Revised Classification of the Species within the *Dryopteris varia* Complex (Dryopteridaceae) in Japan

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The *Dryopteris varia* complex (subg. *Erythrovariae* sect. *Variae* Fraser-Jenk.) is an apogamous fern complex. Most species of the complex are triploid apogamous, show morphological and genetic variation, and present difficulties in their identification. Recent molecular research suggested that the reason that each apogamous species in the complex is so variable is due to reticulate evolution through hybridization between diploid sexual and triploid apogamous species. In this study, we summarized the taxonomic treatment of 11 species within the *D. varia* complex (*D. bissetiana*, *D. chichiimensis*, *D. erythrovaria* sp. nov., *D. hikonensis*, *D. insularis*, *D. kobayashii*, *D. protobissetiana*, *D. sacrosancta*, *D. saxifraga*, *D. subhikonensis* sp. nov., and *D. varia*) on the basis of their genome constituents revealed by molecular analyses.

Key words: apogamous, classification, Dryopteridaceae, hybrid origin, reticulate evolution, the *Dryopteris varia* complex

*Dryopteris* Adans. (Dryopteridaceae), with 225—c. 400 species recognized (Fraser-Jenkins 1986, Pteridophyte Phylogeny Group 2016), is one of the world’s largest genera of ferns. In Japan, 62 species, four varieties and two formae were listed by Iwatsuki (1995). About half of the Japanese species of *Dryopteris* were reported to be apogamous and mostly triploid, rarely diploid or tetraploid (Takamiya 1996).


It is characterized by the markedly elongate lowest bisepalous pinnules on the lowest pinna and the densely scaly petioles. Lin et al. (1995, 2003) recognized five species and two varieties (*D. bissetiana* (Baker) C. Chr., *D. insularis* Kodama var. *insularis*, *D. insularis* var. *chichiimensis* (Nakai ex H. Itô) H. Itô, *D. pacifica* (Nakai) Tagawa, *D. sacrosancta* Koidz., *D. saxifraga* H. Itô, and *D. varia* (L.) Kuntze). Serizawa (2009) separated *D. kobayashii* Kitag. from *D. sacrosancta* sensu lato on the basis that the former has thinner fronds and falcate pinnae. *Dryopteris protobissetiana* K. Hori et N. Murak. from Yakuushima, Japan, is similar to *D. bissetiana* in having slightly bullate scales and dark green laminae, but differs in its flat, serrate margins at the apex of the upper pinnae. At present, seven species and two varieties are recognized in the *D. varia* complex.

Most species of the *D. varia* complex, such as *D. bissetiana* (Hirabayashi 1967, Nakato et al.
1995, Lin et al. 2003, Lee et al. 2006), Dryopteris insularis var. chichisimensis (Lin et al. 2003), D. pacifica (Hirabayashi 1970, Lin et al. 1992; Nakato et al. 1995, Lin et al. 2003, Lee et al. 2006), D. sacrosancta (Mitui 1965, 1968, Hirabayashi 1969, Nakato et al. 1995, Lin et al. 2003, Lee et al. 2006, Ebihara et al. 2014), are triploid apogamous (Table 1). Only two species are known to be diploid sexual; D. saxifraga (Hirabayashi 1967, Mitui 1975, Lee et al. 2006) and D. protobissetiana (Hori et al. 2014). Ebihara et al. (2014) recently reported that D. varia also has a diploid sexual cytotype in Taiwan. A few species, such as D. bissetiana (Hirabayashi 1966, Lee et al. 2006), D. pacifica (Lin et al. 1992, Nakato et al. 1995), and D. varia (Hirabayashi 1966, 1967, 1974) have been reported as having diploid cytotypes, in addition to triploid apogamous cytotypes.

Hori et al. (2014, in prep.) clearly showed that the classification of the apogamous species of the D. varia complex by Iwatsuki (1995) had issues, especially for D. pacifica, because three genotypes (α, β, and γ types), which have completely different genome constituents on the basis of the molecular analyses using five nuclear markers, were recognized within this species. The scientific name of D. pacifica (Nakai) Tagawa, based on Polystichum pacificum Nakai (1925) from Japan, also needs revision, since it is a later homonym of D. pacificum Christ (1912), a name for a Samoan species. Christ (1912) commented that D. pacifica was similar to D. dissecta, which is now placed in Tectaria (Xing et al. 2013). The separation of D. kobayashii from D. sacrosancta sensu lato (Serizawa 2009) was supported by molecular data of Hori et al. (2014). To classify this complex, it is important to elucidate the genetic constitution and variation within each species, especially in the apogamous species.

Recent molecular research suggested that the Dryopteris varia complex experienced reticulate evolution (Lee & Park 2013, Hori et al. 2014, in prep.) through hybridization between diploid sexual species and triploid apogamous species. The nucleotide sequences of the five nuclear markers from five diploid sexual species of the D. varia complex and related species were categorized in five monophyletic groups of sequences (A–E, M): A, D. varia; B, D. saxifraga; C, D. protobissetiana; D, D. caudipinna; E, D. chinensis; and M, D. insularis (only the diploid apogamous type is known from Japan). It was also shown that each triploid apogamous species of the D. varia complex contained two or three nucleotide sequences of the nuclear markers from two or three of the above diploid sexual species: D. bissetiana, B + C; D. pacifica (α), A + C; D. pacifica (β), A + B + C; D. pacifica (γ), A + C + D; D. kobayashii, B + C + E; D. sacrosancta, A + C + E; D. chichisimensis, A + C + M (Fig. 1). Therefore, these apogamous species likely underwent complicated reticulate evolution among the diploid sexual species and the triploid apogamous species. This phenomenon has led to the difficulty of identifying species in the D. varia complex.

