

出國報告（出國類別：其他）

出席『18屆國際植物學大會』報告
International Botanical Conference XVIII

服務機關：行政院農業委員會林業試驗所

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出國期間：100年7月22日~8月1日

報告日期：100年9月20日

摘要

國際植物研討會每六年舉辦一次，目的在聚集各地植物學者，分享彼此之研究成果與經驗，尋求後續之合作共識。本次大會參加之植物學家有 2027 位，來自 73 個國家，台灣則有 20 為植物學者參加；共 171 節的主題研討會，包括 951 個口頭報告及 834 篇海報 (含 722 篇電子海報)，另有 10 場大會演講 (plenary speech) 及 30 場的主題演講 (keynote speech)。由於東南亞至馬來群島地區是一聯接亞洲北半球與南半球(澳洲紐西蘭)之舊熱帶區域，但全球植物學家對此地區之植物資源瞭解卻極為有限；本次植物學大會對此議題，因此籌組了一個研討會，討論本地區之蕨類植物多樣性與演化。該研討會分六個子題，分由日本、中國、台灣、英國(馬來地區)、美國(夏威夷)、紐西蘭學者報告其研究，本人受邀發表「台灣是蕨類植物多樣性的轉運站」。經一星期之研究成果與經驗分享，大家對「植物保育與永續利用」及「資源衍生利益之公平分享」的課題均有所共識，同時認為各國政府應盡速落實 2010 年在日本名古屋第 10 次生物多樣性公約的決定，以達成全球植物保育策略 2020 年的目標。

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壹、計畫目的

全世界約有 350,000 種植物，這些植物有許多是人類賴以維生的種類，包括食用、醫藥、建材及紙張等等之生活用品，同時提供人類一個優質與美麗的生存環境。但因生育地之破壞、過度利用、污染、氣候變遷、入侵種漫延及病虫害等因素，植物學家評估自然界中約有三分之二的種類，在二十一世紀將面臨滅絕的危機。瞭解全球之植物資源及尋求永續利用之道，是人類當務之急。國際植物研討會每六年舉辦一次，該會聚集了全世界的植物學者，目的在分享各地學者之研究成果與經驗，尋求後續之合作共識。

東南亞至馬來群島地區是一聯接亞洲北半球與南半球(澳洲紐西蘭)之舊熱帶區域。由於澳洲大陸近世之北移與接近亞洲地區，影響了過去百萬年來兩區植物誌之變化，但全球植物學家對此地區之植物資源瞭解卻極為有限。本次植物學大會對此議題，因此籌組了一個研討會，討論本地區之蕨類植物誌多樣性與演化；研討會分六個子題，分由日本、中國、台灣、英國(馬來地區)、美國(夏威夷)、紐西蘭學者報告其研究，本人受邀發表「台灣是蕨類植物多樣性的轉運站 (Taiwan as a hub of fern diversity)」。

貳、行程規劃與工作記要

七月二十二日（星期五）：

自台北出發，搭乘菲律賓航空公司航班，至馬尼拉國際機場轉機。

七月二十三日（星期六）：

清晨約 7:00 抵達澳洲墨爾本機場。於機場辦理入境手續後，搭巴士至市區旅館並辦理住宿登記。隨後赴墨爾本皇家植物園 (Royal Botanic Gardens Melbourne) 參訪。

墨爾本皇家植物園設立於 1846 年，佔地 38 公頃，展示植物約 10,000 種 52,000 株，是當地著名的休閒與植物多樣性教育場所，更是卓有聲譽的植物基因保存及研究機關。展示區分兩大類，一為植物類群主題蒐集、一為地區植物蒐集。前者包括殼斗科植物、山茶科植物、藥草植物、蕨類植物、莢蒾屬植物、玫瑰植物、蘇鐵科植物、棕櫚植物、乾旱植物、尤加利植物等；後者有澳洲植物區、紐西蘭植物區、南菲植物區、南中國植物區、加州植物區、熱帶植物區(溫室)及稀有及瀕臨滅絕植物區。園區另有標本館及服務中心，後者提供遊園訪客簡易餐飲服務並販售植物相關書籍與紀念品。

