Phytotaxa 583 (3): 251–259
https://www.mapress.com/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.583.3.3

Resurrection and emended description of *Gastrodia foetida* (Orchidaceae)

KENJI SUETSUGU[1,2,4*], RIN AOKI[3,5] & SHINGO KANEKO[3,6]
[1]*Department of Biology, Graduate School of Science, Kobe University, 1-1 Rokkodai, Nada-ku, Kobe, 657-8501, Japan*
[2]*The Institute for Advanced Research, Kobe University, 1-1 Rokkodai, Nada-ku, Kobe, 657-8501, Japan*
[3]*Faculty of Symbiotic Systems Science, Fukushima University, Fukushima, Fukushima 960-1296, Japan*
[4] *kenji.suetsugu@gmail.com; https://orcid.org/0000-0002-7943-4164*
[5] *bluekirin.0102@gmail.com; https://orcid.org/0000-0003-1455-1797*
[6] *kaneko.shingo@gmail.com; https://orcid.org/0000-0002-9021-8155*
**Corresponding author: kenji.suetsugu@gmail.com*

Abstract

This paper presents a re-evaluation of the taxonomic identity of *Gastrodia foetida* based on molecular and morphological data. The taxon was described from Iriomote Island, Ryukyu Islands, Japan, and has often been treated as a synonym of *G. nipponica* from Wakayama Prefecture, Honshu, Japan. In contrast, we showed that the genetic divergence between *G. foetida* and *G. nipponica* is much more significant than that between *G. foetida* and *G. takeshimensis*. Additionally, *G. foetida* can be distinguished from *G. nipponica* by a few morphological traits, particularly a more dilated column toward a little below the middle. Therefore, we propose that *G. foetida* is recognized as a distinct species based primarily on molecular phylogenetic evidence followed by morphological evidence. Our investigation strongly suggested that these species exhibit distinct geographic separation: *G. nipponica* is restricted in mainland Japan (north of the Ryukyu Islands), whereas *G. foetida* is mainly distributed on the more southern areas (the Ryukyu Islands and possibly Taiwan).

Keywords: cryptic species, *Gastrodia nipponica* species complex, mycoheterotrophy, taxonomy, taxonomic revision

Introduction

Gastrodia Brown (1810: 330; Gastrodieae, Epidendroideae) is a mycoheterotrophic orchid genus across a large geographical area that includes Asia, Oceania, Madagascar, and Africa (Cribb *et al.* 2010; Suetsugu 2022). The key characteristic of *Gastrodia* species includes fleshy tubers, absence of normal leaves, united sepals and petals, and two mealy pollinia without caudicles (Cribb *et al.* 2010; Hsu & Kuo 2010; Hsu *et al.* 2012; Suetsugu 2021, 2022). However, the genus *Gastrodia* has been a source of systematic confusion due to its wide distribution, phenotypic plasticity, convergent morphological features, and short flowering duration (Suetsugu *et al.* 2018). Furthermore, some species still lack detailed descriptions, particularly those first described decades ago (Suetsugu *et al.* 2018). Given these difficulties in identification, adequate taxonomic studies of this genus have not yet been conducted. Despite these limitations, several recent studies have reported many new *Gastrodia* species (Ong & O'Byrne 2012; Tan *et al.* 2012; Hsu *et al.* 2016; Pelser *et al.* 2016; Tsukaya & Hidayat 2016; Metusala & Supriatna 2017; Aung & Jin 2018; Ma *et al.* 2019; Suetsugu 2019, 2021; Bandara *et al.* 2020). Consequently, the genus comprises more than 100 species, making it the most species-rich mycoheterotrophic genus (Suetsugu 2022). However, more extensive taxonomic studies will be required to precisely characterize the diversity of this group, for which the precise identification of individual species remains problematic.

Gastrodia foetida Koidzumi (1940: 71) was first described from Iriomote Island, Ryukyu Islands, Japan (Fig. 1A). This taxon is often a synonym of *G. nipponica* (Honda 1932: 168) Tuyama (1939: 4) described from Wakayama Prefecture, Honshu, Japan (Fig. 1B). Intriguingly, several new taxa within the *G. nipponica* species complex have been described in recent years (Hsu & Kuo 2010; Suetsugu 2013, 2014, 2016, 2017, 2021), and the *G. nipponica* species complex is now recognized as an ideal model for understanding speciation and diversification of mycoheterotrophic plants (Kishikawa *et al.* 2019; Ogaki *et al.* 2019; Suetsugu 2022; Suetsugu *et al.* 2023). Therefore, although a relatively long, narrow perianth tube (ca. 20 mm long) and a well-developed rostellum of *G. foetida* arguably show a close

Accepted by Pankaj Kumar: 8 Jan. 2023; published: 7 Feb. 2023

affinity to *G. nipponica* (Fig. 1–2), *G. foetida* can be a different entity from *G. nipponica*. To clarify the correct taxonomic status of *G. foetida*, we conducted a detailed, comparative study between *G. foetida* and *G. nipponica* based on molecular and morphological data. Subsequently, we revealed that the genetic divergence between *G. foetida* and *G. nipponica* is greater than between *G. foetida* and *G. takeshimensis* Suetsugu (2013: 375). We also showed that the taxon is distinguished from *G. nipponica* by a few morphological characters, such as a more dilated column toward a little below the middle. Therefore, we propose that *G. foetida* is recognized as a distinct species based primarily on molecular phylogenetic evidence followed by morphological evidence.

Materials and methods

Morphological observation

Morphological characteristics of *G. foetida* and *G. nipponica* were compared using herbarium specimens from KAG, KYO and TI as well as living individuals collected throughout Japan during fieldwork between 2015 and 2021 (Table S1). Morphological characters were visually observed under a Leica M165C stereomicroscope and measured using a digital caliper. The dissected flowering specimens were photographed using a Leica MC170 HD digital camera attached to a Leica M165C stereo microscope. Morphological differences among the *G. nipponica* species complex were also investigated by reviewing the relevant literature and online digitized plant collections, such as JSTOR Global Plants (http://plants.jstor.org/). At least one voucher specimen for newly collected samples from each population during our field survey was deposited in KYO and TNS. The herbarium acronyms follow Index Herbariorum (Thiers 2022).