In this study, the species of the D. varia complex in Japan were recircumscribed according to morphological characteristics, reproductive mode, chromosome number, and the genomic constitution of each species.

**Materials and Methods**

**Observation of morphological characteristics**

To classify the members of the Dryopteris varia complex, we first noted differences in the following morphological characteristics: size of lamina, stipe, lamina shape, color and sheen of the lamina, presence/absence of serrations on the margins of the pinnae, type shape and color of the indusia, and form of the scales. We also examined the type specimens of the species of the D. varia complex and sect. Variae in Japan and China.

**Cytological observation and estimation of reproductive mode**

We observed the mitotic chromosome numbers of each member of the complex. Plant materials for the cytological observation are listed in
To observe mitotic chromosomes, root tips from living stocks were pretreated with 0.004-M 8-hydroxyquinoline for 7 h at approximately 15–18 °C. After fixation overnight in ethanol and acetic acid (3:1), the root tips were hydrolyzed in a mixed solution of 1N HCl and 45% acetic acid (1:1) at 60 °C for 10 min before being mashed in a 2% aceto-orcein solution. The chromosomes were observed under a Leica DM2500 microscope and then photographed using a Leica MC170 HD digital camera.

To estimate the reproductive mode of each sample or herbarium specimen, the number of spores in each sporangium were counted. We examined at least five sporangia with normal spores in each specimen. Samples with 64 spores per sporangium were estimated to be sexually reproducing; samples with 32 spores per sporangium were estimated to be apogamous (Manton 1950).

**Classification with genome constitution of each species**

We treated diploid sexual taxa with distinct chloroplasts and nuclear genomes as distinct species. Apogamous cytotypes with different nuclear genome constituents were also treated as independent species. *Dryopteris pacifica* (α) exhibited several genome constituents; ACC, AAC or AC. *Dryopteris bissetiana* had a BCC or B/C constitution. BBC was not recognized because of low genetic variation in *D. saxifraga* (B). However, in this study, we treated these genotypes as belonging to the same species because it was impossible to distinguish them morphologically. Autopolyploid apogamous cytotypes were treated as the same species as the diploid sexual cyto-

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Reproductive mode</th>
<th>Ploidy level</th>
<th>Chromosome number</th>
<th>Locality of materials</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. bissetiana</em></td>
<td>apogamous</td>
<td>2x n = 82</td>
<td>Japan</td>
<td>Hirabayashi (1966)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3x n = 123</td>
<td>Japan</td>
<td>Hirabayashi (1967), Lin et al. (2003)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>China</td>
<td>Nakato et al. (1995)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sexual</td>
<td>4x n = 82</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
<td></td>
</tr>
<tr>
<td><em>D. insularis</em></td>
<td>apogamous</td>
<td>2x n = 82</td>
<td>Japan</td>
<td>Lin et al. (2003)</td>
<td></td>
</tr>
<tr>
<td><em>D. chichisimens</em></td>
<td>apogamous</td>
<td>2x n = 82</td>
<td>Japan</td>
<td>Lin et al. (2003)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>China</td>
<td>Nakato et al. (1995)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
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<tr>
<td><em>D. pacifica</em></td>
<td>apogamous</td>
<td>n = 123</td>
<td>Japan</td>
<td>Hirabayashi (1970)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>3x n = 123, 2n = 123</td>
<td>Japan</td>
<td>Lin et al. (1992)</td>
<td></td>
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<td></td>
<td></td>
<td>2n = 123</td>
<td>China</td>
<td>Nakato et al. (1995)</td>
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<td></td>
<td>2n = 123</td>
<td>Japan</td>
<td>Lin et al. (2003)</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
<td></td>
</tr>
<tr>
<td><em>D. protobissetiana</em></td>
<td>sexual</td>
<td>2x n = 82</td>
<td>Japan</td>
<td>Hori et al. (2015)</td>
<td></td>
</tr>
<tr>
<td><em>D. sacrosancta</em></td>
<td>apogamous</td>
<td>3x n = 123</td>
<td>Japan</td>
<td>Mitui (1965, 1968), Hirabayashi (1969)</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>China</td>
<td>Nakato et al. (1995)</td>
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<td></td>
<td></td>
<td>2n = 123</td>
<td>Japan</td>
<td>Lin et al. (2003)</td>
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<td>2n = 123</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
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<tr>
<td><em>D. saxifraga</em></td>
<td>sexual</td>
<td>2x n = 41</td>
<td>Japan</td>
<td>Hirabayashi (1967), Mitui (1975)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>apogamous</td>
<td>3x n = 123</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
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<tr>
<td></td>
<td>sexual</td>
<td>2x n = 82</td>
<td>Taiwan</td>
<td>Ebihara et al. (2014)</td>
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<tr>
<td></td>
<td></td>
<td>4x n = 82</td>
<td>Taiwan</td>
<td>Tsai &amp; Shieh (1975, 1985)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 82</td>
<td>Japan</td>
<td>Hirabayashi (1966, 1967, 1974)</td>
<td></td>
</tr>
<tr>
<td><em>D. varia</em></td>
<td>apogamous</td>
<td>3x n = 123</td>
<td>Japan</td>
<td>Mitui (1966, 1968), Hirabayashi (1970)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>China</td>
<td>Nakato et al. (1995)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>Japan</td>
<td>Lin et al. (2003)</td>
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<td></td>
<td></td>
<td>2n = 123</td>
<td>Taiwan</td>
<td>Ebihara et al. (2014)</td>
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<tr>
<td></td>
<td></td>
<td>2n = 123</td>
<td>Korea</td>
<td>Lee et al. (2006)</td>
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</tbody>
</table>
types sharing the same genome because there were no significant differences in morphological characteristics.

