

RbcL Phylogeny of Japanese Pteridophyte Flora and Implications on Intrafamilial Systematics

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Abstract A molecular phylogenetic analysis of the Japanese pteridophyte flora was performed using chloroplast *rbcL* sequences of 93% of Japanese taxa. The obtained tree is provided here and noteworthy or novel results on the infrafamilial taxonomy of the pteridophytes are documented by family.

Key words: infrafamilial taxonomy, lycophyte, monilophyte, pteridophyte, *rbcL*.

The pteridophyte flora of Japan comprising 733 taxa has been almost covered by a sequence data-set for DNA barcoding (Ebihara *et al.*, 2010). The barcoding project used two chloroplast DNA regions, *rbcL* and *trnH-psbA*, and the former alone is not enough for solving deep phylogeny at family or higher levels, while the latter seems unsuitable for phylogenetic analysis due to its frequent indels. Even if the resolution is limited, it is worth while to visualize general phylogenetic relationships in rich floristic sampling. In monilophytes, family-level phylogeny has almost been solved using multiple DNA markers (Schuettpelez and Pryer, 2007) and is reflected in recent classifications (Smith *et al.*, 2006). Intrafamilial relationships, especially those that have not yet appeared in previous studies, are discussed in this paper.

Materials and Methods

Chloroplast *rbcL* sequences of 1205 bp in length used for the present analysis are exactly the same as those used in Ebihara *et al.* (2010), but five of 689 sequences examined by Ebihara *et al.* (2010) were excluded from the present analysis because of their incomplete length. A phylo-

genetic analysis was performed by MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003); each of four Markov chain Monte Carlo (MCMC) chains for two independent runs, 20 million generations, sampled every 1000 generations using the GTR+I+G substitution model, using the “constraint” options for the families defined by Smith *et al.* (2006) except for Woodsiaceae and Dryopteridaceae whose monophyly is not supported in the analysis by Schuettpelez and Pryer (2007). The first half (10000) trees were discarded as a burn-in period based on the diagnosis of the result by Tracer 1.5 (Rambaut and Drummond, 2007). The obtained consensus tree is rooted with lycophytes (Lycopodiaceae, Selaginellaceae and Isoetaceae).

Results and Discussion

The tree reconstructed in this paper (a tree divided into ten parts; Figs. 1–10) show the present results of Bayesian inference of infrafamilial relationships and the family or higher-level relationships by Schuettpelez and Pryer (2007). Since two of the Smith *et al.* (2006)’s families, Dryopteridaceae and Woodsiaceae, are possibly non-monophyletic (Schuettpelez and Pryer,

2007), infrafamiliar relationships by Schuettelpeltz and Pryer (2007) are partially adopted for the two families.

Twenty-nine of the 37 families recognized by Smith *et al.* (2006) plus three lycophyte families are distributed in Japan. The following discussion is in sequence of the families adopted by Smith *et al.* (2006), but families without any novel knowledge are omitted. The infrafamiliar classifications generally follow Iwatsuki (1995), but have been modified adopting the results of recent study.

Lycopodiaceae (Fig. 1)

Both the *Huperzia* group and the *Lycopodiella* group are supported as monophyletic, but the *Lycopodium* s.s. group is paraphyletic in the present tree. The latter result does not match the result of Wikström and Kenrick (2000) using *rbcL* and *trnL* intron sequences.

Ophioglossaceae (Fig. 2)

The paraphyletic placement of *Ophioglossum* in the present outcome does not match the result by Hauk *et al.* (2003) which suggested its monophyly. The most diversified group of Ophioglossaceae in Japan is *Botrychium* sect. *Sceptridium* comprising more than 10 taxa. In the sect. *Sceptridium* all the three polyploid species [tetraploid *B. formosanum* Tagawa (Sahashi, 1981), and hexaploid *B. atrovirens* (Sahashi) M. Kato (Sahashi, 1979) and *B. japonicum* (Prantl) Underw. (Sahashi, 1984)] form a distinct clade.

Cyatheaceae (Fig. 3)

Cyathea lepifera (J. Sm. ex Hook.) Copel. and *C. mertensiana* (Hance) C. Chr. et Tardieu belong to the *Sphaeropteris* group, one of the three major groups of the genus (Conant *et al.*, 1996; Korall *et al.*, 2007), and the remaining six Japanese species belong to the *Cyathea* s.s. group. *Cyathea tuyamae* H. Ohba, an endemic species

