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REVIEW

Hypothesizing Origin, Migration Routes and Distribution Patterns of Gymnosperms in Taiwan

Shing-Fan Huang

No. 521, Nanda Road, Hsinchu 300, Taiwan, Department of Applied Science, National Hsinchu University of Education.
** Corresponding author. Phone: 886-3-5213132#2750; Fax:886-3-5257178; Email: sfhuang@mail.nhcue.edu.tw*

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ABSTRACT: Phytogeographical study of gymnosperms in Taiwan is carried out based on reviewing data gathered from published papers on fossils, phylogeny and phylogeography. Following questions are asked. (1) How is the high degree of endemism of gymnosperm flora of Taiwan derived? (2) How many source areas of gymnosperms in Taiwan are there? (3) Is there relation between distribution pattern of endemic gymnosperms in Taiwan and those of their sister species? (4) How do gymnosperms migrate to Taiwan?

In total, 28 taxa including 19 species and 9 varieties of gymnosperms are in Taiwan. Compared to the Flora of Taiwan 2nd edition, *Nageia fleuryi* is excluded and *Pinus taiwanensis* var. *fragilissima* is added in this paper. Species status of *Calocedrus formosana* and *Tsuga formosana* and variety status of *Cunninghamia lanceolata* var. *konishii* are retained. Scientific names are adopted for *Juniperus morrisonicola* instead of *J. squamata* and for *Juniperus tsukusiensis* var. *taiwanensis* instead of *J. chinensis* var. *taiwanensis*. According to distribution patterns, these 28 taxa may be categorized into tropical origin (TO), Southern Hemisphere origin (SMO) and Northern Hemisphere origin (NMO).

Gymnosperms in Taiwan with high degree of endemism, 78.5%, may owe to woody habit, which is wider in ecological niche compared to herbaceous one and would be less sensitive to the environmental changes, and owe to temperate essence that is more easily to find shelters during temperature fluctuations.

Taxa of TO and SMO are inclined to inhabit low altitudes and sporadically distributed, whereas taxa of NMO are inclined to inhabit middle to high altitudes, especially in northern and central Central Mountain Range and may be widely or restrictedly distributed.

Distribution patterns of endemic taxa of NMO in Taiwan are related with those of their sister species. Taxa with sister species in higher latitudes such as Japan, northwestern China and central China are distributed in higher altitudes with midpoint of altitudinal distribution over 1800 m, while those with sister species in lower latitudes such as South China, southern South China, southeastern China are distributed in lower altitudes with midpoint of altitudinal distribution under 2000 m.

Most fossil histories of endemic taxa of NMO may trace back to Asia or North America (NAM) except *Juniperus morrisonicola* that may trace back to Europe. For those traced back to NAM, ancestors in NAM migrated to northeastern Asia via Biringia, from where dispersed southward either to Japan, or to northern China and then to central and eastern China. From Japan, ancestors either migrated southward through the Ryukyus to Taiwan if sister species were restricted to Japan, or they might have dispersed to continental Asia and evolved when Japan was a part of continental Asia and further migrated southward via East China Sea's land bridge to Taiwan. From central or eastern China, ancestors migrated southward either via East China Sea's land bridge or through southeastern China via Tungshan land bridge to Taiwan. Ancestors in Europe migrated southward to the Himalayas, from where through the Yun-Kue Plateau, Nanling via Tungshan land bridge to Taiwan.

Southwestern China (SWC) plus IndoChina is both refuge and dispersal center. Taxa of SMO might have dispersed from the South Hemisphere through southeastern Asia to IndoChina, from where migrated either through southern South China via South China Sea's land bridge to southern Taiwan, or through South China via Tungshan land bridge to central Taiwan. If taxa of NMO share short genetic distance with their sister species in SWC, their migration routes would be like those of SMO. However, if taxa of NMO share longer genetic distance with their sister species in SWC, one lineage of their ancestors, possibly distributed in central China then, migrated through southeastern China via Tungshan land bridge to Taiwan while another lineage in central China further dispersed to SWC and produced disjunct distribution patterns.

Taxa of gymnosperms in Taiwan distributed in higher altitudes are inclined to have sister species distributed in higher latitudes. However, horizontal distribution patterns of gymnosperms in Taiwan may be blurred by long history of colonization. Thus horizontal distribution patterns can only be explained by obtaining more data on fossils and paleogeography of such taxa in Taiwan.

KEY WORDS: Distribution, endemism, gymnosperms, hypothesizing origin, migration route, Taiwan.

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INTRODUCTION

Gymnosperms are seed plants with naked ovules (Bell and Hemsley, 2000). Extant gymnosperms are classified into four classes, namely Cycadidae, Ginkgoidae, Gnetidae and Pinidae, each with 2, 1, 3, 12 families and 10, 1, 3 and 69 genera (Christenhuszi *et al*., 2011). Distribution patterns of genera of Pinidae are either primarily of the Northern or Southern Hemisphere and both patterns are overlapped in southeastern Asia, and each pattern can be further distinguished into restricted or disjunct distribution (Li, 1953; Conteras-Medina and Vega, 2002). Nine areas of endemism of gymnosperms, namely, southwestern China, Japan, New Caledonia, western North America, Mesoamerica, southern South America, eastern Australia, Tasmania and southern Africa are recognized (Conteras-Medina and Vega, 2002). Southeastern Asia plus southwestern China is considered the most important diversity center of gymnosperms regarding species richness per 10,000 km^2 (Mutke and Barthlow, 2005). Taiwan is situated near mainland China and Japan and its gymnosperm flora contains 5 families (Cupressaceae, Cycadaceae, Pinaceae, Podocarpaceae and Taxaceae, based on the classification of Christenhuszi *et al*. (2011)), 17 genera, and 28 taxa (Editorial Committee of the Flora of Taiwan 2nd edition, 1994). They are distributed in Taiwan proper, except one species, *Podocarpus costalis*, in Lanyu, southeastern isle off Taiwan.

Among these 28 taxa, 64.3% is endemic compared to 26.2% for all vascular plants in Taiwan (Hsieh, 2002). Such a high degree of endemism in gymnosperm flora of Taiwan requires an explanation. Regarding distribution pattern, three distribution types have been recognized for genera of conifers in Taiwan (Liu, 1966): primarily of the Northern or Southern Hemisphere, disjunct between eastern Asia and North America, and restricted to East Asia. For family distribution, most families in Taiwan are primarily of the Northern Hemisphere except Cycadaceae of tropics and Podocarpaceae of the Southern Hemisphere.

Liu (1966) carried out an intensive study on phytogeography of gymnosperms in Taiwan by reviewing taxonomy of each taxon and comparing their distribution patterns. He (Liu, 1966) concluded that relationship between gymnosperm flora of Taiwan and China was direct while that between Japan and Taiwan was indirect. By reviewing distribution patterns of gymnosperms of the world, Li (1978) also reached the conclusion that Taiwan was rich in relict conifers and taxads, and gymnosperm flora of Taiwan was more related to mainland China than to Japan. Since then, many phylogenetic studies of gymnosperms based on molecular data have been carried out and many data about geology and fossils have been published. Thus it is attempted to summarize what have known about the phytogeography of gymnosperms in Taiwan based on published data on fossils, phylogeny and phylogeography to further understanding the possible reasons behind the distribution patterns and to serve as a model for extrapolating to the flora of Taiwan. Moreover, it is also to respond the idea proposed by Huang (2011) that determining the relation between distribution patterns of taxa in Taiwan and their source areas or distribution patterns of their sister taxa is a part of the study of historical biogeography of the Flora of Taiwan. Hence following questions are asked in this paper. (1) How is the high degree of endemism of gymnosperm flora of Taiwan derived? (2) How many source areas of gymnosperms in Taiwan are there? (3) Is there relation between distribution pattern of gymnosperms in Taiwan and those of their sister species? (4) How do gymnosperms migrate to Taiwan?

MATERIALS AND METHODS

Taxa of gymnosperms in Taiwan were compiled mainly based on the Flora of Taiwan 2nd edition (Editorial Committee of the Flora of Taiwan 2nd edition, 1994) and published papers afterward. Distribution patterns of gymnosperms in Taiwan, mainly following Liu (1966) and modified with updating data, was compiled and summarized in Table 1. Horizontal distribution pattern of each taxon in Taiwan was described by distribution districts recognized by Huang (2011), and vertical distribution pattern of each taxon was expressed by the average of its elevational distribution as midpoint altitudinal distribution. Sister species were determined by published phylogenies of each taxon and topologies of phylogenies were described in Venn diagrams (*cf*. Kitching *et al*., 1998). Genetic distance ($p = n/l$, where n is the number of substitutions and l is the length of aligned sequences, while number of indels are excluded from counting as variation) between gymnosperms in Taiwan and their sister populations or species were calculated by aligning and comparing the similarity of sequences of gene markers. It was carried out by uploading a sequence belonging to taxon of gymnosperms in Taiwan to GenBank (http://www.ncbi.nlm.nih.gov/) and using BLAST program employed in the website to align and then calculated number of substitions manually.

RESULTS

Phylogeny, fossil history and distribution pattern of each taxon of gymnosperms in Taiwan

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***Cycas* L.**

Cycas contains about 90 species in six sections, namely *Asiorientalis*, *Cycas*, *Indosinenses, Panzhihuaenses*, *Stangerioides* and *Wadeanae* (Hill, 2011), with the species diversity center in IndoChina (40 species), and it is distributed in islands and coast of continents along the Indian and Pacific Ocean (Hill, 2008). One endemic species belonging to section *Asiorientalis* is in Taiwan. Fossil *Cycas* was reported in the Eocene of China and Japan (Hill, 2008), and in the late Miocene of Nanchuang, Taiwan (Li, 2000).

Cycas taitungensis* Shen *et al.

C. taitungensis inhabits dry and open cliff of southeastern Taiwan at elevations of 300–950 m (Shen and Tsou, 1994). Morphologically it differs from *C. revoluta* , distributing in the Ryukyus and southeastern China where natural populations have not found for a long period of time, only by straight flat leaf margin instead of revolute one (Chen and Stevenson, 1999). *C. taitungensis* is a sister species of *C. revoluta* and these two species are related to *C. panzhihuaensis* from Yunnan based on cpDNA data (Kyoda and Setoguchi, 2010). However, nrITS tree (BLAST and shown by distance tree in GenBanK web site, accessed in January, 2013) described in Venn diagram as (*C. revoluta*, (*C. panzhihuaensis*, (*C. taitungensis*, *C. hainanensis*))) implied that *C. hainanensis* was also related to these three species. Based on cpDNA haplotypes (Kyoda and Setoguchi, 2010: Table 2), the linear relationship showed that *C. panzhihuaensis* was three steps to *C. taitungensis* that was one step to *C. revoluta* in the southern Ryukyus and the latter is one step to *C. revoluta* in the northern Ryukyus (Table 1). Although fossil *Cycas* has been found from the late Miocene of Nanchuang, Miaoli County in northwestern Taiwan (Li, 2000), the relationship of the fossil and *C. taitungensis* has not yet determined. Since extant *Cycas* has a tropical distribution pattern (Hill, 2008), according to the haplotype lineage, it is likely that ancestor of *C. taitungensis*, probably inhabiting IndoChina, has migrated through southern South China via South China Sea's land bridge (*cf*. Shen, 1997; Fig. 1) to southern Taiwan during the glaciations. It then further migrated to southeastern part later and colonized there till present.

***Taxus* L.**

Taxus is a genus of Northern Hemisphere with 7-10 species (Page, 1990; Farjon, 2010). One species, *T. sumatrana*, distributing from the eastern Himalayas to southeastern China and Taiwan and to Malesia (Editorial Committee of the Flora of Taiwan 2nd edition, 1994), is in Taiwan.

***Taxus sumatrana* (Miq.) de Laubenfel**

In Taiwan, *T. sumatrana* inhabits moist forest at elevations of 1000–3000 m of Hsueshan and Central Mountain Ridge (Liu, 1966). Delineation of species of *Taxus* is not clear (Hao *et al*., 2008). Farjon (2010) treated Taiwan's species as *T. mariei* distributing mainly in central and southeastern China. Based on DNA data (Liu *et al*., 2011), phylogeny can be described in Venn diagram as (*T. mairie*, (*T. sumatrana*-Taiwan, (*T. sumatrana*-Taiwan, *T. sumatranus*-Philippines))). Taiwan's samples formed a clade with those from the Philippines, and this clade is sister to *T. mairie*. Because in the clade formed by Taiwan's and Philippines' samples, Taiwan's samples were paraphyletic and arose from basal nodes, implying Taiwan's population could be older than that from the Philippines. In consequence, the dispersal direction would be from Taiwan to the Philippines, as the case of *Euphrasia philippinensis* clearly shown by molecular phylogeny (Wu *et al*., 2009). Thus the ancestor of Taiwan's population is probably derived from southeastern China via the Tungshan land bridge (*cf.* Lin, 1982; Fig. 1) and colonized northern Taiwan.