Molecular analysis

16 *G. foetida* individuals (including eight individuals collected around the type locality [Iriomote Island, Okinawa Prefecture, southern Ryukyu, Japan]), 19 *G. nipponica* individuals (including three individuals collected around the type locality [Kamitonda-cho, Wakayama Prefecture, Honshu, Japan]), and 8 *G. takeshimensis* individuals collected around the type locality (Takeshima Island, Kagoshima Prefecture, northern Ryukyu, Japan) were used for molecular analysis (Table S1). Genomic DNA was extracted from a fresh or dried sample using the DNeasy Plant Mini Kit (QIAGEN). 18 microsatellite markers developed by previous studies (*Gtake009, Gtake011, Gtake012, Gtake015, Gtake020, Gtake021, Gtake0226, Gtake029, Gtake032, Gtake037, Gtake042, Gtake043, Gfont027, Gfont028, Gfont034, Gfont035, Gfont043, Gfont048*) were used for genotyping of the 43 ramets (Kishikawa *et al.* 2019; Ogaki *et al.* 2019). PCR amplification was performed in 5μl reactions using the QIAGEN Multiplex PCR Kit (QIAGEN). Each reaction contained the following components: 10 ng of genomic DNA, 2.5 μl of Multiplex PCR Master Mix, 0.2 μM fluorescently labeled forward primer, 0.2 μM reverse primer. Amplifications used the following setting: 95 °C for 15 min; 33 cycles at 94 °C for 30 s, 57 °C for 1.5 min and 72 °C for 1 min; and an extension at 60 °C for 30 min. Product sizes were determined using an ABI PRISM 3130 Genetic Analyzer and GeneMapper software (Applied Biosystems). The genetic relationships among the multilocus genotypes were evaluated by a neighbor-joining (NJ) tree based on the Nei's genetic distances D_A (Nei *et al.* 1983), using Populations 1.2.31 software (Langella 2007).

Results and discussion

Morphological differences between *G. foetida* and *G. nipponica*

A review and analysis of herbarium specimens, protologues, and living plants revealed few morphological characters that consistently differed between *G. foetida* and *G. nipponica* (Fig. 1–2). Nonetheless, we could find a few morphological differences between *G. foetida* and *G. nipponica*. Given that the shape of the column is one of the diagnostic characteristics for *Gastrodia* species delimitation, it is noteworthy that *Gastrodia foetida* possesses a more dilated column toward a little below the middle (2.9–3.6 mm at the widest part vs. 2.1–2.9 mm at the widest part; Fig. 3). In addition, *Gastrodia foetida* tends to have a taller stem during the flowering period (5–18 cm vs. 3–9 cm), a less open flower with sepals curved inward (vs. a more open flower with straight or spreading sepals), narrower free portions of dorsal sepals (4.5–6.1 mm wide vs. 6.2–9.0 mm wide), narrower free portions of lateral sepals (5.9–7.3 mm vs. 7.2–11.1 mm), narrower free portions of petals (2.5–3.3 × 1.9–2.5 mm vs. 3.0–4.5 × 2.5–3.8 mm) (Fig. 1–3 & 6–7).

FIGURE 1. Holotype of *Gastrodia foetida* (A) and *G. nipponica* (B). Scale bars: 50 mm.

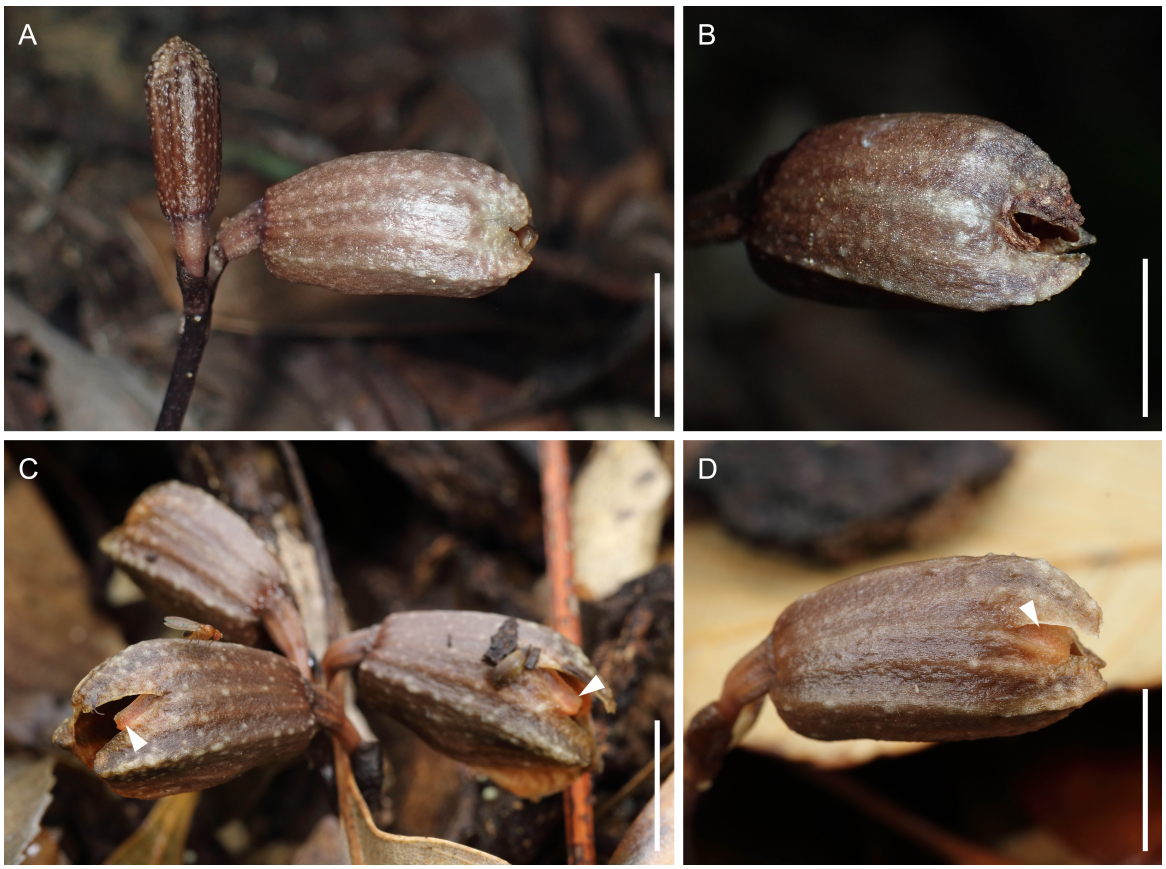

FIGURE 2. *Gastrodia foetida* and *G. nipponica* in the vicinity of each type locality. (A, C) Habit of *G. foetida* and *G. nipponica*, respectively. (B, D) Close-up of flower of *G. foetida* and *G. nipponica*, respectively. Arrows indicate conspicuous petals of *G. nipponica*. Scale bars: 10 mm.

