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Diversity and phytogeography of vascular epiphytes in a tropical–subtropical transition island, Taiwan

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Abstract

We present the first checklist of vascular epiphytes in Taiwan, based on herbarium specimens, literature records, and field observations. Epiphyte phytogeography was analyzed using Takhtajan's modified division in floristic regions. We ascertain the presence of 336 species of vascular epiphytes (24 families, 105 genera) in Taiwan. Pteridophytes contribute most species (171 species), followed by orchids (120 species). Epiphytes contribute 8% to Taiwanese floristic diversity and epiphyte endemism is near 21.3%. The extensive mountain system is probably the most effective driver for epiphyte diversification and endemism in Taiwan. Phytogeographically, Taiwanese epiphytes exhibit equal affinity to the Malesian region, southern China and Indo-China and Eastern Asiatic regions. However, some species have a disjunctive distribution between Taiwan and SW China and/or E Himalaya, presumably related to low habitat similarity with adjacent China and/or the legacy of Late Quaternary climate change. Vascular epiphyte distribution patterns corroborate the phytogeographical separation of the island of Lanyu from the main island of Taiwan along Kanto's Neo-Wallace Line.

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Keywords: Endemism; Epiphyte-quotient; Floristic affinity; Neo-wallace line; Paleotropics; Late Quaternary climate change

Introduction

The conspicuous vascular epiphyte community in the canopy of wet tropical forests has attracted botanists as early as 1888, especially during the second half of the last century (Benzing, 1990; Gentry and Dodson, 1987a; Johansson, 1974; Kress, 1986; Madison, 1977; Richards, 1952). These studies have shown that the epiphytic life-form is a successful adaptation of plants to conditions in

the canopy, comprising ca. 29,000 species, or approximately 10% of all vascular plants, in 83 different families and 876 genera (Gentry and Dodson, 1987a). Whereas the number of epiphyte inventories is gradually increasing, inventories from the paleotropics are still rare and especially from Asia few inventories are available (Wolf and Flamenco-S, 2003). In addition, little is known about epiphytes in tropical–subtropical transition zones. Consequently, the differences in vascular epiphyte diversity and composition between temperate and tropical areas and between paleotropics and neotropics remain ambiguous and lack generally accepted explanations (Benzing, 1987; Gentry and Dodson, 1987a; Zotz, 2005).

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Taiwan (formerly known as Formosa) is a continental island, separated from Southeast China by the ca. 200 km wide Taiwan Strait, which reaches a depth of 70 m. The Tropic of Cancer crosses through the middle of the southern half of the island, and about 70% of the total area is covered by mountains. Taiwan owes its existence to a collision of the Philippines Sea plate with the Eurasian continental margin some 5 million years ago, which induced orogenesis (Ho, 1988). In contrast to many other regions at the tropic of Cancer or Capricorn, Taiwan has a humid climate thanks to the high mountains that induce cloud formation in high-humidity oceanic winds. Frequent typhoons in summer and NE monsoon in winter provide most precipitation throughout the year.

Taiwan floristic diversity is high, comprising ca. 4077 species (Hsieh, 2003). Being a mountainous island, species diversity is the result of great habitat heterogeneity. Furthermore, situated at the transition from tropics to subtropics, in Taiwan many tropical plant species reach their northern limit (Hsueh and Lee, 2000), whereas temperate species are found in the high mountains (Hosokawa, 1958). Phytogeographically, Taiwan belongs to the Eastern Asiatic region (Takhtajan, 1986). Yet the south end of Taiwan, Hanchun

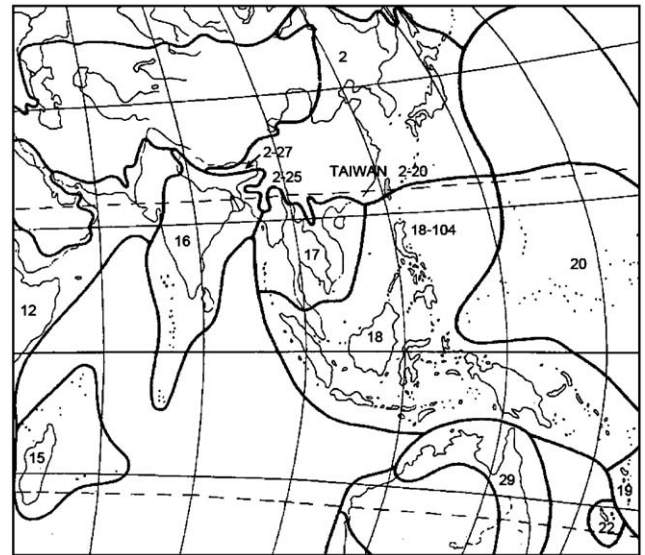


Fig. 2. Takhtajan's floristic regions. Numbers indicated: 2, Eastern Asiatic region; 2–20, Ryukyu islands; 2–25, SW China; 2–27, E Himalaya; 12, Sudano-Zambezian region; 15, Madagascar regions; 16, Indian region; 17, Indochinese region; 18, Malesian region; 18–104, Philippines; 19, Fijian region; 20, Polynesian region; 22, Neocaledonian region; 29, NE Australian region. Regions that not covered in above map but with Taiwanese epiphyte occurrence are: 3, North American Atlantic region; 4, Rocky Mountain region; 6, Mediterranean region; 8, Iran-Turanian region; 9, Madrean region; 10, Guineo-Congolian region; 21, Hawaiian region; 23, Caribbean region; 24, Guayana Highlands; 25, Amazonian region; 26, Brazilian region; 27, Andean region. The figure was modified from Takhtajan (1986).

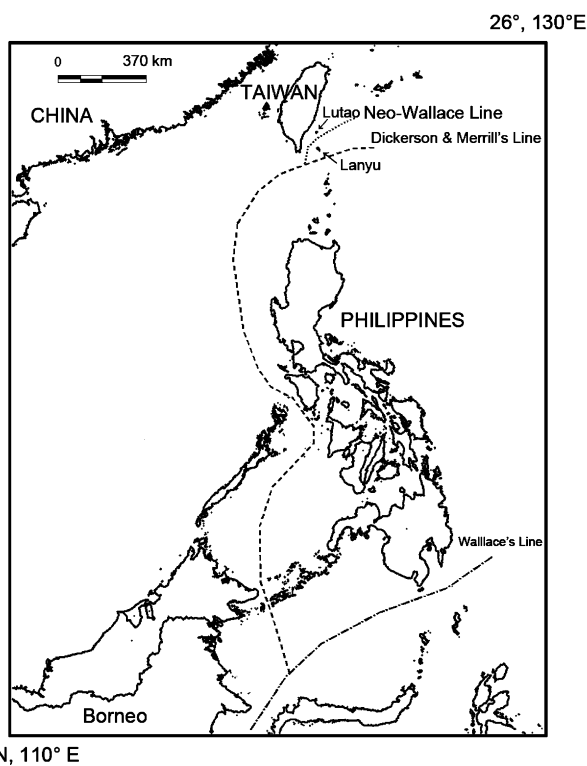


Fig. 1. Location of Taiwan, Lanyu, Lutao, and the Neo-Wallace Line (Kanto, 1933).

Peninsula, and two small volcanic islands, Lanyu and Lutao, located in the south-eastern Taiwan, are pertained to Malesian region (Figs. 1 and 2). The vegetation of Lanyu is characterized by tropical rain forests, and its flora and fauna have more in common with the Philippines than with Taiwan. On this basis, Kanto (1933) proposed the Neo-Wallace Line by extending the boundary of Dickerson and Merrill's Line (Dickerson, 1928) from northern Luzon to Lanyu through the middle sea of Lanyu and Lutao (Fig. 1). Kanto's proposal was corroborated by several subsequent biogeological studies (Hosokawa, 1958; Kanehira, 1935; Yen et al., 2003).

In this study we describe the epiphyte flora of Taiwan for the first time. Specifically, we address the following research questions: (i) Is species richness, endemism, and familial makeup similar to that of other floristic regions such as tropical and temperate areas in the neotropics? (ii) What is the phyto-geographical affinity of epiphytes and several sub-categories? (iii) Do epiphytes corroborate the Neo-Wallace Line?

Materials and methods

Study site

Taiwan is situated between 21°45'N–25°56'N and 119°18'E–124°34'E with an area of 36,000 km² (Fig. 1). The Central Ridge of Taiwan comprises over 200 peaks higher than 3000 m a.s.l., and Yushan is the highest (3952 m) peak in this island. The annual rainfall ranges from 1000 to over 6000 mm (data from 1949 to 2004). Mean monthly temperature in the lowlands ranges from 15 to 20 °C, and is about 28 °C in summer. Based on bioclimatic analyses, Taiwan can be classified into seven climatic regions, and Lanyu is separated independently (Su, 1984, 1992). Lanyu (ca. 46 km², also known as Botel Tobago, Kotosho, and Orchid I.) and Lutao (ca. 16 km², Green I., Kwasyoto I., and Samasana I.) are small tropical islands located at 22°03'N, 121°32'E and 22°40'N, 121°29'E, respectively. During summer and early autumn, typhoons frequently hit Taiwan, which have less impact in western Taiwan, sheltered by the Central Ridge.