In this study, we examined herbarium specimens of the Dryopteris varia complex deposited at MAK, MBK, PE, and TNS. Voucher specimens whose genomic constituents had been fully elucidated were useful especially for describing their morphology and geographic distribution.

Results & Discussion

Cytological observation and estimation of reproductive mode

We estimated the chromosome number of the Dryopteris varia complex as $2n = 123$ (apogamous) in D. bissetiana; $2n = 123$ (apogamous) in D. chichisimensis; $2n = 123$ (apogamous) in D. erythrovaria (newly reported); $2n = 82$ (apogamous) in D. varia complex and revised scientific names of each species. Yellow squares indicate diploid progenitors within the D. varia complex; blue squares indicate related diploid species outside of complex. Ellipses indicate apogamous species. Letters in squares and ellipses indicate genome constituents of nuclear markers. Genome constituents such as A+A+C or A+C+C, are shown as A+C. Letters above squares or ellipses indicate cpDNA genotypes. Red and black arrows indicate maternal and paternal species, respectively. Arrows with red dashes indicate apogamous maternal species. Two courses of hybridization can be supposed related to the formation of D. subhikonensis and are indicated as (a) and (b). *Only diploid apogamous D. insularis is known from Japan.
Table 2. Reproductive system, ploidy level and chromosome numbers of the *Dryopteris varia* complex determined in this study.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Reproductive mode</th>
<th>Ploidy level</th>
<th>Chromosome number</th>
<th>Locality</th>
<th>Voucher</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>D. bissetiana</em></td>
<td>apogamous</td>
<td>2x</td>
<td>2n = 123</td>
<td>Kagawa Pref.: Ayata county, Ayagawa town</td>
<td>K. Hori 532</td>
</tr>
<tr>
<td><em>D. chichisimens</em></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Tokyo Pref.: Ogasawara Is. (including Kazan-</td>
<td>K. Hori 1351</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>retto Is.): Chichijima Is., Higashidaira</td>
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<tr>
<td><em>D. erythrovaria</em></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Tokyo Pref.: Inagi city, Momura</td>
<td>K. Hori 485</td>
</tr>
<tr>
<td>(pacific γ)</td>
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<td><em>D. hikonensis</em></td>
<td>apogamous</td>
<td>2x</td>
<td>2n = 82</td>
<td>Kagawa Pref.: Ayata county, Ayagawa town</td>
<td>K. Hori 531</td>
</tr>
<tr>
<td>(pacific α)</td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Kagawa Pref.: Takamatsu city, Yashima</td>
<td>K. Hori 517</td>
</tr>
<tr>
<td><em>D. insularis</em></td>
<td>apogamous</td>
<td>2x</td>
<td>2n = 82</td>
<td>Tokyo Pref.: Ogasawara Is. (including Kazan-</td>
<td>K. Hori 1350</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>retto Is.): Chichijima Is., Mt. Asahiyama</td>
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<tr>
<td><em>D. kobayashii</em></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Tokyo Pref.: Inagi city, Momura</td>
<td>K. Hori 8</td>
</tr>
<tr>
<td><em>D. protobissetiana</em></td>
<td>sexual</td>
<td>2x</td>
<td>2n = 82</td>
<td>Saga Pref.: Takeo city, Yamauchi town</td>
<td>K. Hori &amp;</td>
</tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td>Y. Inoue 490</td>
</tr>
<tr>
<td><em>D. sacrosancta</em></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Saga Pref.: Takeo city, Yamaguchi town</td>
<td>K. Hori 1756</td>
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<td><em>D. saxifraga</em></td>
<td>sexual</td>
<td>2x</td>
<td>2n = 82</td>
<td>Akita Pref.: Sennboku city, Takigawaeru valley</td>
<td>K. Hori &amp;</td>
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<td>Y. Inoue 1494</td>
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<td><em>D. subhikonensis</em></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Tokyo Pref.: Akiruno city, Youzawa</td>
<td>K. Hori 1146</td>
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<tr>
<td>(pacific β)</td>
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<tr>
<td><em>D. varia</em></td>
<td>sexual</td>
<td>2x</td>
<td>2n = 82</td>
<td>TAIWAN. Taipei city.: Urai</td>
<td>K. Hori 1393</td>
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<tr>
<td></td>
<td>apogamous</td>
<td>3x</td>
<td>2n = 123</td>
<td>Saga Pref.: Kashima city</td>
<td>K. Hori 495</td>
</tr>
</tbody>
</table>

Key to the Japanese species of the *Dryopteris varia* complex (*Dryopteris* subg. *Erythrovariae*).