七月二十四日（星期日）：

上午參訪國家維多利亞標本館(National Herbarium of Victoria, Royal Botanic Gardens Melbourne)，在國際標本館索引(Index Herbarium)的代號為 MEL。館區位於植物園區 F 大門側，不對一般遊客開放，研究人員參訪需先預約。該館館藏約 120 萬份標本，包括維管束植物、真菌與藻類，是研究澳洲地區植物誌與植物多樣性的重要參考資料。館區面臨植物園之一側為圓形造型，牆上有植物標本製作、標本保存意義及植物多樣性保育等相關主題之

展示，做為民眾教育使用。

下午赴本(18)屆國際植物學大會會場註冊，領取會議資料；晚間參加大會開幕。

七月二十五日（星期一）：

早上有兩場大會演講及六個主題演講(分二場次)。大會演講闡述了由化石的研究得到更清楚的植物演化情形，這些證據顯示種子植物多樣性的發生主要在白堊紀(Cretaceous)至新生代(Cenozoic)。另一場則相對的說明這二十年來分子生物技術對人類作物的改良，包括其高抗蟲與抗殺草劑之能力及高生產力。主題演講則以基因體之研究，討論向日葵(*Helianthus*) 及茄屬(*Solanum*) 的演化及自然選擇之影響其種化。

下午參加10個與蕨類相關之研究報告，包括「解開蕨類生物學的基因體時代 (Unfurling fern biology in the genomics age)」、「多面向之蕨類生物地理－瞭解蕨類種化過程的挑戰 (Fern biogeography at multiple scales – the challenge of understanding fern specific process)」、「北美鱗蓋蕨屬植物的親緣、生理與網狀演化 (Phylogeny, physiology, and reticulate evolution: an integrated approach to North American *Dryopteris* (Dryopteridaceae)」、「古生代蕨類的親緣系統新解及對葉器官演化的推論 (New insights on the phylogeny of Paleozoic ferns and implication on foliar organ evolution)」、「古蕨類植物多樣性的生物性 (Paleobiological patterns in fern diversity)」、「蕨類氣孔啓動控制是被動的水壓反應 (Stomatal control started as a passive response to water status)」、「南加州、夏威夷與哥斯大黎加之蕨類種類與環境對葉形與功能變化之影響 (The causes and

consequences of variation in fern leaf form and function across species and environments in Southern California, Hawaii and Costa Rica)」、「陵齒蕨類植物的親緣關係與分化類型 (Phylogenetic relationships and diversification patterns of the Lindsaeoid ferns)」、「澳洲產鐵角蕨科的系統分類 (Systematics of Australasian Aspleniaceae)」、及「澳洲產附生石松的親緣關係與稀有性 (Phylogeny and rarity in Australian ‘tassel-ferns’)」。

七月二十六日（星期二）：

上午之大會演講強調自基因至生態系的調查與研究數據之整合，隨者科學的日新月異，也隨者調查與研究的範圍越來越廣，累積的各式數據分散各地，發表於各期刊；為有效訂定植物之保育與經營策略，整合這些數據實克不容緩。主題演講則強調化石與現生植物資料整合的重要性，同時也強調標本館儲存之標本資料極需整理，藉由長久以來自熱帶地區採集之樣本研究，快速瞭解這廣大地區的多樣性。

下午與來自紐西蘭之 D. Parris 及美國之 Dr. Sundue 與 Dr. Ranker 討論未來禾葉蕨科(Grammitidaceae)之共同合作課題。Dr. Parris 是全世界禾葉蕨科形態分類的權威，Dr. Sundue 與 Dr. Ranker 則過去對該科之分子親緣關係有深入之研究，惟多以新世界之材料為主。本次討論以亞太舊熱帶地區為標的。經多方之討論，彼此同意合作進行。Dr. Parris 並同意先協助鑑定我們已蒐集之台灣、菲律賓與越南等地之標本。

