Pteridaceae), comprising over 250 species. Cytological data from 106 *Pteris* species were reviewed. The base number of chromosomes in *Pteris* is 29. Polyploids are frequently found in *Pteris*, including triploids, tetraploids, pentaploids, hexaploids, and octoploids. In addition, an aneuploid species, *P. deltodon* Bak., has been recorded. Furthermore, the relationship between polyploidy and reproductive biology is reviewed. Among these 106 *Pteris* species, 60% exhibit polyploidy: 22% show intraspecific polyploidy and 38% result from polyploid speciation. Apogamous species are common in *Pteris*. Diploids are the most frequent among *Pteris* species, and they can be sexual or apogamous. Triploids are apogamous; tetraploids are sexual or apogamous. Most *Pteris* species have one to two ploidy levels. The diverse ploidy levels suggest that these species have a complex evolutionary history and their taxonomic problems require further clarification.

## 1. Introduction

Polyploidy provides a rapid route for species evolution and adaptation [1, 2]. Taxa arising from polyploidy are usually characterized by diverse gene expression [3]. This variation in gene expression also has effects on ecological traits, which play an important role in speciation because a specialised niche is a key factor in the formation of new taxa [4–8]. For example, ecological isolation can allow taxa with genetic variation to become segregated [9]. It is estimated that the highest frequency of polyploidy is exhibited in ferns. The frequency of polyploid speciation in ferns is 31%, which is much higher than 15% in angiosperms [10].

In ferns, a special form of asexual reproduction known as apogamy is common [11, 12]. Apogamy provides a bypass to crossover mispairing of chromosomes and stabilises the reproduction of polyploids [13–15]. During metaphase I of meiosis, these polyploids present multivalents, which may have difficulty separating equally. Apogamous species are clonal hybrid genotypes, and, as a result, apogamy creates reproductive barriers that prevent gene flow among closely related taxa, thereby facilitating sympatric speciation [16]. Each taxon maintains an independent genetic lineage, leading eventually to a new species.

*Pteris* L. (Pteridaceae) is a cosmopolitan fern genus with over 250 species. Some *Pteris* species have several different ploidy levels and are found in several geographical areas, such as *P. cretica* and *P. vittata* [11, 17, 18], which likely reflect the ecological differentiation within species. For example, different niche preferences have been found in *P. fauriei* [19]. In addition, polyploidy can also cause morphological novelty. Species complexes in *Pteris* have been frequently reported [20, 21]. Those species complexes are usually composed of a group of taxa with similar morphologies and involved several polyploids. This paper depicts the cytotypes, breeding systems, character variations, and their relationships in the genus *Pteris*.

## 2. Cytotypes of *Pteris* Species

The first studies of polyploidy in *Pteris* focused mainly on ploidy differences and apogamy of *P. cretica* [22]. Walker [12] provided the first comprehensive cytological study of the genus *Pteris*, which included 82 species, and reported that the base number of chromosomes in *Pteris* is 29. In the current study, data from previous cytological studies of 106 *Pteris* species were integrated (Table 1). The data





TABLE 1: Continued.

	Sexual 2X	Apogamous 2X	Apogamous ?2X	Apogamous 3X	Sexual 4X	Apogamous 4X	Apogamous ?4X	Others	Reference
<i>P. tokioi</i> Masam.					V		V		[27, 50, 55]
<i>P. trachyphylla</i> Kunze.		V							[12]
<i>P. tremula</i> R. Br.								Sexual 8X	[12]
<i>P. tripartita</i> Sw.	V				V				[12, 35]
<i>P. umbrosa</i> R. Br.					V				[12]
<i>P. vellucida</i> *			V						[24]
<i>P. vittata</i> L.	V			V	V	V		5X, 6X	[1, 12, 17, 18, 27, 35, 39, 44, 58]
<i>P. wallichiana</i> Agardh	V								[12, 18, 27, 44]
<i>P. wangiana</i> Ching				V					[24]
<i>P. warburgii</i> Christ			V						[54]
<i>P. wernerii</i> (Rosenstock) Holtt.			V						[25]
<i>P. wulaiensis</i> C.M.Kuo		V							[36]
<i>P. xiaoyingae</i> H. He & L. B. Zhang		V							[59]
<i>P. yamatensis</i> (Tagawa) Tagawa					V				[12, 23]

? means unknown.