***Amentotaxus* Pilger**

Amentotaxus contains six species distributing in India, China, Vietnam and Taiwan (Farjon, 2010). One endemic species is in Taiwan (Editorial Committee of the Flora of Taiwan 2nd. edition, 1994), but Farjon (2010) mentioned two species including *A. formosana* and *A. argotaenia*. Without further proof of the existence of *A. argotaenia* in Taiwan, one species is considered here. Fossil *Amentotaxus* were found from the Upper Cretaceous to Miocene of North America (Manchester, 2009) and from the Paleocene to Lower Pliocene of Europe (Ferguson *et al*., 1978; Manchester, 2009), while no fossil records were found from Asia (Manchester, 2009).

***Amentotaxus formosana* Li**

A. formosana inhabits moist broad-leaved forest at elevations of 800–1300 m in southern Taiwan (Liu, 1966). It is a sister species to the clade composed of *A. argotaenia* and *A. yunnanensis* from China based on cpDNA phylogenetic tree (Hao *et al*., 2008). However, *A. formosana* and *A. yunnanensis* shared the shortest genetic distance among related species, and the genetic distance of *A. formosana* and *A. yunnanensis* is the longest among those of Taiwan's gymnosperms and their sister species based on cpDNA and mtDNA (Table 1; Huang, 2011),

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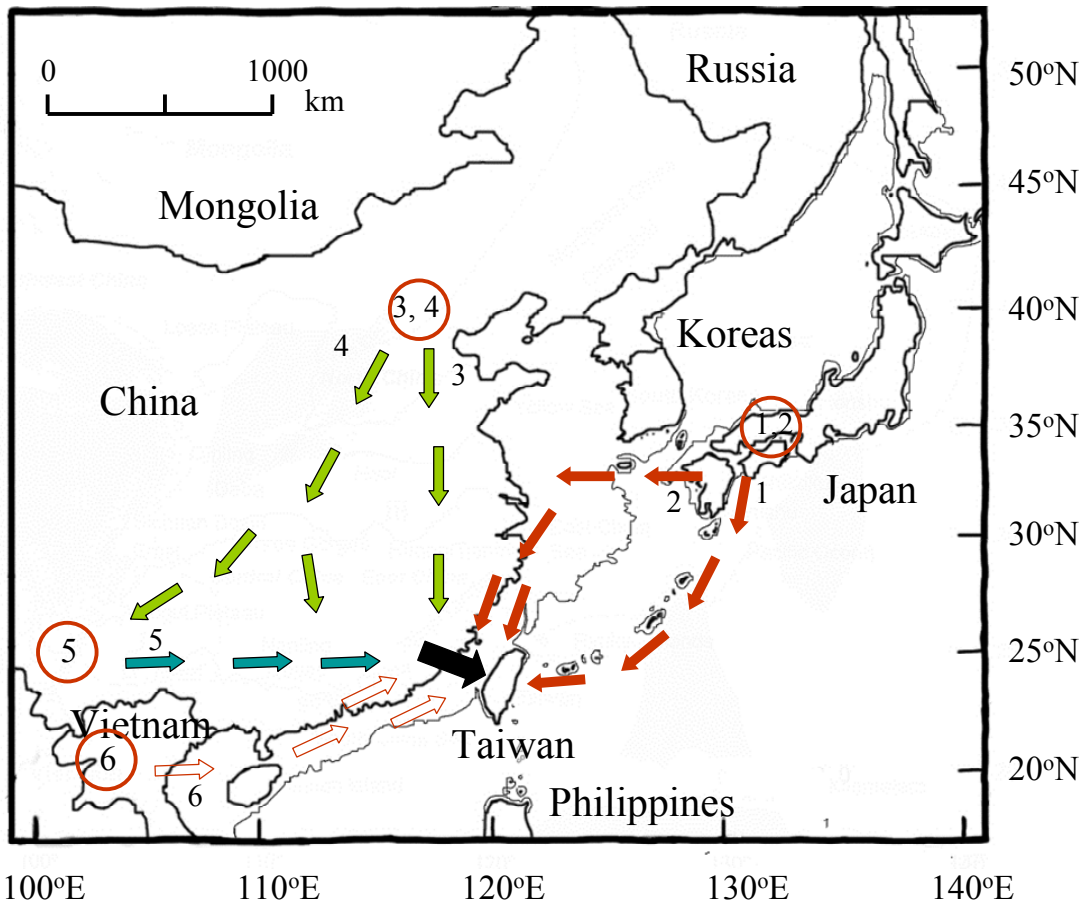


Fig. 1: Postulated migration routes of endemic taxa of gymnosperms in Taiwan. Background map is modified from Qui et al. (2011: Fig. 1). Empty circles represent possible source areas from where migrated to Taiwan. Numbers inside the circles and beside arrows are postulated migration routes. Route 1 indicated that the source area was Japan and from where plants migrated through the Ryukyus to Taiwan. Route 2 indicated that the source area was also Japan and from where plants migrated to eastern China when Japan was a part of continental area and then moved southward to south eastern China, and either through East China Sea's land bridge or Tungshan land bridge to Taiwan. Route 3 indicated that the source area was northeastern China and from where plants migrated southward to eastern China and southeastern China and then moved through Tungshan land bridge to Taiwan. Route 4 indicated that the source area was northeastern China and from where plants migrated to northern China and central China. From central China, plants either migrated southward to southeastern China and then moved via Tungshan land bridge to Taiwan, or continued to migrate to refuge of southwestern China. Route 5 indicated that the source area was southwestern China and from where plants migrated eastward through the Yun-Kue Plateau, Nanling to southeastern China and through Tungshan land bridge to Taiwan. Route 6 indicated that the source area was IndoChina and from where plants migrated through southern South China either from South China Sea's land bridge or Tungshan land bridge to Taiwan.

indicating that it has colonized Taiwan for a long period of time. Evidence of inter simple sequence repeat (ISSR) also suggests that *A. formosana* is more related to *A. yunnanensis* and these three species may have evolved in radiation (Ge *et al*., 2005: Fig. 2). *A. yunnanensis* is distributed in Vietnam and Yunnan and Kuechou, southwestern China, and *A. argotaenia* is distributed in Vietnam and southern, southwestern, and central China excluding Yunnan (Fu *et al*., 1999). Fossil records have suggested that extant *Amentotaxus* has migrated from the northern higher latitude. Since *A. formosana* has diverged for a long time, and it is a sister species to the clade formed by Chinese species, and these three species might have evolved radiately, it is postulated that ancestor of these three species might have migrated from northeastern China to central China. From there, one lineage migrated through southeastern China to Taiwan via Tungshan land bridge to become *A. formosanum*, and another lineage migrated to refuge of southwestern China to become *A. yunnanensis* that further evolved to *A. argotaenia*.

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Table 1: Gymnosperms in Taiwan and their phylogenies and distribution pattern. (A: Mid point of altitudinal range (meter) in Taiwan. B: Distribution pattern in Taiwan by district. C: Related species with the shortest genetic distance and its distribution. D: DNA markers. E: Shortest genetic distance (*p=n/l*), *l*: length of sequence, *n*: number of substitutions. F: Relationship of the species shown by Venn diagram. G: Relationship of the species shown by Venn diagram with area replacing species. H: Possible migration route of the taxa. I: Reference for phylogeny. * 1: Northeastern Taiwan; 2: North-central Taiwan; 3: Center-northern Taiwan; 4. Central Taiwan; 5. Southern Taiwan; 6: South-southern Taiwan; 7. Hengchun peninsula; 8: Southeastern Taiwan; 9: Eastern Taiwan. @ C: central; NAM: North America; NE: northeastern; NW: northwestern; S: southern; SE: southeastern; SS: southern most; SW: southwestern; W: western. N/A: not available).

Taxa	A	B*	C@	D	E	F	G@	H@	I
Cycadaceae									
Cycas taitungensis	600	8	*C. revoluta*; Ryukyus	16S RNA-23S RNA, *matK*, *psbC-trnS*, *rpl20-rpl12*, *rps4-trnL*, *trnL-trnF*, *trnS-trnG*, *trnS-fM* cpDNA	0.0001	(*C. panzhihuaensis*, (*C.taitungensis*, *C. revoluta*))	(SWChina, (Taiwan, (SRyukyu, NRyukyu)))	SWChina through SSChina via South China Sea's land bridge	Kyoda & Setoguchi, 2010
				*Nad*1 mtDNA	0	N/A	N/A		
Taxaceae									
Taxus sumatrana	2000	2-6,9	*T. mairie* E, SEChina	*rbcL*, *matK*, *trnH-psbA*, *trnL-trnF* cpDNA	N/A	(*T. chinensis*, (*T. mairie*, (*T. sumatrana*, *T. sumatrana*)))	(S,CChina, (SEChina, (Taiwan, (Taiwan, Philippine))))	SE China via Tungshan land bridge	Liu *et al*., 2011
				ITS nrDNA	0.006	N/A	N/A		
Amentotaxus formosana	1050	6	*A. yunnanensis*; SWChina;	*matK*, *psbA-trnH*, *rbcL*, *rps4*, *trnL-trnL-trnF* cpDNA	0.0086	(*A. formosana*, (*A. yunnanensis*, *A. argotaenia*))	(Taiwan, (SWChina, China))	CChina through SEChina via Tungshan land bridge	Hao *et al*., 2008
				*Nadh*1 mtDNA	0.0155	N/A	N/A		GenBank
Cephalotaxus wilsoniana	2000	2-6, 9	*C. harringtonia*; Japan.	*chlL*, *matK*, *psbA-trnH*, *rbcL*, *rpoc*1, *trnL-trnF* cpDNA	0.0021	(*C. harringtonia*, (*C. wilsoniana*, (*C. koreana*, *C. harringtonia* cv. *fastigiata*)))	(Japan, (Taiwan, (Korea + NEChina, Japan)))	Japan via Ryukyus	Hao *et al*., 2008
Podocarpaceae									
Nageia nagi	250	1-2, 7, 8-9	*N. nagi*; Vietnam, SChina and SJapan	*psbA-trnH* and *trnL-trnF* cpDNA	0	(*N. fleuyri*, (*C. nagi, C. nagi*))	(SWChina, (SChina, Taiwan))	SSChina via South China Sea's land bridge	Present paper
Podocarpus costalis	20	Lanyu, islet close to 8	*P. costalis*; Philippines	*matK*, *psbA-trnH*, *trnL-trnF* cpDNA	0	(*P. coastalis*, (*P. nakaii,* (*P. fasciculus*, *P. macrocarpus* var. *macrocarpus*, *P. macrocarpus* var. *maki*)))	(Philippines, Lanyu)	Philippines	Present paper
Podocarpus fasciculus	2000	2-4,	*P. macrophyllus;* China, Taiwan, SJapan	*matK*, *psbA-trnH*, *trnL-trnF* cpDNA	0	(*P. fasciculus*, *P. macrocarpus* var. *macrocarpus*, *P. macrocarpus* var. *maki*)	Probably (Taiwan, Taiwan)	Taiwan	Present paper
Podocarpus macrphyllus var. macrophyllus	300	7	*P. macrphyllus* var. *maki*; China, Taiwan, SJapan	*matK*, *psbA-trnH*, *trnL-trnF* cpDNA	0	(*P. fasciculus*, *P. macrocarpus* var. *macrocarpus*, *P. macrocarpus* var. *maki*)	Probably (China, Taiwan)	SSChina via South China Sea's land bridge	Present paper
Podocarpus macrphyllus var. maki	500	1, 6, 8, 9	*P. macrphyllus* var. *macrophyllus*; China, Taiwan, SJapan	*matK*, *psbA-trnH*, *trnL-trnF* cpDNA	0	(*P. fasciculus*, *P. macrocarpus* var. *macrocarpus*, *P. macrocarpus* var. *maki*)	(China, Taiwan)	SSChina through SEChina via South China Sea's land bridge	Present paper
Podocarpus nakaii	650	4	*P. annamiensis*; Myanmar, Vietnam and Hainan, China	*matK* cpDNA	0.0025	(*P. annamensis*, *P. fasciculus*)	Probably (SSChina, Taiwan)	SSChina through SEChina via Tungshan land bridge	Present paper
Pinaceae									