七月二十七日（星期三）：

赴 Dandenong Ranges National Park，參加蕨類小組安排之野外參觀。該國家公園佔地 3215 公頃，以 *Eucalyptus regnans* (mountain ash tree) 為優勢樹種，在許多地方幾成純林狀態。全區多溼，蕨類覆蓋度高，因緯度高，種類不

若熱帶豐富，共記錄蕨類植物 35 種 (附錄 1)，絕大部份都不產於台灣。

七月二十八日 (星期四)：

大會演講介紹經濟作物棉花之起源與演化。今日全世界之棉花於一、兩百萬年前，分別起源於非洲、亞洲及中美洲，除自然演化外，更由於在各地廣被使用，經各地之育種與人為篩選、馴化與流通，形成複雜之基因庫。同時為減少虫害之侵襲，各地之棉花栽培多使用大量之農藥。育種學家可利用已獲得之基因研究資料，培育抗蟲品系，以減少對環境之污染。主題演講闡述不同領域科學的快速發展，一方面有助於解決以往分類學所面臨之困境與瓶頸，另一方面由於大量累積的資料與數據，同時也造成分類學家解決問題之障礙。除了運用各種新知識與技術，植物學家凝聚彼此之力量當可事半功倍。同時由於網路之發達，標本影像與文獻之可快速取得，今日分類學更需注意野外之研究，以掌握物種之特徵與生物學特性。

下午有關全球植物保育策略研討會中，與會之報告雖顯示2010年目標一之「植物名錄建立」已有顯著之成果，但名錄本身之品質仍有待提升。「線上植物誌」之建立再次被強調，並成為2020年之努力目標。保育策略中，「能力之建立(capacity building)」也被提出並認為是極待推動之一環，特別是要瞭解熱帶地區的豐富植物資源，有賴當地經訓練之人員投入調查研究。

七月二十九日 (星期五)：

上午先與本日下午研討會之小組成員討論會議進行之方式，再與來自日本的 Dr. Atsushi Ebihara 討論東亞地區蕨類植物保育議題。雙方均同意為落實全球植物保育策略，應有更具體之做法；並結論由日方於本年 12 月舉辦座談會，邀請區域之相關學者專家進一步深入討論，研擬行動方案。

下午於「印度太平洋地區蕨類植物多樣性之起源 The Origin of Fern Diversity in the Indopacific Realm (SE Asia, Australasia)」研討會中，進行口頭報告。共有六個子題：

1. 東南亞膜蕨類之多樣性(Atsushi Ebihara, The diversification of filmy ferns in Southeast Asia)
2. 喜馬拉雅地區的隆起改變季風型態並造成東南亞地區蕨類的多樣性(Li Wang, The rise of the Himalayas enforced the diversification of SE Asian ferns by altering the monsoon regimes)
3. 台灣是蕨類植物多樣性的轉運站(Wen-Liang Chiou, Taiwan as a hub of fern diversity)
4. 馬來群島蕨類拓殖的演化角色探討(Nadia Bystriakova/Harald Schneider, Exploring niche evolution during the colonization of Malesia by ferns)
5. 東南亞地區對夏威夷群島蕨類的重要性(Tom Ranker, The importance of SE Asia ferns for the Hawaiian islands)
6. 澳洲與西南太平洋蕨類的生物地理(Leon Perrie, Biogeography of the Australasian and south-west Pacific fern floras)

七月三十日（星期六）：

早上先參加植物園在氣候變遷時代的角色(Botanic gardens and their role in the time of climate change)研討會。發表報告之各植物園分別自硬體設施之改善、長期物候調查之結果、外來植物之引種、稀有植物之保育與瓶頸、環境教育等不同角度，探討其植物園因應氣候變遷之作爲。