\* It is accorded to the literature. *P. vellucida* could be misspelling of *P. pellucida*.

of some varieties were combined into species. The degree of polyploidy varies in *Pteris*, including triploid, tetraploid, pentaploid, hexaploid, and octoploid species. In addition, an aneuploid species, *P. deltodon* Bak., with 53, 55, and 82 chromosomes per gamete has been reported [18, 23, 24].

Among the 106 *Pteris* species examined, 43 (40%) are diploid, the most common cytotype in this genus (Figure 1). Among the remaining 40 polyploid species (38%), there are 13 triploids, 26 tetraploids, and 1 octoploid. Octoploidy in *P. tremula* R. Br. is the highest ploidy level recorded. Compared to the 34% level of polyploidy in all leptosporangiate ferns [10], polyploid speciation is apparently much more common in the genus *Pteris*. The highest ploidy levels found in all fern genera, such as dodecaploids and hexadecaploids in *Asplenium* [12], were not found in the genus *Pteris*.

Of the 106 species of *Pteris* examined, most of the individuals in a species have only one ploidy level. In contrast, intraspecific polyploids are found in the other 23 species, 22% of genus *Pteris*. Nine species include both diploid and triploid individuals, and four species include both diploids and tetraploids plants. No species comprised solely triploids or tetraploids. Six species have individuals with three ploidy levels, diploids, triploids, and tetraploids (Figure 1). Four species with other intraspecific ploidy combinations were grouped in the "others" in Figure 1. Specifically, *Pteris biaurita* L. and *P. ensiformis* Burm. include individuals having four ploidy levels, that is, diploids, triploids, tetraploids, and hexaploids. Also, *Pteris vittata* L. exhibits pentaploidy in addition to the above four ploidy levels. Finally, *Pteris deltodon* is aneuploid species. Some of the triploids and tetraploids in the genus clearly arose from autopolyploidy. For example, 29 trivalent chromosomes were found in the triploid *P. fauriei* Hieron (*P. fauriei* var. *fauriei*) [27], and 29 tetravalent chromosomes were found in *Pteris*

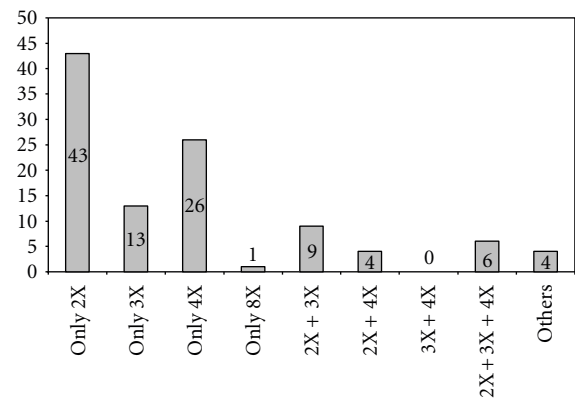


FIGURE 1: The cytotypes of the 106 *Pteris* species in this review.

*tokioi* Masam [27]. Overall, the frequency of the above intraspecific variation in ploidy level in *Pteris* is lower than the 33% reported for all leptosporangiate ferns [10].

### 3. Polyploids and Breeding Systems

The most common breeding system in the genus *Pteris* is sexual (48 species) (Figure 2), followed by apogamous (33 species), then species with both sexual and apogamous reproduction (13 species). Sexual reproduction is more frequent than apogamous in both diploids (28% > 11%) and tetraploids (15% > 7%) (Figure 3). Some other cytotypes could be sexual. For example, *P. tremula* is a sexual octoploid. Although *P. deltodon* is aneuploid, sexual diploids ( $n = 53, 55$ ) are also found in this species [18].