Epiphyte definition

We define epiphytes as organisms that grow on plants without extracting water or nutrients from hosts' living tissues, following Barkman (1958). In this paper, focus is on vascular plants, but many other epiphytic organisms are found in the canopy of the forest. In addition, it is not rare to find accidental epiphytes growing on other plants, which are unable to reproduce in the canopy (Moffett, 2000). We excluded accidental epiphytes from our checklist and classified vascular epiphytes in following sub-categories:

- (i) *Holo-epiphytes*: epiphytes that complete their entire life cycle without contacting the forest floor (Benzing, 1990).
- (ii) *Hemi-epiphytes*: epiphytes that complete part of their life cycle as terrestrial plants. Primary hemi-epiphytes begin their life cycle as epiphytes and eventually send their roots to the ground (e.g. strangler figs), whereas secondary hemi-epiphyte seedlings germinate terrestrially to become epiphytic secondarily when their rooting shoots decompose (e.g. aroids).
- (iii) *Facultative epiphytes*: species in which some individuals are terrestrial.

Epiphyte checklist

Botanically, Taiwan is one of the best explored regions in the tropics. The national database houses over 200,000 botanical records (ca. 60% of herbarium

collections). We gratefully made use of this wealth of information, scrutinizing for epiphytes in well-known epiphytic taxonomic groups (Benzing, 1990). In addition, we used epiphyte records in published plant inventories and floras. Nomenclature follows the 2nd edition of the Flora of Taiwan (Boufford et al., 2003). To compile this checklist, species listed in Flora of Taiwan were examined one by one, and the approximate number of epiphytes was ascertained.

Phytogeography analyses

We assessed the presence of Taiwanese vascular epiphytes in Takhtajan's floristic regions (Takhtajan, 1986). The floristic provinces, SW China, E Himalaya, Ryukyu and Philippines under Eastern Asiatic and Malesian regions of Takhtajan's system, were recognized independently (Fig. 2). Species geographical distributions were characterized based on the flora of Taiwan and collections in the global biodiversity information facility (GBIF) online database. For smaller floristic provinces, such as SW China and Ryukyu, floras of Japan and China were consulted to determine the specific occurrence locations.

Results

Species richness, family makeup, and endemism

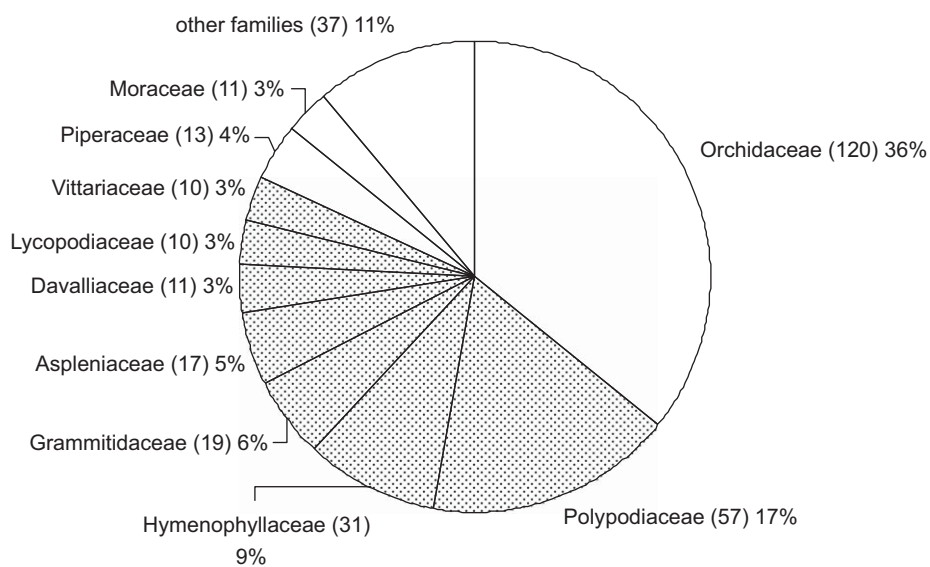
There are 336 species of vascular epiphytes in 105 genera and 24 families in Taiwan and two subsidiary isles, Lanyu and Lutao (Appendix A). Obligate holo-epiphytes comprise 271 (81%) species, 41 (12%) species are facultative holo-epiphytes, and 7 (2%) and 17 (5%) species are primary and secondary hemi-epiphytes, respectively.

The Taiwanese epiphyte flora is dominated by Pteridophytes, i.e. ferns and fern allies, comprising 171 species (Table 1). The number of orchids is also substantial, 120 species (Fig. 3). The 10 most species-rich families contain 89% of all epiphytes and the remaining plant families with epiphytic representatives only contribute about 11% to total epiphyte richness (Fig. 3). At the genus level also, epiphytism is concentrated in few taxa. Only 5% of the genera contain more than 10 species and 54 (51%) genera are represented with one single species only in the region. More than a quarter of native Pteridophytes (Table 1) and 36% of native orchids are epiphytes. In contrast, the Epiphyte-quotient (Ep.-Q, Hosokawa, 1950), i.e. the proportion of epiphytic species in the flora, is only approximately 8% (Table 1).

Of the 336 epiphytes, 75 are endemic species. Sixty-nine species are confined to Taiwan, and one

Table 1. Contribution of vascular epiphytes to the flora of Taiwan in various taxonomic categories (data Flora of Taiwan, Boufford et al., 2003).

| | All vascular plants | Ferns and allies | Angiosperm | Dicotyledons | Monocotyledons |
|----------|---------------------------|------------------|--------------|--------------|----------------|
| Families | 24/235(10%) | 12/37(32%) | 12/190(6%) | 10/151(7%) | 2/39(5%) |
| Genera | 105/1419(7%) | 48/145(33%) | 57/1257(5%) | 16/901(2%) | 41/356(12%) |
| Species | 336/4077(8%) ^a | 171/629(27%) | 165/3420(5%) | 40/2410(2%) | 125/1010(12%) |

^aEpiphyte-quotient.**Fig. 3.** Ten most species-rich epiphytic families and their contribution to total epiphyte flora in Taiwan. Numbers in parentheses are species numbers. Shading indicates Pteridophyta.

disjunctively occurs in Taiwan and Lanyu. Despite the small size of Lanyu and Lutaο, five species are confined here (four species are endemic to Lanyu, and one species is shared by both). The proportion of Taiwan endemic epiphytes (21.3%, Table 2) is less than that in the entire flora (26.2%, Hsieh, 2003). Most endemic epiphytes are orchids (54.2%) despite overall higher number of epiphytic pteridophytes in Taiwan. Of all 114 epiphytic orchids, 38 species (33.3%) are endemic to Taiwan, as opposed to 19 species (11.2%) of pteridophytes (Table 2).

Epiphyte phytogeography

With respect to phytogeographical region, about 41% of epiphytes in Taiwan also occur in the Malesian region, including 10% of species shared with only the Philippines (Table 2). About 39% of species are shared with Indo-China, and about the same proportion is shared with Eastern Asiatic regions, which cover temperate E Asia, E Himalaya, SW China, and Ryukyu. The islands Lutaο and Lanyu share most species (over 70%) with the Malesian region, whilst Lutaο has a high proportion (40%) of species that also occur in temperate

E Asia. Only Lanyu shares an exceptional high proportion (22%) of species with the Philippines (Table 2).

Overall, epiphytic ferns shared more species with other floristic regions than total epiphytic species (Table 2). Over 40% of Taiwanese epiphytic ferns also occurred in Eastern Asiatic, Malesian, and Indochinese regions. Epiphytic orchids exhibited the highest affinity (35%) to Indo-China, yet shared no species with Neotropical and Holarctic areas, except E. Asia.