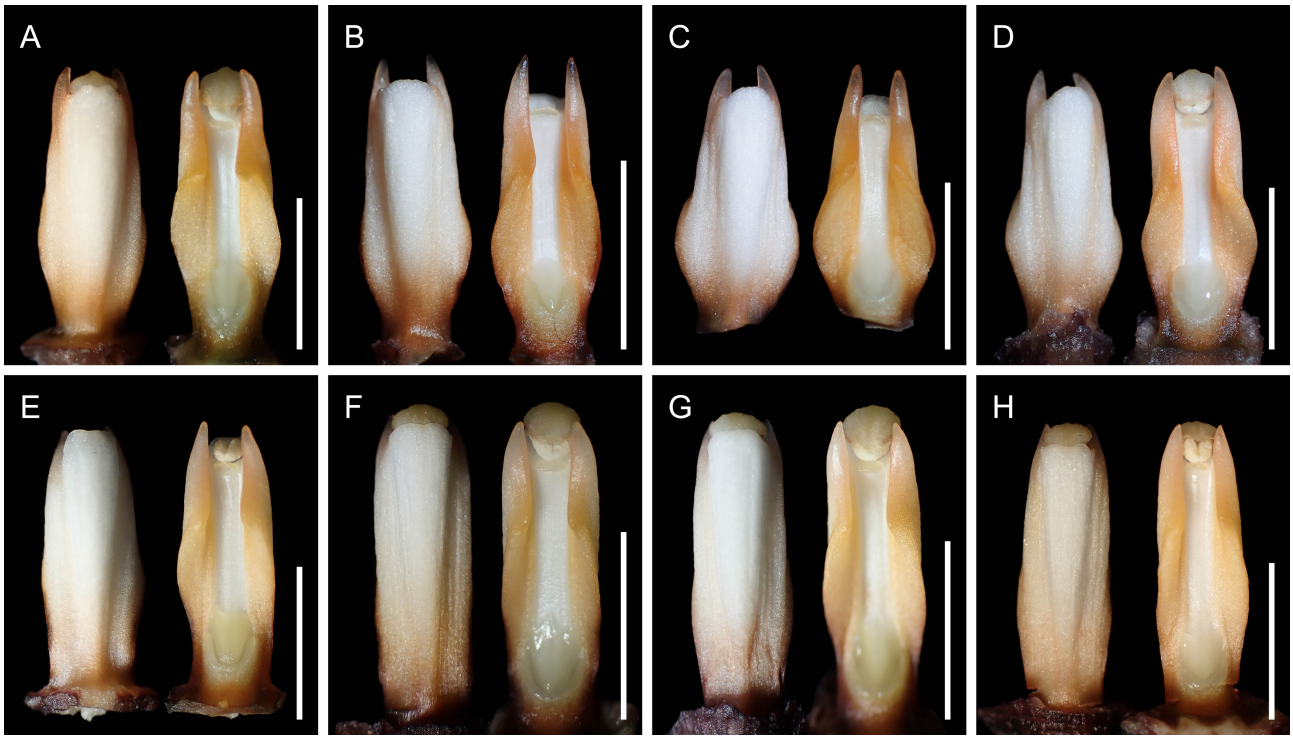

FIGURE 3. Column morphology of *Gastrodia foetida* (A–D) and *G. nipponica* (E–H). Left: dorsal view, right: ventral view. In (B) and (C), the anther cap and pollinia have been removed, while in (E), the anther cap has been removed. In all other cases, both the anther cap and pollinia remain present. Specimen ID: *Suetsugu et al. KS679* (A), *Kenji Suetsugu HNA-Gnipp-01* (B), *Koichi Ueda NND-Gnipp-01* (C–D), *Tetsuro Ikeda Ga12* (E), *Minoru Mizobuchi Ga8* (F), *Minoru Mizobuchi Ga9* (G) and *Masayuki Sato Ga14* (H). Scale bars: 5 mm.

Phylogenetic and ecological differences between *G. foetida* and *G. nipponica*

Our phylogenetic analysis revealed that three *Gastrodia* species form two strongly supported clades (*G. foetida* + *G. takeshimensis* and *G. nipponica*) (Fig. 4). The genetic divergence between *G. foetida* and *G. nipponica* is much greater than that between *G. foetida* and *G. takeshimensis*. Therefore, to better reflect the evolutionary relationships, we propose that *G. foetida* is recognized as a distinct species based primarily on molecular phylogenetic evidence followed by morphological evidence mentioned above. The alternative solution following the phylogenetic species concept would be to expand the circumscription of *G. nipponica* significantly, which would subsume *G. takeshimensis* with significant differences in labellum and column morphology. However, such an extraordinary assemblage of morphologies makes *G. nipponica* undiagnosable.

This notion is also based on the biological species concept, which defines a species as members of populations potentially interbreeding in nature because the completely cleistogamous status of *G. takeshimensis* blocks gene flow with its sympatric species *G. foetida* (Suetsugu 2022; Suetsugu *et al.* 2023). Notably, *G. foetida* and *G. nipponica* are also reproductively isolated by their disjunct distribution (Fig. 5). *Gastrodia nipponica* is restricted in mainland Japan (north of the Ryukyu Islands), whereas *G. foetida* is mainly distributed in the more southern areas (the Ryukyu Islands). Interestingly, *G. foetida* extends its distribution to Goto Island with conditions reminiscent of tropical forests, due to the Tsushima Warm Current. The distributional pattern is reasonable given that Fukuejima Island is known as the northernmost locality of some other plants mainly distributed in Ryukyu Islands (Suetsugu & Fukunaga 2017; Suetsugu 2018). We also note that *Gastrodia* sp. recorded as *G. nipponica* from Taiwan is more likely to be *G. foetida* (Hsu & Kuo 2010; Lin 2019), judging from its distributional pattern as well as morphological characteristics such as a dilated column toward a little below the middle. The more extensive investigation will be needed to reveal a precise distribution of *G. foetida* and *G. nipponica*.