上午 11:00 舉行閉幕式，同時宣佈各分組的主要共識，並接受大會之前的國際植物分類命名(International Code of Botanical Nomenclature) 會議的重要結論。包括：

一、自 2012 年起可在電子出版品上發表新名：

自 2012 年 1 月 1 日起，在印刷出版品上發表新名稱已非必要；於網路上以 pdf 檔發表於具有國際標準書號 (ISBN) 或國際標準期刊號 (ISSN) 之出版品亦可視為有效發表。

二、自明年起命名時可用英文描述

自 2012 年 1 月 1 日起，發表新種時可用拉丁文或英文描述。

三、化石分類群名稱

放棄形態分類群 (morphotaxa) 之概念，若具不同名稱之斷片、生活史階段或儲藏階段之化石可被證實屬同一種時，僅可具有一正當名；該名稱之決定應符合命名法規優先權之相關規定。

四、命名法規名稱更動

國際植物命名法規 (International Code of Botanical Nomenclature) 為有效反映該法規所涵蓋之分類群，更名為國際藻類、真菌及植物命名法規 (International Code of Nomenclature for algae, fungi, and plants)

大會同時通過下次(第 19 屆；2017 年)之國際植物學大會於中國深圳舉行。

下午參觀郊區之 St. Kilda 植物園。該園雖名為植物園，但所有植物均未見名牌，實際上更似一般之休閒公園，但遊客甚少；其植物栽培與環境清潔管理甚佳，亦具一溫室，保存與展示熱帶植物。

七月三十一日（星期日）：

參訪皇家展示博物館(Royal Exhibition Building)及環繞該館四週之 Carlton Garden，此兩者形成之區域於 2004 年被列入世界遺產名錄(World Heritage List)。館內主要展示為墨爾本地區的發展歷史，Carlton Garden 則有各式之庭園景觀配置及一別出心裁設計的兒童遊戲場。全區設施均考量到無障礙空間與環境安全。

晚上赴墨爾本機場，搭乘菲航班機返回。

八月一日（星期一）：

早上抵菲律賓馬尼拉國際機場，轉機後返抵台灣。

參、心得與建議

- 二. 經一週之研究成果與經驗分享，參與之植物學家對「植物保育與永續利用」及「資源衍生利益之公平分享」的課題均有所共識，同時認為各國政府應盡速落實 2010 年在日本名古屋第 10 次生物多樣性公約的決定，以達成全球植物保育策略(Global Strategy for Plant Conservation ; GSPC) 2020 年的目標。台灣之植物學家之研究策略與方向亦應以此為前提。
- 三. 為達成上述目標，對植物資源之瞭解仍為首要課題。在對廣大熱帶地區的植物誌研究仍極貧乏的今天，台灣位於亞洲熱帶邊緣，研究上有地利之優勢。建議政府對此地區的國際合作能多支持，使台灣獲得更多可利用之植物資源；該等地區之植物科學亦相對不足，藉此合作可訓練當地之青年科學家，可獲得更長久的友誼與後續的合作機會。
- 四. 為加速對全球植物資源之瞭解，「分類學」之重要性一再被強調，而發展「線上植物誌 (online flora)」成為各國的努力目標，且期待於 2020 年能完成一具整合且被國際認可的線上植物誌。台灣政府在這方面曾有短暫的兩年國科會支持，惟未能持續完成；建議台灣的植物分類學家仍應朝此方向努力，以與世界潮流接軌。
- 五. 與會人員均意識到：植物園、博物館、標本館、種子庫及其內培育之植物或保存之標本、種子與文獻等，提供了植物保育研究與教育所需之無可替代資源。建議各國政府應支持其長期維護之經費，各管理單位亦應建立完善之經營管理機制，以免蒐集之資源流失。