Discussion

Species richness and taxonomic distribution

For a paleotropical region, the island of Taiwan is with 336 species rich in epiphytes (Table 1). There is no distinct dry season in Taiwan and abundant rainfall and warm climate promote epiphyte species richness and growth. Another reason why epiphyte richness is high may be that Taiwan served as a refuge during Late Quaternary climate change, which has been used to explain the exceptionally high diversity in Taiwan

Table 2. Floristic affinity of Taiwan epiphyte flora with phytogeographical regions, following Takhtajan (1986).

| Floristic regions | Taiwan (324) | Lanyu (69) | Lutao (25) | Pteridophytes (170) | Orchids (114) |
|---------------------------|--------------|------------|------------|---------------------|---------------|
| Eastern Asiatic Region | 38.9 (126) | 50.7 (35) | 64.0 (16) | 48.8 (83) | 25.4 (29) |
| China, Japan, Korea | 27.2 (88) | 21.7 (15) | 40.0 (10) | 31.2 (53) | 20.2 (23) |
| E. Himalaya & S.W. China | 13.0 (42) | 4.4 (3) | 0.0 (0) | 13.5 (23) | 13.2 (15) |
| Ryukyu | 13.0 (42) | 29.0 (20) | 24.0 (6) | 18.2 (31) | 6.1 (7) |
| Malesian Region | 40.9 (132) | 71.0 (49) | 72.0 (18) | 51.8 (88) | 25.4 (29) |
| Malay archipelago | 31.2 (101) | 49.3 (34) | 64.0 (16) | 42.4 (72) | 14.0 (16) |
| Philippines | 9.6 (31) | 21.7 (15) | 8.0 (2) | 9.4 (16) | 11.4 (13) |
| Indo-China | 39.2 (127) | 46.4 (32) | 60.0 (15) | 43.5 (74) | 35.1 (40) |
| India and Sirilanka | 23.5 (76) | 29.0 (20) | 52.0 (13) | 28.8 (49) | 14.9 (17) |
| Melanesia and Hawaii | 12.0 (39) | 26.1 (18) | 44.0 (11) | 20.0 (34) | 1.8 (2) |
| Africa | 4.9 (16) | 8.7 (6) | 8.0 (2) | 7.1 (12) | 0.9 (1) |
| Australia | 9.0 (29) | 18.8 (13) | 36.0 (9) | 12.4 (21) | 1.8 (2) |
| Neotropis | 2.5 (8) | 5.8 (4) | 4.0 (1) | 3.5 (6) | 0.0 (0) |
| Holarctis other than E.A. | 1.5 (5) | 2.9 (2) | 0.0 (0) | 2.9 (5) | 0.0 (0) |
| Endemicity | 21.3 (69) | 5.8 (4) | 0.0 (0) | 11.2 (19) | 33.3 (38) |

Given is the proportion (%) and number of Taiwanese species, in parentheses, of epiphytic Taiwanese species per region.

(4077 plant species; further discussed below). In view of this high floristic diversity, Taiwan may even be considered relatively poor in vascular epiphytes. The contribution of vascular epiphytes to total vascular flora is only 8%, whilst the EP-Q worldwide is nearly 10%. Moreover, about 36% of orchids are epiphytic in Taiwan, which is far less than the 70% worldwide level (Atwood, 1986). Possibly frequent tropical storms have reduced epiphyte diversity in Taiwan. On average, five typhoons hit Taiwan each year (data from 1958 to 2007, Central Weather Bureau). Typhoons may have a dramatic impact on forest canopies and cause understory light levels to increase to 30% of outside levels (Lin et al., 2003). Similarly, low epiphyte diversity in Puerto Rico has been attributed to island isolation and large-scale hurricane disturbances (Migenis and Ackerman, 1993).

Epiphyte richness in neotropical areas, moreover, is generally higher. For example, Wolf and Flamenco-S (2003) report 1173 species for the state of Chiapas, Mexico (75,000 km², 16°N–18°N). Typical for any epiphyte flora, the diversity is concentrated in few taxa (Fig. 3, Table 1). In contrast to the Neotropics, paleotropical areas lack particularly species-rich epiphyte families (e.g. Bromeliaceae, Cactaceae, and Marcraviaceae) and genera in the orchids (e.g. *Pleurothallis*, 1500 spp.; *Epidendrum*, 720 spp.; *Maxillaria*, 570 spp.; *Stelis*, 540 spp.) and in the aroids (*Anthurium*, 600 spp.; *Philodendron*, 350 spp. – Benzing, 1990). In Taiwan, the most abundant epiphytes are ferns, and in this respect Taiwanese epiphyte flora is typical for temperate regions. However, in comparison with other vegetation types, ecosystems, and floristic regions, the relative proportion of epiphytic ferns and orchids of Taiwan is not dramatically different, showing a transition from tropical to temperate regions (Table 3). A high

proportion of ferns and fern allies is probably due to the presence of temperate mountains in Taiwan that favour epiphytic ferns over, for example, orchids (Kessler et al., 2001; Zotz, 2005). In Taiwan, no epiphytic orchids are found above approximately 2300 m a.s.l. (*Gastrochilus hoi*, pers. comm.) in contrast to epiphytic ferns with ultimate altitudes of ca. 3000 m a.s.l. (e.g. *Pyrrosia* spp., *Lepisorus* spp., *Mecodium wrightii*, pers. observ.).

Epiphyte endemism

Many islands are considered global biodiversity hotspots because of high endemism of insular biota (Kreft et al., 2008). Taiwan is no exception, having extraordinary plant endemism. More than 1000 vascular plant species are endemic to the island, comprising 26% of the entire flora. The strikingly high flora endemism can be explained by Taiwan's extensive mountain system. Taiwan was formed from the collision between the Philippines Sea plate and the Eurasian continental margin and gave rise to the Central Ridge of Taiwan in Mid Pliocene (3 Ma) (Ho, 1988). Active orogenesis induced a massive earthquake in central Taiwan as recent as 1999. Orogenesis results in greater microhabitat differentiation of mountainous regions, which promotes island-wide biodiversity and endemism. Kreft et al. (2008) concluded that in continental islands, geographic isolation from the mainland may contribute less to species diversity than mountain isolation. Our data are in agreement with this conclusion. For example, several epiphytic genera of mountainous regions, *Bulbophyllum* (24 spp.), *Gastrochilus* (9 spp.), and *Oberonia* (7 spp.), show exceptionally high endemism of nearly 50%. Furthermore, *Goodyera*, a mid-elevation (ca. 1500–2000 m a.s.l.) species, evolved

Table 3. Epiphyte number of species (*S*) and taxonomic distribution among floristic regions and vegetation types.

| Location | Vegetation type | Latitude | Rainfall (mm) | <i>S</i> | Ferns (%) | Orchids (%) | EQ (%) | Endemism (%) | Source | Regional area/ sampling effort |
|-----------------------------------|---|----------------|---------------|----------|-----------------|-----------------|-----------------|--------------|--|--|
| <i>Paleotropics</i> | | | | | | | | | | |
| Taiwan | Tropical lowland to montane temperate forests | 21.9N–25.3N | 2467 | 324 | 52 | 35 | 8 | 21 | This study | 36,000 km ² |
| Cameroon | Semi-deciduous rain forest | 4.25N–2.5S | ca. 1500–1900 | 78 | 25 | 65 | | | Zapfack et al. (1996) | 150 trees |
| Congo, upper Katanga | Tropical lowland to montane forests | ca. 7.5S–13.4S | 780–1500 | 127 | 28 | 62 | | | Schaijes and Malaisse (2001) | 109,000 km ² |
| SW China, Mt. Ailao | Wet sub-tropical montane forests | 24.53N | 2450–2700 | 32 | 53 | 0.9 | | | Xu and Liu (2005) | 80 trees |
| Liberia, Nimba mountains | Tropical submontane forest | 6N–8N | 1500–3100 | 153 | 25 | 66 | | | Johansson (1974) | 463 trees |
| <i>Neotropics</i> | | | | | | | | | | |
| Mexico, Chiapas | Tropical lowland to montane temperate forests | 16N–18N | 800–5000 | 1173 | 21 | 48 | 14 | | Wolf and Flamenco-S (2003) | 75,000 km ² / 12,276 coll. |
| Ecuador | Tropical lowland to montane temperate forests | 1.4N–5S | 100–4500 | 4231 | ca. 5–20 | ca. 30–53 | ca. 25 | 35 | Küper et al. (2004) | 256,370 km ² |
| Ecuador, Yasuní | Tropical lowland Amazonia | 0.63S | 2750 | 313 | 22 | 30 | 21 ^a | 10 | Kreft et al. (2004) | 650 ha |
| Ecuador, Río Guajalito | Tropical montane forest | 0.23S | 2700 | 122 | 22 | 57 | 28 | | Nieder et al. (2001), Rauer and Rudolph (2001) | 400 ha |
| Ecuador, Río Palenque | Tropical lowland wet forest | ca. 1S | 2980 | 238 | 12 | 34 | 23 | | Gentry and Dodson (1987a) | 170 ha |
| Costa Rica, La Selva | Tropical lowland rainforest | 10.43N | 4000 | 368 | 16 | 30 | 23 | | Gentry and Dodson (1987b) | 1536 ha |
| Costa Rica, Santa Rosa | Seasonal forest (with 6-month dry season) | 10.83N | 1550 | 24 | 29 | 33 | 4 | | Gentry and Dodson (1987a), Janzen and Liesner (1980) | 37,000 ha |
| Costa Rica, Monteverde | Tropical montane forest | 10.3N | 2500 | 878 | 22 ^b | 36 ^b | 29 | | Haber (2001) | 10,500 ha |
| Panama, Barro Colorado | Tropical lowland moist forest | 9.15N | 2750 | 216 | 20 | 38 | 16 | | Croat (1978) | 1560 ha |
| Guyana, Mabura Hill | Tropical lowland moist forest | 5.33N | 2700 | 216 | 18 | 42 | 13 | | Ek (1997) | 10,000 ha |
| <i>Temperate</i> | | | | | | | | | | |
| Chile, Fundo San Martín, Valdivia | Temperate forests | 39.63S | | 16 | 63 | 6 | | | Riveros and Ramirez (1978) | |

