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錫蘭七指蕨在北臺灣之一新分布

New Distribution Area of *Helminthostachys zeylanica* (Ophioglossaceae) from North Taiwan

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Abstract

A new distribution area of *Helminthostachys zeylanica* in North Taiwan was reported at Yangmingshan, which was supposed to be the northern boundary of this species in Taiwan. The phenology, the characters of its habitat, and companions are described in present study.

Key words: Ophioglossaceae, *Helminthostachys zeylanica*, Taiwan, Yangmingshan, rare species

摘要

本文介紹錫蘭七指蕨在臺灣的新分布地區—陽明山也是臺灣島內分布的北界，並描述其物候與生長環境之各項特徵及物候關係與伴生植物。

關鍵字：瓶爾小草科、七指蕨、臺灣、陽明山、稀有植物

Introduction

Helminthostachys zeylanica (L.) Hook. is the only species of the genus *Helminthostachys* in the Ophioglossaceae, this species was utilized as, medicinal properties such as malaria controlling preparation (Cicuzza, 2020). *Helminthostachys zeylanica* distributed in Sri Lanka, India, the Philippines, Ryukyu, Australia, Southern China, Malay Peninsula, and Taiwan (Ito, 1928; Hatsusima, 1975; Kuo, 1985; Shieh & Devol, 1994; Joshi, 2011; Zhang et al., 2013; Bharali et al., 2017). In Taiwan, the populations were reported from Tianchi of Lanyu, the third sector of Kenting Forest Recreation in Hengchun Peninsula (Kuo, 1997), Xiaolanyu (Yeh et al., 2010), Hushan Dam in Yunlin County (Huang et al., 2012), Huisun Experimental Forest Station in Nantou (Wang & Ou, 2002). Due to its scarcity, it needs to be protected. Most of the populations of *H. zeylanica* in Taiwan contained only few individuals, therefore, this was an endangered species in Taiwan (Lu & Chiou, 1997). In the Red List of Vascular Plants of Taiwan 2017, the conservation rank of this species was evaluated as Nationally Critically Endangered (NCR) (Editorial Committee of the Red List of Taiwan Plants, 2017).

In March 2020 our field survey first found plants in Yangmingshan National Park area. Therefore, we started phenological observation, and found more than 30 plants sprout in spring, and then matured with fertile spike in the summer.

Material and Methods

Phenological observations were conducted during Mar. 2020 to Sep. 2021. The different phenophases of *H. zeylanica* were recorded and photographed. Climate data of habitat were obtained from the website of Central Weather Bureau.

Results and discussion

I. Habitat condition of *H. zeylanica* in northern Taiwan

The habitat located in a mountain forest near Erziping in Yangmingshan National Park, the altitude was ca. 650 m and far from roadside. In addition to the ancestors' activities and graveyard, there is only few artificial disturbances. The habitat is located on 25 degrees north latitude, which is belonged to subtropical monsoon climate. The afternoon thundershowers in summer might cause this habitat submerged, under the water. In winter, due to the northeast monsoon, the climate here becoming with low temperature and high precipitation, moreover the habitat might cover by snow under some extremely weather conditions (Fig. 1). The weather data of 2020 from the nearby Zhuzihu weather station was revealed that the yearly sunshine hour of the area is less than 1,400 hours with more than 4,700 mm precipitation. The highest monthly temperature is 33°C in July, and the lowest one was 1.4°C in December (Fig. 2).

This region around 20 m² is featured by open forests gap with high sunlight exposure, many companion species in the understory layer, including *Ludwigia ovalis*,



Fig. 1 Habitat of *Helminthostachys zeylanica*. A. Overview B. Habitat submerged after heavy rain. C. The snow-covered neighboring region in 2018. (2016, 2018, and 2021 all have snowfall records in Yangmingshan)

圖 1. 錫蘭七指蕨 (*Helminthostachys zeylanica*) 環境概況。A. 林下環境概況 B. 低窪處強降雨後可致積水 C. 2018 年鄰近山區覆雪 (2016、2018、2021 年陽明山區皆有降雪紀錄)。

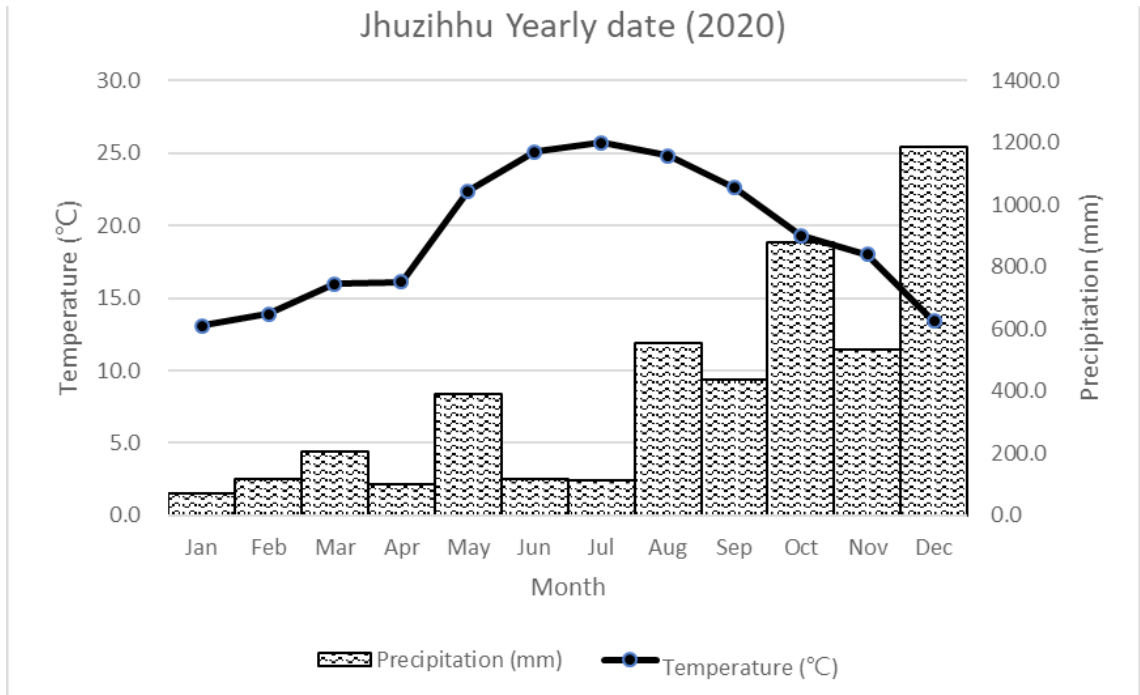


Fig. 2 Climatic data of 2020 from Zhuzihu weather station.

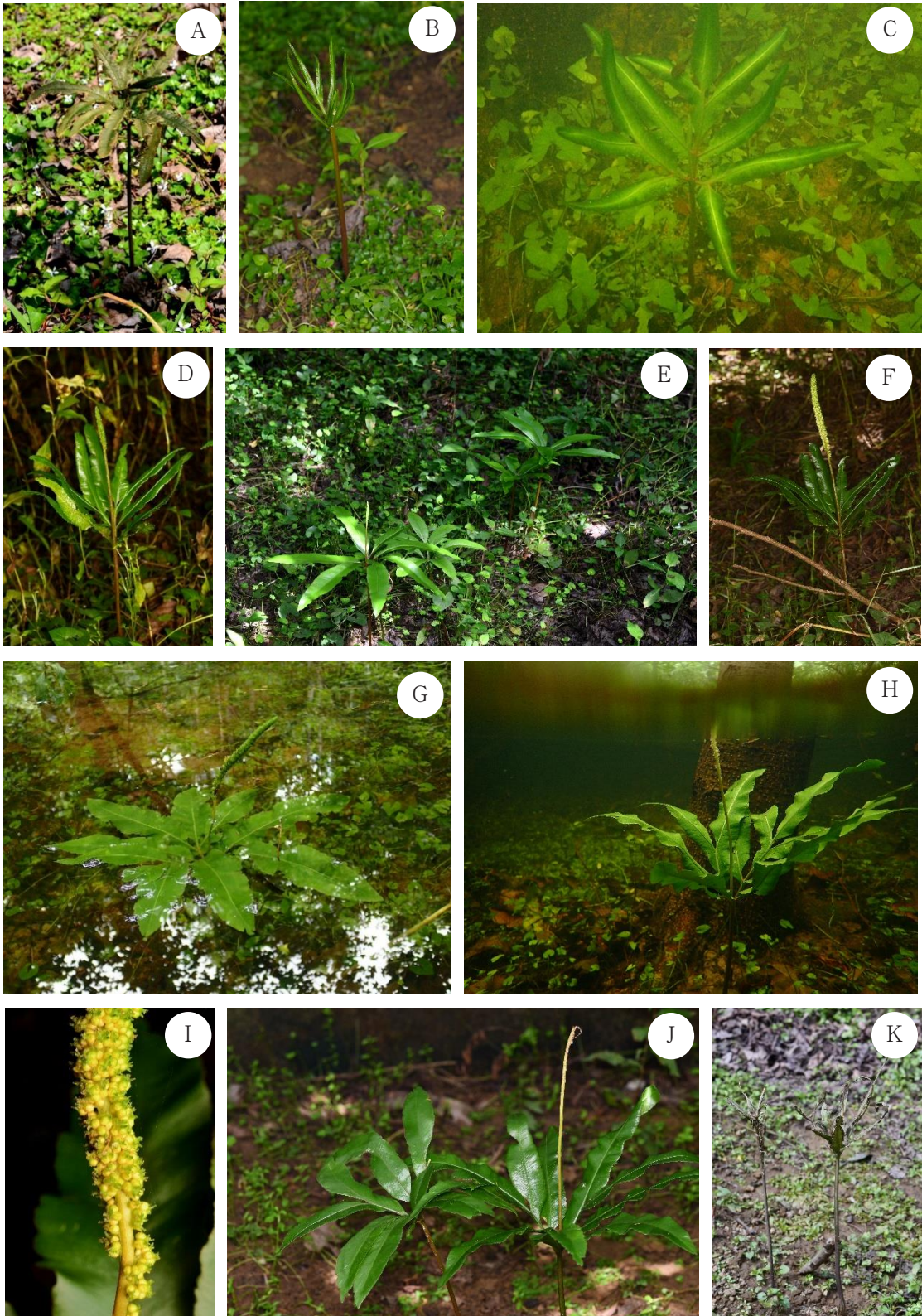
圖 2. 竹子湖氣候站 2020 年度氣象資料。

Ophioglossum petiolatum, *Duchesnea indica*, *Rubus buergeri*, *Persicaria chinensis* var. *chinensis*, *P. pubescens*, *Lobelia chinensis*, *Viola arcuata*, and *V. betonicifolia*, The surrounding canopy layer species, such as *Liquidambar formosana* and *Ardisia sieboldii*, have been identified, with following understory species, e.g., *Pollia Miranda*, *Murdannia keisak*, *Amischotholype glabrata*, and *Paris polyphylla* var. *polyphylla* and some woody species, including *Eleutherococcus trifolius* var. *trifolius*, *Ficus erecta* var. *beecheana*, *Euscaphis japonica*, *Euonymus carnosus*, *Machilus thunbergii*, *Hydrangea angustipetala*, and *Diospyros morrisiana*. The companion species in this region are relatively common in comparison with its adjacent areas, it

can be inferred that the distribution of *H. zeylanica* is not significantly correlated with its companion species. Besides, we also can find some common habitat characteristic between Yangmingshan and Tianchi of Lanyu, both them are known for their temporary wetland environment caused by heavy rainfall. It is noteworthy that such environmental condition can partly inhibit the growth of the understory layer, and thus leading to the dwarf vegetation under forests.

II. Phenology of *H. zeylanica* in northern Taiwan population

This study was conducted in March 2020. We only found a few individuals with leaves in the habitat, we believed that those leaves were persisted from the last winter.



However, as the local climate had become warmer, we detected 13 newly sprout plants on 30th May after heavy precipitation. In the middle of June, the mature plants with fertile spike have been spotted. The fertile spike turned into yellow color and their spores matured in August. The habitat submerged again on 12th August due to the

heavy rain, and spores are likely spreading by water force. Nearly all the fertile spike withered (only an individual remained intact) in September. After then, the habitat had suffered from the disturbance of wild boars, and only 2 of *H. zeylanica* individuals with leaves weathered the winter when we visited again in Feb. 2021 (Fig 3.). According



Fig 4. *Helminthostachys zeylanica* in the summer 2021. A.B. the fertile spike turned into yellow color and then their spores matured 11 July 2020. C.D. the fertile spike dropped from plants on 5 September 2020.

圖 4 錫蘭七指蕨 (*Helminthostachys zeylanica*) 2021 年夏季紀錄。A.B. 7 月 11 日觀測大部分植株孢子囊穗漸趨成熟 C.D. 同 9 月 11 日觀測孢子囊穗脫落後的植株。

to the recorded in 2021, the life cycle starts again. The fertile spike turned into yellow color was spotted on 11th July and dropped from plants on 11th September (Fig 4.).

III. The distribution of *H. zeylanica* in Taiwan

The distribution of *H. zeylanica* in Taiwan is very sporadic and only with few individuals in each locality (Fig. 5), such pattern is probably caused by long-distance dispersal events. Barrington (1993) revealed that pteridophytes are easier carried by other approaches to spread a long distance to other areas due to their small spores. This result is also supported by other recent studies that pointed out the significant effects of long-distance dispersal events on

several fern species (Perrie and Brownsey, 2007; Bauret et al., 2017). However, no robust evidence to prove if the distribution of *H. zeylanica* is associated with the long-distance dispersal events.