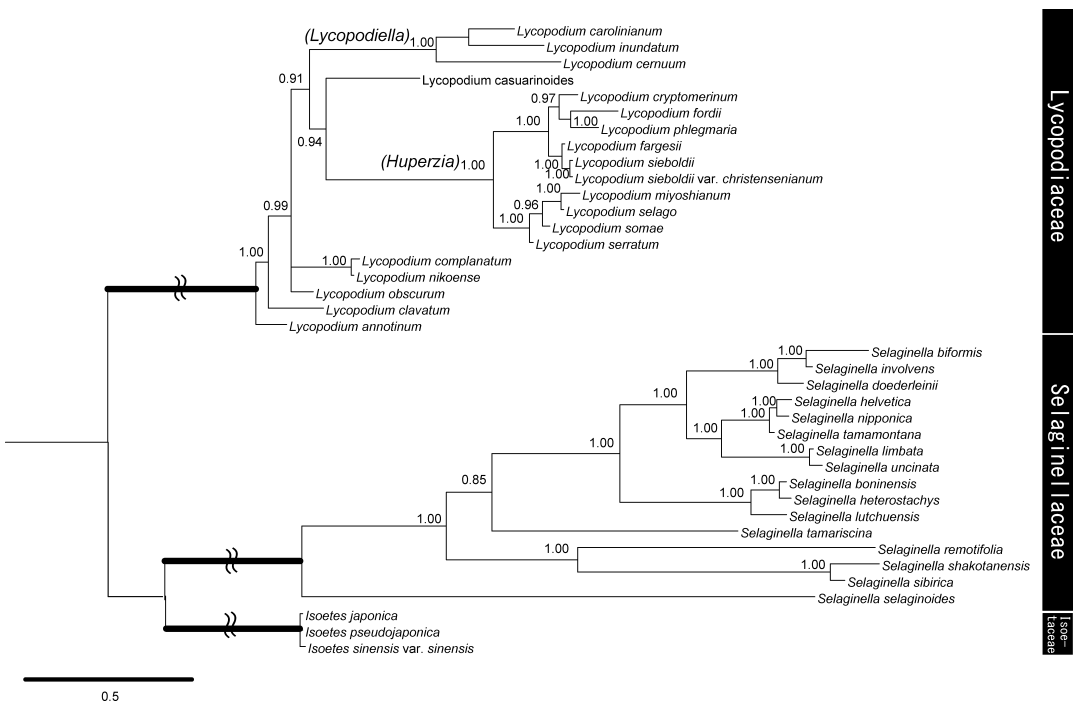


Fig. 1. A part of the results of Bayesian inference of infrafamiliar phylogeny including Lycopodiaceae, Selaginellaceae and Isoetaceae, based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes. Posterior probabilities ≥ 0.90 are shown. Family delimitations, shown by bars on the right side, follow Schuettelpeltz and Pryer (2008).

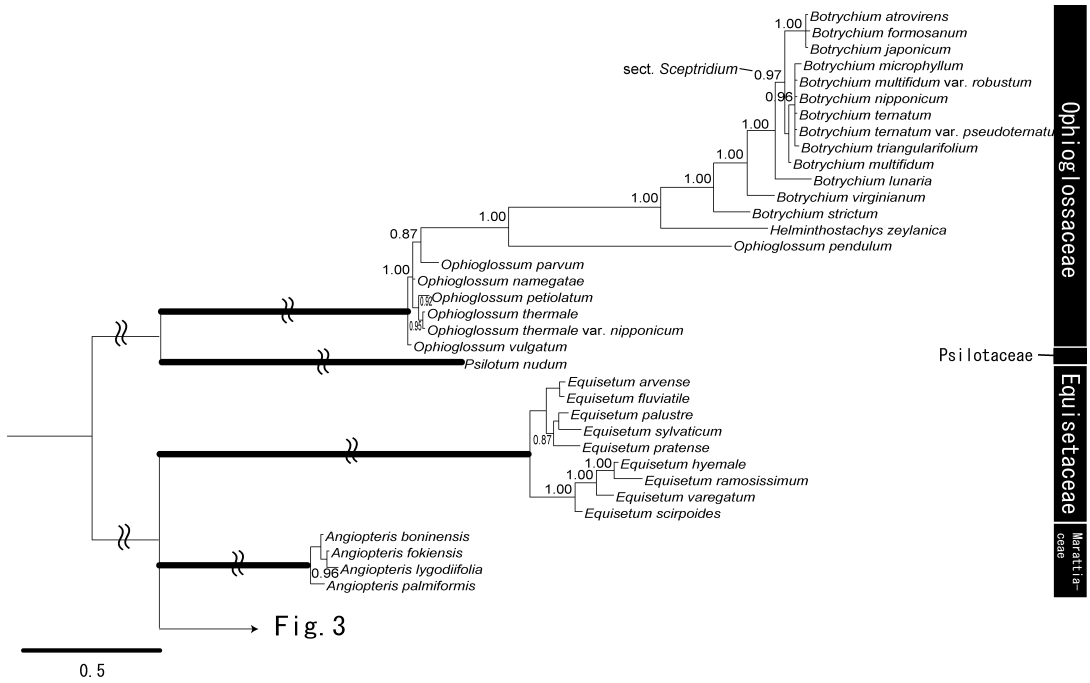


Fig. 2. A part of the results of Bayesian inference of infrafamilial phylogeny including Ophioglossaceae, Psilotaceae, Equisetaceae and Marattiaceae, based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Family delimitations, shown by bars on the right side, follow Smith *et al.* (2006).