| | | | | | | | | | |
|--------------------------------|--------------------------|---------|----------|--------|-----|----|--------|---|-------------------------|
| New Zealand | Temperate rain forests | 34S–47S | 150–5400 | 50 | 70 | 12 | 2 | Oliver (1930) | 268,680 km ² |
| Japan | Temperate forest | 24N–45N | 800–3600 | 52 | 63 | 35 | ca. 1 | Zotz (2005) | 377,873 km ² |
| India, west Himalaya, Nainital | Montane temperate forest | ca. 29N | 1600 | 17 | 76 | 24 | | Gupta (1968), Zotz (2005) | 3422 km ² |
| North Korea | Temperate forest | 38N–43N | 560–1500 | 9 | 100 | 0 | | Kolbeck (1995) | 120,540 km ² |
| World | | | | | | | | Madison (1977) Kress (1986) Gentry and Dodson (1987a) | |
| | | | | 28,200 | 9 | 71 | ca. 10 | | |
| | | | | 23,456 | 11 | 59 | ca. 10 | | |
| | | | | 29,505 | 9 | 77 | ca. 10 | | |

^aFreiberg and Freiberg (2000).

^bIngram et al. (1996) (composition of 256 epiphyte spp.).

three epiphytic species, including two endemics. This is the first report of epiphytism in this genus. Finally, endemism increases with altitude in Taiwan up to nearly 60% above 3500 m a.s.l.

Yet, vascular epiphytes show lower endemism (21.3%) than terrestrial plants (Table 2). This may be due to their superior dispersal ability; 89% of vascular epiphytes in Taiwan disperse by wind. The arboreal habitat and dust-like seeds and diaspores enable long-distance dispersal. Overall, ferns show wider ranges and lower endemism than angiosperms (Gentry and Dodson, 1987a; Kelly et al., 2004) (Table 2). In contrast with epiphytic seed plants, most large epiphytic fern genera are preponderantly pantropical (Gentry and Dodson, 1987a). Apart from dispersal ability, historical factors may also explain species geographical range (Lester et al., 2007). Kelly et al. (2004) reported that in the tropical Andes species endemism increased from primitive to advanced taxonomic groups (bryophytes < pteridophytes < angiosperms). Furthermore, taxa with narrow geographical range are often considered to have high speciation rates (Kelly et al., 2004). In this view, the high endemism (33%) in Taiwanese epiphytic orchids relates to their highly specific pollination system, which, together with the fragmented canopy habitat, promotes rapid speciation (Benzing, 1987; Gentry, 1982; Gentry and Dodson, 1987a; Gravendeel et al., 2004).

Epiphyte phylogeography

Taiwan has a relatively unique vascular epiphyte flora. The regions with closest affinity are the Malesian region, Indo-China, and Eastern Asiatic regions; ca. 40% of Taiwanese species are shared with those regions. Interestingly, about 13% of vascular epiphytes have a disjunctive distribution between Taiwan and SW China and/or E Himalayan regions (Table 2). This floristic disjunction is consistent with Hosokawa's (1958) finding that Taiwan's flora, especially of the highland, is more closely related to SW China and E Himalaya than to adjacent coastal provinces of mainland China. Kuo (1985) indicated similar observations on Taiwanese pteridophyte flora. He found that the pteridophytes of warm-temperate forests (500–1800 m a.s.l.) were closely related to SW China and the Himalayan regions, whilst lowland species showed higher affinity to Ryukyu, south-eastern China and Indo-China.

The simplest explanation for the lower epiphyte affinity of Taiwan with adjacent coastal regions of south-eastern China is lack of suitable habitats (Kuo, 1985). Due to long-term population pressure and associated agricultural activities, south-eastern China has endured extensive habitat change. Since epiphytes are most diverse and abundant in old-growth forests (Cascante-Marin et al., 2006; Köhler et al., 2007; Wolf,

2005), epiphyte diversity is especially affected. Furthermore, lowland south-eastern China shows little habitat similarity with Taiwan mountain areas.

Late Quaternary climate change offers another explanation. On an evolutionary time-scale, epiphytism is relatively recent, occurring in evolutionary advanced families of ferns and seed plants. Orchidaceae did not evolve until the Quaternary (1.6 Ma ago) (Benzing, 1990). Zotz (2005) discussed the possibility that the Pleistocene extinction was one of the limits of epiphytism in temperate zones, whilst few temperate areas (e.g. Chile, New Zealand, Himalayas, Japan) have a high number of epiphytes for being Tertiary refugia. The common feature of the flora in these areas is a high proportion of autochthonous and monotypic taxa. During the ice age in the Quaternary, the sea level in the Taiwan Strait dropped, connecting Taiwan with mainland Eurasia. According to the projected vegetation map of Last Glacial Maximum (LGM, 18,000 ago), Eurasia had relatively scarce tree cover with scattered areas of close forests in the uplands across south-western China and along the south-eastern coast of Eurasia (Ray and Adams, 2001). Presumably, the oceanic climate facilitated Taiwan as a refuge during Quaternary glaciations. Moreover, apart from high endemism, more than half of plant genera in Taiwan are monotypic (Hsieh, 2003). There is an endemic monotypic epiphyte genus *Haraella* (Orchidaceae) in Taiwan. Thus, we propose that Late Quaternary climate change helps explain the disjunctive distribution of many vascular epiphytes between Taiwan and south-western China as well as eastern Himalayan regions.

Interestingly, the epiphyte flora of Lanyu and Lutao is phytogeographically distinct. Lanyu has more affinity with the Philippines (22%) in the Malesian region than Lutao (8%), whereas Lutao shares more species with China, Japan and Korea in the Eastern Asiatic Region (40%) than Lanyu (22%) (Table 2). This pattern is in agreement with the proposed Neo-Wallace Line based on insect distributions (Kanto, 1933).

In summary, this one of the few epiphyte inventories in Asia shows that the Taiwanese epiphyte flora is rich in species and has an extraordinarily high endemism. Regional mountain isolation is probably the most effective driver for epiphyte diversification in Taiwan. Regarding the proportional contribution of epiphytic ferns and orchids, Taiwan is transitional between tropical and temperate zones. The disjunctive distribution of epiphytes between Taiwan and SW China as well as E Himalaya suggests low habitat similarity to adjacent China and/or a legacy of Late Quaternary climate change. Taiwanese vascular epiphyte distributions are in agreement with the Neo-Wallace Line.

Acknowledgement

We thank Chung S.-W., Yu S.-K., Lu P.-F., Chang Y.-H., for sharing personal observations on Taiwanese epiphytes in the field.

Appendix A

See Table A1.

Table A1. The vascular epiphyte checklist of Taiwan.