1a. Sori born only on upper part of lamina ................................................................. 5. *D. insularis*
1b. Sori born on whole lamina ...................................................................................... 2
2a. Scales deflexed ........................................................................................................... 9. *D. saxifraga*
2b. Scales ascending ....................................................................................................... 3
3a. Lamina papyraceous; center of indusia often red ....................................................... 3. *D. erythrovaria*
3b. Lamina herbaceous or coriaceous; center of indusia translucent .............................. 4
4a. Lamina herbaceous ..................................................................................................... 4
4b. Lamina coriaceous ...................................................................................................... 6
5a. Lamina narrowly triangular (length / width = 3/2–2/1); apex of pinnae curved, obtuse ... 6. *D. kobayashii*
5b. Lamina pentagonal (length / width = 4/3–3/2); apex of pinnae straight, acute .......... 8. *D. sacrosancta*
6a. Scales on costa flat .................................................................................................... 11. *D. varia*
6b. Scales on costa bullate ............................................................................................... 7
7a. Scales sub-sparsely on rachis; endemic to the Bonin Islands ........................................ 2. *D. chichisimensis*
7b. Scales dense on rachis; distributed outside the Bonin Island ........................................ 8
8a. Scales on upper part of petiole bullate ......................................................................... 7. *D. protobissetiana*
8b. Scales on upper part of petiole flat ........................................................................... 9
9a. Margin of apex of upper pinnae entire ....................................................................... 1. *D. bissetiana*
9b. Margin of apex of upper pinnae deeply or shallowly serrate ........................................ 10
10a. Margin of apex of upper pinnae deeply serrate; margin of indusia ciliate or entire .......... 4. *D. hikonensis*
10b. Margin of apex of upper pinnae shallowly serrate; margin of indusia entire ............. 10. *D. subhikonensis*

*Key.*

Classification based on morphological characteristics and genome constitution of each species

- We treated the taxonomy of 11 species within the *Dryopteris varia* complex: *D. bissetiana, D.*
chichisimensis, 

\( \textit{Dryopteris erythrovaria} \) sp. nov. = \textit{D. pacifica} (\( \gamma \)), \textit{D. hikonensis} = \textit{D. pacifica} (\( \alpha \)), 

\( \textit{D. insularis} \), \textit{D. kobayashii}, \textit{D. protobissetiana}, 

\( \textit{D. sacrosancta} \), \textit{D. saxifraga}, \textit{D. subhikonensis} 

sp. nov. = \textit{D. pacifica} (\( \beta \)), and \textit{D. varia}.

**Taxonomic treatment**

1. 

\( \textit{Dryopteris bissetiana} \) (Baker) C. Chr., Ind. Fil. 245. 1905. —Fig. 2


Herbs, terrestrial, evergreen; rhizome erect, or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, ascending or deflexed, apex filiform; scales at base of petiole black, margin translucent, flat, narrow, base brown; scales on upper petiole black, flat, spreading, base brown; scales on rachis and costa black, bullate, base brown; lamina bipinnate, occasionally tripinnate at base, narrowly triangular, gradually narrowed to apex, 20–50 cm long, 10–30 cm wide, dark green or whitish green, soft coriaceous, surface shiny or dull, margins recurved; pinnae curved, apex obtuse; apical margin of pinnae entire; lowest basiscopic pinnae on lowest pinna barely longer than second lowest; sori round, medial; indusia reniform or circular, margin entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number \( 2n = 123 \) (Fig. 13a), triploid apogamous (diploid apogamous type unknown in Japan).

**Notes.** \( \textit{Dryopteris bissetiana} \) is an apogamous species of hybrid origin between \( \textit{D. protobissetiana} \) and \( \textit{D. saxifraga} \). It is morphologically similar to \( \textit{D. protobissetiana} \), \( \textit{D. hikonensis} \), and \( \textit{D. subhikonensis} \). However, \( \textit{D. bissetiana} \) differs from them in having pinnae with an entire margin, entire indusia, and gradually narrowed lamina. It is also sometimes similar to \( \textit{D. saxifraga} \). Such intermediate form have been identified as \( \textit{D. saxifragivaria} \) Nakai; however, both \( \textit{D. bissetiana} \) and \( \textit{D. saxifragivaria} \) are of hybrid origin between \( \textit{D. protobissetiana} \) and \( \textit{D. saxifraga} \). They share the same genomes from the two diploid sexual parental species. We therefore treat them as \( \textit{D. bissetiana} \).

From South Korea, Lee et al. (2006) reported diploid apogamous \( \textit{Dryopteris bissetiana} \). Lee & Park (2013) reported several sequences of nuclear \( \textit{Pgi}C \) from \( \textit{D. bissetiana} \). However, all of their sequences nested within the clade of diploid sexual \( \textit{D. saxifraga} \). Their sample may not be the diploid apogamous \( \textit{D. saxifraga} \) because its chloroplast DNA coincided with that of \( \textit{D. protobissetiana} \). It therefore seems possible that they failed to select the nuclear \( \textit{Pgi}C \) sequences belonging to \( \textit{D. protobissetiana} \). Only the triploid apogamous cytotype has been found in \( \textit{D. bissetiana} \) in Japan, even though as many as 25 cytological samples have been analyzed using ploidy analysis or observations of the chromosomes.

Lee et al. (2006) distinguished \( \textit{Dryopteris saxifragivaria} \) Nakai from \( \textit{D. bissetiana} \), because of intermediate morphological characteristics between \( \textit{D. bissetiana} \) and \( \textit{D. saxifraga} \), in Korea. However, continuous morphological variation was observed between \( \textit{D. bissetiana} \) and \( \textit{D. saxifragivaria} \) in Japan, making it difficult to distinguish them morphologically. We conclude that they are \( \textit{D. bissetiana} \) because they share the same genomic constitution (genomes from diploid sexual \( \textit{D. saxifraga} \) and \( \textit{D. protobissetiana} \)).
Weng (1989) reported a tetraploid sexual type ($n = 82$) of *Dryopteris bissetiana* from China, but it did not cite a voucher specimen and we are unable to confirm the identification.