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Abies kawakamii	3050	2-6	*A. ziyuanensis*; CChina;	ITS nrDNA	0.0164	(*A. kawakamii*, *A. homolepis*, *A. ziyuanensis*, *A. chensiensis*)	(Taiwan, CChina, Japan, NChina)	CChina through SEChina via Tungshan land bridge	Xiang *et al*., 2009
Keteleeria davidiana var. formosana	600	1, 6	*K. davidiana* var. *davidiana*; SWChina;	*matK*, *rbcL*, *rps*4, *trnK-matK* cpDNA	0.0006	(*K. fortunei*, (*K. davidiana* var. *davidiana*, *K. davidiana* var. *formosana*))	(EChina, (SWChina, Taiwan))	SWChina through SSChina via South China Sea's land bridge	GenBank
Picea morrisonicola	2750	3-5	*P. torano*; Japan	*petN-psbM-trnD*, *trnT-trnF* cpDNA	0.0011	(*P. morrisonicola*, (*P. torano*, *P. neoveitchii*), *P. chihuanuana*, *P. maximowiczii*)	(Taiwan, (Japan, NChina), Mexico, Japan)	Japan via Ryukyus	Ran *et al*. 2006
			P. maximowiczii; Japan;	*matK*, *rbcL*, *trnT-trnL-trnF* cpDNA	0.0009	N/A	N/A		GenBank
			P. maximowiczii; Japan;	*Nad*5 mtDNA	0.0009	N/A	N/A		Ran *et al*. 2006
Pinus armandii var. masteriana	2800	2-6	*P. kwangtungensis*; SChina; *P. armandii* var. *armandii*; CChina, SJapan,	*LEA* nrDNA	0	(P. *armandii* var. *armandii*, (*P. morrisonicola*, *(P. armandii* var. *masteriana*, *P. dalatensis*), (*P. kwangtungensis*, *P. dalatensis*))	(Himalaya, (CChina, (Taiwan, (Taiwan, Vietnam), (SChina, Vietnam)))	CChina through SEChina via Tungshan land bridge	Syring *et al*., 2007
Pinus massoniana	400	1-3	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Pinus morrisonicola	1300	1-6	*P. kwangtungensis*; S China, Vietnam, and other many species	*matK*, *trnG* cpDNA	0.0009	N/A	N/A	CChina through SEChina via Tungshan land bridge	Liston *et al*., 2007;
			P. kwangtungensis; S China, Vietnam	*LEA* nrDNA	0.0043	(P. *armandii* var. *armandii*, (*P. morrisonicola*, *(P. armandii* var. *masteriana*, *P. dalatensis*), (*P. kwangtungensis*, *P. dalatensis*))	(CChina, (Taiwan, Taiwan, Vietnam, (SChina, Vietnam))		Syring *et al*., 2007
Pinus taiwanensis	1950	2-5, 8-9	*P. thunbergii*, Japan.	*atpB-rbcL*, *matK*, *rbcL*, *rpl*20-*rps*8, *trnV* cpDNA	0.0008	(*P. taiwanensis*, (*P. hwangshanensis*, *P. luchuensis*, *P. thunbergii*, *P. tabuliformis*, (*P. kesiya*, *(P. densata*, *P. yunnanensis*))))	(Taiwan, (China, Japan))	EChina through SEChina via Tungshan land bridge	Present paper
			P. hwanshanensis, E China	*Nadh*1 mt DNA	0	N/A	N/A		
Pinus taiwanensis var. fragilissima	800	8	*P. taiwanensis*; Taiwan	*atpB-rbcL*, *matK*, *rbcL*, *rpl*20-*rps*8, *trnV* cpDNA	0	(*P. taiwanensis*, *P. taiwanensis var. fragilissima*)	(Taiwan, Taiwan)	Taiwan	Present paper
Pseudotsuga wilsoniana	1650	2-5, 8-9	*P. gausenii*; E. China	*atpB-rbcL*, *matK*, *rbcL*, *rpl*20-*rps*8, *trnV* cpDNA	0.0002	(*P. japonicus*, (*P. wilsoniana*, *P. gausenii*, *P. sinensis*, *P. forestii*, *P. brevifolia*))	(Japan, (Taiwan, China))	EChina through SEChina via Tungshan land bridge	Wei *et al*., 2010
			P. forestii; SW China	*LEAFY* nrDNA	0.0024	*(P. forestii*, (*P. wilsoniana*, *P. brevifolia*))	(SWChina, (SWChina, Taiwan)		
			P. gausenii; E. China	*LEAFY* nrDNA	0.0024	(*P. wilsoniana*, (*P. gausenii*, *P. sinensis*, *P. japonicus*))	(Taiwan, (EChina, Japan))		
			P. gausenii; E. China	*Nad*5, *cox*1 mtDNA	0.0004	N/A			
Tsuga formosana	2750	2-6	*T. dumosa*; Himalaya; *T. sieboldii*; Japan	*rpl*16, *trnk-matK*, *trnL-trnL-trnF* cpDNA	0.0033	(*T. canadensis*, (*T. dumosa*, *T. formosana*), (*T. sieboldii*, (*T. chinensis*, *T. forestii*)))	(East NAM, (Himalaya, Taiwan), (Japan, China)))	Japan via Ryukyus	Havill *et al*., 2008

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Tsuga formosana (Continued)			*T. sieboldii*; Japan	ITS nrDNA	0.0133	(*T. dumosa*, ((*T. caroniniana*, (*T. sieboldii*-Korea, *T. diversifolia*)), ((*T. diversifolia*, (*T. sieboldii*, *T. formosana*), *T. chinensis*, *T. forestii*))))	(Himalaya, ((west NAM, (Korea, Japan), (Japan, (Japan, Taiwan), China)))		
Cupressaceae									
Cunninghamia lanceolata var. konishii	2050	2-5, 9	*C. lanceolata* var. *lanceolata*; Vietnam, Laos, China	*petG-trnP*, *trnD-trnT*, *trnL-trnF*, *trnV* cpDNA	0	(*C. lanceolata* var. *lanceolata*, *C. lanceolata* var. *konishii*)	(China, Taiwan)	CChina through SEChina via Tungshan land bridge	Hwang *et al*., 2003
Taiwania cryptomerioides	1950	2-6	*T. florisiana*; SW, S, CChina and Burma	*chlL*, *matK*, *trnL-trnL-trnF* cpDNA	0.0016	(*T. florisiana*, *T. cryptomeroides*)	(SWChina, Taiwan)	Japan via Ryukyus or Echina through SEChina via Tungshan land bridge	Chou *et al*., 2011
Calocedrus formosana	1100	2-5, 9	*C. macrolepis*; SW, SChina	*rbcL*, *trnK* cpDNA	0.0005	N/A	N/A	SWChina through SChina via Tungshan land bridge	GenBank
				ITS nrDNA	0.0064	(*C. decurrens*, (*C. macrolepis*, (*C. rupestris*, (*C. macrolepis*, *C. formosana*)))	(NAM, (Vietnam, (SChina, Taiwan)))		Chen *et al*., 2009
Chamaecyparis formosensis	1800	2-6	*C. pisifera*; Japan	*petG-trnP*, *trnV* cpDNA	0.0032	((*C. thyoides*, (*C. formosana*, *C. pisifera*)), (*C. lawsoniana*, (*C. obtusa* var. *obtusa*, *C. obtusa* var. *taiwanensis*)))	((east NAM, (Taiwan, Japan)), (west NAM, (Japan, Taiwan)))	Japan via Ryukyus	Wang *et al*., 2003;
			C. pisifera; Japan	ITS nrDNA	0.0424	((*C. formosensis*, *C. pisifera*), (*C. lawsoniana*, (*C. thyoides*, (*C. obtusa* var. *obtusa*, *C. obtusa* var. *taiwanensis*)))	((Taiwan, Japan), (west NAM, (east NAM, (Japan, Taiwan))))		GenBank; *cf*. Li *et al*., 2003
Chamaecyparis obtusa var. taiwanensis	2000	2-6	*C. obtusa* var. *obtusa*; Japan	*petG-trnP*, *trnV* cpDNA	0.0009	(*C. lawsoniana*, (*C. obtusa* var. *obtusa*, *C. obtusa* var. *taiwanensis*))	(west NAM, (Japan, Taiwan)	Japan via Ryukyus	Wang *et al*., 2003
			C. obtusa var. *obtusa*; Japan	ITS nrDNA	N/A	(*C. thyoides*, (*C. obtusa* var. *obtusa*, *C. obtusa* var. *taiwanensis*)))	(east NAM, (Japan, Taiwan))		Li *et al*., 2003
Juniperus tsukusiensis var. taiwanensis	2100	9	*J. tsukusiensis* var. *tsukusiensis*; Yakushima, Japan	*petN-psbM*, *trnD-trnT*, *trnS-trnG* cpDNA	N/A	(*J. chinensis*-Japan, (*J. jarkensensis*, *(J. tsukusimensis* var. *tsukusimensis*, *J. tsukusimensis* var. *taiwanensis*)))	(Japan, (Japan, Taiwan))	Japan via Ryukyus or long distance dispersal,	Adams *et al*., 2011
			J. tsukusiensis var. *tsukusiensis*; Yakushima, Japan	ITS nrDNA	0				
Juniperus formosana var. formosana	2650	3-6, 8	*J. formosana* var. *mairei*; N, W, CChina	*matK*, *petB-petD*, *psbB*, *rbcL*, *rps4-trnS*, *trnD-trnT*, *trnS-trnG*, *trnL-trnL-trnF*, *trnV*, cpDNA	0.0002	(*J. rigida*, (*J. formosana* var. *formosana*, *J. formosana* var. *mairei*))	(East Asia, (CChina, Taiwan))	CChina through SEChina via Tungshan land bridge	Mao *et al*., 2010
Juniperus morrisonicola	3400	3-6	*J. squamata* f. *wilsonii* WChina	*petN-psbM*, *trnS-trnG*, *trnD-trnT*, *trnL-trnF*, cpDNA	N/A	((*J. squamata* var. *squamata*, (*J. tibetica*, *J. squamata* f. *wilsonii*), (*J. morrisonicola*, *J. przelwaskii*))	(China, WChina, (Taiwan, NWChina))	SWChina through SEChina via Tungshan land bridge	Adams & Schwarzbach, 2012
				ITS nrDNA	N/A				

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***Cephalotaxus* Sieb. & Zucc.**

Cephalotaxus contains 6–11 species distributing in India, China, Myanmar, Thailand, Malaysia, Taiwan, Japan, and Korea (Page, 2000; Farjon, 2010). One endemic species is in Taiwan, but variety status as *C. harringtonia* var. *wilsoniana* was adopted by Farjon (2010). Species status is followed here until a critical treatment has been done. Fossil *Cephalotaxus* was widely distributed in the middle of Cenozoic, and was wide spread throughout the North Hemisphere (Shi *et al*., 2010). In Europe, It was reported in Cenozoic deposits from the middle Eocene to the Pleistocene (Shi *et al*., 2010). In eastern Asia, it was reported from Kwangchi, China in the Oligocene, but soon disappeared, and it occurred in Japan since the Pliocene (Shi *et al*., 2010). In North America, it was only reported from USA in the Miocene and might have been derived from the eastern Asian lineage (Shi *et al.*, 2010).

***Cephalotaxus wilsoniana* Hayata**

C. wilsoniana inhabits needle-leaved and needle-broad-leaved forest at elevations of 1300–2700 m throughout Central Mountain Range in Taiwan (Liu, 1966). Based on cpDNA (Hao *et al.*, 2008), phylogenetic tree can be described in Venn diagram as (*C. harringtonia*-Japan, (*C. wilsoniana*-Taiwan, (*C. koreana*-Korea, *C. harringtonia* cv. *fastigiata*-Japan))). Thus *C. wilsoniana* is nested inside a clade distributing in Japan and Korea. *C. wilsoniana* and *C. harringtonia* shared the shortest genetic distance among these related species based on cpDNA (Table 1; Huang, 2011). Thus Taiwan's species is possibly derived from lineage of Japan, from where the ancestor of *C. wilsoniana* might have migrated through the Ryukyus to northern Taiwan during the glaciations.

***Nagaia* Gaertn.**

Nageia contains five species in southeastern Asia, eastern Asia and India (Page, 2000; Farjon, 2010). Two sections, *i.e.*, *Nageia* and *Wallichiana*, were proposed to accommodate extant species (Fu, 1992). Section *Nageia* is distributed from Malaysia, Vietnam, southern and southeastern China to southern Japan while section *Wallichiana* is distributed from northeastern India, IndoChina, Malaysia, the Philippines to New Guinea. One species belonging to section *Nageia* is in Taiwan. Another species, *N. fleuryi*, has been reported in Taiwan based on specimens collected from Hsintien, vicinity of Taipei City (Keng, 1987), but the specimens were considered within variation range of *N. nagei* (Yang *et al*., 1997; Farjon, 2010). The later treatment is followed here. Fossil *Nageia* has been reported in Russia and Japan from the early Cretaceous, and in Hainan, China, from the Eocene (Jin *et al.*, 2010).

***Nageia nagi* (Thunb.) O. Ktze.**

N. nagi is distributed in Vietnam, southern to central China and southern Japan (Farjon, 2010). Two species have been reported in Taiwan including *N. formosensis* Dummer from southern Taiwan and *N. nankoensis* Hayata from northern Taiwan (Hu, 1964; Mill, 1999). Based on *psbA-trnH* and *trnL-trnF* cpDNA (unpublished data of the author), no variation was found among four individuals collected from northern and southern Taiwan, and *N. nagi* from GenBank (*AY083103*) but these samples vary with *N. fleuryi* (*AY013734*) by two substitutions. Thus it seems to be appropriate to merge these two Taiwan's species under the name *N. nagi* as the treatment of Yang *et al*. (1997) and Farjon (2010).

