

Taxonomic reappraisal of *Solanum biflorum* var. *kotoense* (Solanaceae)

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Received: June 1, 2018; Accepted: October 16, 2018

Abstract

The identity of *Solanum biflorum* Lour. var. *kotoensis* Y. C. Liu & C. H. Ou is reappraised as its type specimen was rediscovered in TCF. Based on comparative study of related fresh and herbaria materials, *S. biflorum* var. *kotoensis* is treated as a synonym of *Lycianthes boninensis* Bitter. *L. boninensis* could be readily distinguished from closely related *L. biflora* by its glabrous habits and distinct morphology of calyx teeth. *L. boninensis* was regarded as endemic to the Bonin Islands, but presently its distribution range extends to the Ryukyu Islands and Lanyu, forming a remarkable phytogeographic pattern.

Key words: Lanyu, *Lycianthes biflora*, *Lycianthes boninensis*, *Solanum biflorum* var. *kotoense*, Taiwan, taxonomy.

紅頭耳鉤草之分類再議

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收件日期: 2018 年 6 月 1 日; 接受日期: 2018 年 10 月 16 日

摘要

伴隨模式標本重現於 TCF 標本館，本研究探討紅頭耳鉤草 (*Solanum biflorum* Lour. var. *kotoensis* Y. C. Liu & C. H. Ou) 之分類地位。基於新鮮及乾燥標本之觀察比對，我們將 *S. biflorum* var. *kotoensis* 處理為 *Lycianthes boninensis* 之異名。紅頭耳鉤草與近似種紅絲線 (*Lycianthes biflora* (Lour.) Bitter) 可藉由光滑之植物體及相異的萼齒形態區分。*L. boninensis* 過往被認定為小笠原群島之特有種，但目前其地理分布延伸至琉球群島及蘭嶼，形成一獨特之植物地理模式。

關鍵詞: 蘭嶼、紅絲線、紅頭耳鉤草、臺灣、分類學

Introduction

Lycianthes (Dunal) Hassl. is a large genus of Solanaceae comprising 150–200 species (Dean *et al.* 2017), with the majority distributed in the New World from Mexico to Argentina, and only approximately 30 species are found in the Old World between Asia and Australia (Dean 2004). Although sometimes included within *Solanum* by earlier authors (e.g. Hatusima 1969; Liu and Ou 1974, 1978), *Lycianthes* is commonly recognized as a distinct genus in modern studies (e.g. Yamazaki 1993b; Zhang *et al.* 1994; D' Arcy and Peng 1998) as it could be well characterized in morphology by the combination of cup-shaped, 10-veined, mostly 5–10 toothed calyx and poricidal anther dehiscence (D' Arcy 1986; Dean 2004; Olmstead *et al.* 2008; Dean *et al.* 2017). Molecular data has shown that *Lycianthes* is distant from *Solanum* but closely related to the chili pepper genus *Capiscum*, and some recent analyses have revealed that *Lycianthes* is paraphyletic with *Capiscum* nested within (Olmstead *et al.* 2008; Särkinen *et al.* 2013). A systematic recircumscription of *Lycianthes* and/or *Capiscum* is thus ultimately necessary.

In Taiwan, two *Lycianthes* species, *L. biflora* (Lour.) Bitter and *L. lysimachioides* (Wall.) Bitter, are commonly accepted (Zhang *et al.* 1994; D' Arcy and Peng 1998; Yang and Liu 2002; Boufford *et al.* 2003; Editorial Committee of the Red List of Taiwan Plants 2017). An additional taxon, described as *Solanum biflorum* Lour. var. *kotoensis* Y. C. Liu & C. H. Ou (Liu and Ou 1974) from Lanyu island, underwent a more intricate taxonomic history. This variety was accepted in the first edition of the Flora of Taiwan (Liu and Ou 1978) but later reduced by

Liao (1987) as a synonym of *S. biflorum* var. *glabrum* Koidz. ex Hatus. described from the Bonin Islands. Yamazaki (1993b), on the other hand, recombined this taxon under *Lycianthes laevis* (Dunal) Bitter described from Java [as *L. laevis* var. *kotoensis* (Y.C.Liu & C.H.Ou) T.Yamaz.] and simultaneously recorded it from the Ryukyu Islands. Meanwhile, *S. biflorum* var. *kotoense* was sunken into *L. biflorum* in other studies (Zhang *et al.* 1994; D' Arcy and Peng 1998; Yang and Liu 2002).