**Habitat and distribution.** *Dryopteris bissetiana* occurs in both deciduous and broad-leaved evergreen forests and in secondary forests in Japan (Hokkaido, Honshu, Shikoku and Kyushu) (Fig. 14-la.), Korea, and mainland China.

**Japanese name.** Yama-itachishida.


Habitat and distribution. *Dryopteris bissetiana* occurs in both deciduous and broad-leaved evergreen forests and in secondary forests in Japan (Hokkaido, Honshu, Shikoku and Kyushu) (Fig. 14-la.), Korea, and mainland China.

**Japanese name.** Yama-itachishida.


2. **Dryopteris chichisimensis** Nakai ex H. Itô in Bot. Mag. Tokyo 49: 435. 1935. — Fig. 3


Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome and costa, sub-sparse on petiole and rachis; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, flat, base narrow and brown; scales on upper part of petiole and rachis brown, narrow, flat at base; scales on costa brown, bullate; lamina bipinnate, occasionally spininate at base, widely triangular, gradually narrowed to apex, 10–30 cm long, 20–50 cm wide, dark green, soft coriaceous, surface shiny, margin flat; apex of pinnae curved; apical margin of pinnules deeply serrate; lowest bisiscopic pinnules on lowest pinna slightly longer than second one; sori round, medial; indusia reniform or circular, margins ciliate, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$ (Fig. 13b), triploid.
Fig. 2. *Dryopteris bissetiana* (Baker) C. Chr. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 332*, MAK).
Fig. 3. *Dryopteris chichisimensis* Nakai ex H. Itô 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 1351*, MAK).
apogamous.

Habitat and distribution. Subtropical wet evergreen forests. Endemic to Japan (Ogasawara Islands, including Kazan-retto) (Fig. 14-1b.).


Notes. Dryopteris chichisimensis is an apogamous species of hybrid origin between D. hikonensis and D. insularis. The parents of D. chichisimensis are apogamous. However, the sexual type of D. insularis may have existed in the past. The genome constitution of D. chichisimensis consists of those from D. varia, D. protobissetiana and D. insularis. Dryopteris chichisimensis is hardly distinguishable from D. hikonensis based only on morphological traits. It is therefore recommended that the nuclear DNA constitution be determined when reporting new localities. Dryopteris chichishimensis often differs from D. hikonensis in the sparser scales on the petiole.

Iwatsuki (1995) commented on the distribution of Dryopteris chichishimensis in the Izu-Islands without indicating voucher specimens. We found newly collected specimens of D. chichisimensis in MAK from Kita-iwoto Island in addition to specimens from Chichijima. Previous reports have cited this species as Chichijima-Benishida, its Japanese vernacular name. However, it does not have an affinity to Benishida (the D. erythrosora complex), but rather to Itachishida (the D. varia complex). Therefore, a new Japanese name, Chichijima-Itachishida is proposed here.


3. Dryopteris erythrovara K. Hori & N. Murak., sp. nov. — Fig. 4

Dryopteris erythrovara K. Hori & N. Murak. is an apogamous species of hybrid origin between D. hikonensis and D. caudipinna. Its genome consists of those from D. varia, D. protobissetiana, and D. caudipinna. This species is characterized by the combination of large papyraceous lamina and red indusia. A large papyraceous lamina is one of the characteristics of D. caudipinna. Red indusia are also characteristic of D. caudipinna, though it sometimes has translucent indusia. The genomic constitution mentioned above may be the reason for the sometimes translucent indusia of D. erythrovara, like other members of the D. varia complex.

Typus: Japan, Tokyo, Inagi City, Momura, approximately 100 m altitude, on soil cliff near dry road in forests, K. Hori 2478, collected on June 18, 2016 (holo-MAK446760).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 20–50 cm long; scales lanceolate, apex filiform; scales at base of petiole black, flat, base narrow and brown scales on upper part of petiole and rachis black, flat, base spreading and brown; scales on costa black, base bullate and brown; lamina bipinnate to tripinnatifid, widely triangular, subabruptly narrowing to apex, 30–80 cm long, 20–40 cm wide, dark green or yellowish green, papyraceous, surface shiny or dull, margin flat; pinnae straight, apex obtuse; apical margin of pinnules deeply serrate; lowest basiscopic pinnules on lowest pinna slightly longer than second lowest pinnule; sori round, medial; indusia red in center or translucent, reniform or circular, almost entire or rarely margins ciliate, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number 2n = 123 (Fig. 13c), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests and secondary forests in temperate zone. Japan (Honsyu, Shikoku, and Kyushu) (Fig. 14-1c.), Korea (Cheju Island) and eastern China.


4. Dryopteris hikonensis (H. Itō) Nakaikke, New Fl. Jap. 841. 1992. —Fig. 5


Dryopteris immixta Ching in Fl. Tsinling. 2: 225, pl. 41, f. 1–2. 1974. syn. nov. Type: China, Jiangsu, Pao-hwa Shan (C. Pei 3464, Nov. 18, 1933, PE 44572 — holo-).


Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales on rhizome, petiole, rachis and costa dense; petiole 10–40 cm long; scales lanceolate, ascending, apex filiform; scales at base of petiole, upper petiole, and rachis black to blackish brown, flat, base...
Fig. 4. *Dryopteris erythrovaria* K. Hori & N. Murak. 1-4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from type specimen, *K. Hori* 2478, MAK).
Fig. 5. *Dryopteris hikonensis* (H. Itô) Nakaike 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface of upper pinnae. 6: abaxial surface. 7: indusium. (drawn from K. Hori 647, MAK).
spreading and brown; scales on costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, widely triangular, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, dark, yellowish or whitish green, soft coriaceous, surface shiny or dull, margin flat; pinnules curved, apex acute; apical margins of pinnules deeply serrate; lowest basiscopic pinnule on lowest pinna slightly longer than second lowest pinnule; sori round, medial; indusia reniform or circular, entire or margins ciliate, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number 2n = 82 (diploid apogamous, Fig. 13d) or 2n = 123 (triploid apogamous, Fig. 13e).

Habitat and distribution. Warm temperate to subtropical evergreen forests and secondary forests in temperate to subtropical zones. Japan (Honshu, Shikoku, Kyushu and Ryukyu) (Fig. 14-1d.), Korea, and eastern China.

Japanese name. O-Itachishida.

Notes. Dryopteris hikonensis is an apogamous species of hybrid origin between D. varia and D. protobissetiana. It differs from D. varia in having slightly bullate scales on the rachis and from D. protobissetiana in having flat scales on the petiole and lowest basiscopic pinnules on the lowest pinna slightly longer than second basiscopic pinnule.

Dryopteris lungjiensis, D. pudouensis, D. quadrifida and D. yushanensis are treated as synonyms of D. pacifica by Zhang et al. (2013), based on morphological similarities. However, we treat them as synonyms of D. hikonensis in this study because D. pacifica is an illegitimate later homonym. In Zhang et al. (2013), D. consimilis and D. fuyangensis are treated as synonyms of D. varia; D. paravaria and D. shanghaensis are treated as synonyms of D. setosa; and D. tieanzuensis is treated as a synonym of D. sacrosancta. These names can be regarded as synonyms of D. hikonensis based on morphological similarities. In addition, D. immixta (triploid apogamous species, Weng 1989) can also be regarded as a synonym of D. hikonensis. Genome constituents of the members of the D. varia complex in China still need to be clarified.

5. Dryopteris insularis Kodama, Icon. Pl. Koisik. 2: t. 49. 1914.—Fig. 6


Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome and costa, sub-sparse on petiole and rachis; petiole 20–35 cm long; scales brown, lanceolate, ascending, apex filiform; base of scales at base of petiole, upper petiole, and rachis flat, narrow; base of scales on costa bullate; lamina bipinnate to tripinnatifid, widely triangular, gradually narrowing to apex, 35–45 cm long, 25–35 cm wide, yellowish green, soft coriaceous, surface shiny, margin flat; pinnae straight, apex obtuse; pinnae obtuse, apical margin finely serrate; lowest basiscopic pinnae on lowest pinna barely longer than second lowest pinna; sori round, borne on upper part of lamina, sori-bearing pinnae contracted; sori round, medial; indusia reniform, glandular, margins ciliate, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 82$, diploid apogamous (Fig. 13f).

Habitat and distribution. Subtropical dry evergreen forests. Endemic to Japan (Bonin Islands) (Fig. 14-le.).

Japanese name. Munin-Itachishida.

Notes. Dryopteris insularis is characterized by having sori borne only on the upper part of the lamina and indusia with glandular ciliate margins. Its genome differs from other sexual species and apogamous species.

In previous studies, D. insularis cited as Munin-Benishida. However, as indicated for D. chichisimensis, it has no affinity with Benishida (the D. erythrosora complex), but instead definitely belongs to the Itachishida group (the D. varia complex). Thus, the new Japanese name, Munin-Itachishida, is proposed here.


Type: China, Fengtian, Hsiao-ping-tao. (M. Kobayashii 39. October 9, 1932, TI).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, sparse on petiole, rachis and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, margin translucent, base flat, narrow and brown, scales on upper petiole black, flat, narrow, base brown; scales on rachis black, flat, spreading, base brown; scales on costa brown, bullate; lamina bipinnate to tripinnatifid, narrowly triangular, gradually narrowing to apex, 20–40 cm long, 10–20 cm wide, yellowish green, herbaceous, surface dull, margin flat; pinnae curved, apex obtuse; pinnae entire or shallowly serrate or apical margin serrate; lowest basiscopic pinnae on lowest pinna barely longer than second basiscopic pinna; sori round, borne on upper part of lamina, sori-bearing pinnae contracted; sori round, medial; indusia translucent, reniform or circular, margins entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$, triploid apogamous (Fig. 13g).
Fig. 6. *Dryopteris insularis* Kodama 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from K. Hori 1350, MAK).
Fig. 7. *Dryopteris kobayashii* Kitag. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from K. Hori 8, MAK).
egree forests and secondary forests in temperate zone. Japan (Honsyu, Shikoku, and Kyushu) (Fig. 14-1f), Korea, and eastern China.

**Japanese name.** Ryo-to-Itachishida.

**Notes.** *Dryopteris kobayashii* is an apogamous species of hybrid origin between *D. bissetiana* and *D. chinensis*. Its genome comprises those from *D. saxifraga*, *D. protobissetiana* and *D. chinensis*. *Dryopteris kobayashii* is similar in gross morphology to *D. sacrosancta*, but is distinguishable by its narrowly triangular lamina, curved pinnae with an obtuse apex and always whitish green young pinnules.