IV. The significance of *Ludwigia ovalis* in this area

Among those companion species in these regions, *L. ovalis* is the rarest species, one of rare aquatic plant species in Taiwan. Based on the previous records, it was mainly found in mid-altitude lakes, including Shuanglianpi, Lunpi Lake, Caopi, Mingchi, Yuanyang Lake, and Mysterious Lake. (Yang and Yen, 2001) Moreover, it is important to note that *L. ovalis* has been recognized as a NVU species on the Red List of Vascular

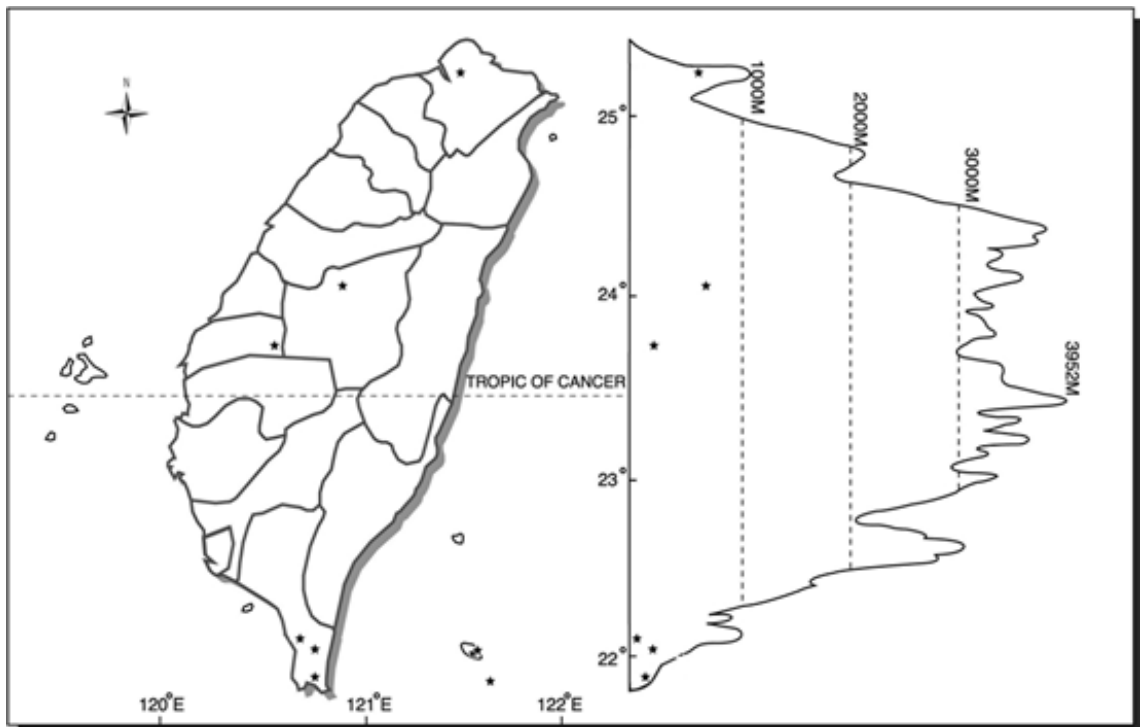


Fig 5. The distribution map of *Helminthostachys zeylanica* in Taiwan.

圖 5. 錫蘭七指蕨 (*Helminthostachys zeylanica*) 分布圖。

Plants of Taiwan (Editorial Committee of the Red List of Taiwan Plants, 2017). The habitat here in northern Taiwan is the only one where both *H. zeylanica* and *L. ovalis* existing together. Therefore, the biodiversity might be underestimated here, and some unknown species might be recorded in the future.

Conclusion

It was widely believed that *H. zeylanica* is a tropical species which was restricted in southern part and Lanyu island. But some northern populations in Yunlin and Nantou County were recently recorded. Moreover, this study further expanded its northernmost boundary in Taiwan to Yangmingshan where did not belong to tropical climate area actually. These findings implied that the distribution of *H. zeylanica* is out of southern Taiwan and remote island. Therefore, it is expected that more populations would be found in other places with similar condition in the future.

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臺灣蕨類植物誌四新增類群

Four new records for the Fern Flora of Taiwan

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Abstract

On account of intensive field and herbaria investigations in Taiwan, new data about the biodiversity and taxonomy of the ferns in Taiwan are proposed. Three native species, *Adiantum roborowskii* var. *faberi* (Baker) Y.X. Lin & J. Prado (Pteridaceae), *Diplazium hachijoense* Nakai (Athryiaceae) and *Polystichum erosum* Ching & K.H.Shing (Dryopteridaceae) and a naturalized species *Cheilanthes viridis* (Forssk.) Sw. (Pteridaceae) are recorded in Taiwan for the first time. We provide the background data of taxonomy, distribution, habitats, photographs, conservation status, and notes for each species.

摘要

經由近年頻繁的野外及標本考察，本文報導臺灣蕨類新資訊，包含三種新紀錄分類群：峨嵋鐵線蕨 (*Adiantum roborowskii* var. *faberi* (Baker) Y.X. Lin & J. Prado)、薄蓋雙蓋蕨 (*Diplazium hachijoense* Nakai) 及蝕蓋耳蕨 (*Polystichum erosum* Ching & K.H.Shing)，以及一新歸化種綠碎米蕨 (*Cheilanthes viridis* (Forssk.) Sw.)。本文亦提供分類、生物地理分布、照片及註記相關資訊。

Key words :Taiwan, Pteridophytes, newly recorded species, naturalized species

關鍵字 : 臺灣、蕨類、新紀錄種、新歸化種

Introduction

Ferns and lycophytes in Taiwan represent an incredibly high diversity which could be due to large extent to warm and wet weather, altitude variation, diverse habitats, and geographical distribution (Moore et al. 2010). Since the latest comprehensive studies (TPG 2019; Hsu et al. 2019a; 2019b), new taxa were continuously reported (Chao et al. 2019; 2021; Hsu et al. 2019c; Lu et al. 2019; Chang et al., 2020; Chang & Hsu 2021; Ebihara et al. 2021; Fan et al. 2021), and currently 816 taxa including natural hybrids and infraspecific taxa has been accepted (TPG 2021).

Apparently, the exact diversity of ferns and lycophytes in Taiwan has not been fully expressed. There are still dozens of taxonomically uncertain materials discovered by researchers and amateurs in recent years, some of which have been introduced as undetermined species (“sp.”) by Knapp (2011, 2013), Knapp and Hsu (2017) and Hsu et al. (2019a; 2019b). After examining floristic documentation and herbarium collections from adjacent georegions, we are now confirming the identity of three native taxa, namely *Adiantum roborowskii* var. *faberi* (Baker) Y.X. Lin & J. Prado (Pteridaceae), *Diplazium hachijoense* Nakai (Athyriaceae) and *Polystichum erosum* Ching & K.H. Shing (Dryopteridaceae). Meanwhile, we recognize a newly naturalized species *Cheilanthes*

viridis (Forssk.) Sw. (Pteridaceae) from northern Taiwan. In this paper, background data of nomenclature, distribution, habitats, taxonomy and conservation status for each species are provided. In addition, their conservation status in Taiwan based on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories and Criteria (IUCN 2017) is evaluated.

Materials and methods

Morphological data of the studied species were mainly gathered from field trips in Taiwan during 2010–2020 and from the specimens preserved in HAST, TAI, TNM and TAIF. The identities of these materials were clarified by consulting related taxonomic literature and also images of related type materials and general collections from the databases of B, BM, K, MO, NY, P, PE and US. We used GeoCAT (Bachman et al. 2011) to help assessing the Extent of Occurrence (EOO) and the Area of Occupancy (AOO) of the discussed species in Taiwan.

Results and discussion

Taxonomic Treatments

Adiantum roborowskii var. *faberi* (Baker) Y.X. Lin & J. Prado, Fl. China 2–3: 249. 2013. [Pteridaceae]. Fig. 1.

≡ *Adiantum faberi* Baker, J. Bot. 26(7): 225. 1888.

≡*Adiantum roborowskii* f. *faberi* (Baker) Y.X. Lin, Fl. Reipubl. Popularis Sin. 3(1): 212. 1990.

Type: CHINA. Sichuan Province: Mt. Omei, 1000m, 1887, *Faber 1033* (syntypes: B 20-0004243 image!, B 20-0004244 image!, MO 1865038 image!, NY 00127467 image!, P 00607858 image!).

Chinensis name: “峨嵋鐵線蕨”, adapted from Lin et al. (2013).

Distribution: This variety was previously recorded from SW China and is newly recorded from Taiwan.

Habitat: Lithophytic, growing in *Abies*–*Tsuga* upper-montane coniferous forest (Li et al. 2013) on stream-side, semi-shaded cliff at ca.2000–2500m elevation in Taiwan.

IUCN Red List Category and Criteria: VU [D1+2]. This species has quite limited EOO (ca. 50 km²), AOO (ca. 10 km²) and mature individuals (< 1000) in central Taiwan estimated from currently available data, though no significant threat has been detected. We hence evaluated it as Vulnerable.

Specimens examined: TAIWAN. Hualien County: Xiulin Township, en route from Ho Huan Chin Kuang to Ping Feng Shan, 2600 m, 5 September 2009, *Huang 4223* (HAST, the central frond only; others are *Adiantum taiwanianum*); Mt. Pingfeng, 2500–2800 m, 25 July 2015, *Hsu 7974* (TAIF); Nantou County: Renai Towbship, Da Yu Ling, 2420 m, 8 November 2014, *Knapp 3537* (P); Pilu Stream, 2000m, 06 April 2006, *Lu 11625* (TAIF); Sung chuan kang, 2450 m, 12 March 2006, *Tsai 01060* (TNM); Sung chuan kang,

2300–2600 m, 14 September 2014, *Hsu 7248* (TAIF); *Hsu 7249* (TAIF); Sung chuan kang, 2400–2500m, 21 June 2020, *Chang ZXC002075* (TAIF). CHINA. Chongqing: Nan chuan District, 800m, 17 March 1995, *Liu 15412* (PE, TAIF). Hubei Province: Li chuan City, 830m, 16 June 2009, *Dong 428* (TAIF).

Note: This taxon has been introduced by Hsu et al. (2019a: pp.231) as “*Adiantum* sp.” with a comprehensive set of images. Among the congeners in Taiwan (TPG 2019), *Adiantum roborowskii* var. *faberi* is closely related to *A. monochlamys* Eaton and *A. taiwanianum* Tagawa in sharing tripinnate fronds and 1 (rarely 2) sori per pinnule. It could be distinguished from *A. taiwanianum* by having larger fronds (20–40 vs. 4–18 cm long) and larger fertile pinnules (5–10 vs. 2–5 mm long) with usually flat (usually strongly revolute) margins and rounded cuneate (vs. cuneate) bases. Meanwhile, it differs from *A. monochlamys* by having orbicular-flabellate (vs. obovate to obtriangular) fertile pinnules with sub entire or shallowly crenate (vs. obtusely to sharply toothed) upper margins.

Cheilanthes viridis (Forssk.) Sw., Syn. Fil. 127. 1806; Schelpe, Fl. Zambesiaca: 133; Crouch et al., Ferns S. Africa: 390, pl. 2011; Yatskievych, Lundellia 23: 22, f. 2. 2020. [Pteridaceae]. Fig. 2.

≡*Pteris viridis* Forssk., Fl. Aegypt.-Arab.: 186. 1775.

≡*Pellaea viridis* (Forssk.) Prantl., Bot. Jahrb. Syst. 3: 420. 1882.

See Roux (2009) for other synonyms.

Type: YEMEM. Montium Hadiensium, *P.*

Forsskål s.n. (lost, according to Roux 2009).

Chinese name: “綠碎米蕨”.

Distribution: *Cheilanthes viridis* is native and widely distributed from South Africa through East Africa toward the Arabian Peninsula and some adjacent islands (Miller 1996; Roux 2009). It also

distributes in Brazil with uncertain origin (Prado et al. 2013) and naturalized in several countries such as USA (Yatskievych 2020), India (Fraser-Jenkins et al. 2017), Sri Lanka (Fraser-Jenkins et al. 2006), Australia (Bostock 1998) and New Zealand (Webb et al. 1995). The record in Taiwan likely

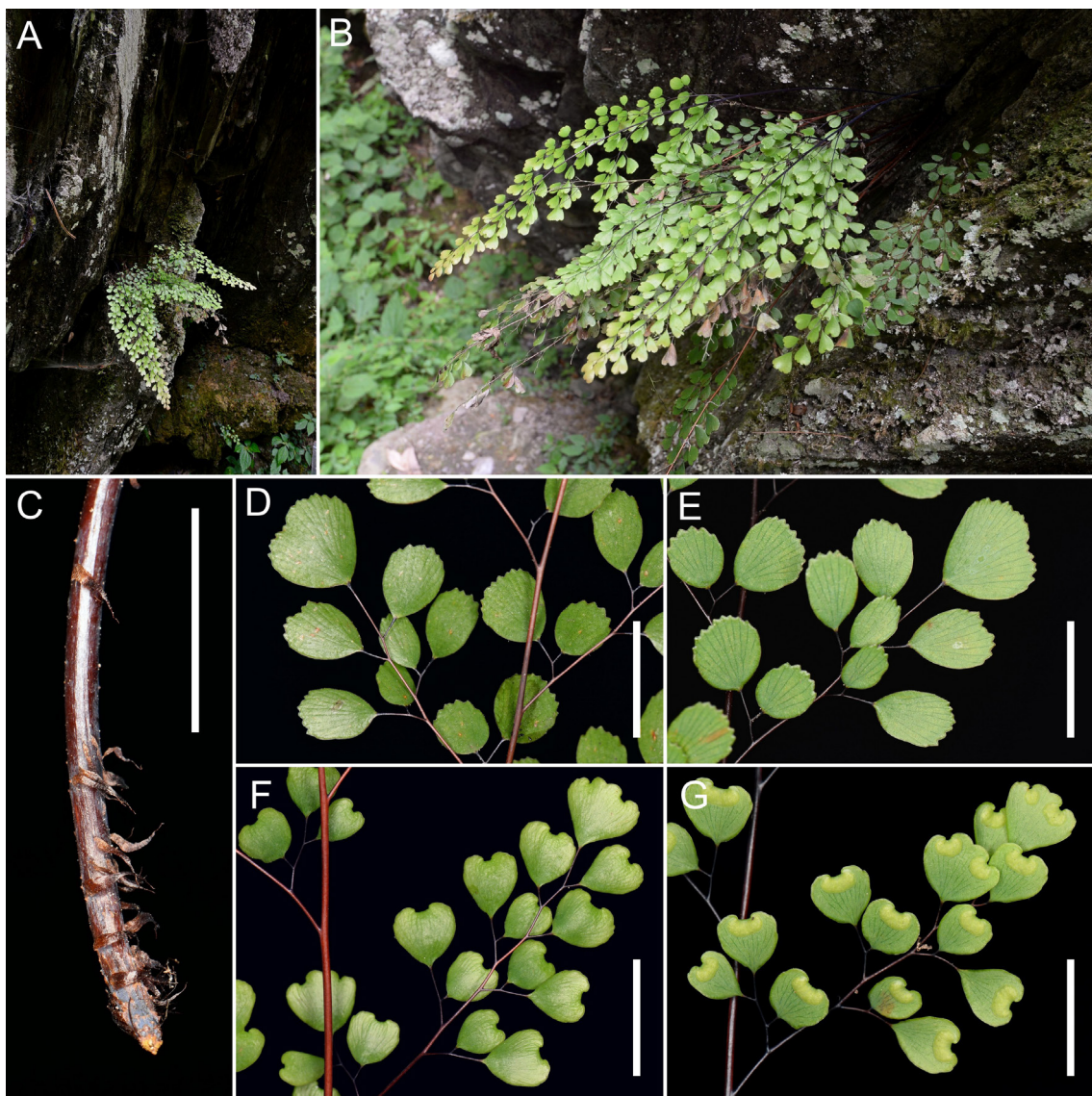


Figure 1. *Adiantum roborowskii* var. *faberi*, from Chang ZXC002075. A–B. Habitat and habits. C. Scales on stipe base. D. Adaxial sterile pinnules. E. Abaxial sterile pinnules. F. Adaxial fertile pinnules. G. Abaxial fertile pinnules. Scale bars = 1 cm.

represents its first record as a naturalized species in East Asia.