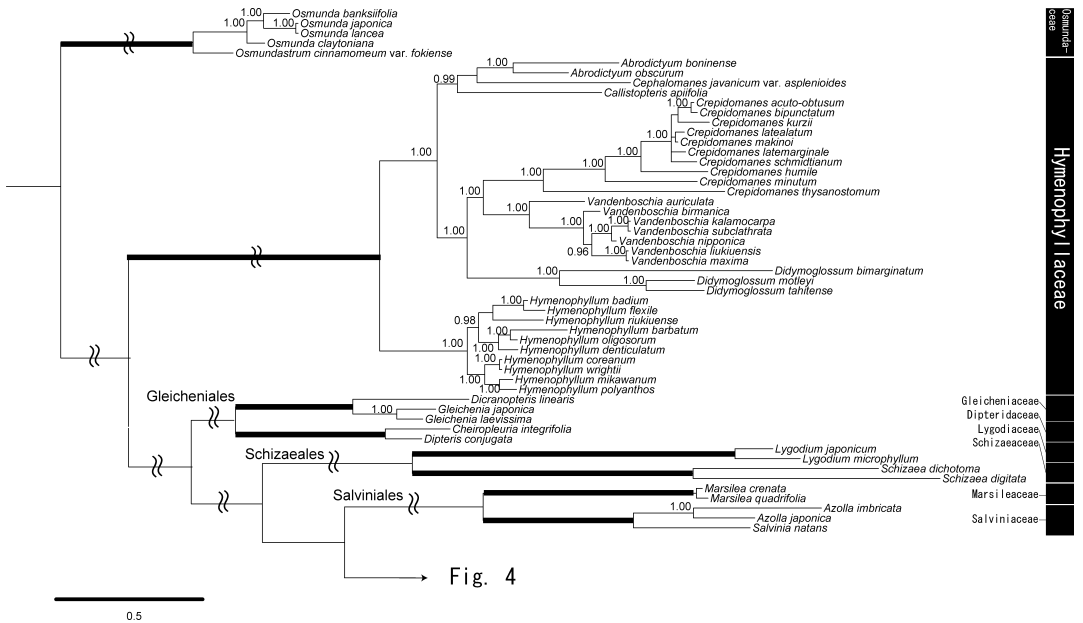


Fig. 3. A part of the results of Bayesian inference of infrafamilial phylogeny including Osmundaceae, Hymenophyllaceae, Gleicheniaceae, Dipteridaceae, Lygodiaceae, Schizaeaceae, Marsileaceae and Salviniaceae, based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Schematic relationships between families follow Smith *et al.* (2006).

of Minami-ijima Isl. (Volcano Isls.) characterized by branching trunks, is closely related to *C. spinulosa* Wall. ex Hook. having non-branching trunks.

Lindsaeaceae (Fig. 4)

The genus *Lindsaea* is apparently polyphyletic; *L. odorata* Roxb. (sect. *Osmolindsaea*) is sister to *Tapeinidium*. Among the other *Lindsaea* species, *L. orbiculata* (Lam.) Mett. ex Kuhn, *L. simulans* Ching, *L. cambodgensis* H. Christ and *L. kawabatae* Sa. Kurata form an unsolved complex. *Lindsaea heterophylla* Dryand. is also included in the complex, and this result does not conflict with the hypothesis of its hybrid origin

(Kramer, 1971). Further careful study is necessary especially for bipinnate *Lindsaea* species.

Dennstaedtiaceae (Fig. 4)

The current generic classifications are supported by the present phylogeny. Five of the eight *Microlepia* taxa share exactly the same *rbcL* sequence—this suggests some Japanese *Microlepia* species are hybrid-origin polyploids, and share a maternal ancestor.

Pteridaceae (Fig. 5)

All of the five robust clades recognized by Schuettpelz *et al.* (2007) within Pteridaceae are distributed in Japan. The PT clade including