CHINA. Shandong Prov.: Mt. Kunyu J. X. Li 97 (PE).

KOREA. Hong dao.: X. C. Zhang 3673 (PE).

7. *Dryopteris protobissetiana* K. Hori et N. Murak. in Acta Phytotax. Geobot. 66: 47–57, 2015. —Fig. 8

Type: Japan, Kagoshima Pref., Yakushima, Mt. Myo jo, 300 m alt, K. Hori 913 (holo-, MAK).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–30 cm long; scales at base of petiole black, flat, spreading, base brown; scales on upper petiole black, base brown, bullate; scales on rachis and costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, narrowly triangular, gradually narrowing to apex, 10–40 cm long, 10–20 cm wide, dark green, soft coriaceous, surface shiny, margin flat; pinnate straight, apex obtuse; apical margin of pinnules finely serrate; lowest basiscopics pinnules on lowest pinna barely longer than second basiscopics pinnule; sori round, medial or relatively nearer to margin than to midrib; indusia reniform or circular, margins entire or erose, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 64; chromosome number 2n = 82 (Fig. 13h) diploid sexual.

**Habitat and distribution.** Warm temperate evergreen forests. Japan (southern part of Yakushima, Kagoshima Pref., Kyushu) (Fig. 14-2g).

**Japanese name.** Moto-Itachishida.

**Notes.** *Dryopteris protobissetiana* is most similar to *D. bissetiana* in having slightly bullate scales and a dark green lamina surface, but differs from it in having flat, serrate margins at the apexes of the upper pinnae and flat margins of the lamina.

**Specimens examined.** JAPAN. KYUSHU. Kagoshima Pref. (Yakushima): Hanage river, T. Nakaie s.n., Aug. 17, 1982 (TNS); Hann-yama, K. Hori 1756 (MAK); Kawahara, K. Hori 1836 (MAK); Koshima, S. Tagane TF269 (TNS); Koyouji, K. Hori 1863 (MAK); Mt. Mochou-dake, K. Hori 917 (MAK); Mt. Myojo, K. Hori 906 (MAK), K. Hori 913 (MAK); Nakabase, K. Hori 1851 (MAK); O-ko, K. Hori 1872 (MAK); Yudomari, T. Oka & K. Hori 1344 (MAK).
8. Dryopteris sacrosancta Koidz. in Bot. Mag. Tokyo 38: 108. 1924.—Fig. 9


Dryopteris bissetiana var. tenerifrons H. Itô in Bot. Mag. Tokyo 50: 37. 1936. Type: Japan, Prov. Aki (Hiroshima Prefecture), Miyazima (U. Faurie 444, T1 – holo-).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, sparse on petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, margin translucent, flat, spreading, base brown; scales on upper petiole, rachis, and costa black, flat, spreading, base brown; lamina bipinnate to tripinnate, pentagonal, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, yellowish green, herbaceous, surface weakly shiny or dull, margin flat; pinnae straight, apex acute; apical margins of pinnules finely serrate; lowest basiscopic pinnules on lowest pinna slightly longer than second basiscopic pinnule; sori round, medial; indusia translucent, reniform or circular, margins entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number 2n = 123 (Fig. 13i), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests. Endemic to Japan (Honshu, Shikoku and Kyushu) (Fig. 14-2h.).


Notes. Dryopteris sacrosancta is an apogamous species of hybrid origin between D. hikoinensis and D. chinensis. Its genome consists of those from D. varia, D. protobissetiana and D. chinensis. Dryopteris sacrosancta and D. kobayashii are similar in having herbaceous, yellowish green lamina. The scales of these two species are sparser than in other members of the D. varia complex. However, D. sacrosancta is distinguished from D. kobayashii by having widely triangular lamina, pinnae with a straight, acute apex, and sometimes reddish brown young pinnules.

Fig. 8. *Dryopteris protobissetiana* K. Hori et N. Murak. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from type specimen, *K. Hori* 906, MAK).
Fig. 9. *Dryopteris sacrosancta* Koidz. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from the specimen of K. Hori & Y. Inoue 490, MAK).
9. Dryopteris saxifraga H. Itô in Bot. Mag. Tokyo. 50: 125 (1936). —Fig. 10


Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis and costa; petiole 5–20 cm long; scales lanceolate, deflexed, apex filiform; scales at base of petiole black, flat, spreading, base brown; scales on upper petiole, rachis and costa usually black, rarely brown, base bullate and brown; lamina bipinnate, occasionally tripinnate at base, oblong, gradually narrowing to apex, 5–30 cm long, 5–15 cm wide, whitish green, soft coriaceous, surface dull, margins recurved; pinnae curved, apex obtuse; pinnales obtuse, apical margin entire or sinuate; lowest basiscopic pinnales on lowest pinna rarely longer than second basiscopic pinnale; sori round, medial; indusia reniform or circular, margins entire or erose, translucent, 1.5–2 mm in diameter; spores per sporangium 64; chromosome number 2n = 82 (Fig. 13j), diploid sexual.