| No | Family | Species/taxon | Habit | Floristic_Region |
|----------------------|--------------|---|-------|--|
| Pteridophytes | | | | |
| 1 | Aspleniaceae | <i>Asplenium adiantoides</i> | FacuE | 15, 18, 22, 29 |
| 2 | Aspleniaceae | <i>Asplenium antiquum</i> | E | 2 |
| 3 | Aspleniaceae | <i>Asplenium australasicum</i> | E | 18, 22, 29 |
| 4 | Aspleniaceae | <i>Asplenium bullatum</i> | E | 16, 17 |
| 5 | Aspleniaceae | <i>Asplenium cuneatifforme</i> | E | EndemicF |
| 6 | Aspleniaceae | <i>Asplenium ensiforme</i> | FacuE | 2–25, 17, 16 |
| 7 | Aspleniaceae | <i>Asplenium griffithianum</i> | FacuE | 2–20, 16, 17 |
| 8 | Aspleniaceae | <i>Asplenium incisum</i> | FacuE | 2 |
| 9 | Aspleniaceae | <i>Asplenium laciniatum</i> | E | 2–27 |
| 10 | Aspleniaceae | <i>Asplenium neolaserpitiifolium</i> | E | 2–20, 17 |
| 11 | Aspleniaceae | <i>Asplenium nidus</i> | E | 2–20, 17, 18, 19, 20, 21, 22, 23, 29, 15, 12 |
| 12 | Aspleniaceae | <i>Asplenium normale</i> | FacuE | 2, 15, 17, 18, 20, 29, 12, 21 |
| 13 | Aspleniaceae | <i>Asplenium oldhami</i> | FacuE | 2–20, 17 |
| 14 | Aspleniaceae | <i>Asplenium planicaule</i> | FacuE | 2, 17, 18–104 |
| 15 | Aspleniaceae | <i>Asplenium prolongatum</i> | FacuE | 16, 17, 2 |
| 16 | Aspleniaceae | <i>Asplenium pseudolaserpitiifolium</i> | E | 17 |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|----|------------------|---|-------|--------------------------|
| 17 | Aspleniaceae | <i>Asplenium ritoense</i> | FacuE | 2, 17 |
| 18 | Davalliaceae | <i>Araiostegia parvipinnata</i> | E | 2–25 |
| 19 | Davalliaceae | <i>Davallia formosana</i> | E | 17 |
| 20 | Davalliaceae | <i>Davallia mariesii</i> | E | 2 |
| 21 | Davalliaceae | <i>Davallia solida</i> | E | 17, 18, 22 |
| 22 | Davalliaceae | <i>Humata chrysanthemifolia</i> | E | 18–104 |
| 23 | Davalliaceae | <i>Humata griffithiana</i> | E | 2–27, 2–25 |
| 24 | Davalliaceae | <i>Humata pectinata</i> | E | 18, 20, 29 |
| 25 | Davalliaceae | <i>Humata repens</i> | E | 2, 15, 17, 18, 29 |
| 26 | Davalliaceae | <i>Humata trifoliata</i> | E | 2–20, 17, 18 |
| 27 | Davalliaceae | <i>Humata vestita</i> | E | 17, 18 |
| 28 | Davalliaceae | <i>Leucostegia immersa</i> | E | 2–27, 16, 17, 18 |
| 29 | Grammitidaceae | <i>Calymmodon cucullatus</i> | E | 16, 18, 22, 29 |
| 30 | Grammitidaceae | <i>Calymmodon gracilis</i> | E | 17, 18 |
| 31 | Grammitidaceae | <i>Ctenopteris curtisii</i> | E | 18 |
| 32 | Grammitidaceae | <i>Ctenopteris merrittii</i> | E | 18 |
| 33 | Grammitidaceae | <i>Ctenopteris mollicoma</i> | E | 18 |
| 34 | Grammitidaceae | <i>Ctenopteris obliquata</i> | E | 16, 17, 18 |
| 35 | Grammitidaceae | <i>Ctenopteris subfalcata</i> | E | 16, 17, 18 |
| 36 | Grammitidaceae | <i>Ctenopteris tenuisecta</i> | E | 18 |
| 37 | Grammitidaceae | <i>Grammitis adspersa</i> | E | 18, 29 |
| 38 | Grammitidaceae | <i>Grammitis congener</i> | E | 17, 18 |
| 39 | Grammitidaceae | <i>Grammitis fenicis</i> | E | 18–104 |
| 40 | Grammitidaceae | <i>Grammitis intromissa</i> | E | 18 |
| 41 | Grammitidaceae | <i>Grammitis jagoriana</i> | E | 18 |
| 42 | Grammitidaceae | <i>Grammitis nuda</i> | E | EndemicF |
| 43 | Grammitidaceae | <i>Grammitis reinwardtia</i> | E | 18 |
| 44 | Grammitidaceae | <i>Prosaptia contigua</i> | E | 16, 18, 19, 20, 22, 29 |
| 45 | Grammitidaceae | <i>Prosaptia urceolaris</i> | E | 17, 18 |
| 46 | Grammitidaceae | <i>Scleroglossum pusillum</i> | E | 17, 18 |
| 47 | Grammitidaceae | <i>Xiphopteris okuboii</i> | E | 2, 17 |
| 48 | Hymenophyllaceae | <i>Abrodicyum cuningii</i> | E | 2, 18 |
| 49 | Hymenophyllaceae | <i>Crepidomanes bilabiatum</i> | E | 2–20, 17, 18 |
| 50 | Hymenophyllaceae | <i>Crepidomanes birmanicum</i> | E | 2, 17, 16 |
| 51 | Hymenophyllaceae | <i>Crepidomanes kurzii</i> | E | 16, 17, 18, 29 |
| 52 | Hymenophyllaceae | <i>Crepidomanes latealatum</i> | FacuE | 2, 16, 17, 18 |
| 53 | Hymenophyllaceae | <i>Crepidomanes latemarginale</i> | FacuE | 2–20, 16, 17, 18 |
| 54 | Hymenophyllaceae | <i>Crepidomanes palmifolium</i> | E | EndemicF |
| 55 | Hymenophyllaceae | <i>Crepidomanes schmidtianum</i> var. <i>latifrons</i> | FacuE | 2–27, 18–104 |
| 56 | Hymenophyllaceae | <i>Gonocormus minutus</i> | E | 2, 16, 17, 18, 20, 22 |
| 57 | Hymenophyllaceae | <i>Hymenophyllum barbatum</i> | E | 2, 16, 17 |
| 58 | Hymenophyllaceae | <i>Hymenophyllum devolii</i> | E | EndemicF |
| 59 | Hymenophyllaceae | <i>Hymenophyllum fimbriatum</i> | E | 18–104 |
| 60 | Hymenophyllaceae | <i>Hymenophyllum productum</i> | E | 17, 18 |
| 61 | Hymenophyllaceae | <i>Hymenophyllum simonsianum</i> | E | 2–27 |
| 62 | Hymenophyllaceae | <i>Hymenophyllum taiwanense</i> | E | EndemicF |
| 63 | Hymenophyllaceae | <i>Mecodium badium</i> | E | 2, 16, 17, 18 |
| 64 | Hymenophyllaceae | <i>Mecodium javanicum</i> | E | 16, 18, 19 |
| 65 | Hymenophyllaceae | <i>Mecodium oligosorum</i> | E | 2 |
| 66 | Hymenophyllaceae | <i>Mecodium polyanthos</i> | E | 2, 15, 17, 18 |
| 67 | Hymenophyllaceae | <i>Mecodium wrightii</i> | E | 2, 4 |
| 68 | Hymenophyllaceae | <i>Meringium blandum</i> | E | 18 |
| 69 | Hymenophyllaceae | <i>Meringium denticulatum</i> | FacuE | 2–20, 16, 17, 18, 19 |
| 70 | Hymenophyllaceae | <i>Meringium holochilum</i> | FacuE | 18 |
| 71 | Hymenophyllaceae | <i>Microgonium bimarginatum</i> | FacuE | 2–20, 16, 17, 18, 20, 29 |
| 72 | Hymenophyllaceae | <i>Microgonium motleyi</i> | FacuE | 2–20, 16, 17, 18, 20 |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|-----|------------------|--|-------|---|
| 73 | Hymenophyllaceae | <i>Microgonium omphalodes</i> | FacuE | 2–20, 18, 20, 29 |
| 74 | Hymenophyllaceae | <i>Microtrichomanes nitidulum</i> | E | 16, 17, 18, 29 |
| 75 | Hymenophyllaceae | <i>Pleuromanes pallidum</i> | E | 16, 17, 18, 20 |
| 76 | Hymenophyllaceae | <i>Vandenboschia auriculata</i> | E | 2, 16, 17, 18, 20 |
| 77 | Hymenophyllaceae | <i>Vandenboschia maxima</i> | FacuE | 2–20, 17, 18 |
| 78 | Hymenophyllaceae | <i>Vandenboschia radicans</i> | E | 2–27, 2–20, 6, 12, 16, 17, 18, 23, 24, 25, 27 |
| 79 | Lomariopsidaceae | <i>Elaphoglossum callifolium</i> | E | 17, 18 |
| 80 | Lomariopsidaceae | <i>Elaphoglossum commutatum</i> | E | 10, 12, 15, 16, 18, 21, 25 |
| 81 | Lomariopsidaceae | <i>Elaphoglossum luzonicum</i> | E | 18 |
| 82 | Lomariopsidaceae | <i>Elaphoglossum marginatum</i> | E | EndemicF |
| 83 | Lomariopsidaceae | <i>Elaphoglossum yoshinagae</i> | E | 2, 17 |
| 84 | Lomariopsidaceae | <i>Lomariopsis spectabilis</i> | E | 2–20, 18 |
| 85 | Lycopodiaceae | <i>Lycopodium carinatum</i> | E | 2–20, 17, 18, 20, 29 |
| 86 | Lycopodiaceae | <i>Lycopodium cryptomerianum</i> | E | 2 |
| 87 | Lycopodiaceae | <i>Lycopodium cunninghamioides</i> | E | 2 |
| 88 | Lycopodiaceae | <i>Lycopodium fargesii</i> | E | 2 |
| 89 | Lycopodiaceae | <i>Lycopodium fordii</i> | E | 2, 16, 17 |
| 90 | Lycopodiaceae | <i>Lycopodium phlegmaria</i> | E | 2, 18, 22, 29, 15, 12 |
| 91 | Lycopodiaceae | <i>Lycopodium salvinioides</i> | E | 2–20, 18–104 |
| 92 | Lycopodiaceae | <i>Lycopodium sieboldii</i> | E | 2 |