附錄 1. Dandenong Ranges National Park 蕨類植物名錄

1. *Adiantum aethiopicum*
2. *Asplenium bulbiferum*
3. *Asplenium flabellifolium*
4. *Crepidomanes venosum*
5. *Ctenopteris heterophylla*
6. *Diplazium australe*
7. *Blechnum cartilagineum*
8. *Blechnum chambersii*
9. *Blechnum fluviatile*
10. *Blechnum minus*
11. *Blechnum nudum*
12. *Blechnum wattsii*
13. *Calochlaena dubia*
14. *Cythea australis*
15. *Cyathea cunninghamii*
16. *Cyathea marcescens*
17. *Dicksonia antarctica*
18. *Glechenia microphylla*
19. *Grammitis billardiarei*
20. *Histiopteris incisa*
21. *Hymenophyllum australe*
22. *Hymenophyllum cupressiforme*
23. *Hymenophyllum flabellatum*
24. *Hypolepis melleri*
25. *Hypolepis glandulifolia*
26. *Hypolepis rugosula*
27. *Lastreopsis acuminata*
28. *Lastreopsis hispida*
29. *Microsorium pustulatum*
30. *Pellaea falcata*
31. *Polystichum proliferum*
32. *Pteridium esculentum*
33. *Pteris comans*
34. *Pteris tremula*
35. *Rumohra adiantiformis*
36. *Sticherus tener*
37. *Tmesipteris obliqua*
38. *Toder barbara*

附錄 2. 論文發表全文

Taiwan as a hub of fern diversity

(“The origin of fern diversity in the Indopacific realm (SE Asia, Australasia)”)

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Abstract

Taiwan, comprising the main island and its associated islets, is located near the boundary between the Holarctic and Paleotropical regions. The complicated topography forms various habitats with different climate patterns, harboring > 4,000 vascular plants, including about 700 species of lycophytes and ferns. The lycophytes and ferns in Taiwan are diverse, with varied components of different geographical regions. The repetitive glacial and interglacial events, followed by vicariance and long distance dispersal due to their tiny spores have resulted lycophytes and ferns colonizing among the Asian Continent, Taiwan and nearby islets, and paleotropical regions. *Athyrium* (mainly distributed in temperate regions), *Humata repens* complex (mainly distributed in paleotropical regions), and *Deparia lancea* complex (mainly distributed in eastern Asia and southern China) are given as examples illustrating Taiwan as a hub of fern diversity.

Keywords: *Athyrium*, *Deparia lancea*, fern, *Humata repens*, Indopacific realm, Taiwan.

INTROUCTION

Taiwan, ca. 36,500 km², comprising the main island and its associated islets, is located near the boundary between the Holarctic and Paleotropical regions. Two-third of the area in Taiwan is occupied by hills and mountains, and the elevation ranges from seaside to about 3,950 m. This complicated topography forms various habitats with different climate patterns, from tropical to temperate, and harbors some 4,000 vascular plants, including about 700 species of lycophytes and ferns.

The lycophytes and ferns in Taiwan are diverse, with about 25% of south to indo-China element, 17% of Asiatic element, 16% of Himalayan element, 11% of Malesian element, 9% of pantropical (*ad hoc* paleotropical) element, 8% of Japan/northeastern-China element, 3% of temperate element, and 11 % of endemism.

The repetitive glacial and interglacial periods caused the plant migration between the Asian Continent and Taiwan. The vicariance thereafter might have caused plant speciation and evolution through hybridization, polyploidization and different reproductive strategies. The functions of northeastern monsoon, southwestern monsoon, typhoon, migratory birds, and probably the jetstream and trade wind promoted the long distance dispersal of lycophytes and ferns among the Asian Continent, Taiwan and nearby islets, and paleotropical regions by their tiny spores. *Athyrium* (mainly distributed in temperate regions), *Humata repens* complex (mainly distributed in paleotropical regions), and *Deparia lancea* complex (mainly distributed in eastern Asia and southern China) are given as examples illustrating Taiwan as a hub of fern diversity.