During a field trip to Lanyu in November, 2006, we met a fruiting *Lycianthes* sp. (Fig. 1A) along the trail to Mt. Hungtou, the highest peak of the islet. The plant was first linked to *L. biflora* due to its erect habit, though it showed somewhat distinct characters such as glabrous habit and shorter, spine-like calyx teeth. After preliminary study, it soon revealed that this taxon might match *Solanum biflorum* var. *kotoensis* and is also very close to *L. boninensis* described from the Bonin Islands of Japan (Liu and Ou 1974, 1978; Toyoda 2003; Yahara and Nagata 2003). To clarify its exact taxonomic position, we planned to examine the type specimen of *Solanum biflorum* var. *kotoense*, which was recorded as being collected by T. Sata from Botel Tobago (an alternative name of Lanyu) on 7 August, 1932, and preserved in the Herbarium of the Department of Botany, National Taiwan University ("Herb. Dept. Bot. Coll. Sci. National Taiwan University") (Liu and Ou 1974), currently the Herbarium of National Taiwan University (herbarium code: TAI). However, we failed to locate any specimen matching Liu and Ou's (1974) record in TAI, and the identity of the Mt. Hungtou *Lycianthes* thus remained uncertain.

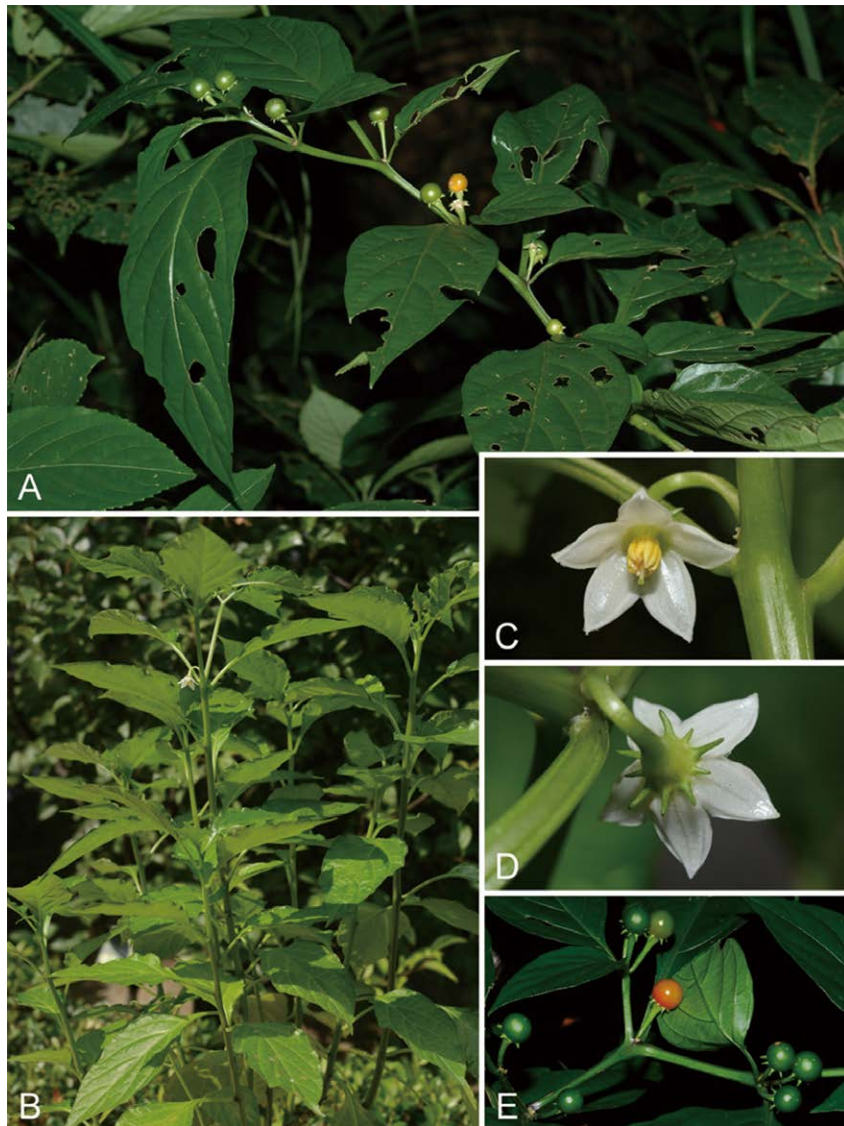


Fig 1. Morphology of *Lycianthes boninense* found in Lanyu (A & E from *Chung 8427*; B–D from *Chung 12223*). A. Fruiting habit. B. Flowering habits. C. Flower, front view. D. Flower, back view, showing calyx teeth. E. Fruits.