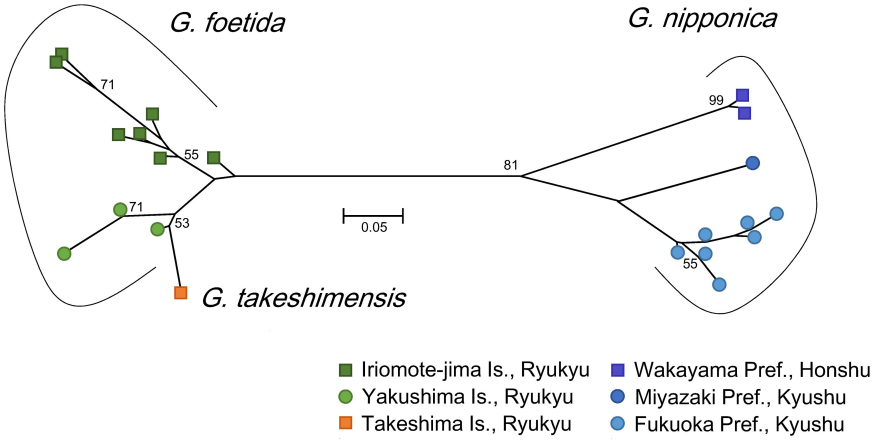

FIGURE 4. Unrooted neighbor-joining tree of *Gastrodia nipponica*, *G. foetida* and *G. takeshimensis* based on the multilocus genotypes. The scale bar indicates the Nei's genetic distances D_A (Nei *et al.* 1983). Node values indicate bootstrap support of ≥50%. Filled square: type locality of each species. Filled circle: other sampling localities.

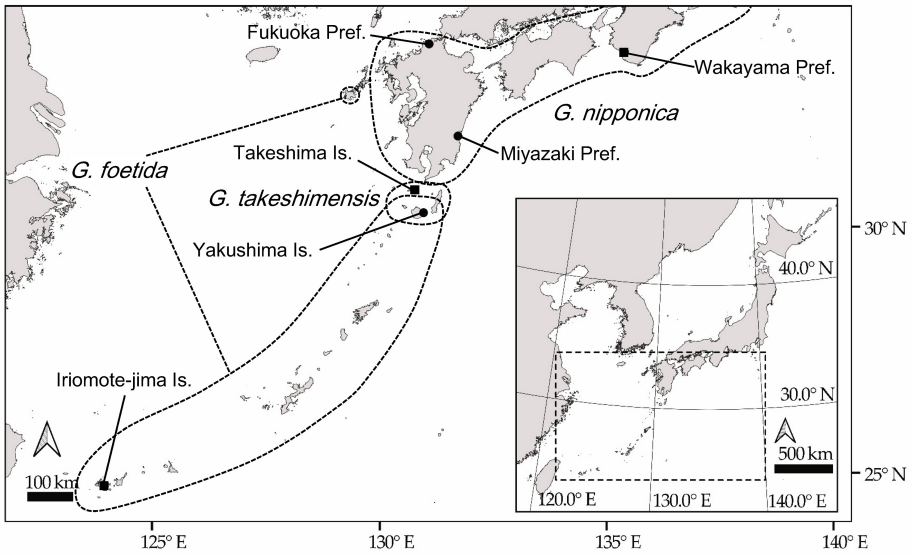

FIGURE 5. Map showing the geographical distribution of *Gastrodia nipponica*, *G. foetida* and *G. takeshimensis*. Filled square: type locality of each species. Filled circle: other sampling localities for molecular analysis.

Taxonomic treatment

Gastrodia foetida Koidzumi (1940: 71) emend. Suetsugu (Fig. 1A, 2A–B, 3A–D, 6)

Type:—JAPAN. Ryukyu Islands—Okinawa Pref.: Iriomote Island, Urata, 25 February 1940, *S. Tawada s.n.* (holotype: KYO!).

Terrestrial, mycoheterotrophic herbs. Roots slender, often produced from the junction between rhizome and inflorescence after the flowering season. Rhizome tuberous, fusiform or cylindrical, 2–8 cm long, 3–11 mm in diameter, yellowish brown, covered with numerous scales and unicellular hairs similar to roots. Stem leafless, erect, pale brown, 5–18 cm long, 1.5–3.5 mm in diameter, 3–4 nodes, with tubular sheaths. Bracts ovate, up to 5 mm long, 4 mm wide. Pedicel and ovary 1.0–1.5 cm long. Flowers 1–5, tubular, slightly nodding, resupinate, 16–22 mm long, 9–12 mm in diameter. Sepals and petals united, forming a five-lobed perianth tube. Sepals subsimilar, 16–22 mm long, connate to ca. 3/4 of their length with petals, lateral sepals connate ca. 2/3 of their length with each other, outer surface pale brown with numerous inconspicuous white warty spots, margin entire or slightly undulate; free portion of dorsal sepal ovate-triangular, obtuse at apex, 3.5–5.5 × 4.5–6.1 mm; free portions of lateral sepals triangular, usually not spreading, obtuse at apex, 4.5–5.7 × 5.9–7.3 mm. Free portions of petals ovate or elliptic, 2.5–3.3 × 1.9–2.5 mm. Lip adnate to column foot, 7.9–9.5 mm × 4.7–5.4 mm; hypochile with 2 well-developed globose calli; epichile pale yellowish

white, ovate-orbicular, base contracted, disc with 4–6-ridges, the central two ridges extending to the wide-triangular to ligulate reddish apex. Column straight, semi-cylindrical, 7.5–8.8 × 2.9–3.6 mm at the widest part and 2.1–2.5 mm wide at base; column foot well developed; lateral column wings (stelidia) distinct, narrow, the edges parallel to column, dilated toward a little below the middle of column, apex acute, slightly exceeding anther cap; rostellum well developed; stigma located at base. Anther hemiellipsoid, 1.3–1.5 mm in diameter, pollinia 2. Capsule cylindrical, 2.6–3.5 cm long, pedicel elongating to more than 30 cm long in fruit.