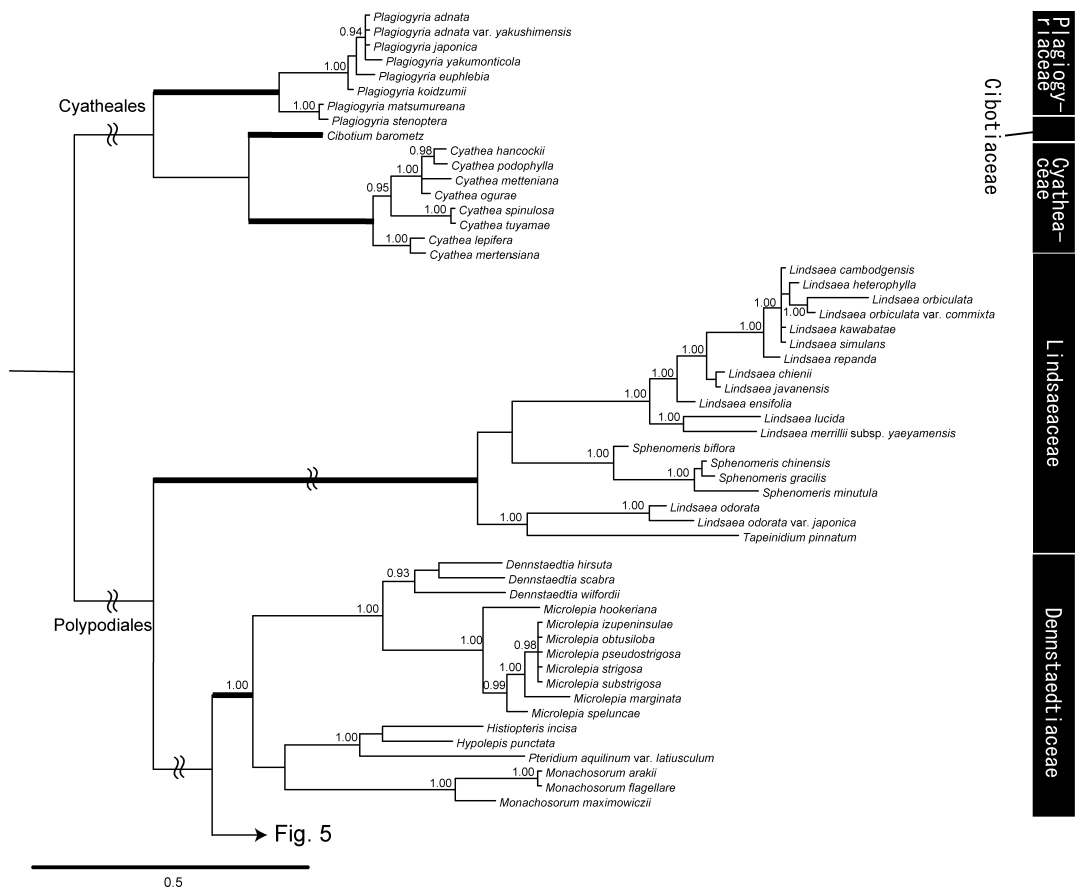


Fig. 4. A part of the results of Bayesian inference of infrafamilial phylogeny including Cyatheales (Plagiogyriaceae, Cibotiaceae and Cyatheaceae), Lindsaeaceae and Dennstaedtiaceae, based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Schematic relationships between families follow Smith *et al.* (2006).

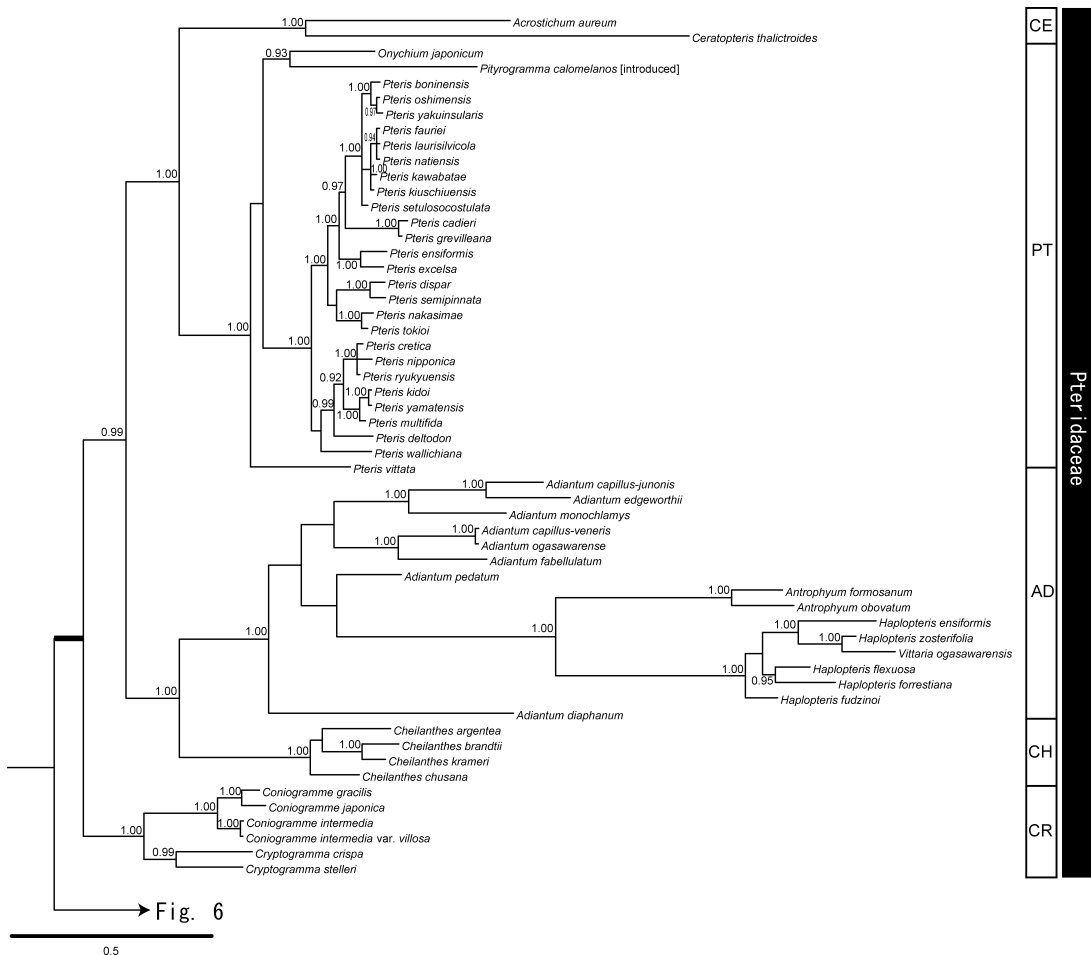


Fig. 5. A part of the results of Bayesian inference of infrafamilial phylogeny including Pteridaceae based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycopytes. Posterior probabilities ≥ 0.90 are shown. Names of the clades are based on Schuettpelz *et al.* (2007). Schematic relationships between families follow Smith *et al.* (2006).