Habitat: In Taiwan, *Cheilanthes viridis* is found growing on a semi-shaded roadside stone pitching concrete wall accompanied with *Pilea microphylla* (L.) Liebm. and *Lemmaphyllum microphyllum* C. Presl in the urban area of Tucheng, New Taipei City.

IUCN Red List Category and Criteria: NA. *Cheilanthes viridis* is presumed as a naturalized species in Taiwan.

Additional specimens examined: TAIWAN. New Taipei City: Tucheng District, Tucheng, ca. 20 m, 9 January 2021, *Hsu 13219* (TAIF). INDIA. Tamil Nadu State: Kodaikanal Botanic Garden, 1400 m, 27 November 2006, *Chiou et al. 15214* (TAIF); *Chiou et al. 15239* (TAIF); Tirunelveli, Kothayar Forest, 700–900 m, 28 November 2006, *Chiou et al. 15263* (TAIF).

Note: *Cheilanthes viridis* is readily distinguished from the other species of subfamily Cheilantheoideae (Pteridaceae) in Taiwan (TPG 2019; 2021) by its relatively large (ca. 15–50 × 6–15 cm), 2-pinnate to 3-pinnatifid laminae and ovate-deltoid to ovate-elliptic, sometimes trifid but never pinnatifid segments (Fig. 2). In fact, its gross outline superficially resembles an unrelated native species, *Lindsaea heterophylla* Dryand. (Lindsaeaceae), but could be differentiated by having false indusia that open toward midribs (Fig. 2H–J; *L. heterophylla* has true indusia that open toward margin).

This species is currently only known from a single wild population in northern

Taiwan, but presumably more records will be added in the future considering its potential of naturalization. The population in Taiwan was first photographed and documented by a citizen naturalist Helen Shine on May 2020 in the “Plant Investigation and Phenology Observation” website (<https://plant.tbn.org.tw/>; accessed 8 January 2021), and the images were named by other data contributors as either “genus *Cheilanthes*” or *Lindsaea heterophylla*. Street view images available in Google Map (<https://maps.google.com.tw/>; accessed 8 January 2021) revealed that a few individuals had grown there on August 2019, and a significantly expansion of population size could be observed by comparing our present observation (Fig. 2A) with these earlier images. Although *C. viridis* has long been a horticultural plant in Europe (Walters 1986), it is in fact seldom sold or cultivated in Taiwan (personal observation), and the origin of the naturalized population is thus uncertain.

The systematics within Cheilantheoideae remains unsettled, and so as the generic placement of *Cheilanthes viridis* (Prado et al. 2013; Yatskievych 2020). Here we tentatively follow the latest study (Yatskievych 2020) which placed it under *Cheilanthes*, though this species is genetically distantly related to the other Taiwanese Cheilantheoideae (Schuettpelz et al. 2007; Zhang et al. 2007). Several infraspecific taxa are recognized in its native areas (Crouch et al. 2011), and the naturalized population in Taiwan belongs to var. *viridis* when subdivided.

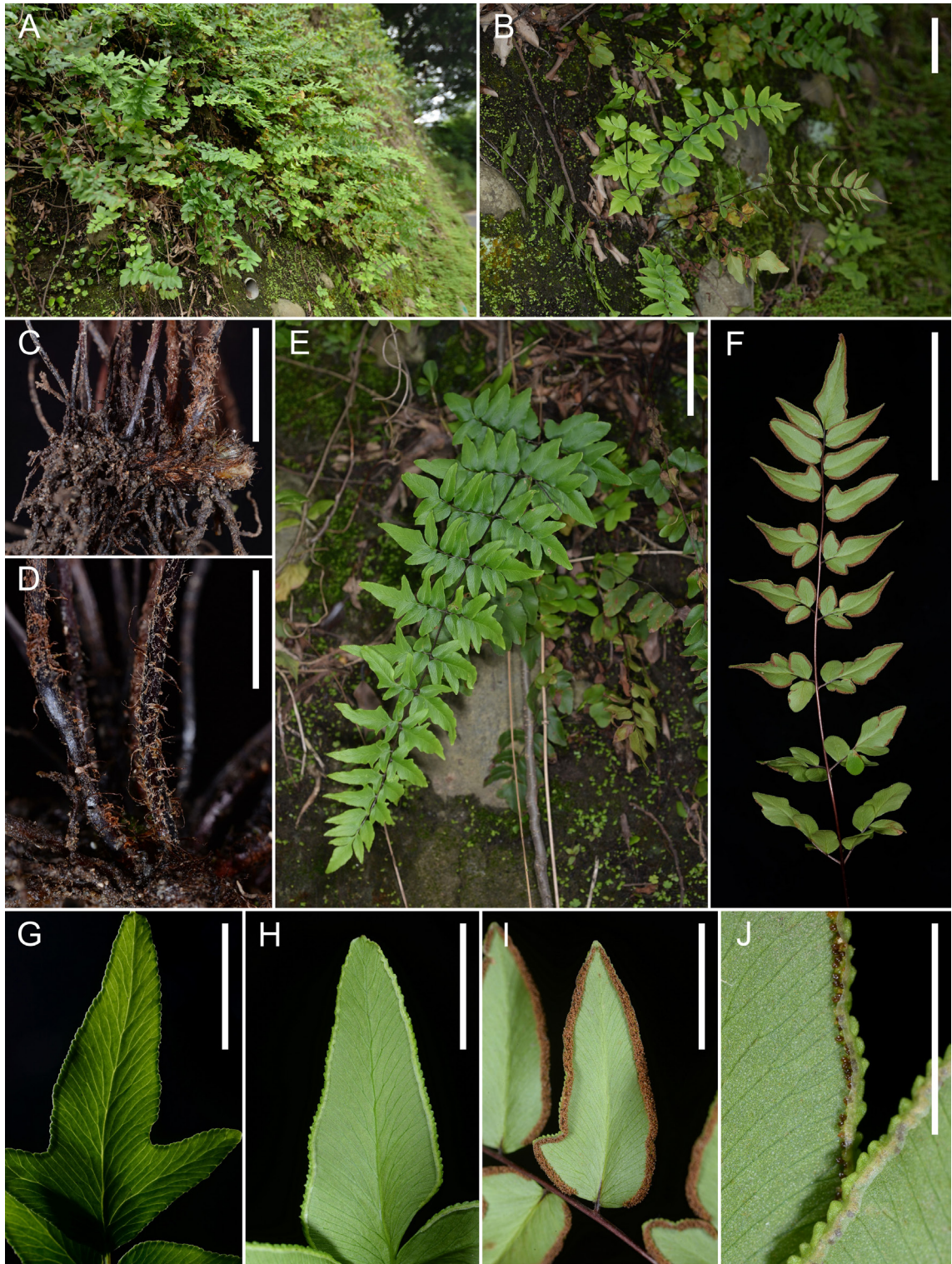


Figure 2. *Cheilanthes viridis*, from Hsu 13219. A–B. Habitat and habits. C. Rhizome. D. Scales on stipe base. E. Adaxial lamina. F. Abaxial lamina. G. Segment with transmitted light, showing venation. H–J. Sori. Scale bars: B, E, F = 5 cm; C, G–I = 1 cm; D, J = 5 mm.

Diplazium hachijoense Nakai, Bot. Mag. (Tokyo) 35(417): 148–149. 1921; Kato, Fl. Japan 1: 227. 1992; Ebihara, Standard Ferns Lycophytes Japan 2: 329, 340, pl. 2-061-6–9. 2017. [Athryiaceae]. Fig. 3.

≡ *Athyrium hachijoense* (Nakai) Ohwi, Bull. Natl. Sci. Mus. 3(2): 100. 1956.

≡ *Allantodia hachijoensis* (Nakai) Ching, Acta Phytotax. Sin. 9(1): 55. 1964.

See Ebihara and Kasetani (2018 onwards) for other synonyms.

Type: JAPAN. Hachijo Island (“insulae Hachijo”), *T. Nakai s.n.* (TI not seen).

Chinese name: “薄蓋雙蓋蕨”, adapted from He and Kato (2013).

Distribution: Korea, Japan, S and SW China and Taiwan

Habitat: Terrestrial, growing in *Pyrenaria-Machilus* winter monsoon forest (Li et al. 2013) under humid shaded forest on mountain slopes at ca. 700–900m in Taiwan.

IUCN Red List Category and Criteria: NT [D1+2]. This species is currently only found in the forests around Mt. Datun in Yangmingshan National Park, where it is locally very abundant and no potential threat is observed. It is hence evaluated as Near Threatened considering the small estimated AOO (ca. 5 km²) and mature individuals (< 2500).

Specimens examined: TAIWAN. New Taipei City: Sanzhi District, Erhtzuping, 850 m, 7 October 2001, *Lu 2037* (TAIF); Erhtzuping, 800m–900m, 23 April 2016, *Hsu 8424* (TAIF). Taipei City: Beitou District,

Palaka Road, 800m–900m, 23 April 2016, *Hsu 8422* (TAIF); Beitou, 850 m, 23 April 2016, *Knapp 4105* (P); 830 m, 23 April 2016, *Knapp 4106* (P); Mt. Datun, 700m, 17 July 2016, *Lu 29608* (TAIF).

Note: This species has been introduced as “*Diplazium* sp. 2” by Hsu et al. (2019b: 91) with a comprehensive set of images. It belongs to a taxonomically and genetically complicated species group with bipinnate to tripinnatifid fronds due to hybridization and polyploidization (Hori and Murakami 2019). Among the morphologically similar species in Taiwan, *D. hachijoense* could be distinguished by having lanceolate, appressed, fugacious scales on stipe base (vs. linear-lanceolate, spreading and ±persistent scales in *D. conterminum*, *D. dilatatum*, *D. okinawaense*, *D. pseudodoederleinii*, *D. taiwanense* and *D. virescens*), sori medial on lateral veins of ultimate segments and spaced from both costulae and segment midribs (vs. sori usually adjacent to costulae in *D. doederleinii* and adjacent to segment midribs in *D. laxifrons*). Preliminary plastid DNA data from Taiwanese materials support that *D. hachijoense* and *D. laxifrons* (= *D. amamianum* recognized by Hori and Murakami 2019) share the same maternal parentage (TPG, unpublished data).

Polystichum erosum Ching & K.H.Shing, Acta. Phytotax. Sin. 10: 303. 1965. Fig. 4

Replaced basionym: *Polystichum lacerum* Christ, Bot. Gaz. 51: 352. 1911. *nom. illeg., non.* (Thunb.) C. Presl, Epimel. Bot. 56. 1851.



Figure 3. *Diplazium hachijoense*, from Hsu 8422. A. Habit. B. Rhizome. C. Scales on stipe base. D. Pinnules. E. Sori. Scale bars: B = 5 cm; C, E = 1 cm; D = 2 cm.

Type: CHINA. Sichuan Province: Baoxing (“Mupin”), August 1908, *E.H. Wilson* 2608 (holotype: BAS; isotypes: BM-001048684 image!, LE, US-00067511 image!, W).

Chinese name: “蝕蓋耳蕨”, adapted from Zhang and Barrington (2013).

Distribution: S and SW China and

Taiwan

Habitat: Lithophytic, growing in *Abies–Tsuga* upper-montane coniferous forest (Li et al. 2013) on stream-side, shaded cliff at ca. 2300–2500m elevation in Taiwan.

IUCN Red List Category and Criteria: VU [D1+2]. *Polystichum erosum* is currently

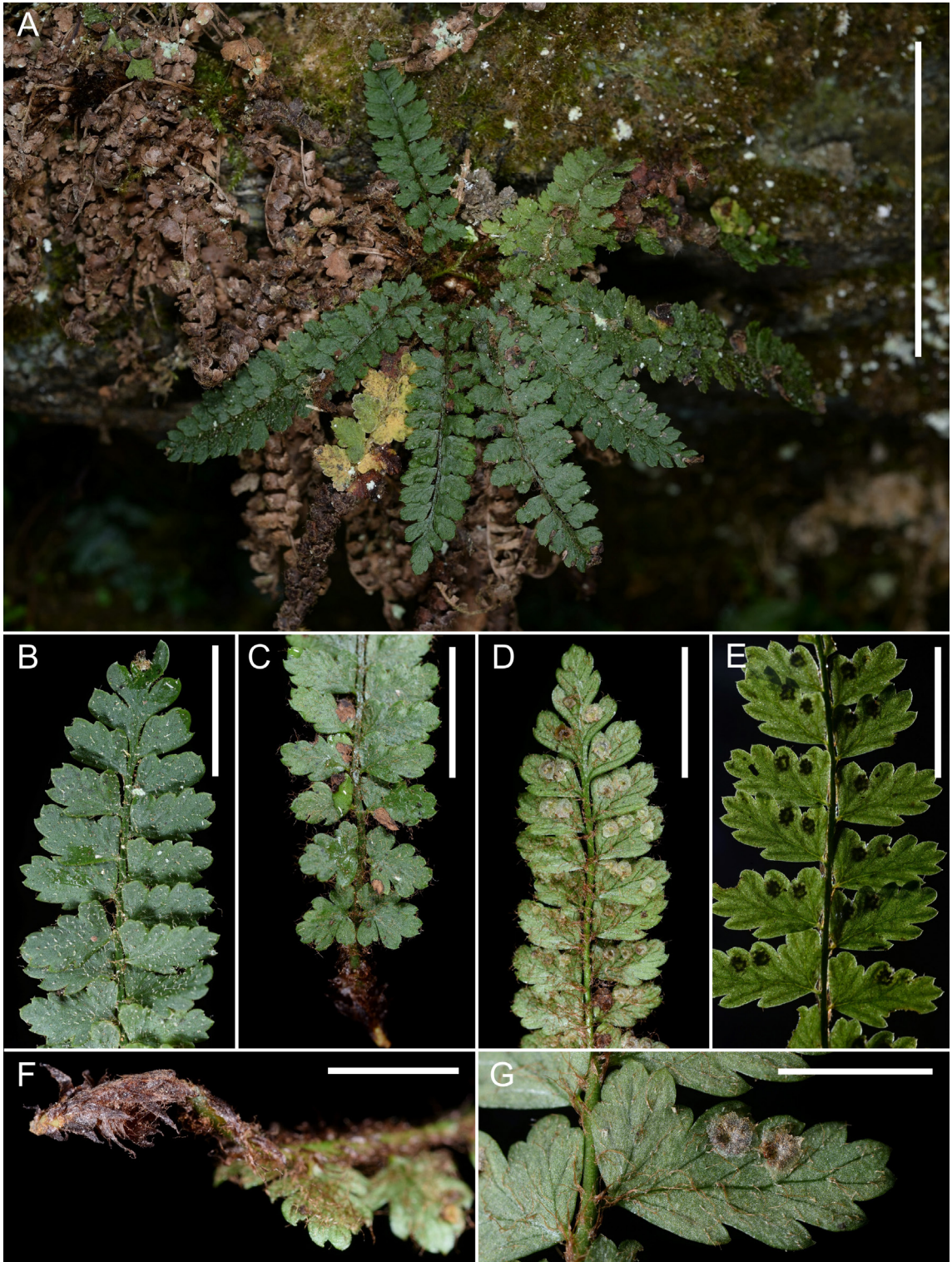


Figure 4. *Polystichum erosum*, from Hsu 11929. A. Habitat. B-C. Adaxial lamina. D. Abaxial lamina. E. Lamina with transmitted light, showing venation. F. Scales on stipe base. G. Abaxial pinna and sori. Scale bars: A = 5 cm; B-E = 1 cm; F-G = 5 mm.

only observed from two locations with totally < 50 mature individuals in central Taiwan. However, we estimate much larger EOO (ca. 100 km²), AOO (ca. 10 km²) and number of mature individuals (< 1000) based on the facts that similar habitats in this region are mostly uninvestigated, and its small, shaded-growing habits are also easily overlooked. Therefore, we evaluate this species as Vulnerable.