In December, 2017, a sheet fitting the record of *Solanum biflorum* var. *kotoense* type (Fig. 2) was eventually found in the Herbarium of National Chung Hsing University (herbarium code: TCF) where Prof. Liu and Prof. Ou, the authors of *S. biflorum* var. *kotoense*, stayed for their entire research careers. On the account that the “National Taiwan University Herbarium” stamp on the sheet implies that this specimen was originally preserved in TAI, and no trace of additional duplicates could be detected so far, the TCF sheet could be directly treated as the holotype of *S. biflorum* var. *kotoense* (see Art. 9.1. Note 1 of the Melbourne Code; McNeill *et al.* 2011). Additionally, several specimens cited under *S. biflorum* var. *kotoense* in the first edition of the Flora of Taiwan (Liu and Ou 1978) were also found in TCF.



Fig 2. Holotype of *Solanum biflorum* var. *kotoense* currently preserved in TCF. Photographed by You-Ting Hsieh.

After a critical study of the rediscovered holotype of *S. biflorum* var. *kotoense* and related fresh and herbaria materials, we are convinced that the unknown *Lycianthes* we encountered at Mt. Hungtou in 2006 along with several *Lycianthes* collections from Lanyu match *S. biflorum* var. *kotoense*, and all these specimens also correspond to *Lycianthes boninensis*. As *L. boninensis* takes priority at species rank, we treated *Solanum biflorum* var. *kotoensis* as a synonym of *L. boninensis* for the first time. The global distribution of *L. boninensis*, previously considered endemic to the Bonin Islands (Yamazaki 1993b; Yahara and Nagata 2003), then extends to the Ryukyu Islands and Lanyu (Fig. 3). To aid identification, the full synonymy, morphological description, voucher specimens and color plates of *L. boninensis* is presented in this study. Its taxonomic identity, phytogeography and conservation status are also discussed.