Pteris, *Onychium* and *Pityrogramma* (introduced), has the largest number of members. The other four clades are: AD (*Adiantum*, *Haplopteris* [*Vittaria*] and *Antrophyum*), CR (*Coniogramme* and *Cryptogramma*), CH (*Cheilanthes*) and CE (*Ceratopteris* and *Acrostichum*). In the PT clade, the position of *Pteris vittata* L. is unsolved, but the tree clearly suggests at least the species occupies the most basal position among Japanese *Pteris* species. *Pteris fauriei* Hieron. and its related species (*P. boninensis* H. Ohba, *P. kawabatae* Sa. Kurata, *P. kiuschiuensis* Hieron., *P. laurisilvicola* Sa. Kurata, *P. natiensis* Tagawa,

P. oshimensis Hieron., *P. setulosocotulata* Hayata and *P. yakuinsularis* Sa. Kurata) form an unsolved complex. Considering the fact that they are mostly known as apogamously reproducing taxa (Takamiya, 1996), detailed study on their origins and relationships is necessary.

Aspleniaceae

(Fig. 6)

There is little discordance with previous phylogenetic analysis (Schneider *et al.*, 2004a). Of nine clades recognized by Schneider *et al.* (2004a), members of the seven clades are distributed in Japan. All the *Hymenasplenium* species

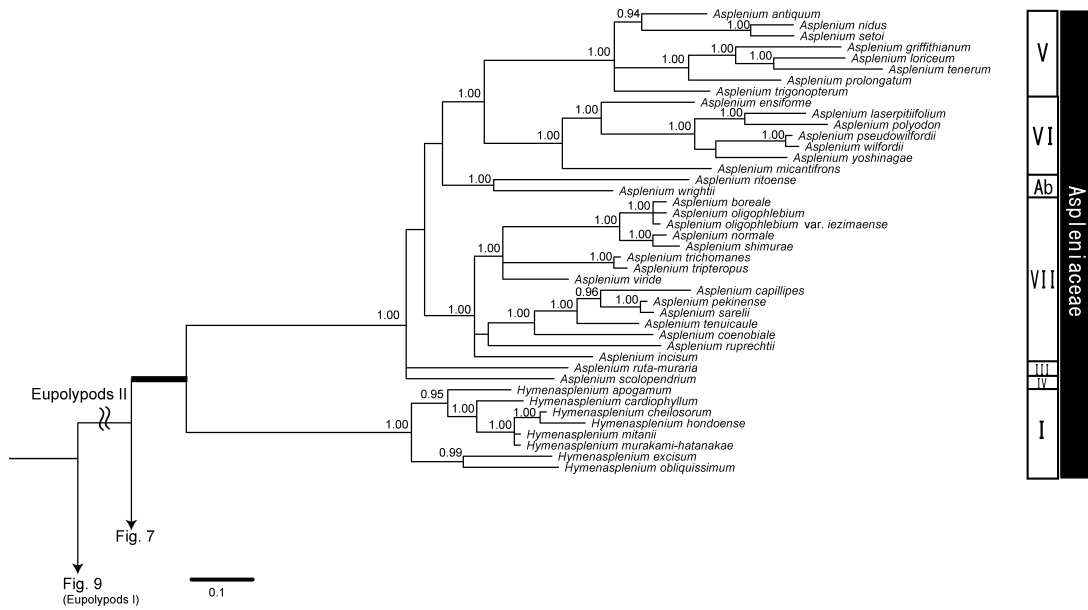


Fig. 6. A part of the results of Bayesian inference of infrafamilial phylogeny including Aspleniaceae based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Names of the clades are based on Schneider *et al.* (2004a) except for Ab, which is an unnamed clade including *Asplenium bullatum*. Schematic relationships between families follow Smith *et al.* (2006).

are included in Clade I [the names of the clades follow those in Schneider *et al.* (2004a)]. *Asplenium ruta-muraria* L. is in Clade III. *Asplenium scolopendrium* L. is in Clade IV. *Asplenium antiquum* Makino, *A. griffithianum* Hook., *A. loriceum* H. Christ ex C. Chr., *A. nidus* L., *A. prolongatum* Hook., *A. setoi* N. Murak. et Seriz., *A. tenerum* G. Forst. and *A. trigonopterum* Kunze are in Clade V. *Asplenium ensiforme* Wall. ex Hook. et Grev., *A. laserpitifolium* Lam., *A. micantifrons* (Tuyama) Tuyama ex H. Ohba, *A. polyodon* G. Forst., *A. pseudowilfordii* Tagawa, *A. wilfordii* Mett. ex Kuhn and *A. yoshinagae* Makino are in Clade VI. *Asplenium boreale* (Ohwi ex Sa. Kurata) Nakaike, *A. capillipes* Makino, *A. coenobiale* Hance, *A. incisum* Thunb., *A. normale* D. Don, *A. oligophlebium*

Baker, *A. pekinense* Hance, *A. ruprechtii* Sa. Kurata, *A. sarelii* Hook., *A. shimurae* (H. Itô) Nakaike, *A. tenuicaule* Hayata, *A. trichomanes* L., *A. tripteropus* Nakai and *A. viride* Huds. are in Clade VII. *Asplenium ritoense* Hayata and *A. wrightii* D. C. Eaton ex Hook. are in an unnamed clade with *A. bullatum* Wall. ex Mett.