| 93 | Lycopodiaceae | <i>Lycopodium squarrosom</i> | E | 2, 20, 18, 22 |
| 94 | Lycopodiaceae | <i>Lycopodium taiwanense</i> | E | 2–27, 2–20, 16 |
| 95 | Oleandraceae | <i>Nephrolepis auriculata</i> | FacuE | 2–20, 16, 17, 18, 9, 23, 24, 25, 26, 27, 22, 21, 15, 29 |
| 96 | Oleandraceae | <i>Nephrolepis biserrata</i> | FacuE | 2–20, 19, 20, 18, 23, 12, 15, 16, 10, 29, 27, 25 |
| 97 | Oleandraceae | <i>Nephrolepis multiflora</i> | FacuE | 2–20, 16, 17, 18–104 |
| 98 | Oleandraceae | <i>Oleandra wallichii</i> | E | 2–25, 2–27, 16, 17 |
| 99 | Opioglossaceae | <i>Ophioderma pendula</i> | E | 17, 18, 15, 21, 29 |
| 100 | Polypodiaceae | <i>Aglaomorpha meyeniana</i> | E | 18–104 |
| 101 | Polypodiaceae | <i>Arthromeris lehmanni</i> | E | 2, 16, 17, 18–104 |
| 102 | Polypodiaceae | <i>Belvisia mucronata</i> | E | 16, 18, 20, 22, 19, 29 |
| 103 | Polypodiaceae | <i>Colysis hemionitidea</i> | FacuE | 2–27, 16, 17, 18–104 |
| 104 | Polypodiaceae | <i>Colysis pothifolia</i> | FacuE | 2, 16, 17, 18–104 |
| 105 | Polypodiaceae | <i>Colysis shintenensis</i> | FacuE | 2 |
| 106 | Polypodiaceae | <i>Colysis wrightii</i> | FacuE | 2–20, 17 |
| 107 | Polypodiaceae | <i>Crypsinus echinosporus</i> | E | EndemicF |
| 108 | Polypodiaceae | <i>Crypsinus engleri</i> | E | 2 |
| 109 | Polypodiaceae | <i>Crypsinus hastatus</i> | FacuE | 2, 18–104 |
| 110 | Polypodiaceae | <i>Crypsinus quasidivariatus</i> | FacuE | 2–27, 16 |
| 111 | Polypodiaceae | <i>Crypsinus taeniatus</i> var. <i>palmatus</i> | FacuE | 18, 20 |
| 112 | Polypodiaceae | <i>Crypsinus taiwanensis</i> | FacuE | EndemicF |
| 113 | Polypodiaceae | <i>Crypsinus yakushimensis</i> | FacuE | 2–20 |
| 114 | Polypodiaceae | <i>Drymotaenium miyoshianum</i> | E | 2 |
| 115 | Polypodiaceae | <i>Drynaria fortunei</i> | E | 17 |
| 116 | Polypodiaceae | <i>Lemmaphyllum diversum</i> | E | 2 |
| 117 | Polypodiaceae | <i>Lemmaphyllum microphyllum</i> | E | 2 |
| 118 | Polypodiaceae | <i>Lepisorus clathratus</i> | E | 2, 8, 16 |
| 119 | Polypodiaceae | <i>Lepisorus kawakamii</i> | E | EndemicF |
| 120 | Polypodiaceae | <i>Lepisorus kuchenensis</i> | E | 2–25 |
| 121 | Polypodiaceae | <i>Lepisorus megasorus</i> | E | EndemicF |
| 122 | Polypodiaceae | <i>Lepisorus monilisorus</i> | E | EndemicF |
| 123 | Polypodiaceae | <i>Lepisorus morrisonensis</i> | E | 2–25, 2–27 |
| 124 | Polypodiaceae | <i>Lepisorus obscurevenulosus</i> | E | 2 |
| 125 | Polypodiaceae | <i>Lepisorus pseudoussuriensis</i> | E | EndemicF |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|---------------------|-----------------|---|-------|---|
| 126 | Polypodiaceae | <i>Lepisorus suboligolepidus</i> | E | 2 |
| 127 | Polypodiaceae | <i>Lepisorus thunbergianus</i> | E | 2, 18–104 |
| 128 | Polypodiaceae | <i>Lepisorus tosaensis</i> | E | 2 |
| 129 | Polypodiaceae | <i>Leptochilus decurrens</i> | FacuE | 16, 17, 18, 20 |
| 130 | Polypodiaceae | <i>Loxogramme confertifolia</i> | E | EndemicF |
| 131 | Polypodiaceae | <i>Loxogramme formosana</i> | E | 2–25 |
| 132 | Polypodiaceae | <i>Loxogramme grammitoides</i> | E | 2 |
| 133 | Polypodiaceae | <i>Loxogramme remotefrondigera</i> | E | EndemicF |
| 134 | Polypodiaceae | <i>Loxogramme salicifolia</i> | E | 2, 17 |
| 135 | Polypodiaceae | <i>Microsorium buergerianum</i> | E | 2, 17 |
| 136 | Polypodiaceae | <i>Microsorium dilatatum</i> | E | 2–20, 16, 17 |
| 137 | Polypodiaceae | <i>Microsorium fortunei</i> | FacuE | 2–27, 2–20 |
| 138 | Polypodiaceae | <i>Microsorium membranaceum</i> | FacuE | 2–25, 2–27, 16, 17, 18–104 |
| 139 | Polypodiaceae | <i>Microsorium punctatum</i> | E | 16, 17, 22, 29 |
| 140 | Polypodiaceae | <i>Microsorium rubidum</i> | E | 2–20, 16, 17, 18, 20 |
| 141 | Polypodiaceae | <i>Polypodium amoenum</i> | E | 2–27, 17 |
| 142 | Polypodiaceae | <i>Polypodium argutum</i> | E | 2–25, 2–27, 17, 18–104 |
| 143 | Polypodiaceae | <i>Polypodium formosanum</i> | E | 2–20 |
| 144 | Polypodiaceae | <i>Polypodium microrhizoma</i> | E | 2–25, 2–27 |
| 145 | Polypodiaceae | <i>Polypodium raishanense</i> | E | EndemicF |
| 146 | Polypodiaceae | <i>Polypodium transpianense</i> | E | EndemicF |
| 147 | Polypodiaceae | <i>Pseudodrynaria coronans</i> | E | 2–20, 2–25, 2–27, 17 |
| 148 | Polypodiaceae | <i>Pyrrosia adnascens</i> | E | 2–20, 16, 17, 18, 20 |
| 149 | Polypodiaceae | <i>Pyrrosia gralla</i> | E | 2–25 |
| 150 | Polypodiaceae | <i>Pyrrosia linearifolia</i> | E | 2 |
| 151 | Polypodiaceae | <i>Pyrrosia lingua</i> | E | 2, 17 |
| 152 | Polypodiaceae | <i>Pyrrosia matsudae</i> | E | EndemicF |
| 153 | Polypodiaceae | <i>Pyrrosia polydactylis</i> | E | EndemicF |
| 154 | Polypodiaceae | <i>Pyrrosia sheareri</i> | E | 17 |
| 155 | Polypodiaceae | <i>Pyrrosia transmorrisonensis</i> | E | EndemicF |
| 156 | Polypodiaceae | <i>Saxiglossum angustissimum</i> | E | 2 |
| 157 | Psilotaceae | <i>Psilotum nudum</i> | E | 2, 17, 18, 21, 22, 29, 10, 12, 15, 23, 9, 3, 25, 27, 26 |
| 158 | Selaginellaceae | <i>Selaginella delicatula</i> | E | 2, 16, 17, 18, 20 |
| 159 | Selaginellaceae | <i>Selaginella involvens</i> | E | 2, 16, 17, 18 |
| 160 | Selaginellaceae | <i>Selaginella stauntoniana</i> | FacuE | 2 |
| 161 | Selaginellaceae | <i>Selaginella tamariscina</i> | FacuE | 2, 16, 18 |
| 162 | Vittariaceae | <i>Antrophyum formosanum</i> | FacuE | 2–20 |
| 163 | Vittariaceae | <i>Antrophyum obovatum</i> | FacuE | 2, 16, 17 |
| 164 | Vittariaceae | <i>Antrophyum parvulum</i> | FacuE | 2–20, 18 |
| 165 | Vittariaceae | <i>Antrophyum sessilifolium</i> | FacuE | 18–104 |
| 166 | Vittariaceae | <i>Vaginularia paradoxa</i> | E | 16, 18, 20, 21 |
| 167 | Vittariaceae | <i>Vaginularia trichoidea</i> | E | 18, 21 |
| 168 | Vittariaceae | <i>Vittaria anguste-elongata</i> | E | 18 |
| 169 | Vittariaceae | <i>Vittaria flexuosa</i> | E | 2, 16, 17, 18 |
| 170 | Vittariaceae | <i>Vittaria taeniophylla</i> | E | 2–27, 2–25, 17, 18–104 |
| 171 | Vittariaceae | <i>Vittaria zosterifolia</i> | E | 2–20, 18, 20 |
| Dicotyledons | | | | |
| 172 | Araliaceae | <i>Schefflera arboricola</i> | E | 17 |
| 173 | Asclepiadaceae | <i>Dischidia formosana</i> | E | EndemicF&L |
| 174 | Asclepiadaceae | <i>Hoya carnosa</i> | E | 2, 16, 17 |
| 175 | Ericaceae | <i>Rhododendron kawakamii</i> | E | EndemicF |
| 176 | Ericaceae | <i>Vaccinium dunalianum</i> var. <i>caudatifolium</i> | E | EndemicF |
| 177 | Ericaceae | <i>Vaccinium emarginatum</i> | E | EndemicF |
| 178 | Gesneriaceae | <i>Aeschynanthus acuminatus</i> | E | 2–27, 16, 17, 18 |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|-----------------------|-----------------|---|---------|--|
| 179 | Gesneriaceae | <i>Lysionotus pauciflorus</i> | E | 2 |
| 180 | Gesneriaceae | <i>Lysionotus pauciflorus</i> var. <i>ikedae</i> | E | EndemicL |
| 181 | Melastomataceae | <i>Medinilla formosana</i> | E | EndemicF |
| 182 | Melastomataceae | <i>Medinilla hayataina</i> | E | EndemicL |
| 183 | Melastomataceae | <i>Pachycentria formosana</i> | E | EndemicF |