Additional specimens examined:

TAIWAN. Taichung City: Heping District, from Hsiangkuliao to Chungyangchien Stream shelter, ca. 2300 m, 20 August 2019, *Hsu 11929*; *Chang ZXC001713* (TAIF); from Chungyangchien Stream shelter to Mt. Chungyangchien, ca. 2450 m, 21 August 2019, *Hsu 11967* (TAIF). CHINA. Sichuan Province: Emeishan City, Mt. Emei, 2200–2400 m, 5 August 2011, *Hsu 4390* (TAIF); same locality, 1700–1800 m, 6 August 2011, *Hsu 4413* (TAIF); Chengdu City, Mt. Xilingxue, 1300–2100 m, 12 August 2011, *Hsu 4468* (TAIF); *Hsu 4469* (TAIF); 2100–2700 m, 13 August 2011, *Hsu 4497* (TAIF).

Note: Among the documented *Polystichum* species in Taiwan (DeVol and Kuo 1975, Shieh et al. 1994, TPG 2019), *P. capillipes* (Baker) Diels and *P. thomsonii* (Hook.f.) Bedd. are morphologically similar to *P. erosum* Ching & K.H.Shing in sharing bipinnatifid, lanceolate frond and basal pinnae with a pair of pinnatisect or free segments. It is easily distinguished by having sparse, linear brown scales on both surface of lamina (vs. covered with clavate brown microscales adaxially in *P. capillipes* and

glabrous in *P. thomsonii*), often bearing 1 proliferous bulbil on rachis apex (vs. 1 proliferous bulbil on junction of basal pinnae and stipe in *P. capillipes* and non-proliferous bulbil in *P. thomsonii*) and only 1–2 pairs of basal pinnae pinnatisect (vs. more than 3 pairs of pinnae pinnatisect with basal auricle segments in *P. capillipes* and *P. thomsonii*).

In Taiwan, *Polystichum erosum* was possibly first collected by Chia-Yu Tsai (蔡佳育) around a branch of Piluchi (畢祿溪) in 2005, but the voucher specimen was lost and only some photos are preserved (Pi-Fong Lu, personal communication on January 2021).

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臺灣靈芝科（多孔菌目）三種新紀錄

Three species of Ganodermataceae (Polyporales) new to Taiwan

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Abstract

Ganodermataceae is a large family of polyporoid fungi, characterized by having double-walled and pigmented basidiospores. In the present study, *Ganoderma gibbosum*, *G. lingzhi* and *Haddowia longipes* are reported as newly recorded from Taiwan. Descriptions, illustrations and photos of these three species are provided.

Key words: Basidiomycota, Ganoderma, Haddowia, taxonomy

摘要

靈芝科 (Ganodermataceae) 是孔狀擔子菌中的一大科，靈芝科獨特之處在於其成員的擔孢子具有雙層壁且有顏色。本研究提出台灣產靈芝科三個新紀錄種：有柄靈芝 (*Ganoderma gibbosum*)、赤芝 (*G. lingzhi*) 和長柄雞冠孢芝 (*Haddowia longipes*)，並提供這些物種的描述、繪圖和照片。

關鍵字：擔子菌門、靈芝屬、雞冠孢芝屬、分類學

Introduction

Ganodermataceae (Donk) Donk is a large family of polyporoid basidiomycetes. Its members are widespread in tropical to temperate regions; and is morphologically characterized by having laccate or non-laccate pileal surface, mostly trimitic hyphal system, and pigmented double-walled basidiospores. In Taiwan, the first report of Ganodermataceae species is *Ganoderma australe* (Fr.) Pat. (Murrill 1909, as *Elfvingia tornata* (Pers.) Murrill), which was collected by a Japanese K. Miyake. Since then, several early records were made by Japanese mycologists. They are *Ganoderma lucidum* (Curtis) P. Karst. (Kanehira 1918a, as *Polyporus lucidus* (Curtis) Fr.), *Ganoderma applanatum* (Pers.) Pat. (Kanehira 1918b, as *Fomes leucophaeus* (Mont.) Cooke), *Ganoderma dimidiatum* (Thunb.) V. Papp (Sawada 1931, as *Ganoderma japonicum* (Fr.) Sawada), *Ganoderma orbiforme* (Fr.) Ryvar den (Sawada 1942, as *Ganoderma fornicatum* (Fr.) Pat.), *Ganoderma tropicum* (Jungh.) Bres. (Sawada 1942), *Sanguinoderma rugosum* (Blume & T. Nees) Y.F. Sun, D.H. Costa & B.K. Cui (Sawada 1942, as *Ganoderma rugosum* (Blume & T. Nees) Pat.) and *Trachyderma tsunodae* (Yasuda ex Lloyd) Imazeki (Sawada 1942, as *Ganoderma tsunodae* (Yasuda ex Lloyd)). Among them, *G. applanatum* and *G. lucidum* were supposed to be misidentified (Yeh and Chen 1990; Moncalvo et al. 1995), and have not been found occurring in Taiwan.

Subsequently new records were added by Taiwanese mycologists, namely *Amauroderma exile* (Berk.) Torrend (Chang et al.

2001), *Ganoderma applanatum* var. *laevisporum* Humphrey & Leus-Palo (Chang 1994), *Ganoderma calidophilum* J.D. Zhao, L.W. Hsu & X.Q. Zhang (Chou and Chang, 2005), *Ganoderma flexipes* Pat. (Wang and Wu 2007), *Ganoderma multiplicatum* (Mont.) Pat. (Wang and Wu 2007), *G. orbiforme* (Chang 1992, as *Ganoderma boninense* Pat.; Chang 1992 as *Ganoderma limushanense* J.D. Zhao & X.Q. Zhang; Wu and Zhang 2003, as *Ganoderma densizonatum* J.D. Zhao & X.Q. Zhang), *Ganoderma rotundatum* J.D. Zhao, L.W. Hsu & X.Q. Zhang (Wu and Zhang 2003), *Magoderma subresinosum* (Murrill) Steyaert (Chang 1996) and *Tomophagus colossus* (Fr.) Murrill (Wu and Zhang 2003).

Four new species have been proposed by domestic mycologists. There were *Ganoderma multipileum* Ding Hou (Hou 1950), which was collected from the lowlands in Taichung, *Ganoderma formosanum* T.T. Chang & T. Chen (Chang and Chen 1984), which was synonymized under *Ganoderma sinense* J.D. Zhao, L.W. Hsu & X.Q. Zhang (Moncalvo et al. 1995; Moncalvo and Ryvar den 1997), and *Ganoderma microsporum* R.S. Hseu (Hseu et al. 1989), which was synonymized under *Ganoderma weberianum* (Bres. & Henn. ex Sacc.) Steyaert (Wang 2005; Wang et al. 2005), and *Ganoderma bambusicola* Sheng H. Wu, C.L. Chern & T. Hatt., which was misidentified as *Ganoderma neojaponicum* Imazeki from Taiwan for thirty years (Hseu 1990). Totally there have been 18 species of Ganodermataceae species known in Taiwan.

In the present study, we report three

new records of Ganodermataceae from Taiwan: *Ganoderma gibbosum*, *Ganoderma lingzhi* and *Haddowia longipes*, which were collected during 2015-2020.

Materials and methods

Morphological studies

All studied specimens are deposited at the herbarium of National Museum of Natural Science (TNM). Descriptions and illustrations are based on dried specimens. Freehand thin sections are mounted in 5% KOH for observations and measurements. Melzer's reagent (IKI) are applied to detect amyloidity and dextrinoidity.

DNA extraction, PCR and sequencing

Dried specimens were prepared for DNA extraction using the Plant Genomic DNA Extraction Miniprep System (Viogene Biotek corporation, New Taipei City, Taiwan), following the manufacturer's protocol. Primer pairs ITS1/ITS4 were used to amplify ITS regions (White et al. 1990). PCR products were purified and sequenced by MB Mission Biotech company (Taipei City, Taiwan). BioEdit v7.2.5 was used to assemble new sequences (Hall 1999). Finally, the newly generated sequences were submitted to GenBank.

Phylogenetic analyses

The dataset of ITS sequences was used to construct the phylogenetic tree. MAFFT v.7. was used to align the sequences. Phylogenetic analyses were carried out for the dataset based on maximum likelihood (ML), using RaxML Black Box (Stamatakis 2014) at the CIPRES Science Gateway. The statistical

supports were shown above branches of ML tree when bootstrap values (BS) ≥ 70 .

The ITS ML tree (Fig. 1) consisted of 26 species and 39 sequences. Twenty-four species from ingroups; two species from outgroups (*Perenniporiella chaquenia* Robledo & Decock and *P. pendula* Decock & Ryvarde), Ingroups contain the members of 8 genera of the Ganodermataceae: *Amauroderma* Murrill, *Ganoderma* P. Karst., *Haddowia* Steyaert, *Humphreya* Steyaert, *Magoderma* Steyaert, *Sanguinoderma* Y.F. Sun, D.H. Costa & B.K. Cui, *Tomophagus* Murrill and *Trachyderma* (Imazeki) Imazeki.

Results

Phylogeny

The final alignment of 39 sequences had 684 sites including gaps, of which 129 sites were parsimony informative. Our new generated *Ganoderma gibbosum* strains (MW887921, MW887922, MW887927, MW888212 and MW888213), *G. lingzhi* (MW888214, MW888223, MW888224 and MW888225) and *Haddowia longiceps* (MW888226) were clustered with *G. gibbosum* strains [AY593856 (Wang and Yao 2005) and KY364271 (Jargalmaa et al. 2017)] *G. lingzhi* holotype strain (JQ781858) and *H. longiceps* strain [MK345423 (Hapuarachchi et al. 2019)], respectively, and with strong support values (BS = 100%). Therefore, phylogenetical analysis supports identification of these three species.

Taxonomy

Ganoderma gibbosum (Blume & T. Nees) Pat., Annales du Jardin Botanique de Buiten-

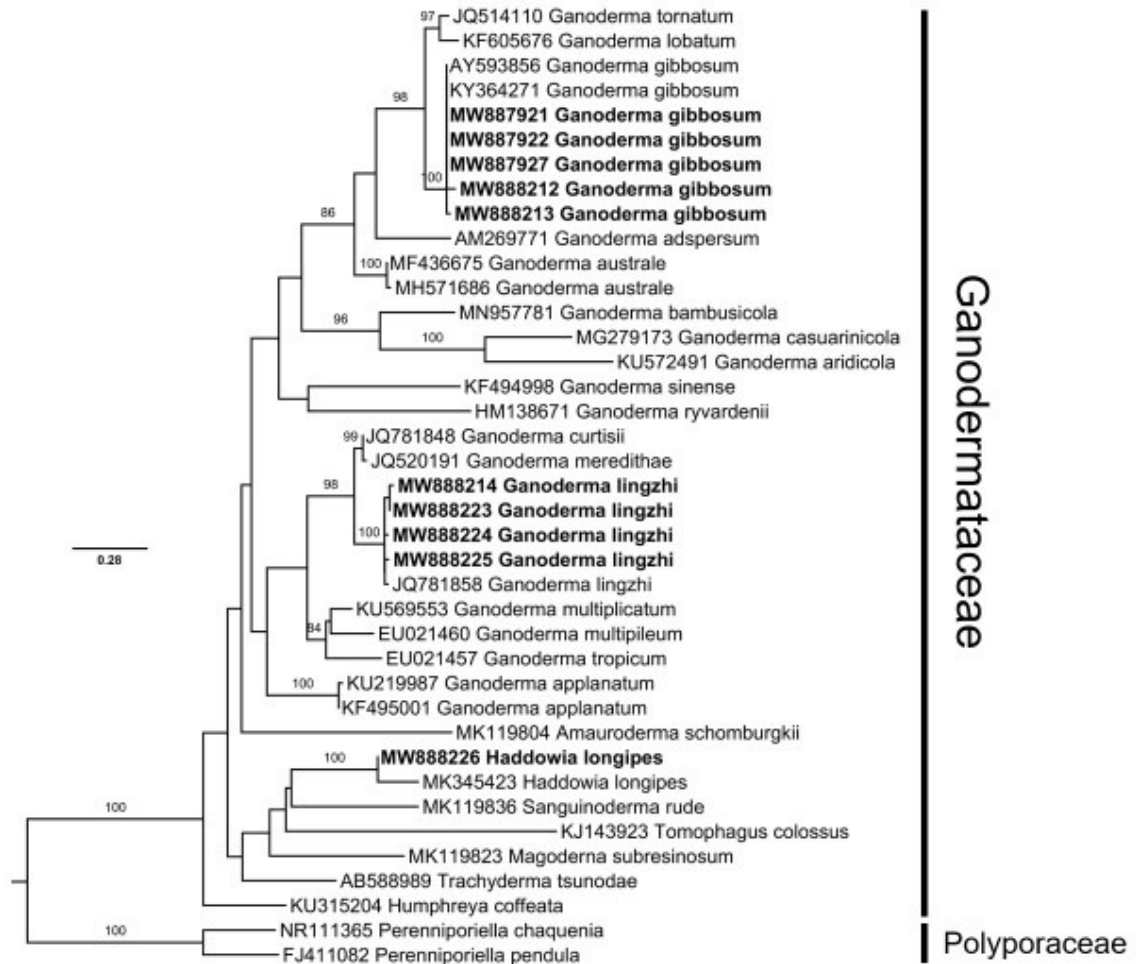


Fig. 1. The phylogram of Ganodermataceae inferred from ML analysis using the ITS dataset. The result presented the position of the three newly recorded species (shown in bold).