Woodsiaceae (Fig. 7)

This family sensu Smith *et al.* (2006) is possibly non-monophyletic according to the succeeding analysis by Schuettpelz and Pryer (2007), and Blechnaceae and Onocleaceae are perhaps in-groups of Woodsiaceae. Most of the Japanese taxa of this family have already been sampled by Sano *et al.* (2000a, 2000b), Adjie *et al.* (2008) and Takamiya (2008), and our result does not

Fig. 7. A part of the results of Bayesian inference of infrafamilial phylogeny including Woodsiaceae, Blechnaceae and Onocleaceae, based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Schematic relationships between families and major clades of Woodsiaceae follow Schuettpelz and Pryer (2007).

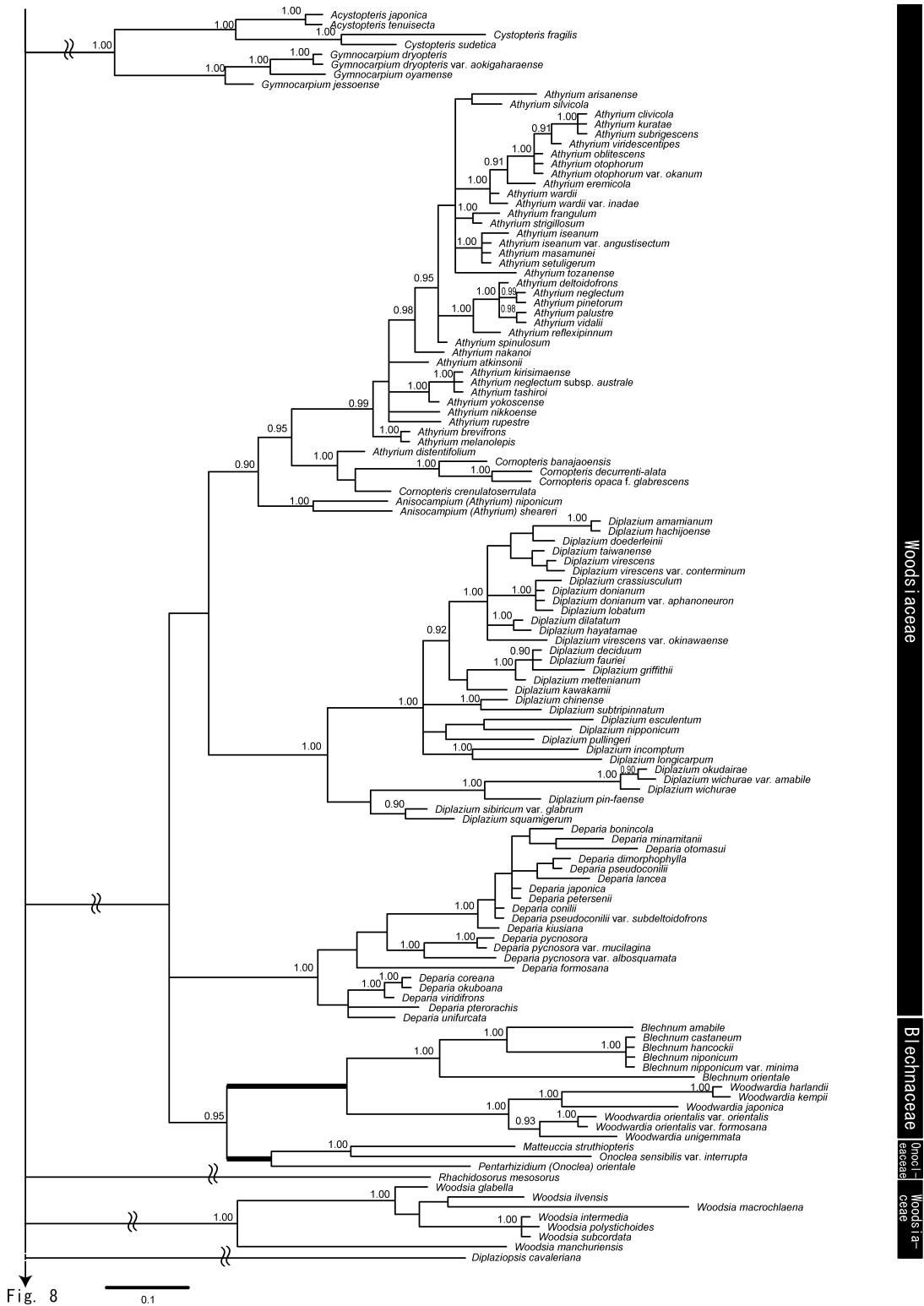


Fig. 8

0.1

show any particular incongruence with them. *Cornopteris* is a genus easily recognizable by its fleshy horn-shaped projections at the base of costules but is clearly nested in *Athyrium* (Adjie *et al.*, 2008). The recent separation of the basal member of *Athyrium* (*A. niponicum* (Mett.) Hance and *A. sheareri* (Baker) Ching) plus *Kuniwatsukia* as a redefined genus *Anisocampium* (Liu *et al.*, 2011) is a practical treatment for keeping *Cornopteris* as a genus, though the position of *A. distentifolium* Tausch ex Opiz is still unsolved.

