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***Gastrodia amamiana* (Orchidaceae; Epidendroideae; Gastrodieae), a new completely cleistogamous species from Japan**

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Introduction

Gastrodia Brown (1810: 330; Gastrodieae, Epidendroideae) is a mycoheterotrophic leafless genus that is distributed throughout the temperate and tropical regions of Asia, Oceania, Madagascar and Africa (Cribb *et al.* 2010, Hsu & Kuo 2010, Suetsugu *et al.* 2018a) and characterized by fleshy tubers, united tepals and two mealy pollinia that lack caudicles (Cribb *et al.* 2010, Hsu & Kuo 2010, Suetsugu *et al.* 2018a,b). Several recent studies have re-examined the diversity of *Gastrodia* in many Asian countries (Hsu *et al.* 2012, 2016, Ong & O’Byrne 2012, Tan *et al.* 2012, Suetsugu 2013b, 2014, 2016, 2017, Huang *et al.* 2015, 2018, Tsukaya & Hidayat 2016, Metusala & Supriatna 2017, Pelser *et al.* 2016, Suetsugu *et al.* 2018a,b). As a result, the genus now comprises ca. 100 species, thereby making it the most diverse mycoheterotrophic genus (Hsu *et al.* 2016, Suetsugu 2017, Suetsugu *et al.* 2018a,b). However, it is likely that the distribution and diversity of *Gastrodia* species remain underestimated because plants are easily overlooked in the field due to their short flowering seasons and small size (Hsu *et al.* 2016, Suetsugu 2017, Suetsugu *et al.* 2018b).

As anticipated, an unknown *Gastrodia* taxon was discovered during a recent botanical survey of the lowland evergreen forest of Amami-Oshima and Tokunoshima Islands, Japan. Detailed morphological examination revealed that the floral morphology differs from that of other known species. Accordingly, I describe my collection as a new species and provide a detailed morphological account.

Taxonomic Treatment

***Gastrodia amamiana* Suetsugu, *sp. nov.* (Figs. 1, 2)**

Type:—JAPAN. Ryukyu Islands: Kagoshima Pref., Amami-Oshima Island, Amami City, Naze, 3 March 2019, Morita *et al.* AN003 (holotype: TNS, a flower in the spirit collection).

Terrestrial, mycoheterotrophic herbs. Rhizome tuberous, fusiform or cylindrical, 3–8 cm long, 4–9 mm in diameter, yellowish brown, covered with numerous scales. Stem leafless, erect, pale brown, 2–4 cm long, 2–3 mm in diameter. Bracts ovate, ca. 4 mm long. Pedicel and ovary 6–10 mm long. Flowers 1–5, tubular, angled slightly upward, resupinate, 10–13 mm long, ca. 7 mm in diameter. Sepals and petals united, forming a 5-lobed perianth tube; perianth tube entirely closed. Sepals similar, 10–13 mm long, connate ca. 2/3 the length of the petals, lateral sepals connate ca. 3/5 their length with each other, outer surface dark brown, densely verrucose, margins entire; free portion of dorsal sepal straight, ovate-triangular, retuse, ca. 4.5 × 4.5 mm; free portions of lateral sepals spreading, apex obtuse. Free portions of petals ovate or elliptic, ca. 3 × 2 mm. Lip adnate to column foot, 6–7 mm long; hypochile with 2 degenerate calli; epichile red-brownish, ovate-triangular, base contracted, with 2(–4) indistinct ridges elevated on upper portion, and 2 ridges extending to the ligulate apex. Column straight, clavate, 5.5–6.5 mm, white tinged with grayish brown at base, with a pair of lateral wings; column foot present; lateral wings red, incurved, edges parallel to column; rostellum absent; stigma located slightly above middle. Anther hemispheric, ca. 1 mm in diameter, pollinia 2.

Additional specimen examined:—JAPAN. Ryukyu Islands: Kagoshima Pref., Tokunoshima Island, Amagi-cho, 27 March 2019, Morita TA009 (TNS, a flower in the spirit collection).



FIGURE 1. *Gastrodia amamiana* at the type locality. A. Flowering plants. B. Flower. *Gastrodia amamiana*, Tokunoshima Island, Japan. C. Flowering plants. D. Flower. Photography by Hidekazu Morita.

Distribution and phenology:—To date, the distribution of *G. amamiana* is restricted to two localities (the type locality on Amami-Oshima Island and the other locality on Tokunoshima Island). In both, ca. 20 flowering individuals were found in a dense forest dominated by *Castanopsis sieboldii* (Makino) Hatusima. Flowering March, fruiting April.