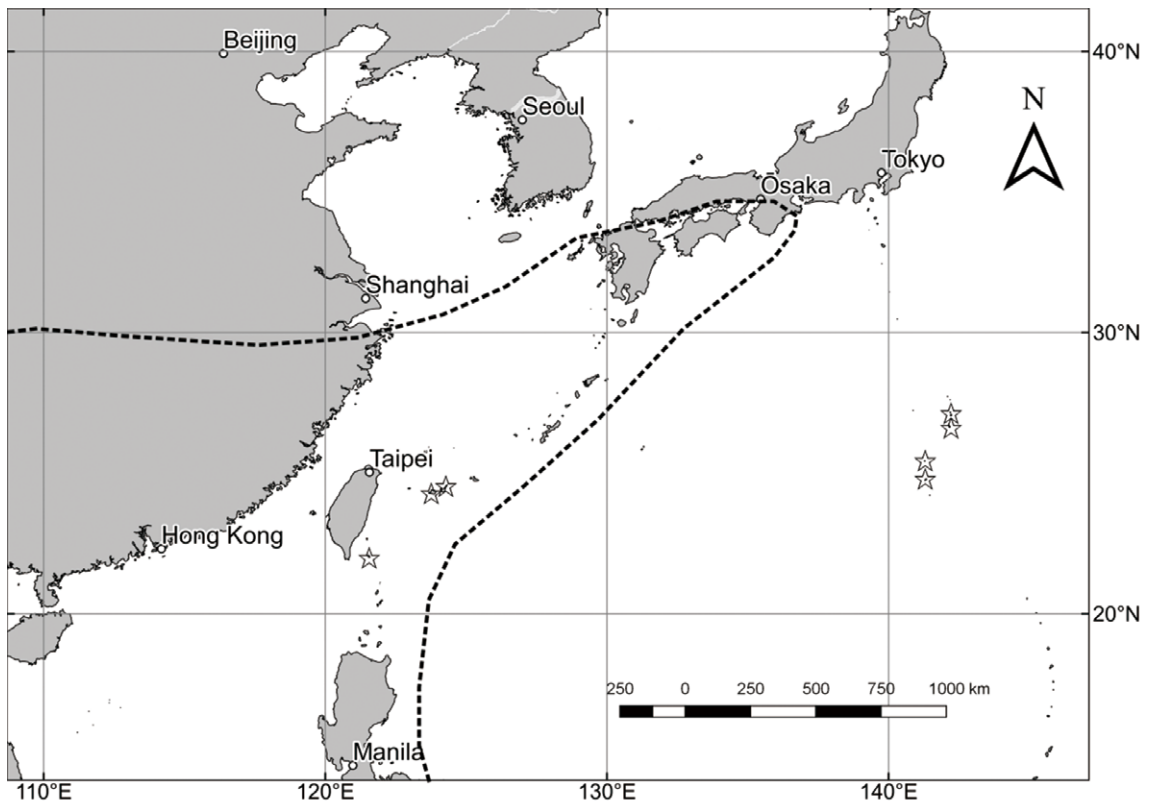


Fig 3. Distribution ranges of *Lycianthes boninensis* (stars) and *L. biflora* (dashed line) in East Asia.

TAXONOMIC TREATMENT

Lycianthes boninensis Bitter, Abh. Nat. Ver. Bremen 24:483. (1919). Figs. 1 & 2. **Type:** JAPAN. Tokyo: Bonin Islands (“Bonininseln”), *Warburg s.n.* (holotype: B, possibly destroyed).

= *Solanum biflorum* Lour. var. *kotoense* Y.C.Liu & C.H.Ou, Quart. J. Chin. For. 7: 151. 1974 [as “*kotoensis*”]. ≡ *Lycianthes laevis* (Dunal.) Bitter var. *kotoensis* (Y.C.Liu & C.H.Ou) T. Yamaz., Fl. Japan. 1993. **syn. nov.** **Type:** TAIWAN. Taitung: Lanyu (Botal Tobago), Mt. Satuja, 7 Aug 1932, *T. Sata s.n.* (holotype: TCF!).

= *Solanum boninense* Nakai ex Tuyama, Bot. Mag. Tokyo 50: 132. 1936. **Type:** JAPAN. Tokyo: Bonin Islands, Chichijima (“Ins. Titizima”), 8 July 1920, *T. Nakai s.n.*, (holotype: TI!).

= *Solanum biflorum* Lour. var. *glabrum* Koidz. ex Hatus., J. Geobot. (Kanazawa) 17:49. 1969. **Type:** JAPAN. Tokyo: Bonin Islands, 1 Oct 1912, *S. Nisimura 81* (holotype: TI!).

Morphology: Subshrubs 0.6–1.0 m tall. Branches glabrous, sometimes sparsely hairy at very young stage. Leaves solitary or unequally paired, thick membranaceous, sparsely hairy at very young stage, soon turning glabrous, petiole 1–3 cm long; major leaves ovate or ovate-oblong, 10–18 cm long, 4.0–8.5 cm wide, apex acute or acuminate, base cuneate or rounded, shortly attenuate into petiole, entire, lateral veins 5–7 pairs; minor leaves broadly ovate to oblong, 3–8 cm long, 2–4 cm wide. Inflorescences 1–6-flowered fascicles in leaf axils. Pedicel 0.5–1.0 cm long, glabrous, retrose in flowering, erect in fruiting. Calyx cup-shaped, 3–4 mm long, ca. 4 mm in diam., glabrous, 10-toothed; teeth spine-

like, attached slightly below the rim, subequal or distinctly unequal in length, 0.3–1.5(–2.0) mm long; corolla rotate-campanulate, white, deeply 5-lobed, lobes ca. 7 mm long, ovate-lanceolate, acute; stamens 5, connivent, inserted in corolla tube, filaments ca. 1 mm long, anthers oblong, ca. 3.5 mm long; style filiform, ca. 5 mm long. Berry red, globose, 0.7–0.9 cm in diam., with saucer-shaped persistent calyx at base.

Chinese name: “紅頭耳鉤草” (Liu and Ou 1978).

Global distribution: *Lycianthes boninensis* is currently reported in Japan and Taiwan (Fig. 3). In Japan, it has been recorded from Chichijima, Hahajima, Kita Iwo Jima and Minami Iwo Jima of the Bonin Islands (Ogasawara Subprefecture, Tokyo Metropolis) (Toyoda 2003) and Ishigakijima and Iriomotejima of the Ryukyu Islands (Okinawa Prefecture) (Yamazaki 1993). In Taiwan, it is currently only recorded in Lanyu (Lanyu Township, Taitung Co.). The record of *Lycianthes boninensis* in Borneo (Beaman and Anderson 2004) is currently rejected as discussed below.

Habitat and phenology: In Lanyu, *Lycianthes boninensis* was found growing under primary broadleaved forest at the elevation of 200–400 m. Flowering was recorded from May to July and fruiting from July to next March.