Thelypteridaceae

(Fig. 8)

Although Iwatsuki (1995) recognized two gen-

era, *Thelyptetis* and *Stegnogramma*, in Japanese Thelypteridaceae, our result shows *Stegnogramma* is nested in *Thelypteris* s.l. and related particularly to *T. flexilis* (H. Christ) Ching and *T. omeiensis* (Baker) Ching (*Cyclogramma*). Though Smith and Cranfill (2002) have already pointed out the 32-generic system by Pichi Sermolli (1977) after Holttum (1971, 1982) is no longer natural (e.g. *Christella* is polyphyletic) in their preliminary study, the system seems useful for grouping the Japanese taxa. Molecular analysis employing global sampling and taxonomic revision is still awaited.

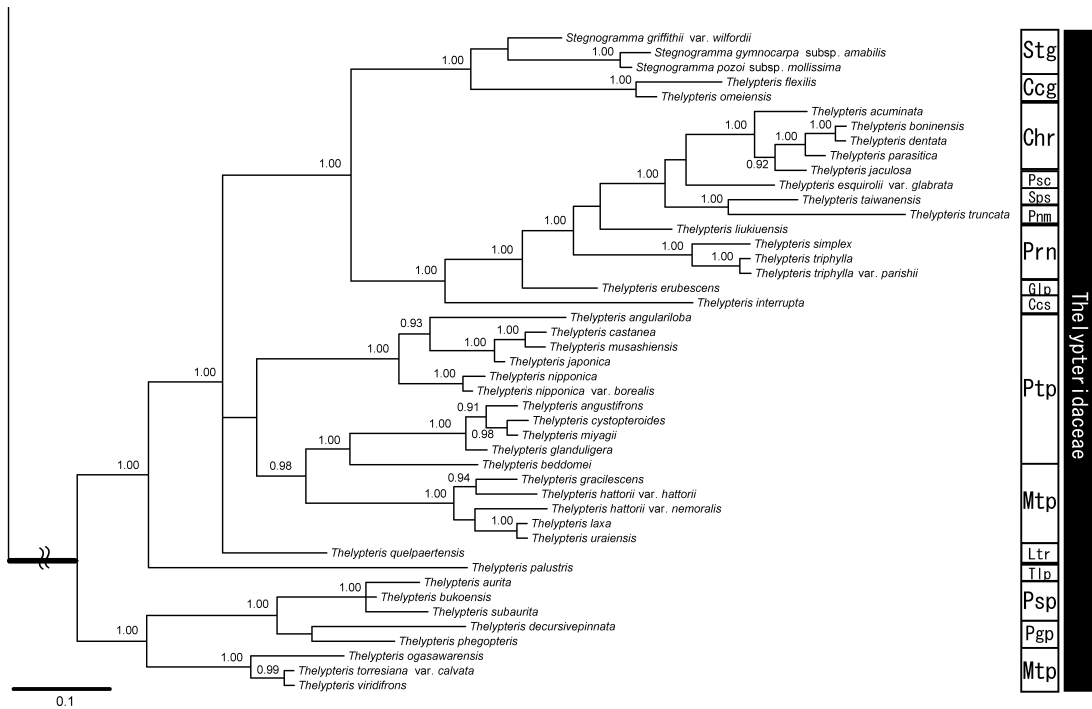


Fig. 8. A part of the results of Bayesian inference of infrafamilial phylogeny including Thelypteridaceae based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Genera by Pichi Sermolli (1977) are also indicated (Ccg: *Cyclogramma*, Ccs: *Cyclosorus*, Chr: *Christella*, Gln: *Glaphyopteridopsis*, Ltr: *Lastrea*, Mtp: *Metathelypteris*, Pgp: *Phegopteris*, Pnm: *Pneumatopteris*, Prn: *Pronephrium*, Psc: *Pseudocyclosorus*, Psp: *Pseudophegopteris*, Ptp: *Parathelypteris*, Sps: *Sphaerostephanos*, Stg: *Stegnogramma* and Tlp: *Thelypteris* s.s.).

Fig. 9. A part of the results of Bayesian inference of infrafamilial phylogeny including Dryopteridaceae based on chloroplast *rbcL* sequences of 684 Japanese pteridophytes, rooted with lycophytes. Posterior probabilities ≥ 0.90 are shown. Schematic relationships between major genera follow Schuettpelz and Pryer (2007).