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Fig. 2A and Fig. 3

Description. Basidiomata perennial, solitary or scattered. Pileus semicircular, applanate, projecting 3.5–9.5 cm, 6–16 cm broad and 2–6.5 cm thick, sessile or laterally substipitate, woody hard. Pileal surface non-laccate, light brown to brown, with concentric sulci, sometimes irregularly swollen. Pore surface cream to light yellowish, brownish in old specimens; pores circular, 4–5 per mm,

120–160 μm diam, dissepiments entire, 60–100 μm diam. Context layer dark brown, 1–3 cm thick. Tube layer concolorous or slightly paler than context layer, 2–4 cm thick. Hyphal system trimitic. Pileipellis of a cutis, 0.4–1.4 mm thick, blackish brown, anamixoderm, composed of compacted interwoven skeleto-binding hyphae, terminal branched, main stems brownish to brown 4–5 μm diam, walls subsolid, lateral branches brownish to subcolorless, 1–2.5 μm diam,



Fig. 2. Photos of basidiomata in situ. A. *Ganoderma gibbosum*. B. *Ganoderma lingzhi*. C. *Haddowia longipes*.

walls subsolid. Context mainly composed of skeleto-binding hyphae, fairly straight, usually over 300 μm long, terminal branched, main stems brownish to brown, 3.5–6 μm diam, walls subsolid, lateral branches yellowish brown, 2–3 μm diam, walls subsolid; generative hyphae not observed. Tube mainly composed of binding hyphae, richly branched, main stems brownish to brown, 3–4.5 μm diam, with 0.8–1.5 thick walls or subsolid, lateral branches brownish to subcolorless, 1–2 μm diam, walls or subsolid; generative hyphae with clamp connections, 2–2.5 μm diam, thin-walled. Basidia not observed. Basidiospores double-walled, ellipsoid to narrowly ellipsoid, exospore smooth and colorless, endospore echinulate and brownish, IKI —, CB —, 8.2–11 \times 5.2–7

μm (with myxosporium), 7–9 \times 4.8–5.8 μm (without outer myxosporium).

Specimen examined. TAIWAN. Nantou County, Jenai Township, Aowanda National Forest Recreation Area, 121°11'E, 23°57'N, alt. 1250 m, on fallen angiosperm trunk, 3 Oct 2016, C.-C. Chen & C.-L. Wei, WEI 16-460 (TNM F31102, GenBank MW888213); 121°10'E, 23°57'N, alt. 1200 m, on fallen angiosperm trunk, 28 Aug 2017, C.-C. Chen, GC 1708-345 (TNM F33086, GenBank MW887927); Wulingshan Trail, 121°10'E, 24°01'E, alt. 1170 m, on fallen angiosperm trunk, 2 Mar 2020, C.-L. Wei, WEI 20-020 (TNM F34691, GenBank MW887921); Y.-C. Lin, L-2003-04 (TNM F34692); New Taipei City, Chinshan District, Shihtoushan Park, 121°38' E, 25°13' N, alt. 12 m, on liv-

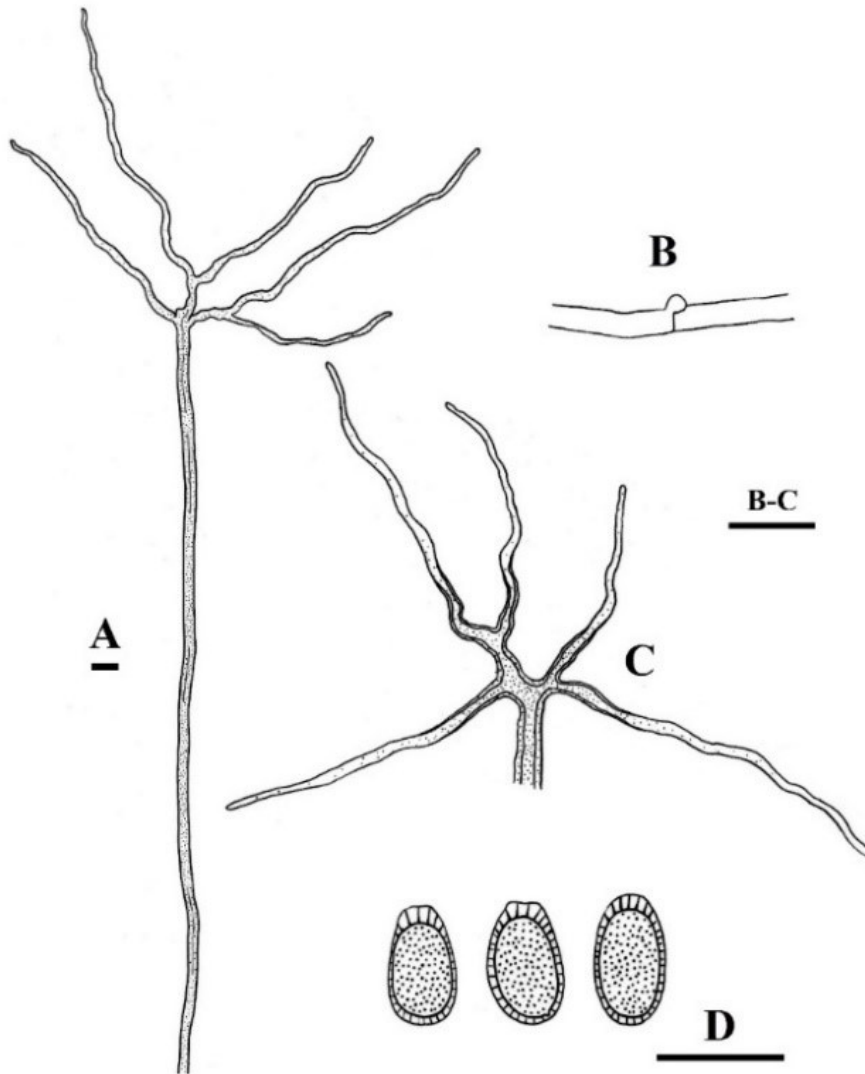


Fig. 3. Micromorphological of *Ganoderma gibbosum*. A. Skeletal-binding hyphae from context. B. Generative hyphae from tube. C. Binding hyphae from tube. D. Basidiospores. Bars = 10 μ m.

ing trunk base of *Casuarina equisetifolia*, 26 Aug 2015, C.-C. Chen, C.-L. Wei, W.-C. Chen & S. Lim, GC 1508-86 (TNM F33086); Taichung City, Hoping District, Henglingshan Trail, 120°55'E, 24°14'N, alt. 990 m, on standing angiosperm trunk, 8 Aug 2017, C.-L. Wei & Y.-L. Huang, WEI 17-602 (TNM F32608); WEI 17-603 (TNM F32609, GenBank MW888212); Taiwan Endemic Species

Research Institute, Low Altitude Experimental Station, 120°57'E, 24°16'N, alt. 1000 m, on standing angiosperm trunk, 7 Aug 2017, C.-L. Wei & Y.-L. Huang, WEI 17-568 (TNM F32583, GenBank MW887922).

Habitat. On dead angiosperm trunks.

Distribution. China, Laos, Myanmar, Thailand and Vietnam (Hapuarachchi et al. 2019; Parmasto 1986; Zhao et al. 1983), and Tai-

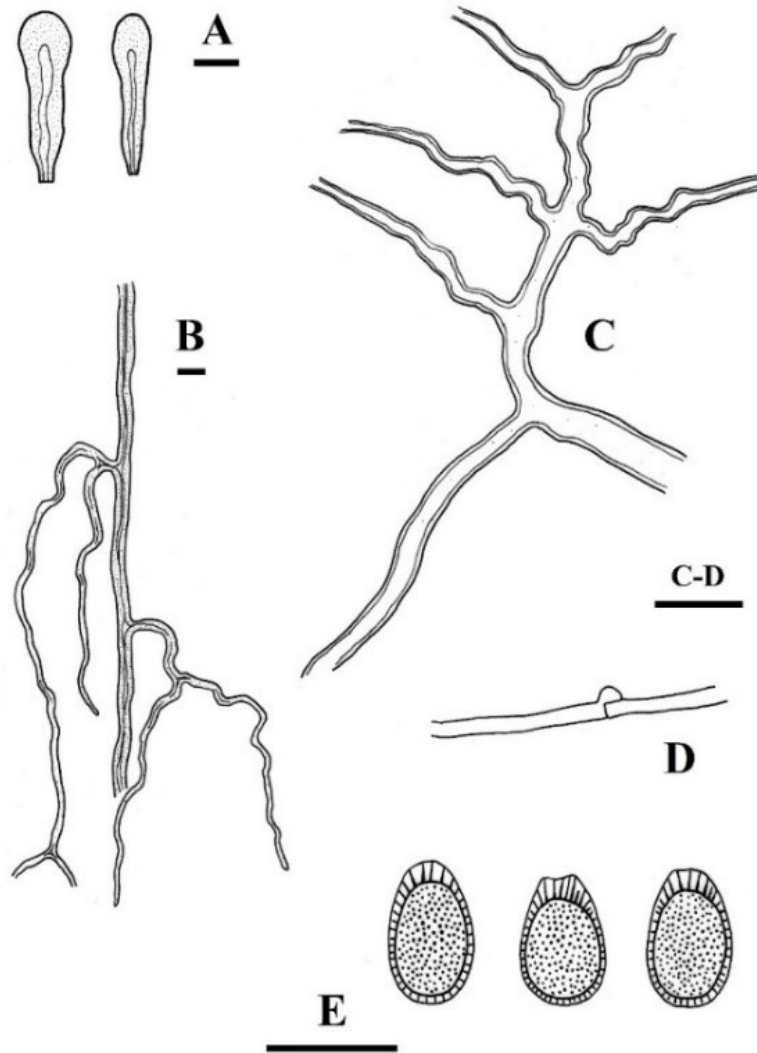


Fig. 4. Micromorphological of *Ganoderma lingzhi*. A. Pileipellis. B. Skeletal-binding hyphae from context. C. Binding hyphae from tube. D. Generative hyphae from tube. E. Basidiospores. Bars = 10 μ m.

wan (this study).

Notes. *Ganoderma gibbosum* is characterized by sessile to laterally substipitate basidiomata, non-laccate pileal surface, pores 4–5 per mm, context skeleto-binding hyphae with terminal branched and ellipsoid to narrowly ellipsoid basidiospore. *Ganoderma australe* (Fr.) Pat. is similar in having

non-laccate pileal surface and same pores size. However, it differs from *G. gibbosum* in having consistently sessile basidiocarps and slightly smaller basidiospores [5.3–7.9 \times 3.4–5.1 μ m (without outer myxosporium) (Hapuarachchi et al. 2019)] Taiwanese collection fits description of Luangharn et al. (2020) in all aspects.

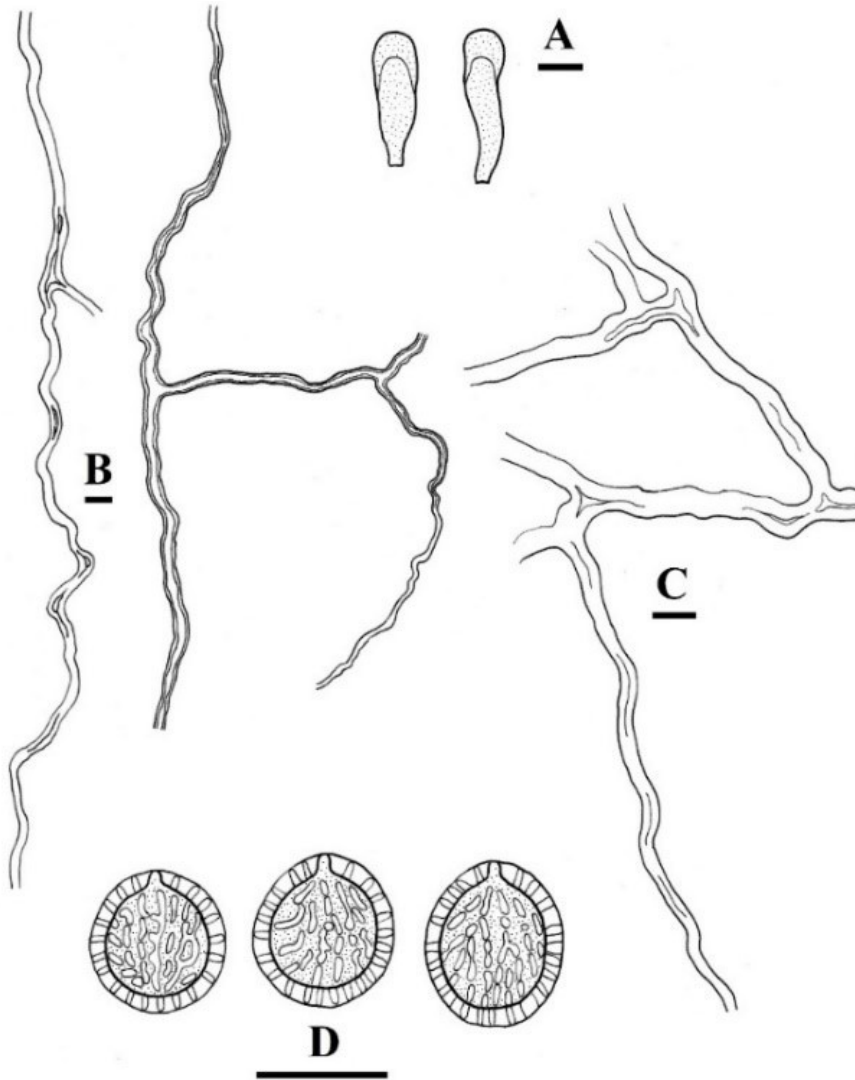


Fig. 5. Micromorphological of *Haddowia longipes*. A. Pileipellis. B. Skeletal-binding hyphae from context. C. Binding hyphae from tube. D. Basidiospores. Bars = 10 μ m.