Taxonomic notes:—*Gastrodia amamiana* is morphologically similar to *G. clausa* Hsu, Chung & Kuo (2012: 271), primarily because both possess dark brown, densely verrucose and completely cleistogamous flowers (Table 1). However, *G. amamiana* can be distinguished by its lip morphology (well developed, ca. 6–7 mm long vs. peloric, <5 mm long), column foot condition (prominent vs. obscure), and column morphology (without ventral appendage vs. with a prominent ventral appendage). In addition, *G. amamiana* is somewhat similar to *G. kuroshimensis* Suetsugu (2016: 266), with both species fully cleistogamous. However, *G. amamiana* can be easily distinguished by its smaller stature at flowering (2–4 cm vs. 8–17 cm) and anther cap morphology (independent vs. joined with column). Finally,

G. amamiana is also similar to *G. uraiensis* Hsu & Kuo (2010: 244). However, *G. amamiana* can be distinguished by its floral condition (cleistogamous vs. chasmogamous), rostellum condition (degenerate vs. ca. 0.7 mm long), stigma position (slightly above middle vs. base), and hypochile condition (degenerate vs. developed; Table 1).

Reproductive notes:—It is notable that the flowers of *G. amamiana* remained completely closed throughout the flowering period (Fig. 1). It is known that most cleistogamous plants adopt mixed pollination strategies, producing some chasmogamous flowers for outcrossing (Culley & Klooster 2007). In contrast, *G. amamiana* appears to be completely cleistogamous species that is obligately self-pollinating. Nevertheless, such obligate self-pollination is relatively common among *Gastrodia* species, having been observed in at least four species: *G. clausa*, *G. kuroshimensis*, *G. takeshimensis* Suetsugu (2013: 375), and *G. flexistylodes* Suetsugu (2014: 270). However, it should be noted that the complete cleistogamous status of *G. amamiana* will need to be confirmed using both the phenological observation of numerous individuals under natural conditions (Culley & Klooster 2007) and genetic analysis (Kishikawa *et al.* 2019). In particular, microsatellite analysis of the completely cleistogamous species *G. clausa* and *G. amamiana* and the putative chasmogamous sister species *G. uraiensis* could help elucidate whether the species are subject to either current or historical outbreeding.

Importantly, the evolutionary advantage of complete cleistogamy among *Gastrodia* species remains unclear. Because mycoheterotrophic plants often grow on the dense forest floor, where they are shaded by woodland or scrub, it is plausible that mycoheterotrophy developed as an adaptation for survival under low-light conditions (Bidartondo 2005). However, such low-light environments are unsuitable for most of the insect species and, therefore, would limit reproduction (Herrera 1997). Indeed, it appears that most mycoheterotrophic species (especially nectarless species) have abandoned insect-mediated pollination in favor of cleistogamy (Suetsugu 2013a, 2015, but also see Martos *et al.* 2015, Suetsugu 2018). Therefore, the fully cleistogamy observed among *Gastrodia* species is likely a means of reproductive assurance that compensates for the pollinator limitation owing to these species lack of nectar and their pollinator-unfriendly habitat.

TABLE 1. Morphological comparison among *Gastrodia amamiana* and related species.

Character	<i>G. amamiana</i>	<i>G. clausa</i>	<i>G. kuroshimensis</i>	<i>G. uraiensis</i>
Plant height	2–4 cm	2–4 cm	8–17 cm	1–6 cm
Floral condition	cleistogamous	cleistogamous	cleistogamous	chasmogamous
Perianth tube size	10–13 mm long	9–13 mm long	11–13 mm long	11–13 mm long
Perianth tube condition	densely verrucose, dark brown	densely verrucose, dark brown	verrucose, dark greenish brown	densely verrucose, dark brown
Column shape	clavate, ca. 6 mm long without any prominent appendage	clavate, ca. 6 mm long with a prominent ventral appendage	semi-cylindrical, ca. 7 mm long without any prominent appendage	terete, ca. 6–7 mm long without any prominent appendage
Rostellum condition	absent	absent	absent	just below the anther cap
Position of stigma	slightly above middle	near middle	slightly above middle	basal
Anther cap	independent	independent	joined with column	independent
Lip size	6–7 mm long	peloric, less than 5 mm long	8–10 mm long	6–7 mm long
Lip connection	joined with the perianth tube	joined with perianth tube	joined with the perianth tube	adnate to the column foot
Number of ridges on the lip	2–4	none	2–4	4
Hypochile	with two degenerate calli	without any appendages	with two degenerate calli	with two developed globose calli

Data of related species from Hsu *et al.* (2010, 2012) and Suetsugu (2016).