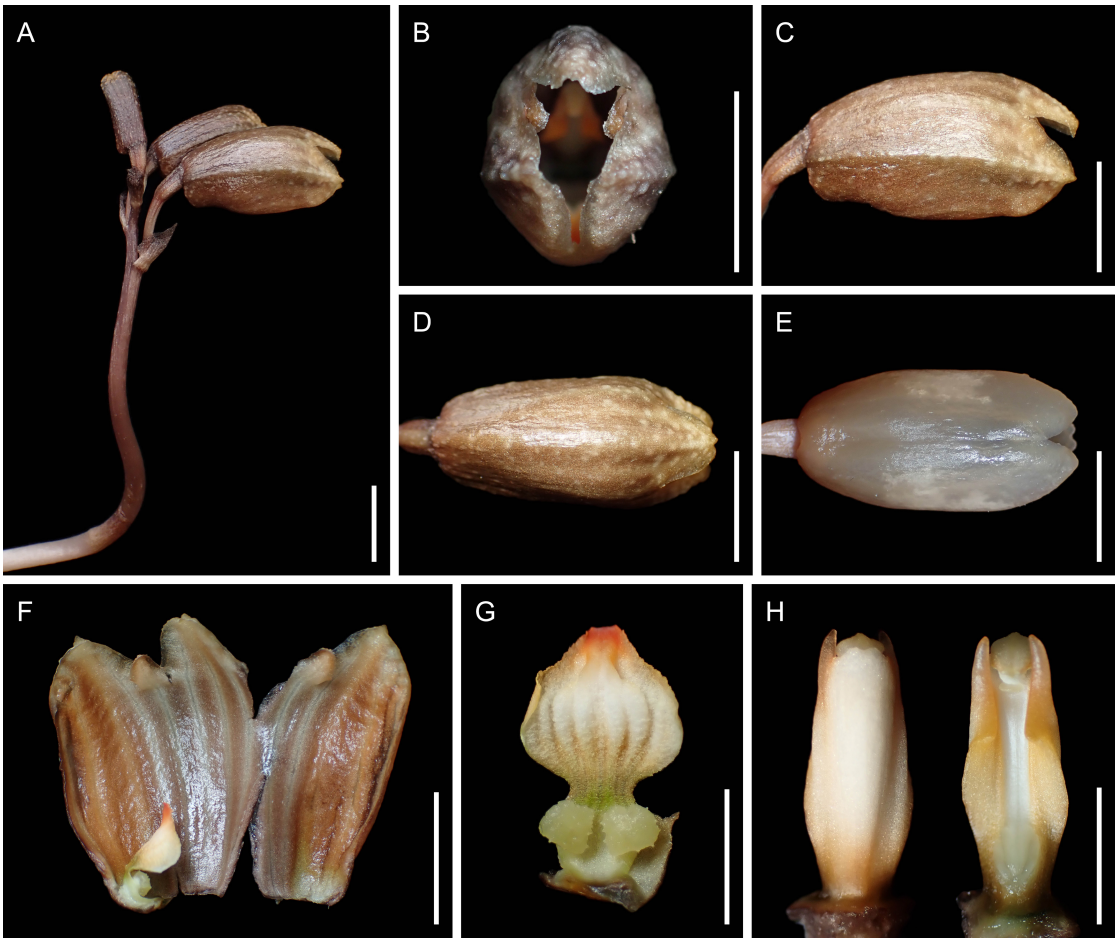

FIGURE 6. *Gastrodia foetida* (*Suetsugu et al. KS679*, TNS) collected around its type locality. (A) Plant. (B) Flower, front view. (C) Flower, lateral view. (D) Flower, dorsal view. (E) Flower, ventral view. (F) Flattened perianth tube and lip. (G) lip. (H) Column (left: dorsal view, right: ventral view). Scale bars: 10 mm (A–F) and 5 mm (G–H).

Additional specimens examined:—JAPAN. Ryukyu Islands—Okinawa Pref.: Iriomote Island, 18 March 1968, *Yamazaki et al. s.n.* (TI!); loc. cit.,13 March 1987, *Yahara et al. 873017* (TI!); Iriomote Island, Otomi-rindo, 25 February 2020, *Suetsugu et al. KS679* (TNS!, spirit collection); Ishigaki Island, Mt. Omotodake, 13 May 1971, *Kunio Nakajima 47822* (KAG!); loc. cit., 29 February 2020, *Hiroshi Kazui KS688* (TNS!, spirit collection); loc. cit., 6 March 2021, *Hiroshi Kazui KS829* (TNS!, spirit collection). Kagoshima Pref.: Yakushima Island, Anbo, 10 April 2015, *Kenji Suetsugu ANB-Gnipp-01* (TNS!, spirit collection); Yakushima Island, Anbo, along the Hanaage River, 10 April 2018, *Kenji Suetsugu HNA-Gnipp-01* (KYO!), loc. cit., 6 April 2022, *Hiroaki Yamashita Ga27* (KYO!); Yakushima Island, Tashirokaigan, 10 April 2018, *Kenji Suetsugu TSR-Gnipp-01* (TNS!, spirit collection). **Kyushu—**Nagasaki Pref.: Goto City, Kishikumachi, Nakadake, Nanatsudake, 9 May 2018, *Koichi Ueda NND-Gnipp-01* (KYO!); Goto City, Kishikumachi, Nakadake, Happongiyama, 9 May 2018, *Koichi Ueda HPG-Gnipp-01* (KYO!).

Gastrodia nipponica (Honda 1932: 168) Tuyama (1939: 4) emend. Suetsugu (Fig. 1B, 2C–D, 3E–H, 7)

Type:—JAPAN. Wakayama Pref.: Nishimuro County, Iwatamura (= Kamitonda-cho), 1 May 1931, *Kaichi Kashiyama no. 2* (holotype: TI!).