Ganoderma lingzhi Sheng H. Wu, Y. Cao & Y.C. Dai, Fungal Diversity 56 (1): 54 (2012) Fig. 2B and Fig. 4

Description. Basidiomata annual, solitary or scattered, stipitate. Pileus reniform, semi-circular to flabelliform, projecting 4–7 cm, 5–12 cm broad and 1.5–2.5 cm thick, hard corky to corky. Stipe lateral, subcylindrical, laccate, dark reddish brown to dark purplish

brown, up to 27 cm long and 1.5–3 cm thick. Pileal surface laccate, orange brown, reddish brown to dark reddish brown. Pore surface cream to yellow, yellowish brownish in old specimens; pores circular, 5–6 per mm, 100–180 μ m diam, dissepiments entire, 50–100 μ m diam. Context layer rather homogeneous, buff to brownish, about 0.5 cm thick. Tube layer concolorous with context layer,

up to 2 cm thick. Hyphal system trimitic. Pil-eipellis of a cutis, hymeniderm, composed of clavate hyphal elements, brown, 30–50 × 8–10 μm, with narrow lumens, more or less amyloid. Context mainly composed of skeleto-binding hyphae, intercalary, main stems brownish to brown, 4–6 μm diam, with 1–2 μm thick walls or subsolid, lateral branches brownish, 1.5–3 μm diam, walls subsolid; generative hyphae rarely, 2.5–3 μm diam, thin-walled. Tube mainly composed of binding hyphae, richly branched, main stems subcolorless, 4–6 μm diam, with 0.5–1 μm thick walls, lateral branches colorless, 1.5–3 μm diam, with 0.5 μm thick walls; generative hyphae with clamp connections, 2–3 μm diam, thin-walled. Basidia not observed. Basidiospores double-walled, ellipsoid to ovoid, exospore smooth and colorless, endospore echinulate and brownish, IKI —, CB —, 9.5–11.5 × 6.2–7.2 μm (with myxosporium), 7.5–9 × 5.5–6.5 μm (without outer myxosporium).

Specimen examined. TAIWAN. Nantou County, Jenai Township, Aowanda National Forest Recreation Area, 121°10'E, 23°57'N, alt. 1200 m, on the ground, 12 Aug 2015, C.–C. Chen, *GC 1508-3* (TNM F29033); 8 Sep 2016, K.-Y. Lin, *GC 1609-38* (TNM F31387); *GC 1609-39* (TNM F31388); 27 Sep 2016, N.A., *GC 1609-47* (TNM F31394); *GC 1609-48* (TNM F31395); 28 Aug 2017, C.–C. Chen, *GC 1708-346* (TNM F33087); 12 Sep 2018, C.–C. Chen & C.–C. Chang, *GC 1809-43* (TNM F33756, GenBank MW888225); 14 Jun 2020, C.–C. Chen, *GC 2006-1* (TNM F34693); 121°11'E, 23°57'N, alt. 1250 m, on

the ground, 3 Oct 2016, C.–C. Chen & C.–L. Wei, *WEI 16-418* (TNM F31078); 21 Aug 2017, C.–C. Chen & C.–L. Wei, *WEI 17-606* (TNM F34297); *WEI 17-607* (TNM F32614); 28 Aug 2017, S.–H. Wu, *Wu 1708-309* (TNM F31664), *Wu 1708-313* (TNM F31668), *Wu 1708-314* (TNM F31669), *Wu 1708-315* (TNM F31670); 28 Apr 2018, C.–L. Wei, *WEI 18-017* (TNM F33181); 12 Sep 2018, C.–L. Wei, *WEI 18-403* (TNM F34461); *WEI 18-409* (TNM F34224); Yuchih Township, Lienhuachih, 120°53'E, 23°56'N, alt. 700 m, on the ground, 30 Aug 2006, S.–Z. Chen, *Chen 1562*, (TNM F25901); on rotten trunk base, 2 Jun 2018, S.–Z. Chen, *Chen 3968* (TNM F34511, GenBank MW888224); on the ground, *Chen 3969* (TNM F34512); *Chen 3970* (TNM F 34513); Taichung City, Hoping District, 3.5 km of Tungmaoshan Trail, 120°57'E, 24°11'N, alt. 1200 m, on standing dead trunk, 27 May 2018, C.–L. Wei & C.–P. Huang, *WEI 18-127* (TNM F33559, GenBank MW888214); Hsinshue District, Takeng Walking Road No. 4, 120°48'E, 24°11'N, alt. 780 m, on the ground, 10 Jun 2018, C.–L. Wei & C.–P. Huang, *WEI 18-378* (TNM F34444, GenBank MW888223).

Habitat. Usually on the ground near angiosperm tree, rarely on trunk.

Distribution. China, Japan and Korea (Cao et al. 2012), and Taiwan (this study).

Notes. *Ganoderma lingzhi* is a famous medicinal fungus in China for more than two thousand years (Cao et al. 2012). It is characterized by having laccate pileus, yellow pore surface, skeleto-binding hyphae with intercalary branch and ellipsoid to ovoid

basidiospore. *Ganoderma lucidum* (Curtis) P. Karst. shares similar pileal surface and basidiospores sized with *G. lingzhi*. However, it differs from *G. lingzhi* in having white pore surface and longer cuticle cells (47–70 μm). Besides, Moncalvo et al. (1995) indicated that *G. lucidum* have not been distributed in Taiwan, here we follow their opinions. In Taiwan, *G. lingzhi* occurs at the elevation of 700–1200 meters, usually grow under trees of Fagaceae spp. This observation corresponds with Cao et al. (2012). Morphological features of Taiwanese collections fit description of Cao et al. (2012) for this species.

Haddowia longipes (Lév.) Steyaert, Persoonia 7 (1): 109 (1972) Fig. 2C and Fig. 5

Description. Basidiomata annual, solitary, stipitate, light in weight. Pileus reniform, projecting 4 cm, 4.5 cm broad and about 1.2 cm thick, soft corky. Stipe eccentric, cylindrical, laccate, black, 12 cm long and about 0.7 cm thick. Pileal surface weakly laccate, orange brown, with concentric shallow sulci. Pore surface cream; pores subcircular to subangular, 1.5–2.5 per mm, 300–500 μm diam, dissepiments entire, 100–140 μm diam. Context layer buff, 0.2–0.3 cm thick. Tube layer concolorous with context layer, 0.7–0.9 cm thick. Hyphal system trimitic. Pileipellis of a cutis, hymeniderm, composed of clavate hyphal elements, yellowish brown, 25–35 \times 9–11 μm , with wide lumens, swollen in KOH. Context mainly composed of skeleto-binding hyphae, intercalary, main stems colorless, 3.5–6 μm diam, with 1–1.5 μm thick walls or subsolid, lateral branches

colorless, 1.5–3 μm diam, walls up to 1 μm thick or subsolid; generative hyphae not observed. Tube mainly composed of binding hyphae, richly branched, main stems colorless, 3–5 μm diam, walls up to 1.5 μm thick or subsolid, lateral branches colorless, 1.5–3 μm diam, walls up to 1 μm thick; generative hyphae 3–4 μm diam, thin-walled. Basidia not observed. Basidiospores broadly ellipsoid to subglobose, double-walled, exospore with longitudinal ridges partly connected with short transverse walls, colorless, endospore smooth, brownish, IKI —, CB —, 10–13 \times 9–11.5 μm (with myxosporium), 9–11 \times 8.5–9.5 μm (without outer myxosporium).

Specimen examined. TAIWAN. Pingtung County, Mudan Township, Shimen Village, 120°45'E, 22°09'N, alt. 240 m, on the ground near *Melia azedarach*, 11 Nov 2020, S.-H. Wu, S.-Z. Chen & C.-L. Wei, Wu 2011–62 (TNM F34694, GenBank MW888226).

Habitat. On the ground near angiosperm tree.

Distribution. Africa—Angola and Kenya, Asia—China, India, Laos and Philippines, South America—Brazil, Costa Rica and French Guiana (Corner 1983; Hapuarachchi et al. 2019; Ryvarden and Johansen 1980; Zhao 1989; Zhao and Zhang 2000) and Taiwan (this study).

Notes. *Haddowia longipes* was initially collected from South America (French Guiana) and subsequently reported to widespread in other tropical regions (Zhao and Zhang 2000). This species is characterized by having weakly to strongly laccate pileus, large pores (1.5–2.5 per mm), skeleto-binding

hyphae with intercalary branch and broadly ellipsoid to subglobose basidiospores with crest-like ornamentations. Taiwanese collection fits description of Ryvarden and Johansen (1980) in all aspects, except for the slightly smaller basidiospores, i.e., 10–13 × 9–11.5 μm (with myxosporium) in this study vs. 12–17 × 10–14 μm (with myxosporium) in Ryvarden and Johansen (1980). The ITS sequence derived from *Wu 2011-62* (GenBank MW888226) has a 99% similarity with the strain *LPDR17072709*, (GenBank MK345423 (Hapuarachchi et al. 2019) of this species.

Acknowledgments

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不同光量下小扭口苔氣體交換與葉綠素 螢光之研究

Study on the Gas Exchange Quantitative and Chlorophyll Fluorescence of *Barbula indica* under Different Irradiations

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摘要

本研究量測小扭口苔 (*Barbula indica* (Hook.) Spreng.) 於不同光量梯度下之氣體交換及葉綠素螢光參數，發現小扭口苔因不具有氣孔構造，呈現蒸散速率與光合作用速率無論處於何種光量下，蒸散速率皆維持固定速率 (約 $21 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$)。同時具有較高的光飽和點 (light saturation point, LSP at $800\text{-}1,200 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$) 及光補償點 (light compensation point, LCP at $68.19 \pm 12.36 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$)，以及較低的暗呼吸速率 (dark respiration rate, Rd at $3.31 \pm 0.48 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)，這或許其為廣布型的原因之一。在光化學效能 (electron transport rate, ETR) 方面，ETR 與光合速率 (net photosynthesis rate, Pn) 呈現顯著相關 ($P < 0.0001$)，且高光下 ($1,200\text{-}2,000 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$)，非光化學消散 (non-photochemical quenching, NPQ) 能量比例佔全部能量之 80%，顯示小扭口苔的光合系統已具

有相當功能性的非光化學消散機制，藉由葉綠素螢光量測的技術，具方便、快速及非破壞性等優點，可藉此監測苔蘚植物生態生理的狀態，有助了解光合系統的演進，並開發新的應用於這類廣泛存在的苔蘚植物。

關鍵字：苔蘚、氣體交換、光合作用、葉綠素螢光、非光化學消散

Abstract

The gas exchange and chlorophyll fluorescence parameters of *Barbula indica* (Hook.) Spreng. were measured under different irradiation gradients. The results show that *B. indica* is lack of stomatal structure, and regardless of the amount of irradiation, the evapotranspiration rate maintained a constant rate around $21 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$. *B. indica* had a higher light saturation point at $800\text{-}1,200 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$ and a light compensation point at $68.19 \pm 12.36 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$, and low dark respiration rate at $3.31 \pm 0.48 \text{ } \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. This may be one of the reasons for the widespread type. In terms of photochemical efficiency, ETR of *B. indica* was significantly correlated with photosynthetic rate ($P < 0.0001$). Under high light at $1,200\text{-}2,000 \text{ } \mu\text{mol photon m}^{-2} \text{ s}^{-1}$, the proportion of non-photochemical quenching energy accounted for 80% of the total energy, indicating that the photosynthetic system of *B. indica* was capable with the functional non-photochemical quenching mechanism. The chlorophyll fluorescence measurement technology has not only the advantages of convenience, speed, and non-destructiveness which can monitor the ecological and physiological state of moss, but also will help understand the evolution of the photosynthetic system and develop new applications for such widespread moss.

Key words: moss, gas exchange, photosynthesis, chlorophyll fluorescence, non-photochemical quenching

前言

生物土殼 (biological soil crusts, BSCs) 是指地衣 - 苔蘚植物微生物群落，分布相當廣泛，在某些地區甚至占生物覆蓋的 70% (Belnap & Lange, 2001)，其散布在土壤表層最上層土壤中複雜的土壤顆粒和生物體，主要由細菌、真菌、藻類、地衣、地草和苔蘚組成 (Eldridge & Greene, 1994; Evans & Johansen, 1999; Belnap & Lange, 2001)。BSCs 可以促進後期演替物種的建立，是世界眾多陸地生態系統恢復的必要組成部分 (Bowker, 2007)，BSCs 和其他孢子植物往往被忽視，因為它們是屬於演替早期的物種，生物量較低，任何影響都可以被認為是次要的。然而，BSCs 在演替早期階段可以克服養分限制，任何外部因子都有可能啟動這一過程，從而產生比預期更大的影響 (Breen & Levésque, 2006; Marleau *et al.*, 2011)。

苔蘚在演化上是介於藻類及蕨類之間的植物，是由水生向陸生過渡的類群，使得苔蘚在植物構造上具有特殊性 (胡人亮, 1987; 徐仁, 1980)。苔蘚是屬尚未被充分研究的植物，被認為具有維管束植物的植物光合系統功能較原始的型態，但苔蘚在結構上彼此有很大差異 (Waite and Sack, 2010)。光合作用是綠色植物獲取碳水化合物化合物的主要功能，光合系統的構造隨著植物在離水的過程也逐步在演化 (施定基等, 1983; Thornton *et al.*, 2005)。確定苔蘚性狀功能具有很重要的意義，因為苔蘚反映原始植物的狀況，其組織比維管束植物更簡單，成為遺傳和功能演

化的模型 (Thornton *et al.*, 2005; Cove *et al.*, 2006)，而且它們被認為是生態系統碳循環的主要貢獻者，這個重要性正逐漸提高 (Gorham, 1991; Lagerstrom *et al.*, 2007)，針對苔蘚植物光合作用之效能與結構性功能之研究正逐步被重視，Yan 等 (2021) 研究指出小立碗蘚 (*Physcomitrella patens*) 的天線構造 (antenna, PSI-LHCI) 與陸生植物的天線構造具有相似的結構，並且發現綠藻、苔蘚和陸生植物之間葉綠素的排列存在一些差異，顯示苔蘚 PSI-LHCI 具有光能收集和能量轉移的機制。Carbonera 等 (2012) 使用螢光檢測磁共振 (fluorescence-detected magnetic resonance, FDMR) 技術量測小立碗蘚，可知非光化學消散 (non-photochemical quenching, NPQ) 可有效保護小立碗蘚光合核心和外圍天線複合體。Gerotto 等 (2011) 指出當小立碗蘚對暴露於強光或低溫時，會使 Psbs (LHCII 的次單位) 和 LHCSR (light-harvesting complex stress-related proteins) 等蛋白質增加，這兩種蛋白質的含量與 NPQ 效能有關，顯示在這種苔蘚中，具有快速反應的 NPQ 機制及環境長期馴化的表現。NPQ 中最快和最重要的組成部分是 qE (Müller *et al.* 2001; Johnson and Ruban 2011)，這與以下三項密切相關：1) 類囊體膜質子梯度 ΔpH 的變化，2) 參與葉黃素循環的色素總量，以及 3) PSII 中次單位 PsbS 的存在 (Müller *et al.* 2001; Lavaud and Lepetit 2013)。Nilkens 等 (2010) 指出當 qE 的反應完成後，玉米黃質 (Zeaxanthin, Z) 與 PsbS 結合以消散 H^+ 。因此，qE 反應後的部分稱為 qZ，是

一種較慢的 NPQ 反應 (Maxwell & Johnson, 2000)。苔蘚植物之受光面積與氣體交換較少進行定量之研究，因此，本研究利用面積換算及氣體交換的技術，以臺灣低海拔廣布型小扭口苔樣本，測量其氣體交換與葉綠素螢光，藉此瞭解小扭口苔生態生理的特性，並有助於瞭解光合系統的演進，以開發新的應用於這類廣泛存在的苔蘚植物。