Fu (1992) considered that the refuge and dispersal center of the genus would be around southwestern China although northeastern Asian origin of the genus has been proposed based on fossil records (Jin *et al*., 2010). However, a fossil species, *N. hainanensis* Jin *et al*., from the Eocene of Hainan, not distinguishable morphologically from the extant *N. nagi* was described (Jin *et al*., 2010). In addition, distribution pattern of *Nageia* in Taiwan, in low altitudes of the north and the south, make it unlikely to consider that ancestor of Taiwan's population has migrated from northeastern Asia. Hence Taiwan's population could have derived from southern China. It is postulated that *N. nagi* could have originated from the boarder of China and IndoChina as suggested by Fu (1992), and ancestor of Taiwan's population could have migrated from southern South China via South China Sea's land bridge to southern Taiwan during the glaciations, and then dispersed through eastern Taiwan to northern Taiwan.

***Podocarpus* L'Herit ex Pers.**

Podocarpus contains about 100 species mainly in the Southern Hemisphere extending to West Indies, Mexico, southern China and southern Japan (Page, 1990; Farjon, 2010). Two subgenera, *Foliatus* and *Podocarpus*, each with nine sections, were classified (De Laubenfels, 1985). Treatment of two subgenera is supported by phylogenetic tree based on *rbc*L cpDNA (Conran *et al*., 2000) and *matK* cpDNA (unpublished data from GenBank). Subgenus *Podocarpus*, composed of 41 species, is distributed in the Southern Hemisphere, while subgenus *Foliatus*, composed of 53 species, is distributed in tropical Asia, Australia and

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Pacific islands (De Laubenfels, 1985). Five taxa, namely, *P. costalis, P. fasciculus*, *P. macrocarpus* var. *macrocarpus*, *P. macrocatrpus* var. *maki* and *P. nakaii,* are in Taiwan and they all belong to subgenus *Foliolatus*.

Based on *psbA-trnH*, *trnL-trnF* and *matK* cpDNA (unpublished data of the author), pylogenetic tree of these five taxa could be described in Venn diagram as (*P. costalis,* (*P. nakaii,* (*P. fascisulus, P. macrocarpus* var. *macrocarpus*, *P. macrocatrpus* var. *maki*))). No variation was found among Taiwan's *P. fasciculus, P. macrocarpus* var. *macrocarpus* and *P. macrocatrpus* var. *maki*. Based on *matK* cpDNA by integrating sequences deposited at GenBank and author's unpublished data, phylogenetic tree of species related to Taiwan's taxa can be described in Venn diagram as ((*P. polystachyus*, *P. elatus*), (*P. longifoliolatus*, *P. dispermus*), *P. brevifolius*, *P. costalis*, *P. rumphii*, ((*P. nakaii*, *P. annamiensis*), (*P. nerifolia*, *P. macrophyllus* var. *macrophyllus*, *P. fasciculus*, *P. macrophyllus* var. *maki* (= *P. chinensis*), *P. chingiana*))).

***Podocarpus costalis* Presl.**

P. costalis is distributed in northern Luzon, the Philippines, and isles between it and Taiwan (Yang *et al*., 1997; Farjon, 2010). It inhabits open coastal area at Lanyu, an isle off southeastern Taiwan. It is a sister species to the clade formed by the other Taiwanese species. Since the genus could be of Southern Hemisphere origin, judging from present distribution pattern, it is plausible that it has colonized Lanyu in recent time from southern nearby islands.

***Podocarpus fasciculus* de Laubenfels**

P. fasciculus inhabits moist forest at elevations of 1500–2500 m of northern Central Mountain Range in Taiwan (Yang *et al*., 1997). It was endemic to Taiwan when described (De Laubenfels, 1985), but populations of the southern Japan and Iriomote of the Ryukyus have been considered as members of the species (Farjon, 2010). Morphologically, only character of long vs. sessile receptacle of male cones distinguishes *P. fasciculus* from *P. macrophyllus* var. *maki* (Yang and Lu, 1994), and this character is hardly found on the specimens. Therefore it is considered as endemic species to Taiwan here. *P. fasciculus* and *P. macrophyllus* var. *maki* are hard to distinguish from vegetative specimens and they showed no variation based on cpDNA data, implying their close relationship. In Taiwan, *P. fasciculus* and *P. macrophyllus* var. *maki* are distributed allopatrically. The former is in middle altitudes of north-central part of western Taiwan while the latter is in relatively lower altitudes of northern, eastern and southern Taiwan. Since morphological and molecular variation of these two taxa is limited, it is likely that *P. fasciculus* is recently evolved when *P. macrophyllus* var. *maki* in Taiwan dispersed to higher altitude.

Podocarpus macrophyllus* (Thunb.) Sweet var. *macrophyllus

P. macrophyllus var. *macrophyllus*, distributing in China, Taiwan and southern Japan, inhabits tropical rain forest in southern Taiwan and Lanyu (Yang and Lu, 1994; Farjon, 2010). Since Taiwan's population is distributed in southern part, its ancestor very likely has migrated from the southern South China as Hainan via South China Sea's land bridge to southern Taiwan.

***Podocrpus macrophyllus* (Thunb.) Sweet var. *maki* Sieb & Zucc.**

P. macrophyllus var. *maki* is distributed in southern, central and eastern China, and southern Japan (Earle, 2011). It inhabits moist broad-leaved forest in northern, eastern and southern Taiwan and it is distributed in relatively higher altitude than its typical form in Taiwan. This variety could have derived from ancestor of the southern South China via South China Sea's land bridge and invaded southern Taiwan, like its typical form, then migrated northward from the eastern part.

***Podocarpus nakaii* Hayata**

P. nakaii is endemic and inhabits broad-leaved forest in central Taiwan (Yang and Lu, 1994; Farjon, 2010). Phylogenetic tree based on *matK* cpDNA relates *P. nakaii* to *P. annamiensis* from Myanmar, Vietnam and Hainan, China. It belongs to the section *Globulus* distributing from Vietnam, Taiwan, to Sumatra, Borneo and New Caledonia (De Laubenfels, 1985). Hence *P. nakaii* is the most northern species in this section. Because central Taiwan is near the entrance of Tungshan land bridge (Huang, 2011), it is postulated that ancestor of *P. nakaii* has migrated from IndoChina through southern China via Tungshan land bridge to central Taiwan during the glaciations.

***Abies* Miller**

Abies contains 10 sections and 47 species in the Northern Hemisphere (Farjon, 2010). One endemic species, *A. kawakamii*, is in Taiwan. Farjon (2010) related it to *A. homolepis* and treated them under subsection *Homolepides* of section *Monii*. *Abies* was proposed to have originated from the middle and high latitudes of the Northern Hemisphere in the middle

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Cretaceous and might have dispersed southward in the Eocene (Xiang *et al*., 2009). Megafossils in Asia were found in Japan in the Miocene and Pleistocene and in Yunnan in the Pliocene (Xiang *et al*., 2009).

***Abies kawakamii* (Hayata) Ito**

A. kawakamii forms pure stands at the elevations of 2800–3700 m throughout Taiwan (Liu, 1966). Based on nrITS phylogenetic tree, it forms a clade with *A. chensiensis* in northern China, *A. homolepis* in Japan, and *A. ziyuanensis* in central China (Xiang *et al*., 2009). Thus it belongs to a clade of Sino-Japanese subregion (*sensu* Wu and Wu, 1998). *A. kawakamii* and *A. ziyuanensis* share the shortest genetic distance among related species based on nrITS (Table 1), although Farjon (2010) taxonomically treated *A. kawakamii* under subsection *Homolepides* including *A. homolepis* while *A. chensiensis* and *A. ziyuanensis* were treated in another subsection. The close relationship between *A. kawakamii* and *A. ziyuanensis* is also exemplified by sharing two common haplotypes (*A* & *B sensu* Shih *et al*., 2007) of *GapC* intron nrDNA (GenBank, accessed in December, 2012). Because Japan's *A. homolepis* and northern Chinese *A. chensiensis* are also related to Taiwan's species, their ancestors could have originated and diversified from northeastern Asia. From there, one lineage went into Japan, one lineage dispersed to northern China, and one lineage migrated southward to central China. Sequentially, one lineage from central China went further southward through southeastern China via Tungshan land bridge to Taiwan.

***Keteleeria* Carriere**

Keteleeria contains three species in China, Laos, Vietnam and Taiwan (Farjon, 2010). One endemic variety is in Taiwan. *Keteleeria* might have occurred in the late Cretaceous of East Asia and became widespread throughout the Northern Hemisphere in the Tertiary (Wang *et al*., 2006). Manchester (2009) reported that fossil *Keteleeria* occurred in the early Eocene and Oligocene in North America, and was present in both Europe and Asia from Oligocene to Pliocene. Present diversity center is in southwestern China from where thinned to central and eastern China.

***Keteleeria davidiana* (Franchet) Beissner var. *formosana* Hayata**

K. davidiana var. *formosana* is disjunctly distributed in northern and southern Taiwan at elevations of 300–600 m in the north and 500–900 m in the south (Liu, 1966). *K. davidiana* var. *formosana* and *K. davidiana* var. *davidiana* in central-western China share the shortest genetic distance among related taxa based on cpDNA (Table 1). Liu (1966) hypothesized that the northern Taiwan's population was derived from those of southeastern China, while the southern Taiwan's population from those of southwestern and southern China during the glaciations. This view was adopted by Shen (1997). However, *K. shanwangensis* Y.-F. Wang *et al*., the Miocene species from Shantung of eastern China, is more similar to *K. fortunei* (distributing in southwestern, central and southeastern China) rather than to *K. davidiana* (Wang *et al*., 2006). Hence Miocene distribution pattern of *K. davidiana* could be consistent with the present one (Wang *et al*., 2006: Fig. 1), implying that during the glaciations, populations in southeastern China might belong to *K. fortunei* rather than to *K. davidiana*. Thus it seems less likely that two sources colonized northern and southern Taiwan respectively. In addition, mtDNA haplotype *e* of *Cyclobalanopsis glaucus* in Taiwan (Lin *et al*., 2003: Table 1) showed a similar disjunct pattern as *K. davidiana* var. f*ormosana* and it was derived from single source, Hong Kong (mtDNA haplotype *f*). Thus colonization of ancestor of *K. davidiana* var. *formosana* from one source and becoming disjunct is quite plausible. In the case of one source of colonization, ancestor of *K. davidiana* var. *formosana* could have migrated from southwestern China, present center of diversity and dispersal, through southern China via South China Sea's land bridge and colonized southern Taiwan. It then migrated northward from eastern Taiwan to northern as *Nageia nagi* did because *K. davidiana* var. *formosana* and *N. nagi* have similar distribution pattern in Taiwan.

***Picea* A. Dietrich**

Picea contains two sections and 38 species in the Northern Hemisphere (Farjon, 2010). One endemic species, *P. morrisonicola*, is in Taiwan, and it is treated under series *Picea*, at least including *P. maximowiczii* in Japan and *P. chihuahuana* in Mexico, of section *Picea* (Farjon, 2010). Based on molecular phylogeny and fossil evidence, Ran *et al*. (2006) proposed that *Picea* has originated from North America and migrated to Asia through Beringia during the early Tertiary, and then moved westward to Europe. Since Miocene, one lineage in northern Eurasia might have migrated southward to the eastern Himalayas when the Himalaya was uplifted and the climate became cooler, and another lineage migrated to Japan (Ran *et al*., 2006).

***Picea morrisonicola* Hayata**

P. morrisonicola is the southern most species of the genus (Earle, 2011) and it is distributed sporadically

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among the pure stands of *Tsuga* and *Abies* in Central Mountain Range in Taiwan at elevations of 2300–3200 m (Liu, 1966). Phylogenetic tree based on cpDNA (Ran *et al*., 2006) may be described in Venn diagram as (*P. morrisonicola*, (*P. orientalis*, (*P. torano, P. neoveitchii*), *P. chihuahuana*, ((*P. wilsonii*, *P. purpurea*, (*P. maximowiczii*, *P. brachytyla*)))), with *P. chihuahuana* in Mexico, *P. orientalis* in western Asia and the other species in eastern Asia, while *P. morrisonicola*, *P. orientalis*, *P. torano*, and *P. mzximowiczii* share the same mtDNA haplotype which is different from other species (Ran *et al*., 2006). *P. morrisonicola* and *P. maximowiczii* in Japan share the shortest genetic distance among related species based on cpDNA (Table 1). Biogeography of the genus was discussed by Ran *et al*. (2006), but that of *P. morrisonicola* was not mentioned. Because *P. morrisonicola* is a sister species to the other related species and contains five autapomorphies (Ran *et al*., 2006: Fig. 1), implying its long time divergence, the ancestor of *P. morrisonicola*, might have migrated from Japan in the Pliocene southward via the Ryukyus to northern Taiwan.