Terrestrial, mycoheterotrophic herbs. Roots slender, often produced from the junction between rhizome and inflorescence after the flowering season. Rhizome tuberous, fusiform or cylindrical, 1.5–8.5 cm long, 3–13 mm in

diameter, yellowish brown, covered with numerous scales and unicellular hairs similar to roots. Stem leafless, erect, pale brown, 3–9 cm long, 1.5–4 mm in diameter, 2–4 nodes, with tubular sheaths. Bracts ovate, up to 5 mm long, 4 mm wide. Pedicel and ovary 1.0–1.5 cm long. Flowers 1–4, tubular, slightly nodding, resupinate, 19–24 mm long, 10–14 mm in diameter. Sepals and petals united, forming a five-lobed perianth tube. Sepals subsimilar, 19–24 mm long, connate to 3/4–4/5 of their length with petals, lateral sepals connate 2/3–3/4 of their length with each other, outer surface dark brown with numerous inconspicuous white warty spots, margin entire or slightly undulate; free portion of dorsal sepal ovate-triangular, obtuse at apex, 4.5–6.0 × 6.2–9.0 mm; free portions of lateral sepals triangular, spreading, obtuse at apex, 5.2–7.2 × 7.1–12.1 mm. Free portions of petals ovate or elliptic, 3.0–4.5 × 2.5–3.8 mm. Lip adnate to column foot, 8.2–9.2 × 4.6–6.1 mm long; hypochile with 2 well-developed globose calli; epichile pale yellowish white, ovate-orbicular, base contracted, disc with 4–6-ridges, the central two ridges extending to the ligulate reddish apex. Column straight, semi-cylindrical, 7.9–9.0 × 2.1–2.9 mm at the widest part and 2.0–2.5 mm wide at base; column foot well developed; lateral column wings (stelidia) distinct, narrow, the edges parallel to column, slightly dilated toward a little below the middle of column, apex acute, not exceeding anther cap; rostellum well developed; stigma located at base. Anther hemiellipsoid, 1.4 mm in diameter, pollinia 2. Capsule cylindrical, 2.5–3.4 cm long, pedicel elongating to more than 30 cm long in fruit.

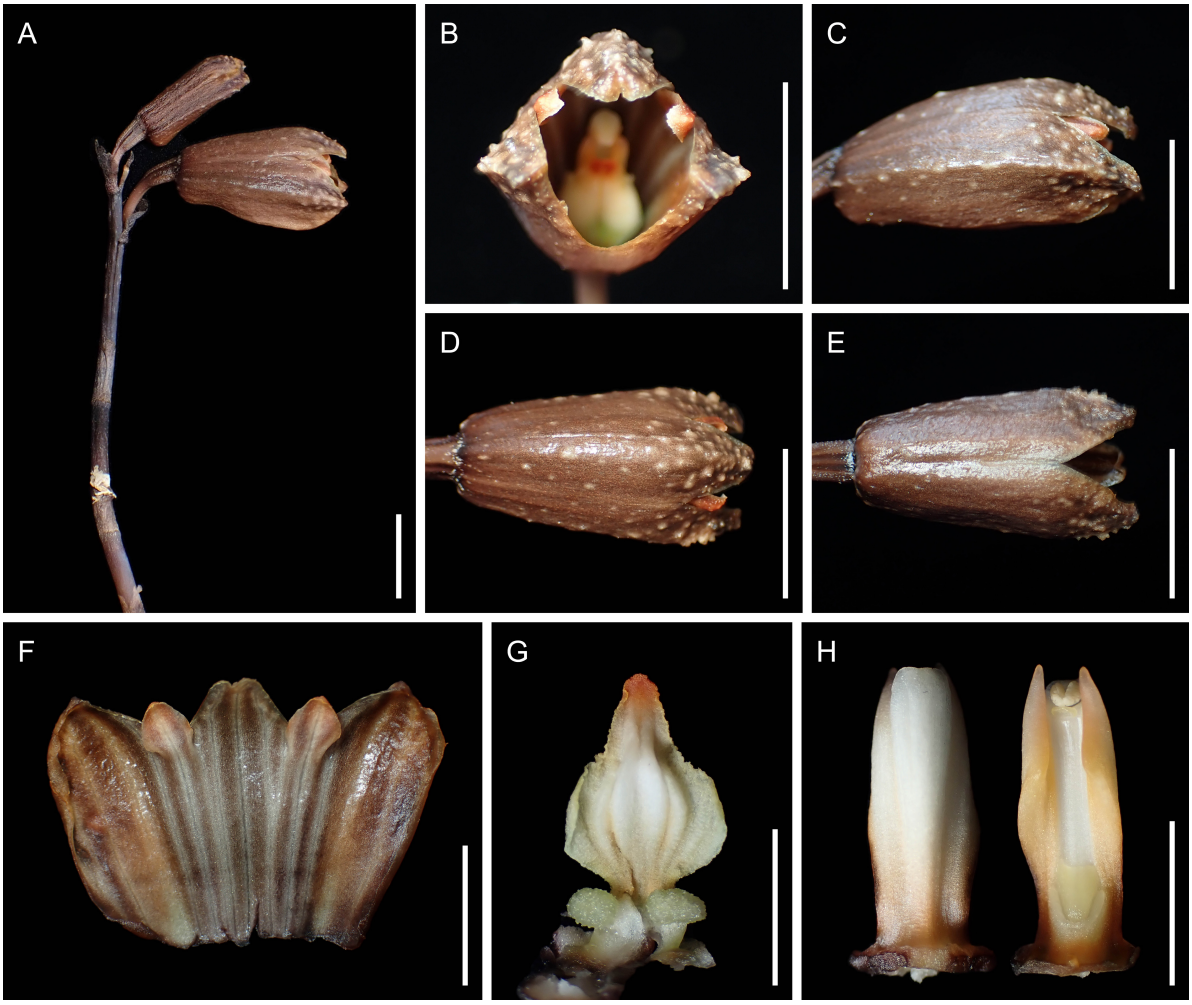

FIGURE 7. *Gastrodia nipponica* (*Tetsuro Ikeda Ga12*, KYO) collected around its type locality. (A) Plant. (B) Flower, front view. (C) Flower, lateral view. (D) Flower, dorsal view. (E) Flower, ventral view. (F) Flattened perianth tube. (G) lip. (H) Column (left: dorsal view, right: ventral view). Scale bars: 10 mm (A–F) and 5 mm (G–H).