Apogamy is found in 39% of all cytotypes and 28% of polyploids (Figure 3; diploids 11%, triploids 21%,

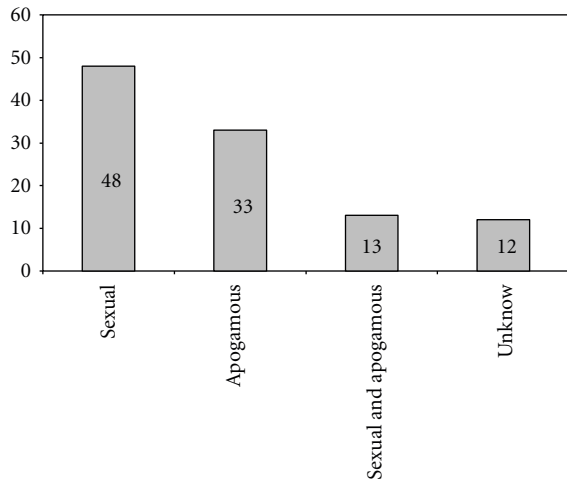


FIGURE 2: The breeding systems of the 106 *Pteris* species in this review.

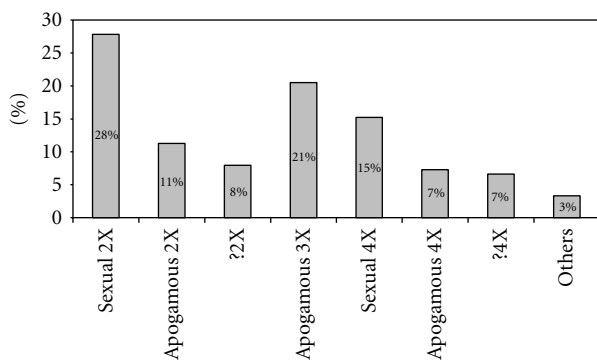


FIGURE 3: The breeding systems and cytotypes of the 106 *Pteris* species in this paper.

tetraploids 7%). Apogamous diploids are considered to originate from the hybridisation of two sexual diploid species followed by acquired apogamy or from genetic change of a sexual diploid species [11]. Apogamous triploids could derive from a cross between sexual diploid and tetraploid species or between apogamous diploids (unreduced, diploid gametes, functionally male) and sexual diploids [5, 11–14, 48, 60]. Diploids appear to be the ancestors of the triploids; however, ploidy reduction is also possible: triploids produced the diploid apogamous *Dryopteris pacifica*. Such diploids may be derived from partial synapsis and segregation [61].

All triploids were found to be apogamous. In both autotriploids and allotriploids, disordered chromosome separation occurs; trivalents in autotriploids and a bivalent plus a univalent in allotriploids cannot be resolved into balanced products. Without apogamous reproduction, spores from autotriploids do not have balanced chromosome complements and, thus, are not viable [62, 63].

The number of sexual tetraploids is greater than that of apogamous ones. Tetraploids could arise via chromosome doubling in a diploid and maintain sexual reproduction thereafter. Tetraploids can also arise from another mechanism, the so-called “triploid bridge” [2]. In this case, a

triploid arises from the fusion of a reduced (haploid) and an unreduced (diploid) gamete. Furthermore, crossing of the unreduced gametes of that apogamous triploid with the haploid gametes of a sexual diploid could produce apogamous tetraploids [64].

#### 4. Polyploidy and the Variation of *Pteris* Species

The variation among infraspecific polyploids may reveal the contribution of polyploidy to speciation. Such variation could include differences in morphology, ecology, cytology, and reproduction. These variations might not be easily distinguished in infraspecific polyploids, which are usually referred to as a “species complex.” Furthermore, possible cryptic species could lurk inside. Below are some examples of these phenomena in *Pteris* species.

*Pteris fauriei* includes sexual diploids and apogamous triploids, *P. fauriei* var. *minor* and *P. fauriei* var. *fauriei*, respectively [46]. Because the triploids have 29 trivalents at meiosis [27], it is likely that they arose via autopolyploidy. Diploids of this species often grow in exposed sites and grasslands and prefer warmer habitats than the triploids [19]. Although only genome dosage distinguishes the diploid and triploid taxa, polyploidy caused ecological differentiation between the taxa.