***Pinus* L.**

Pinus contains two subgenera, *i.e.*, *Pinus* and *Strobus*, and 113 species mainly in the Northern Hemisphere (Farjon, 2010). Five taxa, *i.e. P. armandii* var. *masteriana*, *P. morrisoniacola*, *P. massoniana*, *P. taiwanensis*, and *P. taiwanensis* var. *fragilissima*, occur in Taiwan with the first two taxa belonging to subsection *Strobi* of section *Quinquefolius* of subgenus *Strobus*, and the latter three belonging to subsection *Pinus* of section *Pinus* of subgenus *Pinus*. Based on *atpB-rbc*L spacer, *matK* gene, *rbc*L gene, *rpl*20-*rps*8 spacer and *trnV* intron cpDNA (unpublished data), no variation was found among samples from Taiwan including *P. massoniana* from Huoyenshan, Miaoli, *P. taiwanensis* from Chenghsipao, Hsinchu, and *P. taiwanensis* var. *fragilissima* from eastern South Cross Way, Taitung.

***Pinus armandii* Franchet var. *masteriana* Hayata**

P. armandii var. *masteriana* inhabits relatively dry needle-leaved forest in Central Mountain Range at elevations of 2300–3300 m in Taiwan (Liu, 1966). Based on Late Embryogenesis Abundant (*LEA*)-like gene nrDNA (Syring *et al*., 2007), the phylogenetic tree of *P. armandii* var. *masteriana* and its related species can be described in Venn diagram as (P. *armandii* var. *armandii*, (*P. morrisonicola*, *(P. armandii* var. *masteriana*, *P. dalatensis*), (*P. kwangtungensis*, *P. dalatensis*)). *P. armandii* var. *armandii* is distributed sporadically in southwestern, southern and central China and southern Japan, *P. morrisonensis* in Taiwan, *P. kwangtungensis* in southern China and Vietnam and *P. dalatensis* in Vietnam (Earle, 2011). *P. armandii* var. *masteriana* and both *P. kwangtungensis* and *P. morrisonicola* share the shortest genetic distance among related species based on *LEA* gene nrDNA (Table 1), but morphologically *P. armandii* var. *masteriana* is most related to *P. armandii* var. *armandii*. Thus relationship of *P. armandii* var. *masteriana* is unclear, but its related taxa are distributed in southern China and central China. It is proposed that ancestor of *P. armandii* var. *masteriana* in central or eastern China could have migrated southward to southeastern China via Tungshan land bridge to Taiwan.

***Pinus massoniana* Lamb.**

P. massoniana is distributed in southern central and southeastern China. In Taiwan, Liu (1966) reported that it inhabited northern and central open dry area at elevations of 300–1300 m and also occurred in Coastal Range of eastern Taiwan. However, population with intermittent morphology between *P. taiwanensis* and *P. massoniana* in eastern South Cross Way turned out to be *P. taiwanensis* var. *fragilissima* (Businsky, 2003, Farjon, 2010). Therefore, distribution range of *P. massoniana* is here considered restricted to low elevations of central and northern Taiwan. Judging from species distribution range, ancestor of Taiwan's population should have migrated via Tungshan land bridge to Taiwan.

***Pinus morrisoniacola* Hayata**

P. morrisonicola is endemic to Taiwan and inhabits open mountain forest at elevations of 300–2300 m (Liu, 1966). It formed a clade with *A. armandii* var. *masteriana*, *P. kwantungensis* and *P. dalatensis* based on a *LEA* gene nrDNA phylogenetic tree (Syring *et al*., 2007). Based on cpDNA phylogenetic tree (Liston *et al*., 2007), *P. morrisonicola* is nested inside a clade with relatively long branch. *P. morrisonicola* and *P. kwangtungensis* share the shortest genetic distance among related species based both on *LEA* gene nrDNA, and cpDNA (Table 1). However, *P. morrisonicola* is distantly related to *P. parviflora* in Japan, once the latter species circumscription including Taiwanese specimens. Molecular data strongly suggested that *P. morrisonicola* was closely related to *P. kwangtungensis*. Thus ancestor of *P. morrisonensis* could have migrated from southern China via Tungshan land bridge to Taiwan.

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***Pinus taiwanensis* Hayata**

P. taiwanensis is endemic to Taiwan and inhabits open dry areas at elevations of 750–3000 m in Central Mountain Range and usually form a pure stand (Liu, 1966). *P. taiwanensis* and *P. hwangshanensis* have been treated as subspecies of *P. luchuensis* (Li, 1997). Based on cpDNA phylogenetic tree, *P. taiwanensis* was a sister species to a clade including *P. hwangshanensis*, *P. luchuensis*, *P. thunbergii*, *P. tabuliformis*, *P. kesiya*, *P. densata*, and *P. yunnanensis* (Gernadt *et al*., 2005), or it formed a clade with *P. thunbergii* and became a sister to a clade including *P. kesiya*, *P. yunnanensis* and *P. hwangshanensis*, while *P. densata* is in neighboring clade (Eckert *et al*., 2006). *P. taiwanensis* and *P. thunbergii* in Japan share the shortest genetic distance among related species based on cpDNA data while *P. taiwanensis* and *P. hwangshanensis* in eastern China show no differentiation based on mtDNA (Table 1). As *P. taiwanensis* is more related to Japanese and eastern Chinese species, migration route from southeastern China possibly via Tungshan land bridge is proposed.

***Pinus taiwanensis* Hayata var. *fragilissima* (Businski) Farjon**

P. taiwanensis var. *fragilissima* is endemic to Taiwan and inhabits open dry area at elevations 300–1000 m in eastern South Cross Way. It is intermetten morphologically between *P. massoniana* and *P. taiwanensis* (Businski, 2003). Farjon (2010) reduced it to *P. taiwanensis* var. *fragilissima* due to overlapping and slight difference in morphology. *P. taiwanensis* var. *fragilissima* and both *P. thunbergii* and *P. hwangshanensis* share the shortest genetic distance based on plastome data (GenBank, accessed in January, 2013, *cf*. Parks *et al*., 2012) with the absence of sequence of *P. taiwanensis*. Thus Farjon (2010) could be right in reducing it to a variety. Hence it is recently derived from *P. taiwanensis in situ*.

***Pseudotsuga* Carriere**

Pseudotsuga contains 4–8 species in northern Pacific coast (Farjon, 2010; Wei *et al*., 2010). One endemic species, *P. wilsoniana*, is in Taiwan (Wei *et al*., 2010), although it has been treated conspecific with *P. sinensis* (Farjon, 2010). The genus could have originated from North America based on fossil records (Struass and Doerksen, 1990) and molecular phylogeny (Wei *et al.*, 2010). It then migrated to Asia through Beringia possibly during the late Oligocene to the middle Miocene (Wei *et al.*, 2010).

***Psudotsuga wilsoniana* Hayata**

P. wilsoniana inhabits needle-leaved forest from north-central to south-central Central Mountain Range at elevations of 800–2500 m in Taiwan (Liu, 1966). Phylogenetic tree reconstructed by various DNA markers showed that North American species formed a clade and was a sister to eastern Asian clade (Wei *et al*., 2010). Based on cpDNA, phylogenetic tree of Asian species could be described in Venn diagram as (*P. japonica*, (*P. wilsoniana*, *P. gausenii*, *P. sinensis*, *P. forrestii*, *P. brevifolia*)), while *P. wilsoniana* has an autapomorphic substitution based on *nad*5 mtDNA (Wei *et al*., 2010: Fig. 1a). Hybrid origin of *P. wilsoniana* was revealed by *LEAFY* nrDNA phylogenetic tree because two haplotypes in two clades were found (Wei *et al*., 2010). One clade was (*P. forrestii*, (*P. brevifolia, P. wilsoniana*)) distributing in southwestern China, southern China and Taiwan respectively, and the other was (*P. wilsoniana*, (*P. gaussenii, P. sinensis, P. japonica*)) distributing in Taiwan, southeastern China, central China and Japan respectively. *P. wilsoniana* and *P. gausenii* share the shortest genetic distance among related species based on cpDNA and mtDNA data, while *P. wilsoniana* and both *P. gausenii* and *P. forestii* share the shortest genetic distance among related species based on *LEAFY* nrDNA (Table 1). In addition, *P. wilsoniana* contains diversified *LEAFY* haplotype in *P. sinensis*-*P. gausenii* clade, while shows no variation in *LEAFY* haplotype in *P. brevifolia*-*P. forestii* clade, implying that it might have mainly originated from *P. sinensis*-*P. gausenii* lineage. Thus *P. wilsoniana* is most closely related to *P. gausenii* and possibly receives another source of genome from ancestor of *P. forrestii* through gene flow. This view is not mentioned by Wei *et al*. (2010) because they thought *P. wilsoniana* was derived from *P. forestii*-*P. brevifolia* lineage and they propose historical biogeography of *Psudotsuga* based on *LEAFY* phylogenetic tree. Their story on biogeography of *P. wilsoniana* went as follows. The ancestor of *P. wilsoniana* derived from *P. forestii*-*P. brevifolia* lineage in the middle Miocene. In accordance with deterioration of the climate, it migrated southward to the refuge of southwestern China. In the process of migration, it hybridized with *P. sinensis*-*P. gausenii*-*P. japonica* lineage before moved to Taiwan.

Since *P. wilsoniana* may be derived from *P. sinensis*-*P. gausenii* lineage, the other story based on cpDNA and mtDNA phylogenetic tree would be suggested as follows. The ancestors of *Pseudotsuga* in northeastern Asia further migrated to Japan and China respectively in the middle Miocene when they have

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migrated from North America to northeastern Asia. From Japan, it then recolonized Asian continent in the late Miocene-early Pliocene when Japan was a part of Asian continent, and some populations evolved into *P. sinensis*-*P. gausenii* lineage. Part of the lineage received pollen from *P. brevifolia*-*P. forestii* lineage, occurring in eastern China then and on the course of migrating to southwestern China, and moved southward. This hybrid further migrated through southeastern China and possibly via Tungshan land bridge to central Taiwan and became *P. wilsoniana*.

Tsuga Carriere

Tsuga contains 14 species in eastern Asia and North America (Page, 1990), although classification of 9 species in 2 sections was proposed by Farjon (2010). One endemic species, *T. formosana*, is in Taiwan although Farjon (2010) treated it conspecific with *T. chinensis*. Center of origin of *Tsuga* is unknown. It was widely spread in the Northern Hemisphere in the Cenozoic and gradually went extinct in Europe since the Pleistocene (LePage, 2003a, b).

Tsuga formosana Hayata

T. formosana forms a pure stand at elevations of 2000–3500 m in Central Mountain Range in Taiwan (Editorial Committee of the Flora of Taiwan 2nd edition, 1994). It formed a clade with *T. sieboldii* in Japan according to nrITS phylogenetic tree, while it is related to *T. dumosa* in the Himalayas based on cpDNA data (Havill *et al*., 2008), although geographically it is more close to *T. chinensis* in China (Havill *et al*., 2008: Fig. 1). Species status of *T. formosana* is retained instead of variety status of *T. chinensis* var. *formosana* because it did not form a clade with *T. chinensis* in China based on nrITS phylogenetic tree (Havill *et al*., 2008). Based on nrITS, phylogenetic tree may be described in Venn diagram as (*T. dumosa*, ((*T. caroniniana*, (*T. sieboldii*-Korea, *T. diversifolia*)), ((*T. diversifolia*, (*T. sieboldii*-Japan, *T. formosana*), *T. chinensis*, *T. forestii*)))), which could be described by replacing taxa with areas as (Himalaya, (eastern North America, (Korea, Japan), (Japan, Taiwan, China))). Based on cpDNA, phylogenetic tree may be described in Venn diagram as (*T. canadensis*, (*T. dumosa*, *T. formosana*), (*T. sieboldii*, (*T. chinensis*, *T. forestii*))), which could be described by replacing taxa with areas as (eastern North America, (Himalaya, Taiwan), (Japan, China)). *T. formosana* and both *T. sieboldii* and *T. dumosa* share the shortest genetic distance among related species based on cpDNA data, while *T. formosana* and *T. sieboldii* share the shortest genetic distance among related species based on nrITS (Table 1), implying that *T. formosana* may be more related to *T. sieboldii*, as *T. dumosa* was supposed to be of hybrid origin (Havill *et al*., 2008). Both phylogenetic trees of *Tsuga* based on either cpDNA or nrITS (Havill *et al*., 2008: Figs. 2, 3) show that North America is possibly a center of dispersal and from where migrated to Asia progressively from high latitude to low latitude. Based on cpDNA dta, the genetic distance of *Tsuga formosanan* and *T. sieboldii* is the second highest among those of gymnosperms in Taiwan and their sister species, and the genetic distance is nearly equal to that of *Chamaecyparis formosensis* and *C. pisifera* (Table 1) implying its old age in Taiwan. In such a scenario, ancestor of *T. formosana* might have migrated from Japan via the Ryukyus to Taiwan at least during the Pliocene.

Cunninghamia R. Brown

Cunninghamia contains two species, *C. lanceolata* and *C. konishii* in Vietnam, Laos, China and Taiwan (Page, 1990). However, phylogeographic study based on cpDNA showed that large proportion of sampled individuals shared the same ancestral haplotype between *C. lanceolata* and *C. konishii*, although few individuals of each species contains its own unique haplotypes (Hwang *et al*., 2003). Liu (1966) considered *C. konishii* to be conspecific with *C. lanceolata*. Since differentiation do occur between these two taxa (Hwang *et al*., 2003), variety status is retained and one species with two varieties is followed. One variety is endemic to Taiwan. Fossils were reported from the early Cretaceous in northern Hemisphere (Brink *et al*., 2009).