Additional specimens examined:—**JAPAN. Kyushu—**Kagoshima Pref.: Isa City, Okuchitashiro, 25 April 2021, *Hironobu Kanemitsu Ga11* (TNS!, spirit collection). Miyazaki Pref.: Miyazaki City, Shimokitakatamachi, Heiwadai Park, 22 May 2017, *Kenji Suetsugu HWD-Gnipp-01* (KYO!). Kumamoto Pref.: Yatsushiro District, Taneyamamura, June 1909, *Tomoki Yamada s.n.* (TI!, paratype); Ashikita District, Tsunagimura, 29 May 1932, *K. Mayebara s.n.* (TI, paratype). Fukuoka Pref.: Munakata City, Yoshidome, 11 May 2015, *Kenji Suetsugu YSD-Gnipp-01* (KYO!). **Shikoku—**Kochi Pref.: Takaoka District, Nakatosa Town, Mt. Kiuchi-gamori, 31 May 2005, *Taku Miyazaki no. 505022* (TI!);

Kochi City, Haruno Town, Kamado Shrine, 10 April 2021, *Minoru Mizobuchi Ga8* (TNS!, spirit collection); Kochi City, Haruno Town, Nyakuichi-Oji Shrine, 10 April 2021, *Minoru Mizobuchi Ga9* (TNS!, spirit collection). **Honshu—** Wakayama Pref.: Nishimuro County, Iwatamura (= Kamitonda Town), 4 June 1922, *Nuizo Ui s.n.* (TI!); loc. cit., 9 May 1929, *Kaichi Kashiyama no. 1* (TI!, paratype); loc. cit., 24 May 1929, *Tozo Nakajima s.n.* (TI!); loc. cit., 13 June 1929, *Kaichi Kashiyama no. 5* (TI!, paratype); loc. cit., 24 June 1929, *Kaichi Kashiyama no. 6* (TI!, paratype); loc. cit., 17 May 1930, *Kaichi Kashiyama no. 4* (TI!, paratype); loc. cit., 24 May 1931, *Tozo Nakajima s.n.* (TI!); loc. cit., 15 May 1931, *Kaichi Kashiyama no. 3* (TI!, paratype); loc. cit., 9 May 1933, *Kaichi Kashiyama s.n.* (TI!, paratype); loc. cit., 12 May 1940, *Shuichiro Kitazima s.n.* (TI!); loc. cit., 30 April 2021, *Tetsuro Ikeda Ga12* (TNS!, spirit collection). Mie Pref.: Minamimuro County, Kiho Town, 30 April 2021, *Tetsuro Ikeda Ga13* (TNS!, spirit collection). Shizuoka Pref.: Shizuoka City, Suruga Ward, 28 April 2021, *Masayuki Sato Ga14* (TNS!, spirit collection).

Acknowledgments

The authors thank Atsushi Abe, Hiroaki Yamashita, Hironobu Kanemitsu, Hiroshi Kazui, Koichi Ueda, Koji Yonekura, Masaharu Amano, Masayuki Sato, Mikio Kashima, Minoru Mizobuchi and Tetsuro Ikeda for providing specimens and photographs for this study. The authors are grateful to the curators of KAG, KYO and TI for herbaria access. We also appreciate Tian-Chuan Hsu for the valuable discussions on the identity of the Taiwanese *Gastrodia nipponica* species complex. We are also grateful to Kazuma Takizawa and Toshihito Takagi for their technical assistance. This study was financially supported by PRESTO (JPMJPR21D6, KS).

References

Aung, Y.L. & Jin, X. (2018) *Gastrodia kachinensis* (Orchidaceae), a new species from Myanmar. *PhytoKeys* 94: 23–29. https://doi.org/10.3897/phytokeys.94.21348

Bandara, C., Priyankara, T., Atthanagoda, A.G., Lakkana, T., Ediriweera, S. & Kumar, P. (2020) *Gastrodia gunatillekeorum* (Gastrodieae, Epidendroideae, Orchidaceae), a new species from a lowland rainforest of Sri Lanka. *Phytotaxa* 436 (1): 55–62. https://doi.org/10.11646/phytotaxa.436.1.5

Brown, R. (1810) *Prodromus florae novae Hollandae et insulae Van-Diemen*. 1st ed. Taylor, London, 592 pp.

Cribb, P., Fischer, E. & Killmann, D. (2010) A revision of *Gastrodia* (Orchidaceae: Epidendroideae, Gastrodieae) in tropical Africa. *Kew Bulletin* 65: 315–321. https://doi.org/10.1007/s12225-010-9193-4

Honda, M. (1932) On a new species of *Didymoplexis*. *The Botanical Magazine (Tokyo)* 46: 168. https://doi.org/10.15281/jplantres1887.46.168

Hsu, T.C., Chung, S.W. & Kuo, C.M. (2012) Supplements to the orchid flora of Taiwan (vi). *Taiwania* 57: 271–277.

Hsu, T.-C., Fanerii, M., Yang, T.-Y.A., Pitisopa, F. & Li, C.-W. (2016) *Gastrodia isabelensis* and *G. solomonensis* (Gastrodieae, Epidendroideae, Orchidaceae): two new species representing a new generic record in the Solomon Islands. *Phytotaxa* 270 (2): 137–145. https://doi.org/10.11646/phytotaxa.270.2.6

Hsu, T.C. & Kuo, C.M. (2010) Supplements to the orchid flora of Taiwan (IV): Four additions to the genus *Gastrodia*. *Taiwania* 55: 243–248.

Kishikawa, K., Suetsugu, K., Kyogoku, D., Ogaki, K., Iga, D., Shutoh, K., Isagi, Y. & Kaneko, S. (2019) Development of microsatellite markers for the completely cleistogamous species *Gastrodia takeshimensis* (Orchidaceae) that are transferable to its chasmogamous sister *G. nipponica*. *Genes & Genetic Systems* 94: 95–98. https://doi.org/10.1266/ggs.18-00057

Koidzumi, G. (1940) Contributiones ad cognitionem florae Asiae Orientalis. *Acta Phytotaxonomica et Geobotanica* 9: 71. https://doi.org/10.18942/bunruichiri.KJ00002594589

Langella, O. (2007) Populations ver. 1.2. 30: population genetic software (individuals or populations distances, phylogenetic trees). [http://bioinformatics.org/~tryphon/populations/]

Lin, T.-P. (2019) *The orchid flora of Taiwan: A collection of line drawings*. National Taiwan University Press, Taipei, 1012 pp.