| 184 | Moraceae | <i>Ficus benjamina</i> | HemiE-P | 17, 18, 29 |
| 185 | Moraceae | <i>Ficus caulocarpa</i> | HemiE-P | 2–20, 17, 18, 16 |
| 186 | Moraceae | <i>Ficus heteropleura</i> | HemiE-P | 2–27, 18, 17 |
| 187 | Moraceae | <i>Ficus microcarpa</i> var. <i>microcarpa</i> | HemiE-P | 2–20, 18, 17, 16, 29 |
| 188 | Moraceae | <i>Ficus microcarpa</i> var. <i>crassifolia</i> | HemiE-P | 18–104 |
| 189 | Moraceae | <i>Ficus pumila</i> | HemiE-S | 2, 16 |
| 190 | Moraceae | <i>Ficus pumila</i> L. var. <i>awkeotsang</i> | HemiE-S | EndemicF |
| 191 | Moraceae | <i>Ficus sarmentosa</i> var. <i>henryi</i> | HemiE-S | 2 |
| 192 | Moraceae | <i>Ficus sarmentosa</i> var. <i>nipponica</i> | HemiE-S | 2 |
| 193 | Moraceae | <i>Ficus superba</i> var. <i>japonica</i> | HemiE-P | 2, 16, 17, 18 |
| 194 | Moraceae | <i>Ficus virgata</i> | HemiE-P | 2–20, 16, 17, 18, 29, 22 |
| 195 | Piperaceae | <i>Peperomia japonica</i> | E | 2 |
| 196 | Piperaceae | <i>Peperomia nakaharai</i> | E | EndemicF |
| 197 | Piperaceae | <i>Peperomia reflexa</i> | E | 2, 23, 26, 25, 21, 12, 10, 15, 25, 29 |
| 198 | Piperaceae | <i>Peperomia rubrivenosa</i> | E | 18–104 |
| 199 | Piperaceae | <i>Peperomia sui</i> | E | EndemicF |
| 200 | Piperaceae | <i>Piper arborescens</i> | HemiE-S | 18 |
| 201 | Piperaceae | <i>Piper betle</i> | HemiE-S | 18 |
| 202 | Piperaceae | <i>Piper interruptum</i> var. <i>multinervum</i> | HemiE-S | 18 |
| 203 | Piperaceae | <i>Piper kadsura</i> | HemiE-S | 2 |
| 204 | Piperaceae | <i>Piper kawakamii</i> | HemiE-S | EndemicF |
| 205 | Piperaceae | <i>Piper kwashoense</i> | HemiE-S | EndemicL&G |
| 206 | Piperaceae | <i>Piper sintenense</i> | HemiE-S | EndemicF |
| 207 | Piperaceae | <i>Piper taiwanense</i> | HemiE-S | EndemicF |
| 208 | Rubiaceae | <i>Psychotria serpens</i> | HemiE-S | 2, 17 |
| 209 | Saxifragaceae | <i>Hydrangea integrifolia</i> | E | 18–104 |
| 210 | Saxifragaceae | <i>Pileostegia viburnoides</i> | E | 2–20, 16, 17 |
| 211 | Urticaceae | <i>Procris laevigata</i> | E | 2–25, 15, 16, 17, 18 |
| Monocotyledons | | | | |
| 212 | Araceae | <i>Epipremnum formosanum</i> | HemiE-S | EndemicF |
| 213 | Araceae | <i>Epipremnum pinnatum</i> | HemiE-S | 2, 18, 20, 29 |
| 214 | Araceae | <i>Pothodium lobbianum</i> | HemiE-S | 18 |
| 215 | Araceae | <i>Pothos chinensis</i> | HemiE-S | 2 |
| 216 | Araceae | <i>Remusatia vivipara</i> | E | 2–25, 15, 16, 17, 18, 12, 29, 10, 25 |
| 217 | Orchidaceae | <i>Acampe rigida</i> | E | 2–27, 16, 17, 18 |
| 218 | Orchidaceae | <i>Appendicula fenixii</i> | E | EndemicL |
| 219 | Orchidaceae | <i>Appendicula reflexa</i> | E | 17, 18 |
| 220 | Orchidaceae | <i>Arachnis labrosa</i> | E | 17 |
| 221 | Orchidaceae | <i>Ascocentrum pumilum</i> | E | EndemicF |
| 222 | Orchidaceae | <i>Bulbophyllum affine</i> | E | 2–27, 16, 17 |
| 223 | Orchidaceae | <i>Bulbophyllum albociliatum</i> | E | EndemicF |
| 224 | Orchidaceae | <i>Bulbophyllum aureolabellum</i> | E | EndemicF |
| 225 | Orchidaceae | <i>Bulbophyllum chitouense</i> | E | EndemicF |
| 226 | Orchidaceae | <i>Bulbophyllum drymoglossum</i> | E | 2 |
| 227 | Orchidaceae | <i>Bulbophyllum electrinum</i> | E | 2–25, 17 |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|-----|-------------|---------------------------------------|-------|--------------------|
| 228 | Orchidaceae | <i>Bulbophyllum hirundinis</i> | E | 17 |
| 229 | Orchidaceae | <i>Bulbophyllum insulsum</i> | E | 17 |
| 230 | Orchidaceae | <i>Bulbophyllum japonicum</i> | E | 2 |
| 231 | Orchidaceae | <i>Bulbophyllum macraei</i> | E | 2, 16 |
| 232 | Orchidaceae | <i>Bulbophyllum melanoglossum</i> | E | EndemicF |
| 233 | Orchidaceae | <i>Bulbophyllum omerandrum</i> | E | 2 |
| 234 | Orchidaceae | <i>Bulbophyllum pectenvenensis</i> | E | 17 |
| 235 | Orchidaceae | <i>Bulbophyllum pectinatum</i> | E | 17 |
| 236 | Orchidaceae | <i>Bulbophyllum pingtungense</i> | E | EndemicF |
| 237 | Orchidaceae | <i>Bulbophyllum retusiusculum</i> | E | 2–27, 17, 16 |
| 238 | Orchidaceae | <i>Bulbophyllum riyantum</i> | E | 17 |
| 239 | Orchidaceae | <i>Bulbophyllum rubrolabellum</i> | E | EndemicF |
| 240 | Orchidaceae | <i>Bulbophyllum setaceum</i> | E | EndemicF |
| 241 | Orchidaceae | <i>Bulbophyllum taitungianum</i> | E | EndemicF |
| 242 | Orchidaceae | <i>Bulbophyllum taiwanense</i> | E | EndemicF |
| 243 | Orchidaceae | <i>Bulbophyllum tokioi</i> | E | EndemicF |
| 244 | Orchidaceae | <i>Bulbophyllum umbellatum</i> | E | 2–27, 16, 17 |
| 245 | Orchidaceae | <i>Bulbophyllum wightii</i> | E | 16 |
| 246 | Orchidaceae | <i>Chiloschista segawai</i> | E | EndemicF |
| 247 | Orchidaceae | <i>Cleisostoma paniculatum</i> | E | 17 |
| 248 | Orchidaceae | <i>Cleisostoma uraiensis</i> | E | 2–20, 18–104 |
| 249 | Orchidaceae | <i>Cymbidium dayanum</i> | E | 2, 16, 17, 18 |
| 250 | Orchidaceae | <i>Dendrobium catenatum</i> | E | 2 |
| 251 | Orchidaceae | <i>Dendrobium chameleon</i> | E | 18–104 |
| 252 | Orchidaceae | <i>Dendrobium chryseum</i> | E | 2, 16, 17 |
| 253 | Orchidaceae | <i>Dendrobium crumenatum</i> | E | 16, 17, 18 |
| 254 | Orchidaceae | <i>Dendrobium equitans</i> | E | 18–104 |
| 255 | Orchidaceae | <i>Dendrobium falconeri</i> | E | 2–27, 16, 17 |
| 256 | Orchidaceae | <i>Dendrobium furcatopedicellatum</i> | E | EndemicF |
| 257 | Orchidaceae | <i>Dendrobium goldschmidtianum</i> | E | 18–104 |
| 258 | Orchidaceae | <i>Dendrobium leptocladum</i> | E | EndemicF |
| 259 | Orchidaceae | <i>Dendrobium linawianum</i> | E | 2 |
| 260 | Orchidaceae | <i>Dendrobium moniliforme</i> | E | 2 |
| 261 | Orchidaceae | <i>Dendrobium somae</i> | E | EndemicF |
| 262 | Orchidaceae | <i>Dendrochilum uncatum</i> | E | 18–104 |
| 263 | Orchidaceae | <i>Diploprora championii</i> | E | 2–27, 16, 17 |
| 264 | Orchidaceae | <i>Epigeneium fargesii</i> | E | 2–27, 17 |
| 265 | Orchidaceae | <i>Epigeneium nakaharae</i> | E | EndemicF |
| 266 | Orchidaceae | <i>Eria amica</i> | E | 2–25, 2–27, 17 |
| 267 | Orchidaceae | <i>Eria corneri</i> | E | 2–20, 17 |
| 268 | Orchidaceae | <i>Eria japonica</i> | E | 2–20, 17 |
| 269 | Orchidaceae | <i>Eria javanica</i> | E | 2, 16, 17, 18 |
| 270 | Orchidaceae | <i>Eria ovata</i> | E | 2–20, 18 |
| 271 | Orchidaceae | <i>Eria robusta</i> | E | 18 |
| 272 | Orchidaceae | <i>Eria tomentosiflora</i> | E | 18–104 |
| 273 | Orchidaceae | <i>Flickingeria comata</i> | E | 18, 29, 19, 20, 22 |
| 274 | Orchidaceae | <i>Flickingeria tairukounia</i> | E | EndemicF |
| 275 | Orchidaceae | <i>Gastrochilus ciliaris</i> | E | 2 |
| 276 | Orchidaceae | <i>Gastrochilus formosanus</i> | E | 2 |
| 277 | Orchidaceae | <i>Gastrochilus fuscopunctatus</i> | E | EndemicF |
| 278 | Orchidaceae | <i>Gastrochilus hoi</i> | E | EndemicF |
| 279 | Orchidaceae | <i>Gastrochilus japonicus</i> | E | 2 |
| 280 | Orchidaceae | <i>Gastrochilus linii</i> | E | EndemicF |
| 281 | Orchidaceae | <i>Gastrochilus matsudai</i> | E | EndemicF |
| 282 | Orchidaceae | <i>Gastrochilus rantabunensis</i> | E | 2 |
| 283 | Orchidaceae | <i>Gastrochilus raraensis</i> | E | EndemicF |