材料與方法

(一) 試驗材料與處理

試驗材料為小扭口苔 (*Barbula indica* (Hook.) Spreng.)，在臺灣常見於平地的公園、花圃或溫室，生長在潮濕、稍有遮陰的土上，高約 0.5 - 2 cm 左右 (Fig. 1)。本實驗用之小扭口苔種植於特有生物研

究保育中心的溫室內 (23° 49' 42.4" N 120° 48' 04.2" E)，月平均日/夜溫度為 32/27°C，給予充分澆水 (每周 3-4 次)，光量約為外界的 80%，最大光量為 1,000-1,400 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ PPFD。將生長良好之小扭口苔進行 1 cm^2 (1cm X 1cm) 之面積 (M) 取樣，並排列平整後以直尺量測植體之長度 (L)，由下列公式計算出受光植體面積 (A)，於光合作用分析儀 chamber 內平鋪量測，並於儀器系統內進行面積設定，用以計算氣體交換 (修改自王經文等，2008)。

$$M \times L = A, \text{ 受光植體面積}$$

(二) 試驗項目及方法

本次光合作用的試驗使用氣體交換及螢光光合作用分析儀 (portable gas exchange fluorescence system, GFS3000FL,

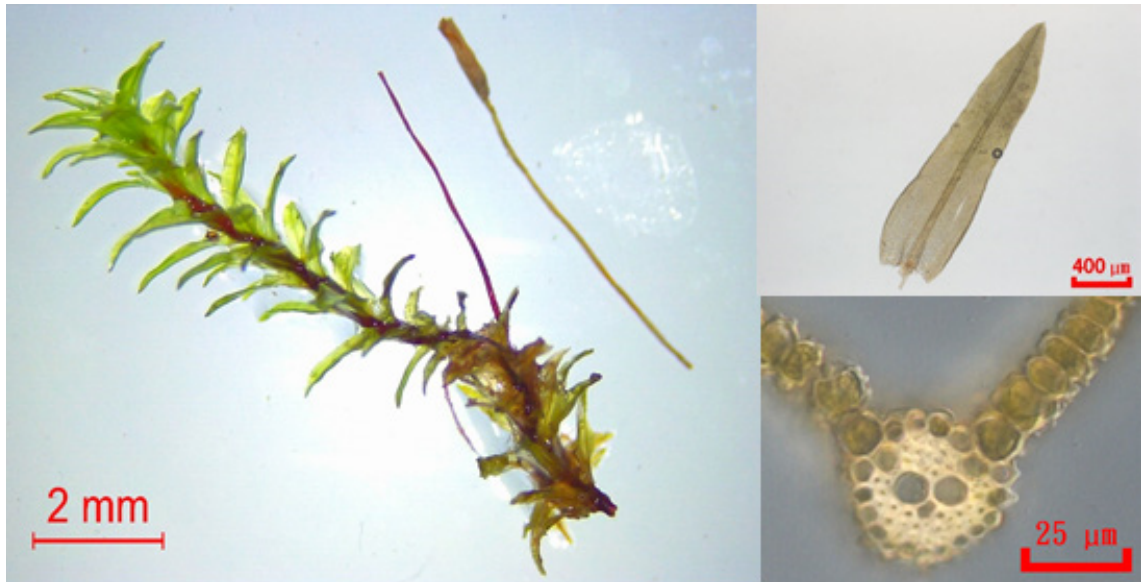


圖 1. 小扭口苔 (*Barbula indica*) 外觀及葉之微觀照片。A. 植物體。B. 葉。C. 葉橫切面，無氣孔。標本編號：K.-Y. Yao 9067。

Fig. 1. The appearance and microscopic photos of *Barbula indica*. Spreng. A. mature plant. B. blade (leaf). C. part of a cross-section of a blade, no stomata. Specimen number: K.-Y. Yao 9067.

Walz, Germany), 其基礎參數設定為：氣體流速 $750 \mu\text{mol s}^{-1}$ 、氣體混均器風扇速度 7 級、同化箱溫度 25°C 、相對溼度 75%，並用開放性系統透過緩衝瓶抽取外界 CO_2 (濃度約 380-420 ppm)。

不同光量變化之淨光合作用量測

於 2021 年 4-5 月測量，隨機取樣 1 cm^2 之小扭口苔，量測植株高度 (取樣為 3.4、3.7、4.2、4.4、4.6 cm) 後，計算受光面積後進行氣體交換之量測，將量測的數值平均，為 5 重覆。依序設定光量 0、5、10、15、25、50、75、100、200、400、800、1,200、1,500、1,800 及 2,000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ photosynthetic photon flux density (PPFD) 等 15 種光量，待每一光量的淨光合作用速率穩定後紀錄，並計算出下列參數 (王經文等 2020a)：

暗呼吸速率 (dark respiration rate, Rd)，為植株呼吸作用。

光量子收率 (light quantum yield, Qy)，為植株利用光能效率。

光補償點 (light compensation point, LCP)，為植株所需最低光量。

最大光合值 (maximum photosynthetic rate, Amax)，為植株最大光合作用速率。

不同光量變化之葉綠素螢光參數量測

將前述處理之小扭口苔，於設定 15 種光量變化下，進行葉綠素螢光參數量測，照光前先測量未照光前之螢光值，測定各項葉綠素螢光，並計算出下列參數 (王經文等，2020a；Demmig-Adams *et al.*, 1996; Johnson & Ruban, 2011)：

F_0 (minimum fluorescence)，代表天線系統的最小放射量。

F_m (maximum fluorescence)，其放出的最大螢光放射量，是代表天線系統及 PS II 反應中心放出的螢光總量。

F_v (variable fluorescence, $F_v = F_m - F_0$)，為暗適應後由 PSII 反應中心所放出之螢光放射量，可代表具活性之 PSII 反應中心的潛在量。

F_0' (minimum fluorescence in the light-adapted state)，照光下的最小螢光量。

F_s (the steady state fluorescence)，光照下 PSII 經由電子傳遞鏈將電子傳至 PSI 達到穩定階段的螢光放射量。

F_m' (maximum fluorescence in the light-adapted state)，光照下 PSII 關閉時最大螢光放射量。

$\text{ETR} = \Phi_{\text{PSII}} \times 0.5 \times 0.84 \times \text{PPFD}$ ，電子傳遞速率 (electron transport rate)

$\Delta F / F_m' = (F_v' / F_m') / (F_v / F_m)$ ，實際 PSII 效率之比例

$\text{NPQ} = (F_m / F_m') - 1$ ，非光化學消散 (non-photochemical quenching)

$\text{ETR} / \text{PG} = \text{ETR} / (\text{Pn} + \text{Rd})$ ，電子傳遞速率與總光合作用速率 (gross photosynthesis rate, PG) 之比值

$P = (F_m' - F_s) / F_m'$ ，光化學消散占吸收能量的比例

$D = 1 - F_v' / F_m' = (F_m' - F_0') / F_m'$ ，為熱消散占吸收能量之比例

$E = 1 - P - D$ ，為過多能量占吸收能量之比例

3. 統計分析

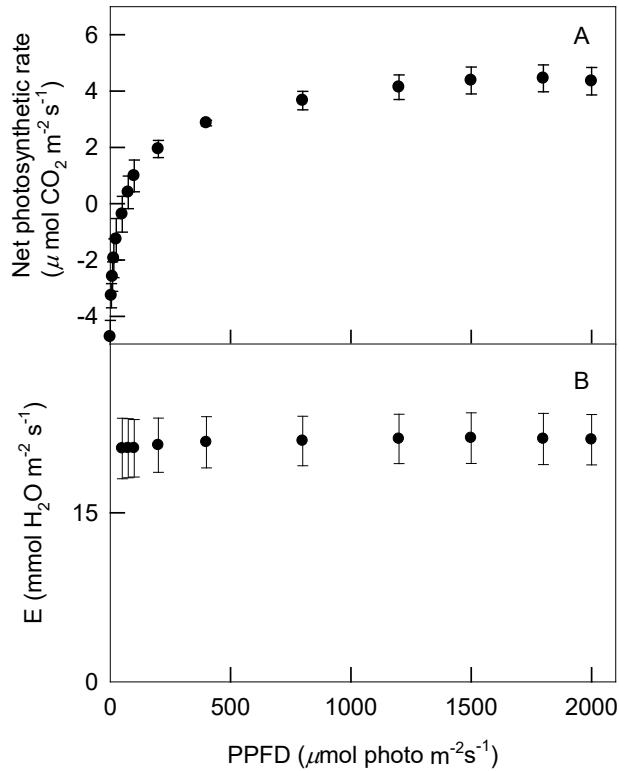


圖 2. 小扭口苔 (*Barbula indica*) 於 0、5、10、15、25、50、75、100、200、400、800、1,200、1,500、1,800 及 2,000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ 光強度變化下之淨光合作用速率 (net photosynthetic rate, Pn) (A) 與蒸散速率 (transpiration rate, E) (B)。Error bar= standard error, n = 5。

Fig. 2. The measurement of net photosynthetic rate (Pn, panel A) and transpiration rate (E, panel B) in *Barbula indica* under 0, 5, 10, 15, 25, 50, 75, 100, 200, 400, 800, 1200, 1500, 1800 and 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Error bar = standard error. n = 5.

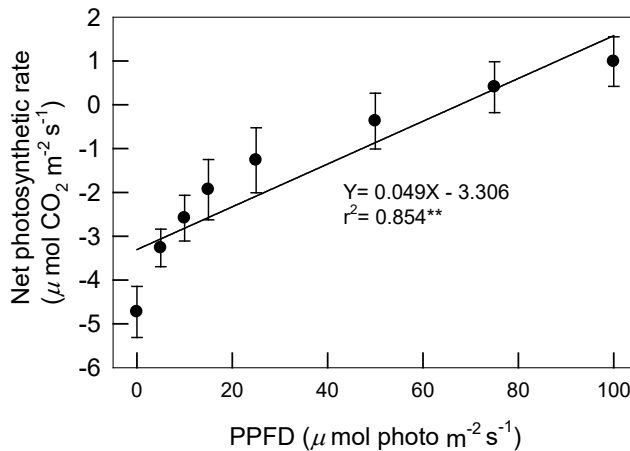


圖 3. 小扭口苔 (*Barbula indica*) 於 0、5、10、15、25、50、75 及 100 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ 光強度下與淨光合作用速率 (net photosynthetic rate, Pn) 之線性關係。** 表示 $P < 0.01$, n = 8。

Fig. 3. The relationship between PPFD and Pn of *Barbula indica* under 0, 5, 10, 15, 25, 50, 75 and 100 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. **, $P < 0.01$. n = 8.

Photosynthetic parameters

Rd ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	3.31±0.48
Qy (CO ₂ /photon)	0.05±0.01
LCP ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$)	68.19±12.36
Amax ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	4.46±0.47

±: standard error (SE). n = 5.

表 1. 小扭口苔 (*Barbula indica*) 於 0-100 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 光強度的進行氣體交換之量測暗呼吸速率 (dark respiration rate, Rd)、光量子收率 (light quantum yield, Qy)、光補償點 (light compensation point, LCP)、最大光合值 (maximum photosynthetic rate, Amax) 平均值及其 SE.

Table 1. Dark respiration rate (Rd), light quantum yield (Qy), light compensation point (LCP) and maximum photosynthetic rate (Amax) of *Barbula indica* under 0-100 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$.

以套裝軟體 PASW Statistics 18 與 SigmaPlot 10.0 進行統計分析與繪圖。光量、氣體交換與葉綠素參數間以線性及二次回歸進行相關性分析與繪圖。

結果

(一) 不同光量變化之氣體交換

圖 2 所示小扭口苔在光量 800-1,200 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 時達到光飽和 (light saturation point, LSP)，因小扭口苔無氣孔構造 (圖 1)，其蒸散速率係靠擴散作用而出，穩定維持約在 21 $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ，而光飽點在光量 800-1,200 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 。

將前述 0-100 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 光量的淨光合作用速率值做線性分析 (圖 3)，發現小扭口苔的淨光合作用速率與光量變化成正比，達到顯著相關 ($P < 0.01$)，由方程式 ($Y = 0.049X - 3.306, r^2 = 0.854^{**}$)，可得小扭口苔之暗呼吸速率 (Dark respiration

rate, Rd) 為 3.31±0.48 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ 、光量子收率 (quantum yield, Qy) 為 0.05±0.01 CO₂/photon、光補償點 (light compensation point, LCP) 為 68.19±12.36 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 及最大淨光合作用速率 (Maximum net photosynthesis rate, Amax) 為 4.46±0.47 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (表 1)。

(二) 不同光量變化之葉綠素螢光

由圖 4 可知，小扭口苔的電子傳遞速率 (electron transport rate, ETR，圖 4A) 與非光化學消散 (NPQ，圖 4C) 會隨著光量提高而調節升高，於光量 2,000 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 達到最高，分別為 57.75±6.86 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ 及 4.07±0.35，而實際 PSII 效率之比例 ($\Delta F / F_m'$ & F_v / F_m ，圖 4B) 於光量 > 1,200 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ ，就維持於 30% 左右，顯示其光合效率已達到飽和，而電子傳遞速率與粗光合作用速率之比值 (ETR/PG) 於光量 1,200 $\mu\text{mol photon m}^{-2} \text{ s}^{-1}$ 以上

時，有多餘的電子必需消耗，否則會有過剩能量的危害 (圖 4D)。

為了解電子傳遞速率 (ETR) 與光合速率 (net photosynthesis rate, Pn) 之關係，由圖 5 可知，ETR 與 Pn 為二次回歸曲線的關係 ($Y = 0.3157X + (-0.0031) X^2 - 3.523$, $r^2 = 0.982^{***}$)，達到顯著相關 ($P < 0.0001$)。顯示 ETR 的表現對於小扭口苔的 Pn 佔有相當大的影響。

為了解小扭口苔在不同光量的能量流動狀態。由圖 6 可知，在低光 (0-200

$\mu\text{mol photon m}^{-2} \text{s}^{-1}$) 時，小扭口苔的光化學消散能量比例 P 維持在 30-60% 間；但在光量 $200 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ 時，非光化學消散能量比例 D 已達 50%，特別在高光時，小扭口苔之非光化學消散能量比例仍逐步提升，為主要能量流向，於光量 $1,200-2,000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ 時占全部能量之 80%，顯示小扭口苔的光合系統已具有相當功能性的非光化學消散機制，而過剩能量比例則維持在 11-16% 間。