Ma, L., Chen, X., Liu, J. & Chen, S. (2019) *Gastrodia fujianensis* (Orchidaceae, Epidendroideae, Gastrodieae), a new species from China. *Phytotaxa* 391 (4): 269–272.

https://doi.org/10.11646/phytotaxa.391.4.5
Metusala, D. & Supriatna, J. (2017) *Gastrodia bambu* (Orchidaceae: Epidendroideae), a new species from Java, Indonesia. *Phytotaxa* 317 (3): 211–218.
https://doi.org/10.11646/phytotaxa.317.3.5
Nei, M., Tajima, F. & Tateno, Y. (1983) Accuracy of estimated phylogenetic trees from molecular data - II. Gene frequency data. *Journal of Molecular Evolution* 19: 153–170.
https://doi.org/10.1007/BF02300753
Ogaki, K., Suetsugu, K., Kishikawa, K., Kyogoku, D., Shutoh, K., Isagi, Y. & Kaneko, S. (2019) New microsatellite markers recognize differences in tandem repeats among four related *Gastrodia* species (Orchidaceae). *Genes & Genetic Systems* 94: 225–229.
https://doi.org/10.1266/ggs.19-00025
Ong, P. & O'Byrne, P. (2012) Two new species of *Gastrodia* from Terengganu, Peninsular Malaysia. *Malesian Orchid Journal* 10: 7–16.
Pelser, P.B., Doble, K.J.S., O'BYRNE, P., Ormerod, P. & Barcelona, J.F. (2016) *Gastrodia cajanoae* (Orchidaceae: Epidendroideae: Gastrodieae), a new species from the Philippines. *Phytotaxa* 266 (1): 53–56.
https://doi.org/10.11646/phytotaxa.266.1.9
Suetsugu, K. (2013) *Gastrodia takeshimensis* (Orchidaceae), a new mycoheterotrophic species from Japan. *Annales Botanici Fennici* 50: 375–378.
https://doi.org/10.5735/085.050.0613
Suetsugu, K. (2014) *Gastrodia flexistyloides* (Orchidaceae), a new mycoheterotrophic plant with complete cleistogamy from Japan. *Phytotaxa* 175 (5): 270–274.
https://doi.org/10.11646/phytotaxa.175.5.5
Suetsugu, K. (2016) *Gastrodia kuroshimensis* (Orchidaceae), a new mycoheterotrophic and complete cleistogamous plant from Japan. *Phytotaxa* 278 (3): 265–272.
https://doi.org/10.11646/phytotaxa.278.3.6
Suetsugu, K. (2017) Two new species of *Gastrodia* (Gastrodieae, Epidendroideae, Orchidaceae) from Okinawa Island, Ryukyu Islands, Japan. *Phytotaxa* 302 (3): 251–258.
https://doi.org/10.11646/phytotaxa.302.3.4
Suetsugu, K. (2018) The northernmost locality of the mycoheterotrophic orchid *Gastrodia flexistyloides* from Fukuejima island, Nagasaki Prefecture, Japan. *Japan. Journal of Japanese Botany* 93: 61–64.
Suetsugu, K. (2019) *Gastrodia amamiana* (Orchidaceae; Epidendroideae; Gastrodieae), a new completely cleistogamous species from Japan. *Phytotaxa* 413 (3): 225–230.
https://doi.org/10.11646/phytotaxa.413.3.3
Suetsugu, K. (2021) *Gastrodia longiflora* (Orchidaceae: Epidendroideae: Gastrodieae), a new mycoheterotrophic species from Ishigaki Island, Ryukyu Islands, Japan. *Phytotaxa* 502 (1): 107–110.
https://doi.org/10.11646/phytotaxa.502.1.9
Suetsugu, K. (2022) Living in the shadows: *Gastrodia* orchids lack functional leaves and open flowers. *Plants, People, Planet* 4: 418–422.
https://doi.org/10.1002/ppp3.10281
Suetsugu K. & Fukunaga, H. (2017) A new locality of *Lecanorchis tabugawaensis* (Orchidaceae) from Fukuejima Island, Nagasaki Prefecture, Japan. *Bunrui* 17: 71–73.
https://doi.org/10.18942/bunrui.01701-11
Suetsugu, K., Fukushima, K., Makino, T., Ikematsu, S., Sakamoto, T. & Kimura, S. (2023) Transcriptomic heterochrony and completely cleistogamous flower development in the mycoheterotrophic orchid *Gastrodia*. *New Phytologist* 237: 323–338.
https://doi.org/10.1111/nph.18495
Suetsugu, K., Suleiman, M. & Tsukaya, H. (2018) A new species of *Gastrodia* (Gastrodieae, Epidendroideae, Orchidaceae) from the Maliau Basin Conservation Area, Sabah, Borneo. *Phytotaxa* 367 (1): 78–84.
https://doi.org/10.11646/phytotaxa.367.1.9
Tan, Y.H., Hsu, T.C., Pan, B., Li, J.W. & Liu, Q. (2012) *Gastrodia albidoides* (orchidaceae: Epidendroideae), a new species from Yunnan, China. *Phytotaxa* 66 (1): 38–42.
https://doi.org/10.11646/phytotaxa.66.1.6
Thiers, B. (2022) Index Herbariorum, New York Botanical Garden. Available from: http://sweetgum.nybg.org/science/ih/ (6 October, 2022)
Tsukaya, H. & Hidayat, A. (2016) A new species of *Gastrodia* (Orchidaceae: Gastrodieae, Epidendroideae) from Java. *Phytotaxa* 273 (1): 77–80.
https://doi.org/10.11646/phytotaxa.273.1.9
Tuyama, T. (1939) Plantæ Boninenses Novæ vel Criticæ. XII. *The Botanical Magazine (Tokyo)* 53: 1–7.
https://doi.org/10.15281/jplantres1887.53.1