Cunninghamia lanceolata (Lamb.) Hook. var. *konishii* (Hayata) Fujita

C. lanceolata var. *konishii* is at elevations of 1300–2800 m in the north and central of Central Mountain Range in Taiwan (Liu, 1966). Since *C. lanceolata* var. *lanceolata* is distributed in southwestern China to southeastern China but not in southern China, ancestor of *C. lanceolata* var. *konishii* might have migrated from southeastern China to Taiwan, possibly via Tungshan land bridge.

Taiwania Hayata

Taiwania contains 2–3 species in Myanmar, China and Taiwan (Page, 1990). One endemic species, *T. cryptomeroides*, is in Taiwan. It has been considered to be conspecific with *T florisiana*, distributing in Burma and southwestern China and scattered in Kuechou, Chiangchi and Fuchien, southern China (Liu, 1966; Farjon, 2010). Based on cpDNA, the genetic distance of Taiwan's *T. cryptomeroides* and Chinese *T. florisiana* is

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relatively higher among those of gymnosperms in Taiwan and their sister species (Table 1). Thus independent species is adopted. The earliest fossil records of *Taiwania* occurred in Alaska from the middle Albian of Cretaceous and it was distributed throughout North America and Eurasia from the late Cretaceous to the Pliocene (LePage, 2009). Fossils from the Miocene to the Pliocene were reported in eastern Asia mainly in Japan (LePage, 2009: Fig. 31). Comparison of the earliest Alaskan fossils with *T. cryptomeroides* reveals indistinguishable morphological characters implying morphological stasis of this genus (LePage, 2009).

***Taiwania cryptomeroides* Hayata**

T. cryptomerioides inhabits needle-leaved forest at elevations of 1300–2600 m in Central Mountain Range in Taiwan (Liu, 1966), and it is a component species in *Chamaecyparis* forest (Editorial Committee of the Flora of Taiwan 2nd edition, 1994). Because *T. cryptomeroides* and *T. florisiana* were estimated to be separated about three million years ago based on molecular dating (Chou *et al*., 2011), it has been proposed that a lineage probably from eastern China migrated through southeastern China, via East China Sea's land bridge (*cf*. Shen, 1997, Fig. 1) to Taiwan, while another lineage went on and spread to refuge of Yunnan and Vietnam. However, possible migration route from Japan via the Ryukyus to Taiwan was not ruled out as *T. cryptomeroides* is usually associated with *Chamaecyparis* species (Chou *et al*., 2011) and the Asian fossils from the Pliocene were mainly deposited in Japan (LePage, 2009: Fig. 31).

***Calocedrus* Kurz**

Calocedrus contains four species in western North America, western China, IndoChina and Taiwan respectively (Farjon, 2010), but two species represented in North America and Asia respectively were suggested by Long *et al*. (2011) by reducing Taiwan's and Vietnam's endemic species to variety due to low degree of variation of nrITS. However, *C. formosana* is monophyletic and morphologically separable such as thicker leaves and shorter receptacles of cones (Chen *et al*., 2009; Long *et al*., 2011). Hence species status is adopted. Fossil records were reported in the Northern Hemisphere (Chen *et al*., 2009). In Europe they were from the early Oligocene of Czech Republic and Hungary, from the early Miocene of Greece and from the Pliocene of Poland (Chen *et al*., 2009). In North America, they were from the Oligocene of Oregon, from the Oligocene-Miocene boundary of Alaska, and from the Miocene of Idaho (Chen *et al*., 2009). In Asia, they were from the Miocene of Yunnan and Japan (Chen *et al*., 2009).

***Calocedrus formosana* (Florin) Florin**

C. formosana inhabits moist forest at elevations of 300–1900 m in central and northern Taiwan (Liu, 1966). Topology of nrITS phylogenetic tree can be described in Venn diagram as (*C. decurrens*, (*C. macrocarpa*, (*C. macrocarpa*, *C. formosana*))) with each species in western North America, Vietnam, China and Taiwan respectively (Chen *et al*., 2009). *C. macrocarpa* and *C. formosana* formed a clade while *C. macrocarpa* was paraphyletic and arose from the basal nodes, suggesting that *C. formosana* is derived from *C. macrocarpa*. Because *C. macrocarpa* is distributed in Yunnan, Kuechou, Kwangtung and Hainan (Wang *et al*., 2004) and Miocene fossil from Yunnan has been reported (Chen *et al*., 2009), ancestor of *C. formoana* could have migrated from southwestern China to southern China and further migrated to central Taiwan via Tungshan land bridge.

***Chamaecyparis* Spach**

Chamaecyparis contains five species in temperate North America (NAM), Japan and Taiwan (Farjon, 2010). Two taxa, *C. formosensis* and *C. obtusa* var. *taiwanensis* are in Taiwan. Reliable fossils of the genus were reported in NAM from the early Eocene to Pliocene, in Europe from the late Oligocene to Pleistocene, in Caucasus and Ural from the Miocene to the Pleistocene, and in Japan from the Pliocene (Liu *et al*., 2009). Center of origin of *Chamaecyparis* is still unknown. Intercontinental floral exchange between NAM and Europe may have happened before the Oligocene (Liu *et al*., 2009). However, European species vanished after the last glacial (Liu *et al*., 2009). Eastern Asian *Chamaecyparis* most likely came from NAM via Beringia during the Paleogene (Liu *et al*., 2009).

***Chamaecyparis formosensis* Matsumura**

C. formosensis inhabits moist forest in Central Mountain Range at elevations of 1000–2600 m (Liu, 1966) and forms a pure stand or mingled with *C. obtusa* var. *taiwanensis*. *C. formosensis* is closely related to *C. pisifera* in Japan based on cpDNA (Wang *et al*., 2003; Liao *et al*., 2010) and nrITS (Li *et al*., 2003). Liu *et al*. (2009) thought that *Chamaecyparis* migrated westward through Beringia to eastern Asia and became established in Japan and Taiwan because no reliable fossil records of this genus from Central Asia and continental eastern Asia were discovered. This scenario is consistent with that proposed by Wang *et al*. (2003).

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According to Wang *et al*. (2003), a lineage of *Chamaecyparis* migrated from NAM to northeastern Asia and moved into Japan because no fossil records were reported in Korea and China. The ancestor of *C. formoensis* from Japan migrated to Taiwan through the Ryukyus.

***Chamaecyparis obtusa* Sieb. & Zucc. var. *taiwanensis* (Hay.) Rehd.**

C. obtusa var. *taiwanensis* inhabits moist forest in Central Mountain Range at elevations of 1200–2800 m in Taiwan (Liu, 1966). Based on cpDNA, *C. obtusa* var. *taiwanensis* is nested inside the clade of *C. obtus*a in Japan, and no substitutions between these two varieties was found except some indels (Liao *et al*., 2010), but differentiation among Taiwan's individuals did happen (Wang *et al*., 2003). Thus it is postulated that ancestor of *C. obtusa* var. *taiwanensis* migrated from Japan to Taiwan through the Ryukyus in recent time.

***Juniperus* L.**

Juniperus contains three sections, *i.e.*, *Caryocedrus*, *Juniperus* and *Sabina*, and 53 species in temperate Northern Hemisphere (Farjon, 2010). Three endemic taxa are in Taiwan. *J. formosana* belongs to section *Juniperus*, while *J. morrisonicola* and *J. tsukusiensis* var. *taiwanensis* belong to section *Sabina* (Mao *et al*., 2010). Fossil records of section *Sabina* were reported from the Eocene/Oligocene boundary in Europe, and from the late Oligocene to early Miocene in North America, and from the late Pliocene in Asia, and fossils of section *Juniperus* appeared in Europe from the middle Miocene onwards while no reports in North America or Asia (Mao *et al*., 2010).

***Juniperus tsukusiensis* L. var. *taiwanensis* (R.P. Adams and C-F. Hsieh) R.P. Adams**

J. tsukusimensis var. *taiwanensis* is restricted to lime stone area of Chingshuishan in eastern Taiwan (Editorial Committee of the Flora of Taiwan 2nd edition, 1994). It is closely related to *J. tsukusiensis* var. *tsukusiensis* based on cpDNA (Adams *et al*., 2011). It is suggested that Taiwan's plants could have derived from Japanese population either through the Ryukyus to Taiwan, or by long distance dispersal since no records of *J. tsukusiensis* have been reported in the Ryukyus.

Juniperus formosana* Hayata var. *formosana

J. formosana var. *formosana* inhabits open and relatively dry areas in Central Mountain Range at elevations of 2300–3000 m in Taiwan (Liu, 1966). It is closely related to *J. formosana* var. *mairei*, distributing in China, based on cpDNA (Mao *et al*., 2010). Taiwan's samples are related to those from southeastern China, rather than from northern China, based on RAPD (Adams *et al*., 2002), implying migration route might be from southeastern China via Tungshan land bridge to Taiwan.

***Juniperus morrisonicola* Hayata**

J. morrisonicola inhabits alpine area and is distributed sporadically in Central Mountain Range at elevation above 3000 m in Taiwan (Editorial Committee of the Flora of Taiwan 2nd edition, 1994). It can form a pure stand at moist valley and is often treated under the name *J. squamata*, distributing from southeastern Asia to eastern Asia. Based on nrITS and cpDNA, *J. morrisonicola* formed a clade with *J. przelwaskii*, distributing in northwestern China, (Adams *et al*., 2012), which is nested inside a clade including *J. squatamta* and *J. tibetica*, distributing in the Himalayas. *J. morrisonicola* and *J. squamata* f. *wilsoni*, distributing in western China, share the shortest genetic distance among related species (Adams *et al*., 2012). Thus ancestor of *J. morrisonicola* could have migrated from western China, through the Yun-Kue Plateau, Nanling (southern Chinese mountain system), Fuchien, via Tungshan land bridge to Taiwan.

Diversity and endemism of gymnosperms in Taiwan

Based on the above review of each taxon of gymnosperms in Taiwan, there are 28 taxa including 19 species and 9 varieties belonging to 16 genera and 5 families in Taiwan (Table 1). Among them, 16 species and 6 varieties are endemic, about 78.5% (22/28) of the gymnosperm flora of Taiwan (Table 2). These endemic taxa mostly have evolved from source areas outside Taiwan, except *Pinus taiwanensis* var. *fragilissima* and *Podocarpus fasciculus*, and their midpoint altitudinal distributions are above 500 m (Table 2). Endemism is almost 100% above 1000 m except at elevations of 2000–2500 m, which house *Taxus sumatrana* that has further dispersed to the Philippines possibly by birds due to fleshy receptacle and seed aril (*cf.* Willson *et al*., 1996). Most non-endemic species belong to Podocarpaceae, a family primarily of the Southern Hemisphere origin, such as *Nageia nagi*, *Podocarpus costalis*, *P. macrophylla* var. *macrophylla*, *P. macrophylla* var. *maki*, except *Pinus massoniana* in China, belonging to Pinaceae, and *Taxus sumatrana* from the Himalaya to Malesia, belonging to Taxaceae.

Distribution patterns of gymnosperms in Taiwan

Distribution patterns of gymnosperm flora of Taiwan

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may be classified into horizontal and vertical one. Horizontally, it may be further subdivided into nine districts (Table 1; Huang, 2011). Many taxa are distributed along Central Mountain Range (including Hsueshan Ridge, Central Mountain Ridge, Alishan Ridge and Yushan Ridge), whereas other taxa are either restricted to Lanyu (*Podocarpus costalis*), north-central Taiwan (*Podocarpus fasciculus*), central Taiwan (*Podocarpus nakaii*), southern Taiwan (*Amentotaxus formosana*, *Podocarpus macrophyllus*, var. *macrophyllus*), southeastern Taiwan (*Cycas taitungensis*, *Pinus taiwanensis* var. *fragilissima*), eastern Taiwan (*Juniperus tsukusiensis* var. *taiwanensis*), or disjunct in northern and southern Taiwan (*Keteleeria davidiana* var. *formosana*) (Table 1).