Conservation status: EN. See the discussion below.

Additional specimens examined: TAIWAN. Taitung: Lanyu Township, Mt. Hungtou (Mt. Hon-tou;), 12 Jul 1935, *Hosokawa 8128* (TCF); 12 Jul 1935, *Kano s.n.* (TCF); 20 Sep 1972, *Huang & Kao 6236* (TCF); 12 Nov 2006, *Chung 8427* (TAIF); 12 Oct 2013,

Lu 26059 (TAIF); 10 Jun 2015, *Chung 12223* (TAIF); Mt. Yamada, *Sata 1691*, Jul 19, 1932 (TAI); Tungching Stream, 30 Sep 2010, *Jung 5166* (TAIF); en route from Yehyu Bridge to hill peak up the Yehyu River, 27 Feb 1993, *Ho 1072* (HAST). JAPAN. Tokyo Metropolis, Ogasawara Subprefecture: Chichijima, 14 Jul 1905, *Hattori s.n.* (TI); Hahajima, 6 Aug 1905, *Hattori s.n.* (TI); 19 Jun 1920, *Nakai s.n.* (TI); 28 Jul 1930, *Tuyama s.n.* (TI); 26 Jun 1932, *Hara T215* (TI); 30 Jun 1932, *Kuwanok s.n.* (TI); 7 Apr 1934, *Tuyama s.n.* (TI); 4 Apr 1936, *Tuyama s.n.* (TI); 400 m, 16 Jul 1969, *Yamazaki s.n.* (TI); Kita Iwo Jima (“Kita-iwo-zima”), 20 Nov 1935, *Tuyama s.n.* (TI); 16 Jun 1940, *Tuyama s.n.* (TI); 300 m, 28 May 1970, *Yamazaki & Enomoto s.n.* (TI); 13 Jul 1993, *Yasui s.n.* (TI); Minami Iwo Jima, 31 Mar 1936, *Tuyama s.n.* (TI); 15 & 16 Jun 1982, *Ohba 826074* (TI).

DISCUSSION

Typification and taxonomic affinity of *Lycianthes boninensis*

All but few loaned ones of the Solanaceae types preserved in the Herbarium Berolinense were unfortunately destroyed during WWII (Hiepko 1987), and currently we could not find any surviving original materials of *Lycianthes boninensis* from online databases of B and other European herbaria. The identity of this name is therefore based on the comparison with original description (Bitter 1919), previous studies (Yamazaki 1993b; Toyoda 2003; Yahara and Nagata 2003) and specimens collected from its type locality. Neotypification would be ultimately necessary if no extant type materials could be discovered after an extensive search.

Lycianthes boninensis is closely related to

the widespread and variable *L. biflora* but readily distinguished by the hairiness of plant bodies and the morphology of calyx teeth. In *L. boninensis*, the stems and leaves are only sparsely hairy at very young stage and soon become entirely glabrous, the calyx is entirely glabrous, with conical-subulate teeth attached slightly below calyx rim, and the calyx teeth are sometimes unequal in length, up to 2 mm and generally 0.3–1.5 mm long. While in *L. biflorum*, the annual stems, leaves and calyx are always sparsely to densely pubescent, and the calyx teeth are linear-subulate, nearly equal in length, generally 2–3 mm long and attached onto the calyx rim. It should be noted that both *L. boninensis* and *L. biflorum* could be found in Lanyu, where they tend to grow allopatrically. *L. biflorum* [voucher specimens: *Sata 1687* (TAI); *Huang 10675* (TAI); *Chang 2841* (TAIF); *Jung 5030* (TAIF)] is often found in open and semi-open waste places or forest margin near sea-level, but *L. boninensis* is only discovered under moist rain forests in the northern mountainous region. All specimens currently examined are clearly separable by the characters mentioned above.

Yamazaki's (1993b) treatment of *Solanum biflorum* var. *kotoense* was somehow impractical. Firstly, he placed this taxon as a variety of Javanese *Lycianthes laevis*, but *L. laevis*, as described in Bitter's (1919) monograph and also seen on its holotype [*J.B.L.T. Leschenault de la Tour 683* (P image!)], bears shortly 5-toothed calyx which is strikingly distinct from the present taxon. Secondly, he stated that *Lycianthes laevis* var. *kotoensis* differs from *L. boninensis* in having membranaceous (vs. thick membranaceous), oblong (vs. ovate) leaves, attenuately acuminate (vs. acute) leaf apices