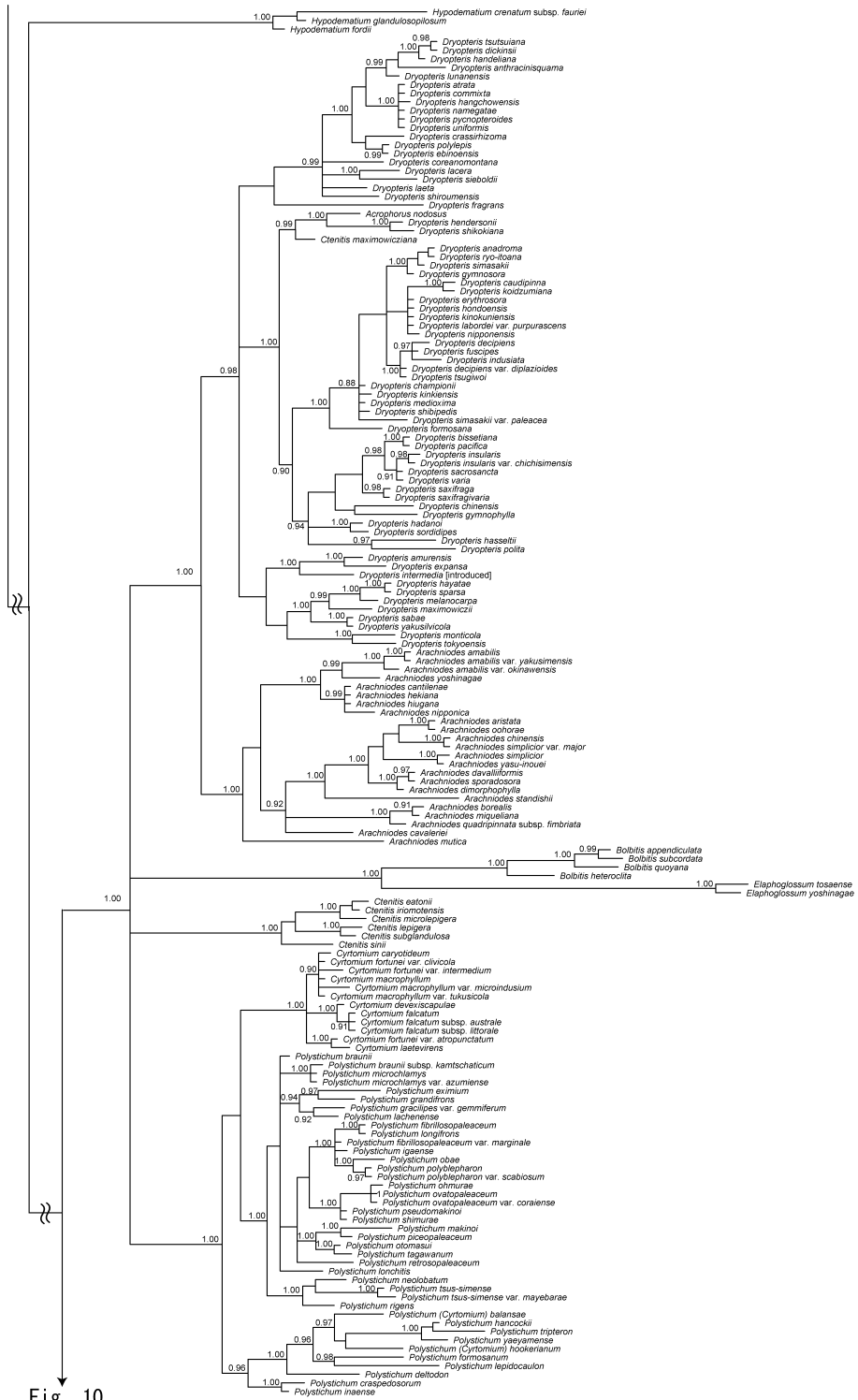


Fig. 10

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Dryopteridaceae

other, at least in the chloroplast DNA marker. As Japanese *Dryopteris* is known for its high percentage of apogamous taxa (Takamiya, 1996), phylogeny using chloroplast DNA needs careful interpretation.

Polystichum–*Cyrtomium*

Lu *et al.* (2005) suggested the polyphyly of *Cyrtomium*. Concerning Japanese species, *C. balansae* (H. Christ) C. Chr. and *C. hookerianum* (C. Presl) C. Chr., without terminal pinna, should be transferred to *Polystichum*. The present result concerning *Polystichum* does not contradict the sectional classification by Daigobo (1972), but relationships within sect. *Metapolystichum*, the most diversified section in Japan, is still unsolved.

Polypodiaceae (Fig. 10)

As already reviewed by Schneider *et al.* (2004b), the present taxonomy of Polypodiaceae has many problems; e.g., *Polypodium* and *Microsorium* are not monophyletic. Monotypic genus *Drymotaenium* is clearly nested in *Lepisorus* (Wang *et al.*, 2010), so *Lepisorus miyoshianus* (Makino) Fraser-Jenk. et Subh. Chandra is an appropriate generic combination. Wang *et al.* (2010) also proposed a new classification of the tribe Lepisorae. According to them, *Neocheiropteris ensata* (Thunb.) Ching and *Microsorium fortunei* should be transferred to *Neolepisorus*. *Microsorium buergerianum* (Miq.) Ching and *Neocheiropteris subhastata* (Baker) Tagawa should be transferred to *Lepidomicrosorium*. Japanese species of *Polypodium* are separated into the “Neotropical clade” and the “Platynerioid-microsoroid clade” sensu Schneider *et al.* (2004b), but not to the “*Polypodium* clade”. Monotypic *Pleurosoriopsis* is also in the Neotropical clade (Schneider *et al.*, 2004b). For the other tribes, global taxonomic revision reflecting molecular phylogeny has not yet been published.

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