Vertically, they are distributed from coastal area to above 3400 m (Table 1). Non-endemic species are either of southern East Asian distribution such as *Nageia nagi*, *Podocarpus macrophyllus*, var. *macrophyllus*, *P. macrophyllus* var. *maki*, or shared with southeastern China such as *Pinus massoniana*, or shared with the Philippines such as *Podocarpus costalis* and *Taxus sumatrana*. However, most species received sources outside Taiwan except *T. sumatrana* which from Taiwan dispersed to the Philippines. For endemic taxa, four taxa (*Cycas taitungensis*, *Podocarpus nakaii, Keteleeria davidii* var. *formosana*, *Pinus taiwanensis* var. *fragilissima*) are distributed between 500 to 1000 m regarding midpoint altitudinal distribution, seven species (*Amentotaxus formosana*, *Pinus morrisonicola*, *P. taiwanensis*, *Pseudotsuga wilsoniana*, *Taiwania cryptomeroidea*, *Calocedrus formosana*, *Chamecyparis formosana*) between 1000–2000 m, nine taxa (*Cephalotaxus wilsoniana*, *Podocarpus fasciculus*, *Picea morrisonicola*, *Pinus armandii* var. *masteriana*, *Tsuga formosana*, *Cunninghamia lanceolata* var. *konishii*, *Juiperus tsukusimensis* var. *taiwaniana*, *J. formosana* var. *formosana*) between 2000 to 3000 m, and two species (*Abies kawakamii*, *Juniperus morrisonicola*) above 3000 m. Apparently, endemic species are more diverse in mid-altitude between 1000 to 3000 m.

Relation between distribution patterns of endemic taxa of gymnosperms in Taiwan and those of their sister species

Distribution patterns of sister species of Taiwan's endemic gymnosperms may be classified into 10 types, namely, northwestern China (NWC), southwestern China (SWC), South China (SC), southern South China (SSC), central China (CC), southeastern China (SEC), eastern China (EC), Japan, Ryukyus, and Taiwan (Table 3). There are six taxa (*Cephalotaxus wilsoniana, Picea morrisonicola, Tsuga formosana, Chamaecyparis formosensis, C. obtuse* var. *taiwaniana, Juniperus tsukusimensis* var. *taiwaniana*) of Taiwan's gymnosperms with sister species in Japan, four taxa (*Amentotaxus formosana, Keteleeria davidii* var. *formosana*, *Taiwania cryptomeroidea*, *Calocedrus formosana*) with sister species in SWC, three taxa (*Abies kawakamii*, *Cunninghamia lanceolata* var. *konishii*, *Juniperus formosana* var. *formosana*) with sister species in CC, two species (*Pinus taiwaniana*, *Pseudotsuga wilsoniana*) with sister species in EC, two taxa (*Pinus armandii* var. *formosana*, *P. morrisonicola*) with sister species in SC, one species (*Podocarpus nakaii*) with sister species in SSC, two taxa (*Podocarpus fascisulu*s, *Pinus taiwanensis* var. *fragilissima*) with sister species in Taiwan, one species (*Juniperus morrisonicola*) with sister species in NWC, and one species (*Cycas taitungensis*) with sister species in the Ryukyus (Table 3).

Midpoint altitudinal distributions of endemic gymnosperms in Taiwan with their sister species in SWC are distributed from 1800 to 2750 m, those in Japan are from 650 to 1950 m, those in CC are from 2050 to 3050 m, those in SC are from 1300 to 1800m, those in EC are from 1650 to 1850 m, that in NWC is at 3400 m, those in Taiwan are from 800 to 2000 m, and that in the Ryukyus is at 600 m (Table 3). Thus midpoint altitudinal distributions in Taiwan are above 1800 m for endemic gymnosperms related to sister species in higher latitudes such as Japan, NWC, and CC, while they are below 2000 m for those related to sister species in lower latitudes such as SWC, SC, SSC and EC.

DISCUSSIONS

Contrasting distribution patterns among taxa of tropical, Southern Hemisphere and Northern Hemisphere origin in Taiwan

In Taiwan, Cycadacea with one species is considered of tropical origin (TO), and Podocarpaceae with six taxa including four species and two varieties is considered of Southern Hemisphere origin (SMO), while three families, namely, Taxaceae (including Amentotaxaceae and Cephalotaxacae), Pinaceae and Cupressaceae (includingTaxodiaceae) are considered of Northern Hemisphere origin (NMO) and they contain 21 taxa including 14 species and seven varieties. Four taxa of SMO are non-endemic and they are either shared with the Philippines (*Podocarpus costalis*), or shared with southern East Asia (*Nageia nagi*, *Podocar pus macrophyllus* var. *macrophyllus*, *P. macrophyllus* var. *maki*) and they are distributed below 650 m, contrasting to two non-endemic taxa of NMO either

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Table 2: Percentage of endemism of gymnosperms in Taiwan based on midpoint altitudinal distribution (average of vertical distribution range).

Midpoint altitudinal distribution (m)	Number of endemic species	Number of non-endemic species	Percentage of endemism	Percentage of endemism
0–500	0	4	0	44.4
500−1000	4	1	80	
1000−1500	3	0	100	100
1500−2000	4	0	100	
2000−2500	5	1	83	90
2500−3000	4	0	100	
3000 and up	2	0	100	100
Total	22	6	78.5	78.5

Table 3: Distribution patterns of endemic gymnosperms in Taiwan and distribution types of their sister taxa.

Distribution type of sister species of endemic taxa of gymnosperms in Taiwan	Taxa of endemic gymnosperm in Taiwan	Midpoint altitudinal distribution of taxa of gymnosperm in Taiwan (m)	Total number of taxa
Northwestern China (NWC)	*Juniperus morrisonicola*	3400	1
Southwestern China (SWC)	*Amentotaxus formosana*, *Keteleeria davidii* var. *formosana*, *Taiwania cryptomeroidea*, *Calocedrus formosana*	1800–2750	4
South China (SC)	*Pinus armandii* var. *masteriana*, *Pinus morrisonicola*	1300–1800	2
southern South China (SSC)	*Podocarpus nakaii*	650	1
Central China (CC)	*Abies kawakamii*, *Cunninghamia lanceolata* var. *konishii*, *Juniperus formosana* var. *formosana*	2050–3050	3
East China (EC)	*Pinus taiwaniana*, *Pseudotsuga wilsoniana*	1650–1850	2
Japan	*Cephalotaxus wilsoniana*, *Picea morrisonicola*, *Tsuga formosana*, *Chamaecyparis formosana*, *Chamaecyparis obtuse* var. *taiwaniana*, *Juniperus tsukusimensis* var. *taiwaniana*	650–1950	6
Ryukyus	*Cycas taitungensis*	600	1
Taiwan	*Podocarpus fascisulus*, *Pinus taiwanensis* var. *fragilissima*	800–2000	2

shared with southeastern China (*Pinus massoniana*) at 400 m or shared with Malesia (*Taxus sumatrana*) at 2000 m (Tables 4 & 5). One species, *Cycas taitungensis*, of TO, and two species, *Podocarpus fasciculus* and *P. nakaii*, of SMO, contrasting 12 species plus 7 varieties of NMO are endemic (Table 4). Midpoint altitudinal distributions of endemic taxa of TO and SMO is below 650 m except *P. fasciculus* at 2000 m, contrasting to those of NMO above 600 m (Table 4).

Horizontal distribution patterns of taxa of TO and SMO are spotted and restricted while taxa of NMO either are distributed widely and become important forest component such as *Pinus taiwanensis*, *Chamaecyparis formosensis*, *Tsuga formosana*, *Abies kawakamii*, *Juniperus morrisonicola* or are spotted and restricted. Endemism of taxa of TO plus SMO is 43% (3/7) contrasting 90.5% (19/21) of taxa of NMO (Table 4). Species of TO, *Cycas taitungensis*, an endemic

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species and possibly derived from lineage of *C.panzhihuaensis* in Yunnan, China, has dispersed to the Ryukyus and evolved to *C. revoluta* and it possibly has inhabited Taiwan for a long time due to having relatively high degree of molecular variation with *C. panzhihuaensis* (Kyoda and Setoguchi, 2010). Taxa of SMO are recently immigrants as shown by non-endemic status or have evolved within a short period of time as shown by sharing relatively short genetic distance with their sister species as *P. fasciculus* and *P. nakaii* (Table 1). However, taxa of NMO could either have evolved within a short period of time as shown by non-endemic or variety status, or they are relics and have evolved for a long time as shown by sharing relatively long genetic distance (Table 1) and by disjunct distribution with their sister species.

How is high degree of endemism of the gymnosperm flora of Taiwan derived?

The endemism of the gymnosperm flora of Taiwan is 78.5% (22/28). Such a high endemicity is contributed by two *in situ* endemic taxa, namely, *Podocarpus fasciculus* and *Pinus taiwanensis* var. *fragilissima*, and 20 other endemic taxa including 14 species and six varieties. Endemic varieties share relatively short genetic distance with their sister varieties, implying that such varieties have isolated and evolved within a relatively short period of time. Meanwhile, endemic species may be relict elements as shown by disjunct distribution or they share longer genetic distance with their sister species, especially with those distributed in Japan, northwestern China, southwestern China and central China (Table 1), implying that they have colonized Taiwan for a long period of time. Woody habit and inhabiting higher altitudinal distribution patterns seem to contribute to high degree of endemism in the Flora of Taiwan (Hsieh, 2002: Fig. 3 & Table 5) and both characters are found in gymnosperms in Taiwan. In addition, the oldest species in Taiwan seem to inhabit middle altitudes (Huang, 2011). Thus explanation may be given as follows. Long life spans and wider ecological niches shown by woody habit make gymnosperms slow to evolve to new species *in situ* and would be less sensitive to environmental changes and, especially, temperate essence as shown by distribution being mostly in middle altitudes makes them easily to find shelters during temperature fluctuations and makes them evolve accordingly over time.

Migration routes of gymnosperms in Taiwan

Possible source areas and migration routes have been reviewed and proposed for each taxon of gymnosperms in Taiwan based on fossil histories and distribution patterns of their sister species and they are summarized in Table 5. For non-endemic species, Philippines, southern South China (SSC), central China (CC), eastern China (EC), and southeastern China (SEC) are the source areas from where either via South China Sea's or Tungshan land bridge to Taiwan (Table 5). For endemic species, four source areas outside Taiwan are recognized (Huang, 2011), namely, Sino-Himalayan subregion (sister species are distributed in northwestern China (NWC) and southwestern China (SWC)), IndoChina-Hainan (SSC), Sino-Japanese subregion (CC, EC, SC, SEC), and Japan.

For endemic taxa with sister species distributed in Sino-Japanese subregion or Japan, their fossil histories may trace back to Asia or North America. For fossil histories trace back to North America, their ancestors crossed Beringia to northeastern Asia, and then either dispersed to Japan, CC, or EC, and further migrated to SEC, SC and SWC. From Japan, they further migrated through the Ryukyus to Taiwan. From EC they migrated via East China Sea's land bridge or further through SEC via Tungshan land bridge to Taiwan. From CC they migrated through SEC via Tungshan land bridge to Taiwan.

For taxon with sister species distributed in NWC, *ex.*, *Juniperus morrisonicola*, fossil history may trace back to Europe, from where ancestors might have dispersed to the Himalayas, and from the eastern Himalayas migrated through Yunn-Kue Plateau, Nanling to Kwangtung and Fuchien (*cf.* Wang, 1992a,b), and from where further migrated via Tungshan land bridge to Taiwan.

For taxa with ancestors or sister species mainly in SWC, *ex.*, *Cycas taitungensis*, *Amentotaxus formosanus*, *Keteleeria davidiana* var. *formosana*, *Taiwania cryptomeroides*, and *Calocedrus formosana*, four migratory routes were proposed. The first route is that ancestors could have migrated from SWC through SSC via South China Sea's land bridge to southern Taiwan such as *Cycas taitungensis* and *Keteleeria davidiana* var. *formosana* because they are distributed in southern Taiwan and inhabiting low altitudes. The second route is that ancestors could have migrated from SWC through SC and SEC via Tungshan land bridge to Taiwan such as *Calocedrus formosana* because it is distributed in central or northern Taiwan. The third route is that ancestors could have migrated from CC or EC through SEC via Tungshan land bridge to central Taiwan and further dispersed to other part of Taiwan while thier sister lineages could have migrated from CC to SWC and thus produced disjunct patterns, and such taxa in Taiwan is distributed in middle altitudes and have colonized Taiwan for a long time such as *Amentotaxus formosana*. The fourth route is that ances-

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Table 4: Comparisons of diversity and distribution patterns of gymnosperms in Taiwan among tropical origin (TO), South Hemisphere origin (SMO) and North Hemisphere origin (NMO).

Type of origin	Taxa (boldface indicates endemic status)	Number of taxa		Midpoint altitudinal distribution (m)	
		Endemic	Non-endemic	Endemic	Non-endemic
Tropical origin (TO)	***Cycas taitungensis***	1	0	650	-
Southern Hemisphere origin (SMO)	***Podocarpus fasciculus***, ***Podocarpus nakaii***, *Podocarpus costalis*, *Nageia nagi*, *Podocarpus macrophyllus* var. *macrophyllus*, *Podocarpus macrophyllus* var. *maki*	2	4	600 and 2000	Below 650
Northern Hemisphere origin (NMO)	*Pinus massoniana*, *Taxus sumatrana*, ***Amentotaxus formosana***, ***Cephalotaxus wilsoniana***, ***Abies kawakamii***, ***Keteleeria davidiana*** var. ***formosana***, ***Picea morrisonicola***, ***Pinus armandii*** var. ***masteriana***, ***Pinus morrisoniacola***, ***Pinus taiwanensis***, ***Pinus taiwanensis*** var. ***fragilissima***, ***Psudotsuga wilsoniana***, ***Tsuga formosana***, ***Cunninghamia lanceolata*** var. ***konishii***, ***Taiwania cryptomeroides***, ***Calocedrus formosana***, ***Chamaecyparis formosensis***, ***Chamaecyparis obtuse*** var. ***taiwanensis***, ***Juniperus tsukusiensis*** var. ***taiwanensis***, ***Juniperus formosana*** var. ***formosana***, ***Juniperus morrisonicola***	19	2	Above 600	400 and 2000

tors could have migrated from Japan through the Ryukyus to Taiwan, while their sister lineages could have migrated from EC through CC to SWC and thus produced disjunct patterns, and such taxa in Taiwan is distributed in middle altitudes and have colonized Taiwan for a long time such as *Taiwania cryptomeroides*.