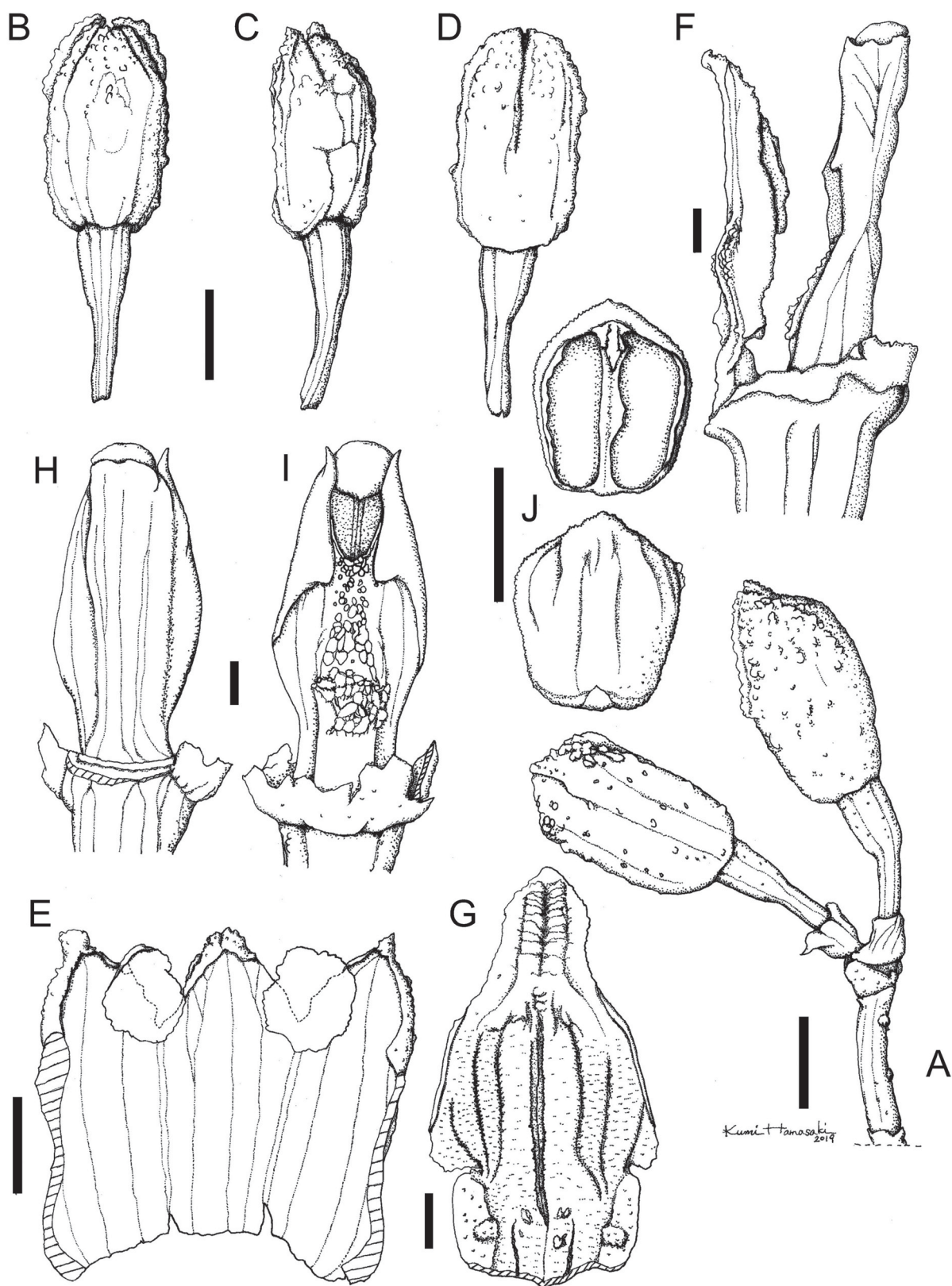


FIGURE 2. *Gastrodia amamiana*. A. Habit. B. Flower, top view. C. Flower, side view. D. Flower, bottom view. E. Flattened perianth tube. F. Column and lip. H. Column, top view. I. Column, bottom view. G. Lip. J. Anther cap. A–D. Bar = 5 mm. E. Bar = 3 mm. F–J. Bar = 1 mm. Drawing by Kumi Hamasaki.

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