Table A1. (continued)

| No | Family | Species/taxon | Habit | Floristic_Region |
|-----|-------------|-------------------------------------|-------|----------------------------|
| 284 | Orchidaceae | <i>Goodyera bilamellata</i> | E | EndemicF |
| 285 | Orchidaceae | <i>Goodyera pendula</i> | E | 2 |
| 286 | Orchidaceae | <i>Goodyera nantoensis</i> | E | EndemicF |
| 287 | Orchidaceae | <i>Haraella retrocalla</i> | E | EndemicF |
| 288 | Orchidaceae | <i>Holcoglossum quasipinifolium</i> | E | 2 |
| 289 | Orchidaceae | <i>Liparis bootanensis</i> | E | 2, 17, 18 |
| 290 | Orchidaceae | <i>Liparis caespitosa</i> | E | 17, 18, 16, 12, 15, 19, 20 |
| 291 | Orchidaceae | <i>Liparis condylobulbon</i> | E | 17, 18 |
| 292 | Orchidaceae | <i>Liparis cordifolia</i> | FacuE | 2–27, 2–25, 16 |
| 293 | Orchidaceae | <i>Liparis elliptica</i> | E | 2, 16, 17 |
| 294 | Orchidaceae | <i>Liparis grossa</i> | E | 17, 18–104 |
| 295 | Orchidaceae | <i>Liparis nakaharai</i> | E | EndemicF |
| 296 | Orchidaceae | <i>Liparis somai</i> | E | EndemicF |
| 297 | Orchidaceae | <i>Liparis viridiflora</i> | E | 2–27, 16, 17, 18 |
| 298 | Orchidaceae | <i>Luisia cordata</i> | E | EndemicF |
| 299 | Orchidaceae | <i>Luisia megasepala</i> | E | EndemicF |
| 300 | Orchidaceae | <i>Luisia teres</i> | E | 2 |
| 301 | Orchidaceae | <i>Microtatorchis compacta</i> | E | 18–104 |
| 302 | Orchidaceae | <i>Oberonia arisanensis</i> | E | 2–20 |
| 303 | Orchidaceae | <i>Oberonia caulescens</i> | E | 2–25, 2–27, 17 |
| 304 | Orchidaceae | <i>Oberonia gigantea</i> | E | EndemicF |
| 305 | Orchidaceae | <i>Oberonia japonica</i> | E | 2 |
| 306 | Orchidaceae | <i>Oberonia pumila</i> | E | EndemicF |
| 307 | Orchidaceae | <i>Oberonia rosea</i> | E | 17 |
| 308 | Orchidaceae | <i>Oberonia seidenfadenii</i> | E | EndemicF |
| 309 | Orchidaceae | <i>Papilionanthe taiwaniana</i> | E | EndemicF |
| 310 | Orchidaceae | <i>Phalaenopsis aphrodite</i> | E | 18–104 |
| 311 | Orchidaceae | <i>Phalaenopsis equestris</i> | E | 18–104 |
| 312 | Orchidaceae | <i>Pholidota cantonensis</i> | E | 17 |
| 313 | Orchidaceae | <i>Phreatia caulescens</i> | E | 18–104 |
| 314 | Orchidaceae | <i>Phreatia formosana</i> | E | 2–25, 17 |
| 315 | Orchidaceae | <i>Phreatia morii</i> | E | EndemicF |
| 316 | Orchidaceae | <i>Phreatia taiwaniana</i> | E | EndemicF |
| 317 | Orchidaceae | <i>Pleione bulbocodioides</i> | FacuE | 2 |
| 318 | Orchidaceae | <i>Pomatocalpa acuminata</i> | E | EndemicF |
| 319 | Orchidaceae | <i>Schoenorchis vanoverberghii</i> | E | 18–104 |
| 320 | Orchidaceae | <i>Staurochilus luchuensis</i> | E | 2–20 |
| 321 | Orchidaceae | <i>Sunipia andersonii</i> | E | 2–27, 16, 17 |
| 322 | Orchidaceae | <i>Taeniophyllum complanatum</i> | E | EndemicF |
| 323 | Orchidaceae | <i>Taeniophyllum glandulosum</i> | E | 2, 17, 18, 29 |
| 324 | Orchidaceae | <i>Thelasis pygmaea</i> | E | 2–27, 16, 17, 18 |
| 325 | Orchidaceae | <i>Thrixspermum annamense</i> | E | 17 |
| 326 | Orchidaceae | <i>Thrixspermum eximium</i> | E | 18–104 |
| 327 | Orchidaceae | <i>Thrixspermum fantasticum</i> | E | 2–20, 18–104 |
| 328 | Orchidaceae | <i>Thrixspermum formosanum</i> | E | 17 |
| 329 | Orchidaceae | <i>Thrixspermum laurisilvaticum</i> | E | 2 |
| 330 | Orchidaceae | <i>Thrixspermum merguense</i> | E | 17, 18 |
| 331 | Orchidaceae | <i>Thrixspermum pensile</i> | E | 17, 18 |
| 332 | Orchidaceae | <i>Thrixspermum saruwatarii</i> | E | EndemicF |
| 333 | Orchidaceae | <i>Thrixspermum subulatum</i> | E | 17, 18 |
| 334 | Orchidaceae | <i>Trichoglottis rosea</i> | E | 18–104 |
| 335 | Orchidaceae | <i>Tuberolabium kotoense</i> | E | EndemicL |
| 336 | Orchidaceae | <i>Vanda lamellata</i> | E | 2–20, 18–104 |

Abbreviations: E: epiphyte, FacuE: facultative epiphyte, HemiE-P: primary hemi-epiphytes, HemiE-S: secondary hemi-epiphyte, EndemicF: endemic species in Taiwan, EndemicL: endemic species in Lanyu, EndemicG: endemic species in Lutao, floristic codes refer to Fig. 2.

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