*Pteris cretica* is widely distributed in warm-temperate and tropical parts of the Old World [65]. It could be one of the most attractive materials in *Pteris* studies. Early studies revealed apogamy and different ploidy levels in the species [11], while subsequent studies reported variable morphology and ploidy levels, including diploids, triploids, and tetraploids [12, 34–36] (Table 1). Although the sexual diploid *P. cretica* has been reported, apogamous diploids, triploids, and tetraploids of this species suggest possible hybridisation events. The presence of a bivalent plus a univalent during meiosis provides distinct evidence of such hybridization [37, 66]. Based on allozyme banding patterns, the triploid *P. cretica* may derive from the diploid apogamous *P. cretica* and the diploid sexual *P. kidoi* [48]. Furthermore, an apogamous intermediate form between the sexual tetraploid *P. multifida* and the apogamous diploid *P. cretica* has been reported [34].

*Pteris ensiformis* occurs in India, Sri Lanka, SE Asia, and Polynesia, although now it is also widely naturalised elsewhere in the tropics [65]. Its cytotypes include diploid, triploid, tetraploid, and pentaploid. The triploid may have arisen from a cross between sexual diploids and sexual tetraploids. The origin of the pentaploid is more complicated to infer; however, hybridisation is suggested by the failure of chromosome pairing at meiosis [41]. *Pteris ensiformis* var. *victoriae* Ba. was reported to be aneuploid ( $2n = 84, 168$ ) [42]. Given the various morphologies of *P. ensiformis*, this species likely underwent multiple hybridisations and possibly contains cryptic species.

*Pteris quadriaurita* is a well-known species complex that includes *P. quadriaurita sensu stricto*, *P. multiaurita*, *P. confusa*, and *P. otaria* [20, 21]. Their radically different morphologies make these taxa difficult to identify. Field

hybridisation experiments have provided evidence that this species complex arose from recurrent hybridisation events, that is, a hybrid swarm. The fact of both sexual and apogamous reproductive systems and diverse ploidy levels, including diploid, triploid, and tetraploid, indicates the undergoing speciation of this complex.

*Pteris deltodon* has diploids and triploids. Furthermore, its aneuploid cytotypes,  $n = 53$  and  $55$ , indicate that it is also hypotetraploid (Table 1). The appearance of aneuploids is limited, with only two records in China and Japan [18, 23]. The species likely arose from allopolyploidy, but it is now a “stable” species because of its sexual reproduction and 64 spores per sporangium [18].

The Chinese ladder brake *P. vittata* shows considerable morphological variations and wide geographical distribution throughout the world. Diverse ploidy levels and reproductive modes have been recorded, including sexual diploids, triploids, sexual and apogamous tetraploids, pentaploids, and hexaploids (Table 1). Furthermore, the spore mother cells show a variety of multivalents, such as  $20I + 26II + 5III$ ,  $9I + 45II + 3III + 2IV$ ,  $29II + 29I$ , and  $29II + 87I$  [17, 18], indicating the occurrence of allopolyploidy. The species involved are not clear, and further taxonomical study on this species complex is needed.

## 5. Conclusion

We reviewed the cytological data of 106 *Pteris* species, and 60% of them exhibit polyploidy, with a frequency of polyploid speciation 38%. This ratio, however, could be underestimated. Since the taxonomy of *Pteris* remains unclear, some cryptic species may exist in the 22% species with intraspecific polyploidy. Integration of further cytological data with reproductive and morphological studies should clarify *Pteris* systematics including species delimitations and also the evolutionary history of its taxa.

## Authors' contribution

Y. S. Chao and H. Y. Liu contributed equally to this work.

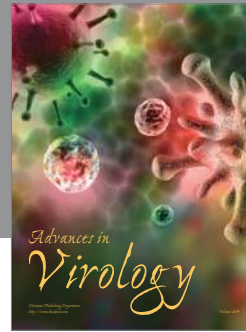
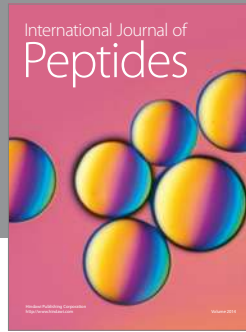
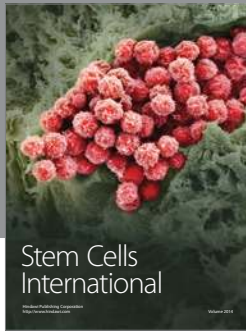
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