and irregular (vs. subequal) calyx. However, the holotype of *Solanum biflorum* var. *kotoensis* (Fig. 2) bears ovate leaves and subequal calyx teeth, both conflicting Yamazaki's observation. The distinction in leaf texture is too subtle to serve as diagnosing character, and specimens from Lanyu comprise leaves varied from ovate to oblong with acute to acuminate apices and calyx teeth varied from obviously irregular to subequal. Based on these observations, we are convinced that none of the characters mentioned by Yamazaki (1993b) are usable to distinguish *Solanum biflorum* var. *kotoense* from *L. boninensis*, and hence we agree with Liao (1987) that *S. biflorum* var. *kotoense* is identical to the Bonin taxon. However, as this taxon could be readily distinguished from *L. biflora* not only by glabrous habits but also by the morphology of calyx teeth, we believe it is better to recognize it as an independent species, namely *L. boninensis*, instead of a glabrous variety of *L. biflora*.

Conservation status of *Lycianthes boninensis*

Lycianthes boninensis was evaluated as EN (Endangered) in Japan (Ministry of the Environment, 2015). In Taiwan, *L. boninensis* is currently only recorded in the northern mountainous region of Lanyu. Although it is recorded in four locations (Mt. Hongtuo, Mt. Yamada, Tungching Stream and Yehyu River) according to specimen data, all these locations are actually closely adjacent and thus better considered as a single subpopulation. A total of ca. 100 mature individuals and ca. 10 km² area of occupancy are estimated based on our field investigation between 2006–2018. As neither population decline nor immediate threat has been observed, this species is evaluated as EN (D1) at national level based on IUCN Red List

Categories and Criteria (IUCN 2012a; 2012b; Editorial Committee of the Red List of Taiwan Plants 2017).

Phytogeography of *Lycianthes boninensis*

The Bonin-Ryukyu-Lanyu distribution pattern of *Lycianthes boninensis* is remarkable and not known from any other vascular plants (Hsieh 2003). The only similar case is *Limonium wrightii* (Hance) Kuntze (Plumbaginaceae), although it occurs in a slightly wider range including the Izu Islands, southern Taiwan and Penghu Islands (Yamazaki 1993a; Li 1998; Toyoda 2003). All other native species sharing among the Bonin Islands, the Ryukyu Islands and Lanyu are globally much more widespread.

The geographic location and flora of the Bonin Islands is rather isolated, with about 43% of vascular plants considered endemic (Kobayashi and Ono 1987). On the other hand, the floras of the Ryukyu Islands and Lanyu, each with fewer than 12% endemic species (Ohba 1996; unpublished data), are more correlative to closely adjacent areas such as southern Japan, Taiwan and northern Philippines. It could therefore be hypothesized that the speciation of *L. boninensis* more likely took place on the Bonin Islands, and its emigration to the Ryukyu Islands and Lanyu might have happened more recently. The small, bright reddish and smell-less berries of *L. boninensis* well fit the syndrome of ornithochory (Albuquerque *et al.* 2006), and it thus has the potential of long-distance dispersal among these oceanic islets. The Bonin-origin hypothesis could further demonstrate that the co-occurrence of closely related *L. boninensis* and *L. biflora* in the Ryukyu Islands and Lanyu (Fig. 3) might be a result of multiple independent

colonization, though phylogenetic and population genetic studies are eventually needed in seeking its origin and evolution history.

Besides Taiwan and Japan, *Lycianthes boninensis* was also recorded from Borneo based on a single collection from the Mount Kinabalu region (Beaman and Anderson 2004). However, the voucher specimen [Kokawa & Hotta 5609 (L image!)] differs from Japanese and Taiwanese materials in having much narrower leaves and linear-subulate calyx lobes. We thus believe that this record was a result from misidentification. Nevertheless, since *L. boninensis* could be easily confused with *L. biflorum* if not carefully studied, there is still a chance to find out additional records of *L. boninensis* within the broad distributing range of *L. biflorum* if a comprehensive re-examination of herbaria and field survey is conducted.

ACKNOWLEDGEMENTS

We are grateful of You-Ting Hsieh (謝侑廷) for taking specimen photos in TCF, the curators of HAST, TAI, TAIF, TCF and TI for herbaria access; Che-Wei Lin (林哲緯), Shen-Kun Yu (余勝焜), Pi-Fong Lu (呂碧鳳), Chiu-Mei Wang (王秋美), Chih-Hsiung Chen (陳志雄) and Hsin-Chieh Hung (洪信介) for accompanying field trips, and two anonymous reviewers for their valuable comments.

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