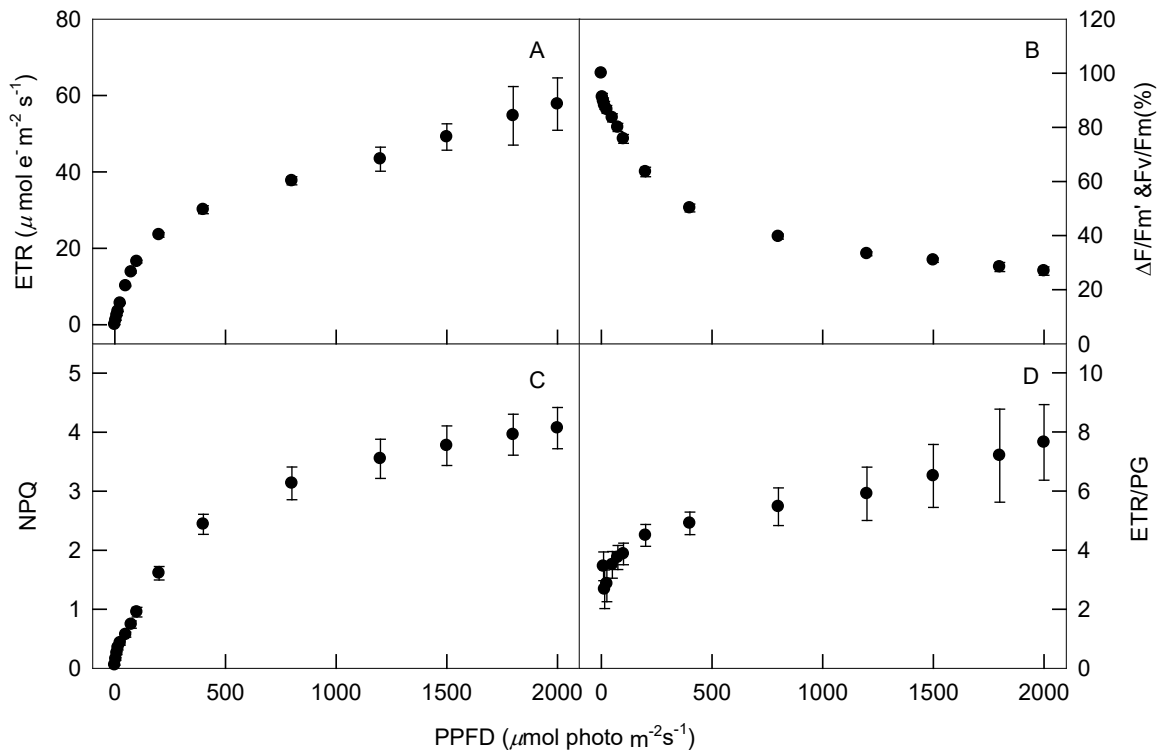


圖 4. 小扭口苔 (*Barbula indica*) 於 0、5、10、15、25、50、75、100、200、400、800、1,200、1,500、1,800 及 2,000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ 光強度變化下之電子傳遞速率 (ETR, A)、實際 PSII 效率之比例 ($\Delta F/Fm' \& Fv/Fm$, B)、非光化學消散 (NPQ, C) 與 ETR/PG (D)。Error bar= standard error, $n = 5$ 。

Fig. 4. The measurement of ETR (panel A), $\Delta F/Fm' \& Fv/Fm$ (panel B), non-photochemical quenching (panel C), and ETR/PG (panel D) in *Barbula indica* under 0, 5, 10, 15, 25, 50, 75, 100, 200, 400, 800, 1200, 1500, 1800 and 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Error bar= standard error. $n = 5$.

討論

(一) 不同光量變化之氣體交換

在一般維管束植物中，當葉片開始暴露在光照下時，Pn 在達到最大速率之前會需要一段誘導的時間，而這種植物光誘導現象會隨著其生態區位而有所不同 (Urban *et al.*, 2007; Bai *et al.*, 2008; Wong *et al.*, 2012; Deans *et al.*, 2019)。在光合作用的誘導過程中，CO₂ 固定的延遲通常與生化和氣孔限制有關 (Bai *et al.*, 2008; Urban *et al.*, 2007)。維管束植物具有氣孔構造，可

以透過氣孔導度的控制來水分消耗 (Taiz & Zeiger, 2002)，特別處於逆境時，耐逆境植物在可忍耐的生理範圍內，可藉由嚴格的氣孔控制來提高用水效率，達到節水的目的 (王經文等, 2020a; 王經文等, 2020b; Reef & Lovelock, 2014)，因此，在氣體交換的研究中 (王經文等, 2020a; 王經文等, 2020b)，特別關注光合下降是否為氣孔因素或非氣孔因素 (光保護或光抑制)，而本試驗材料小扭口苔並未具備氣孔構造 (圖 1) 及維管束構造 (胡人亮，

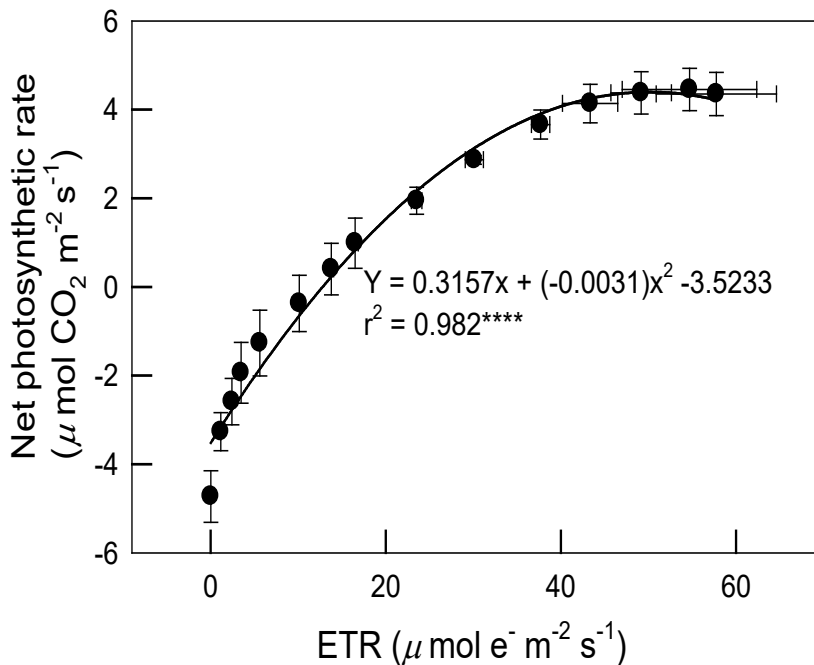


圖 5. 小扭口苔 (*Barbula indica*) 於 0、5、10、15、25、50、75、100、200、400、800、1,200、1,500、1,800 及 2,000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ 光強度變化下之電子傳遞速率 (electron transport rate, ETR) 與淨光合作用速率 (net photosynthetic rate, Pn) 之曲線關係。Error bar= standard error。**** 表示 $P < 0.0001$ 。n = 15。

Fig. 5. The relationship between ETR and Pn of *Barbula indica* under 0, 5, 10, 15, 25, 50, 75, 100, 200, 400, 800, 1200, 1500, 1800 and 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Error bar= standard error. **** = $P < 0.0001$. n = 15.

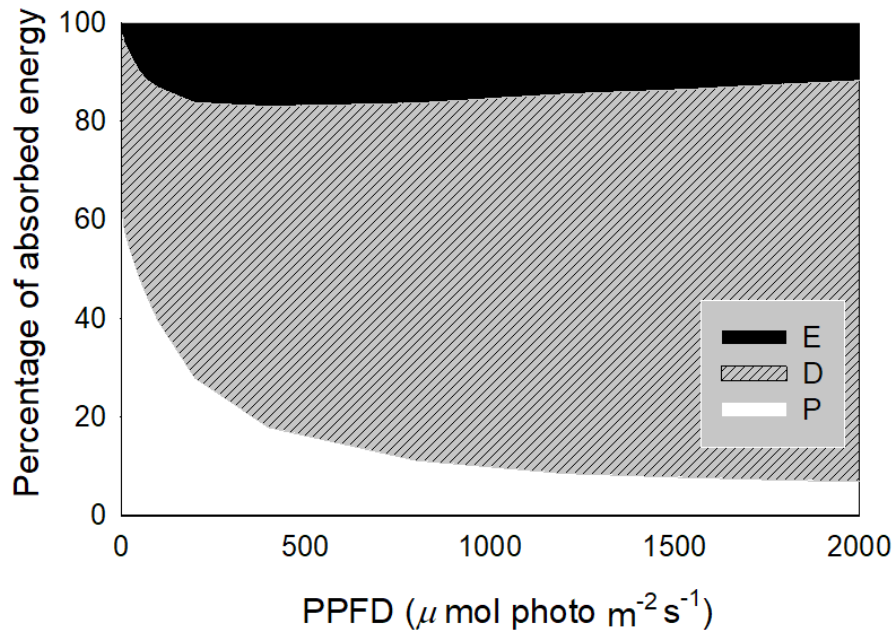


圖 6. 小扭口苔 (*Barbula indica*) 於 0、5、10、15、25、50、75、100、200、400、800、1,200、1,500、1,800 及 2,000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ 光強度變化下，光化學消散占吸收能量的比例 (P%)、熱消散占吸收能量之比例 (D%) 與過剩能量占吸收能量之比例 (E%) 之變化。Error bar= standard error. n = 5。
 Fig. 6. The measurement of P (photochemical quenching), D (thermal quenching accounted for the proportion of absorbed energy) and E (excessive energy) in *Barbula indica* under 0, 5, 10, 15, 25, 50, 75, 100, 200, 400, 800, 1200, 1500, 1800 and 2000 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$. Error bar= standard error. n = 5.

1987; 徐仁, 1980; Waite and Sack, 2010), 因此, 在其進行氣體交換時, 係以細胞間擴散作用的方式來進行, 故圖 2B 的蒸散速率之變化, 無論處於何種光量下皆維持固定速率 (約 $21 \text{ mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)。而小扭口苔不具氣孔構造使得其在非缺水逆境時, 光合系統能在缺少氣孔的因素下忠實反映光量、光質對其的影響, 對於研究光合系統功能的演進是良好的材料。

苔蘚是耐陰生物 (Glime, 2007a), 即使在光量很低下也能保有葉綠素, 甚至可以通过降低輻照度來增加葉綠素含量 (Glime, 2007a, b), 而圖 2A 可知, 小扭口苔的光飽點在光量 $800\text{-}1,200 \mu\text{mol photon}$

$\text{m}^{-2} \text{s}^{-1}$ 間, 相較一般陰性種有較高的光飽點, 惟此時其非光化學消散占吸收能量比例為 72-76% (圖 6), 另於低光 ($0\text{-}200 \mu\text{mol photon m}^{-2} \text{s}^{-1}$) 時, 小扭口苔的光化學消散能量比例 (P) 維持在 30-60% 間 (圖 6), 顯示低光較適合其光合系統, 但仍需要進一步進行不同光量下培養的光適應性研究, 才可明確了解其較佳的光量生態棲位。

光補償點可做為植物評估耐陰能力的參考 (陳忠義和廖天賜, 2007), 大部分的陽性植物光補償點在 $10\text{-}20 \mu\text{mol photon m}^{-2} \text{s}^{-1}$, 陰性植物之光補償點在 $1\text{-}5 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ (Taiz & Zeiger, 2002)。而小扭

口苔光補償點為 $68.19 \pm 12.36 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ ，為陽性植物的特徵，而較低的 R_d ($3.31 \pm 0.48 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$)，則呈現陰性植物的特徵 (郭耀綸和賴幸榆, 2007)，而陳忠義和廖天賜 (2007) 指出當構樹 (*Broussonetia papyrifera*) 苗木培養於相對光量為 100%、40%、10% 的環境下，其光合特性 (如光補償點及最大光合值) 會隨生長環境光量提高，光合特性逐步調整為陽性，對比本試驗的小扭口苔，培養環境相對光量為 80%，這或許其部分光合特性為陽性的原因，也顯示小扭口苔為廣布存在物種的特性。

(二) 不同光量變化之葉綠素螢光

一般而言，光合作用速率與 ETR (或 ΦPSII) 會維持固定比例 (Sun *et al.*, 2007)，而 ETR 被廣泛用於評估光合活性和生產力 (Longstaff *et al.*, 2002; Carr and Björk, 2003; Lesser *et al.*, 2010)。由圖 2A 及圖 4A 可知，光合曲線與 ETR 曲線相似，進一步進行兩者二次曲線回歸分析 (圖 5)，可知兩者呈現顯著相關 ($P < 0.0001$)，這與其他維管束 C4 和 C3 植物有相似的結果 (Cheng *et al.*, 2001; Pérez-Torres *et al.*, 2007; Ripley *et al.*, 2007; Wong *et al.*, 2014)。

維管束植物對於光量變化相當敏感，在其光合作用達到穩定前，需藉由非光化學消散來保護光合系統 (Han *et al.*, 1999; Allen & Percy, 2000; Bai *et al.*, 2008; Wong *et al.*, 2012)。由圖 4C 可知 NPQ 隨著光量提高而調節升高，於光量 $2,000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ 達到最高，而實際 PSII 效率

之比例 ($\Delta F/F_m'$ & F_v/F_m ，圖 4B) 於光量 $1,200 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ 以上，就維持於 30% 左右，顯示其光合效率以達到飽和，而淨光合作用 (圖 2A) 與 NPQ (圖 4C) 趨勢相似，表示隨著淨光合作用速率的增加，相對的過剩光能也在增加，需以利用 NPQ 將其消散 (圖 6)，再對照圖 4D 亦可知，於光量 $1,200-2,000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ 有較高的 ETR/PG，有多餘的電子必需消耗，顯示有其他代替 CO_2 之電子接受者，也就是光呼吸或葉黃素循環，來避免 PSII 受到光傷害，這是植物體因應高光傷害主要的光保護機制 (王經文等, 2008; 王經文等, 2020a; 王經文等, 2020b; Leakey *et al.*, 2003)。由此可知，小扭口苔的光合系統功能已具備相當的非光化學消散能力，惟仍後續進一步進行光誘導試驗研究其光保護及光抑制機制，才可明確了解其較佳的光量生態棲位。

結論

經本試驗可知小扭口苔因不具有氣孔構造，呈現蒸散速率與光合作用速率脫鉤的現象，無論處於何種光量下，蒸散速率皆維持固定速率，其光合系統能在缺少氣孔的因素下反映光量、光質對其的影響，為研究光合系統功能演進的良好材料。小扭口苔同時具有較高的光飽和點及光補償點的陽性植物特徵，以及較低的 R_d 的陰性植物特徵，這或許為其廣佈型的原因之一。小扭口苔與其他維管束 C4 和 C3 植物的光合系統相似，ETR 與 Pn 呈現顯著相關且具備相當的非光化學消散

能力。藉由葉綠素螢光量測的技術，具方便、快速及非破壞性等優點，可藉此監測苔蘚植物生態生理的狀態，有助了解光合系統的演化並開發新的應用於這類廣泛存在的苔蘚植物。

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