Notes. Lee & Park (2006) reported the triploid apogamous cytotype of Dryopteris saxifraga from South Korea. Lee & Park (2013) reported sequences of nuclear PgiC from the triploid apogamous D. saxifraga, which formed a clade with the diploid sexual D. saxifraga in their PgiC molecular tree. Dryopteris bissetiana is sometimes similar to D. saxifraga in gross morphology because D. bissetiana is of hybrid origin between D. saxifraga and D. protobissetiana. The samples of Lee & Park (2013) were confirmed to be triploid apogamous. Only diploid sexual cytotypes have been found in D. saxifraga in Japan. These facts suggest that the triploid apogamous D. saxifraga in Lee & Park (2013) might be D. bissetiana.

Habitat and distribution. Deciduous broad-leaved forests. Japan (Hokkaido, Honshu, Shikoku and Kyushu) (Fig. 14-2i), Korea, and north-east China.

Japanese name. Iwa-Itashishida.

Notes. Dryopteris saxifraga, a sexual diploid with a distinct genome, is characterized by having pinnales with entire margins and oblong lamina.

Dryopteris subhikonensis K. Hori & N. Murak., sp. nov. —Fig.11

Dryopteris subhikonensis K. Hori & N. Murak. is an apogamous species of hybrid origin between D. hikonensis and D. saxifraga or between D. bissetiana and D. varia. Its genome consists of those from D. protoyoburiana, D. saxifrage, and D. varia. It is hardly distinguishable from D. hikonensis based only on morphology. It is therefore recommended that the nuclear DNA constitution be determined before reporting new localities. Dryopteris subhikonensis usually differs from D. hikonensis in having shallowly serrate or entire pinnules, as well as entire indusia. Dryopteris hikonensis is common in forests along the Pacific Ocean and Seto Inland Sea, whereas D. subhikonensis is in the mountains in southeastern Honshu and in forests along the Sea of Japan.

Typus: Japan, Saitama, Han-nou City, Shirako, 200 m, on soil cliff near dry road in forests, K. Hori 2270, July 2, 2016 (holo-, MAK 449117).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves espineuse; scales dense on rhizome, petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole and upper petiole black, flat, narrow, base brown; scales on rachis black, flat, spreading, base brown; scales on costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, widely triangular, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, dark green, soft coriaceous, surface weakly shiny, margin flat; pinnae curved, apex acute; apical margins of pinnules shallowly serrate or entire; lowest basiscopic pinnules on lowest pinna slightly longer than second basiscopic pinna; sori round, medial; indusia reniform or circular, margins entire, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number 2n = 123 (Fig. 13k), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests and secondary forests in temperate zone. Endemic in Japan (southeastern and south Japan sea side of Honshu) (Fig. 14–2j).

Japanese name. Iwa-O-Itachishida.


11. Dryopteris varia (L.) Kuntze, Revis. Gen. Pl. 2: 814. 1891. —Fig. 12

Polypodium varium L., Sp. Pl. 2: 1090. 1753. Type: China, P. Osbeck. s.n., 1.1.9.75, SB! — neo- designated
Fig. 10. *Dryopteris saxifraga* H. Itô 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori & Y. Horii 1494*, MAK).
Fig. 11. *Dryopteris subhikonensis* K. Hori et N. Murak. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface of upper pinnae. 6: abaxial surface. 7: indusium. (drawn from type specimen, *K. Hori* 2270, MAK).
Fig. 12. *Dryopteris varia* (L.) Kuntze 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 1387*, MAK).


Fig. 14-1. Distribution maps of the Dryopteris varia complex in Japan. a, D. bissetiana; b, D. chichisimensis; c, D. erythrovaria; d, D. hikonensis; e, D. insularis; f, D. kobayashii.
Fig. 14-2. Distribution maps of the *Dryopteris varia* complex in Japan. g, *D. protobissetiana*; h, *D. sacrosancta*; i, *D. saxifraga*; j, *D. subhikonensis*; k, *D. varia*. 


**Dryopteris varia** Zhang et al. in Zhang (1963, diploid sexual, known only from Taiwan, Fig. 13) or 123 (triploid apogamous, Fig. 13m).

**Habitat and distribution.** Warm temperature to subtropical evergreen forests and secondary forests in temperate to subtropical zones. Japan (Honshu, Shikoku, Kyushu and Ryukyu) (Fig. 14-2k.), Korea, China, Taiwan, India, Thailand, Indochina and the Philippines.

**Japanese name.** Nankai-Itachishida.

**Notes.** Dryopteris varia is variable in morphology, but can be characterized by having the apex of the lamina abruptly narrowed, the hard coriaceous texture of the lamina and flat scales. Infraspecific cytological variation was observed in this species, but the genome constitution differs from other members of the *D. varia* complex. Tsai & Shieh (1975, 1985) reported a tetraploid sexual cytotype of *Dryopteris varia* from Taiwan. However, even though Ebihara *et al.* (2014) and we (present study) reexamined the cytology of several individuals of *D. varia* from the same localities in Taiwan, we never found tetraploid cytotypes.

**Dryopteris caudifolia**, *D. glabrescens*, *D. lingii* and *D. nanchuanensis* were treated as synonyms of *D. varia* by Zhang *et al.* (2013), while *D. sinobissetiana* and *D. pseudobissetiana* were treated as synonyms of *D. setosa* in Zhang *et al.* (2013). These names can be regarded as synonyms of *D. varia* based on morphological characteristics. The genome constitution of *D. varia* in China need further investigation.


**TAIWAN.**  **Taipei city.**: Urai, K. Hori 1387 (MAK); K. Hori 1393 (MAK).

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**References**


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