For taxa with sister species distributed in Indochina-Hainan, *ex*., *Podocarpus nakaii*, ancestors might have migrated either via South China Sea's land bridge to southern Taiwan and further dispersed to other part of Taiwan or through SC and SEC via Tungshan land bridge to central Taiwan.

In summary, endemic taxa with fossil histories tracing back to Europe and their sister species belonging to Sino-Himalayan subregion are distributed in high altitudes in Taiwan. Endemic taxa with fossil histories tracing back to Asia or North America and their sister species in Japan or China's Sino-Japanese subregion are distributed mainly in middle altitudes. Endemic taxa with fossil histories tracing back to North America and their sister species in SWC are distributed in low altitudes if they share short genetic distance with their sister species, while they are distributed in middle altitudes if they share long genetic distance with their sister species. Endemic taxa with sister species in Indochina-Hainan are distributed in low altitudes.

Conclusions

There are 28 taxa including 19 species and 9 varieties of gymnosperms in Taiwan. Compared to the Flora of Taiwan 2nd edition (Editorial Committee of the Flora of Taiwan 2nd edition, 1994), *Nageia fleuryi* is excluded and *Pinus taiwanensis* var. *fragilissima* is added in this paper. Species status of *Calocedrus formosana* and *Tsuga formosana* and variety status of

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Table 5: Postulated source areas and migration routes of gymnosperms in Taiwan based on distribution patterns of their sister populations or sister taxa.

Distribution of sister species of taxa of gymnosperms in Taiwan	Possible source area and migration route of taxa of gymnosperms in Taiwan	Examples
Philippines	From Luzon to Lanyu	*Podocarpus costalis*
	From Taiwan to Philippines	*Taxus sumatrana*
Southern South China (SSC)	From Hainan or southern Kwangtung through South China Sea's land bridge to southern Taiwan,	*Nageia nagii*, *Podocarpus macrophyllus* var. *macrophyllus*, *Podocarpus macrophyllus* var. *maki*
	from SSC further disperse to SEC through Tungshan land bridge to central Taiwan	*Podocarpus nakaii*
South China (SC)	From SC via Tungshan land bridge to central Taiwan	*Pinus armandii* var. *masteriana*, *Pinus morrisonicola*
Southeastern China (SEC)	From SEC through Tungshan land bridge to central Taiwan	*Pinus massoniana*
Central China (CC)	From CC disperse to SEC through Tungshan land bridge to central Taiwan	*Abies kawakamii*, *Cunninghamia lanceolata* var. *konishii*, *Juniperus formosana* var. *formosana*
East China (EC)	From EC disperse to SEC through Tungshan land bridge to central Taiwan, or from CC disperse to SEC through East China Sea's land bridge to central- north Taiwan	*Pinus taiwaniana*, *Pseudotsuga wilsoniana*
Northwestern China (NWC)	From the eastern Himalayas through the Yun-Kue plateau, Nanling to SEC, via Tungshan land bridge to central Taiwan	*Juniperus morrisonicola*
Southwestern China (SWC)	From SWC to southern South China through South China Sea's land bridge to southern Taiwan	*Keteleeria davidii* var. *formosana*,
	From SWC disperse to South China through Tungshan land bridge to central Taiwan	*Calocedrus formosana*
	Ancestors of extant *Amentotaxus* species might have migrated from northeastern China to central China. From there, one lineage migrated through southeastern China to Taiwan via Tungshan land bridge to become *A. formosanum*, and another lineage migrated to refuge of southwestern China and became disjunct distribution	*Amentotaxus formosana*
	One lineage of *Taiwania* either migrated from eastern China through southeastern China via East China Sea's land bridge to central-north Taiwan, or from Japan through the Ryukyus to northern Taiwan. Whereas another lineage either from EC or CC further disperse to SWC	*Taiwania cryptomeroidea*
Japan	From Japan through the Ryukyus to northern Taiwan	*Cephalotaxus wilsoniana*, *Picea morrisonicola*, *Tsuga formosana*, *Chamaecyparis formosana*, *Chamaecyparis obtuse* var. *taiwaniana*
	From Japan to Taiwan through long distance dispersal	*Juniperus tsukusimensis* var. *taiwaniana*
Ryukyus	From SSC via South China Sea's land bridge to southern Taiwan and further dispersed to the Ryukyus	*Cycas taitungensis*
Taiwan	From lower altitudes in Taiwan dispersed to higher altitudes and evolved	*Podocarpus fascisulus*
	Locally differentiated populations	*Pinus taiwanensis* var. *fragilissima*

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Cunninghamia lanceolata var. *konishii* are retained. Scientific names are adopted for *Juniperus morrisonicola* instead of *J. squamata* and for *Juniperus tsukusiensis* var. *taiwanensis* instead of *J. chinensis* var. *taiwanensis*. These taxa may be categorized into tropical origin (TO), Southern Hemisphere origin (SMO) and Northern Hemisphere origin (NMO).

Gymnosperm flora of Taiwan with high degree of endemism should owe to woody habits with wider ecological niches that are more adaptive to the environmental changes, and owe to temperate essence that is more easily to find shelters during temperature fluctuations.

Taxa of TO and SMO are inclined to inhabit low altitudes and sporadically distributed, whereas taxa of NMO are inclined to inhabit middle to high altitudes, especially in northern and central Central Mountain Range and may widely or restrictedly distributed. Distribution patterns of endemic taxa of NMO in Taiwan are related with those of their sister species. In Taiwan, taxa with sister species in higher latitudes such as Japan, NWC and CC are distributed in higher altitudes with midpoint of altitudinal distributions over 2000 m, while taxa with sister species in lower latitudes such as SC, SSC, SEC are distributed in lower altitudes with midpoint of altitudinal distributions under 2000 m. While vertical distribution patterns in Taiwan are related with those of their sister species, horizontal ones may be blurred by long history of colonization in Taiwan. For example, *Amentotaxus formosana* is considered the oldest colonizer of gymnosperms in Taiwan (Huang, 2011) and would be derived from the north, but its distribution in Taiwan is restricted to the southern part at present. Apparently, one can explain horizontal distribution patterns of taxa in Taiwan only through the study of historical biogeography of such taxa. Hence data on fossil histories and paleogeographical studies of such taxa in Taiwan should be obtained to explain thier distribution patterns.

Most fossil histories of endemic taxa of NMO may trace back to Asia or North America (NAM) except *Juniperus morrisoniocola* that may trace back to Europe. Ancestors in NAM migrated to northeastern Asia via Biringia, from where dispersed southward either to Japan, or to northern China and then to central and eastern China. From Japan, ancestors either migrated southward to the Ryukyus and to Taiwan if sister species are in Japan, or they might have dispersed to continental Asia and evolved when Japan is a part of continental Asia and further migrated southward via East China Sea's land bridge to Taiwan such as *Pseudotsuga wilsoniana*. From central or eastern China, ancestors migrated southward either via East China Sea's land bridge or through southeastern China via Tungshan land bridge to Taiwan. Ancestors in Europe migrated southward to the Himalayas, through Yun-Kue Plateau, Nanling via Tungshan land bridge to Taiwan.Southwestern China (SWC) plus Indochina is both refuge and dispersal center. Taxa of SMO may disperse from the South Hemisphere through southeastern Asia to Indochina, from where migrated either through southern South China via South China Sea's land bridge to southern Taiwan, or through South China via Tungshan land bridge to central Taiwan. When taxa of NMO share short genetic distance with their sister species in SWC, their migration routes are like those of SMO, whereas taxa of NMO share long genetic distance with their sister species in SWC, one lineage of their ancestors, possibly in central China or Japan, migrated to Taiwan while another lineage further dispersed to SWC and produced disjunct distribution patterns.

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台灣裸子植物之可能起源、傳播路線及分布

黃星凡

1. 國立新竹教育大學應用科學系，新竹市南大路 521 號。
* 通信作者。*Phone: 886-3-5213132#2750; Fax:886-3-5257178; Email: sfhuang@mail.nhcue.edu.tw*

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摘要: 本文旨在回顧整理台灣裸子植物分類群之化石紀錄，親緣關係及親緣地理研究，試圖回答下列的問題：(1) 台灣裸子植物之高特有性是如何造成的? (2) 台灣裸子植物之來源區域有哪些? (3) 台灣特有裸子植物之分布樣式與他們的姐妹群之分布樣式有何關聯? (4) 裸子植物如何由來源區域傳播到台灣?

台灣之裸子植物總共有28 個分類群，包括19 種及9 變種。相較於台灣植物誌第二版，長葉竹柏 (*Nageia fleuryi*) 被排除於台灣之裸子植物相，而天龍二葉松 (*Pinus taiwanensis* var. *fragilissima*) 則加入。台灣肖楠 (*Calocedrus formosana*)及鐵杉 (*Tsuga formosana*) 維持種的階級，香杉 (*Cunninghamia lanceolata* var. *konishi*) 則維持變種階級。香青之學名則以*Juniperus morrisonicola* 代替*J. squamata*，清水圓柏之學名則以*Juniperus tsukusiensis* var. *taiwanensis* 代替 *J. chinensis* var. *taiwanensis*. 這28 個分類群依其分布樣式可分成熱帶起源，南半球起源及北半球起源三類。

台灣特有之裸子植物佔台灣裸子植物相之78.5%。如此高的特有性可能歸因於(1) 木本的習性：若與草本習性相較，木本習性具有較寬的生態棲位，因此對環境的變異比較不敏感而更具適應性；(2) 生存於溫帶的本質：台灣地形高低起伏，在溫度高低起伏變化大時，溫帶植物更容易在台灣找到避難所而存活下來。

屬於熱帶起源或南半球起源之分類群在台灣傾向於低海拔分布及零星分布，屬於北半球起源之分類群則傾向於中高海拔分布，尤其是中央山脈之中北部，而有些種類是成片分布，有些則是局限分布。

屬於北半球起源之台灣特有裸子植物，其分布樣式與他們的姐妹群的分布樣式具相關性。若姊妹群的分布在高緯度地區如日本，華西北，華中等，台灣之特有裸子植物屬高海拔分布，且其海拔分布中心高於1800 公尺。若姊妹群的分布在低緯度地區如華南，華極南，華東南等，台灣之特有裸子植物分布屬低海拔分布，且其海拔分布中心低於2000 公尺。北半球起源之台灣特有裸子植物之化石歷史，除香青 (*Juniperus morrisoniocola*) 可回溯至歐洲外，其餘種類可回溯至亞洲或北美洲。北美洲之始祖經白令海峽遷移至東北亞，再從東北亞往南傳播或到日本，或經華北而達華中或華東。定居在日本者，再從日本或經琉球而傳播到台灣，或當日本為亞洲大陸之一部分時，再傳播至華東，同時繼續往南傳播，經東海陸橋而到達台灣。定居華中或華東者，再往南傳播或經東海陸橋而到達台灣，或傳播至華東南經東山陸橋而到達台灣。歐洲之始祖則往南傳播到東喜瑪拉雅山，再經雲貴高原，南嶺到達廣東，福建等地，再經東山陸橋到達台灣。華西南及中南半島既是避難所也是傳播中心。南半球起源之分類群可能由南半球經東南亞而到達中南半島及華西南。再從中南半島及華西南或經華極南，南海陸橋而到達南台灣，或經華南，再由東山陸橋到達中台灣。如果北半球起源之分類群與姐妹群之遺傳距離短，而且其姐妹群之分布在華西南，他們的傳播路徑與南半球起源之分類群由中南半島及華西南之傳播路徑一樣。如果北半球起源之分類群與姐妹群之遺傳距離長，而且其姐妹群之分布在華西南，則可能分布於華中之一支始祖往南傳播，經華東南，東山陸橋而到達台灣; 另一支始祖則繼續由華中往華西南傳播，造成姐妹群間斷分布之現象。

雖然台灣裸子植物之垂直分布與姐妹群之分布樣式有關聯性，但是水平分布則缺少關聯性，可能是因其在台灣具有長久之演化及傳播歷史而混淆了分布樣式。因此欲解釋台灣裸子植物水平之分布樣式，需要更多有關台灣裸子植物的化石及其歷史生物地理學之資料。

關鍵詞：分布、特有性、裸子植物、起源、傳播路線、台灣。

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