Athyrium

The lady ferns (*Athyrium* Roth) comprising about 200 species are mainly distributed in temperate and tropical-subtropical mountainous regions of Asia. Nucleotide sequences of the chloroplast *trnL-trnF*, *rbcL*, *atpA*, *rps4-trnS*, and *matK* were obtained from over 70 species representative of the infrageneric classification. Integrating those molecular data and morphological characteristics, seven clades are strongly supported and recognized as sections. Among them, species of sect. *Athyrium* are mainly distributed in the temperate zone of the northern hemisphere; sect. *Wallichiana* and *Yokoscentia* are restricted distributed in Himalayan and NE Asia, respectively. These sections are the basal clades in the *Athyrium* phylogeny tree. Section *Biserrulata*, *Echinoathyrium*, and *Strigoathyrium* are wide distributed in eastern Asia, somewhat extending to India and Africa. The members of sect. *Polystichoides* are endemic to Himalayan or disjunctively distributed in this area and on western Pacific islands. These biogeographical patterns are considered as the results of vicariance or/and long distance dispersal.

The ratio of endemism of *Athyrium* in the western Pacific islands is high, especially in the tropical regions which include many mountainous islands. They are at the margin of the Asia Continent and experienced the repetitive glacial and interglacial periods. Our results show that those historical geographic events and the margin effect have caused the formation of these endemics and their further evolution.

The spatial dispensation of the *Athyrium* species in the western Pacific islands might be resulted by different events. Phylogeny of several restricted distribution or endemic species in the eastern Asia were studied to reveal their genetic relationship and then the reasons of their distribution. From the north, Japan has 36 including ten endemic

species and their affinities could be found in Asian temperate zone such as mountains of Taiwan. There are 24 *Athyrium* species in Taiwan, seven species are wide distributing in eastern Asia, eight species disjunctive distribution between Himalayan and western Pacific islands, and nine species including four endemics restrictedly distributed in western Pacific islands. The sister species of the two endemic to the Philippines were found in Taiwan. Based on the phylogenetic tree of the endemism and comparison of the species composition of these islands, it suggests that the *Athyrium* species common in Japan and Taiwan was mainly relic after vicariance as glacial effect; whereas the endemic species occurring in the Philippines should be caused by the long distance dispersal events because there was no continental junction event occurred before.

Humata repens complex

Humata repens (L. f.) Diels and its close relatives were defined as a species complex because of the continuum in their morphological variations. It widely distributes in Pacific islands, Asia, to Africa, with eastern boundary at south Pacific to the west boundary at east Africa and south boundary at north Australia to the north boundary at Taiwan and Okinawa islands.

Four scientific names have been used for the *Humata repens* complex in Taiwan. However, the principal components analysis of 14 morphological characters revealed nine morphological forms within the *H. repens* complex in Taiwan, where both triploid ($2n=120$) and tetraploid ($2n=160$) existed.

Diploid individuals ($2n = 80$) were found outside of Taiwan. Examining the spore sizes of different ploids, results show that the average spore size of diploids was

35.47±4.12µm, which is significant smaller than that of polyploids, including triploid (53.56±7.91µm) and tetraploid (53.13±7.81µm). The spore sizes of triploids and tetraploids were not significantly different. Based on this observation, the diploids can be distinguished from the polyploids which including the tri and tetraploids.

According to the spore sizes, the diploid plants were only found in the Melasian regions, whereas the polyploidy plants were mostly found in the margin areas, i.e., Taiwan, Indochina, west Indonesia to Africa, and north Australia.

To determine the relationships of the complex components, sequences of cpDNA (*atp-rbcL* + *rbcL-accD* + *rps16-matK* IGS + *matK*) and nrDNA (*PgiC*) trees of *Humata repens* complex in Taiwan, Japan, Vietnam, and Philippines were analyzed. The incongruence between cpDNA and nrDNA (*PgiC*) trees indicates that the hybrid origin of most individuals. Both phylogenetic trees also show that at least two close ancestors belonging to this complex in its diversity center. Through hybridization and polyploidization, some polyploidy genotypes dispersed to elsewhere and shaped the extant distribution.

There are two spore numbers per sporangium in this complex which indicate their ploids and different reproductive strategies. Those diploids have 64 spores per sporangium, whereas those polyploids have 32 spores per sporangium. It indicates that the former reproduced sexually, and the latter reproduced apogamously.

Assuming the diploids were the ancestral group, after polyploidizing (hybridization or autopolyploidization) the offspring move to other places. Because of the characters of apogamous reproduction, polyploids had a better strategy to produce offspring and colonize on the new habitat by a single spore through long distance dispersal. After the successful colonization, speciation and subsequent multi-genetic progenies have

occurred. The alternative scenario is that the multi-genetic progenies occurred in the original localities and disperse elsewhere, but only those apogamous polyploids have survived successfully. Taiwan, due to its complicated geographical topography and various habitats, is an ideal location to adopt those complex components.

Deparia lancea complex

Deparia is a fern genus in Woodsiaceae (*sensu* Smith et al., 2006, 2008), comprising around 70 species and mainly distributed in Asia, while several species are distributed and endemic in the Hawaiian Islands, North America, and Africa. We conducted a phylogenetic analysis of DNA sequence data and found support for seven major clades within *Deparia*. The East Asian + Southeast Asian clade had greater diversity and/or species richness than the other clades. According to their distribution, these clades could be further identified as either oceanic or continental. Basal clades were composed of continental taxa while derived clades were composed of oceanic taxa. Molecular dating analyses were undertaken to estimate the divergence times of all clades. The results suggested that *Deparia* taxa dispersed from Asia, and then colonized Pacific islands, North America, and Africa during the Pliocene. In addition to these ancient dispersal events, there were some recent expansions in oceanic groups, and the cytogeographical pattern of these oceanic groups implied that polyploidization may play an important role in their expansion.

Deparia lancea group (Woodsiaceae) comprising *Deparia lancea* (Thunb.) Fras.-Jenk. and *Deparia tomitaroana* (Masam.) R. Sano (Woodsiaceae) is particularly interesting in that there were five cytotypes found, from diploid to hexaploid. Although they were widespread in eastern Asia, little was known about the link of their biogeography and evolution of polyploids. To reveal their cytogeography and

phylogeography, individuals from Japan, Taiwan, China, Vietnam, Thailand, Burma, Nepal, N. India, and Borneo were analyzed in this study. The haplotypes inferred from *rps16-matK* + *trnL-L-F* + *nadhF* regions were separated into two distinct groups (A & B). Haplotype group A was consisted of both diploids and polyploids, and distributed in Japan, Taiwan, China, Vietnam, Nepal, and N. India. However, diploids in haplotype group A were only found in Taiwan. Haplotype group B was only consisted of polyploids, and mainly distributed in Japan (Honshu and Kyushu). Diploids in haplotype group B were probably extinct; or were distributed restrictedly, and thus were not discovered by our current samplings. Estimated from ate-smoothing by penalized likelihood, the divergent time of these two haplotype groups was around 0.8 million years.

Based on these results, we proposed the scenario of their biogeographical history. The ancestral diploidy population had been suffered fragmentation during the early to middle Pleistocene, during when the land-bridge of Japan-Ryukyu-Taiwan were disappearing. The possible refuges of diploids were in pacific regions of eastern Asia, such as Japan and Taiwan, in where subsequent polyploidization might occur. The polyploidy individuals, which are generally considered with higher ability in long distance establishment than diploids in ferns, were further selected due to land/habitat discontinuity of islands in pacific regions, and then dispersed to continental East Asia and other regions.