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Living in the shadows: *Gastrodia* orchids lack functional leaves and open flowers

1 | INTRODUCTION

From bryophytes to angiosperms, most terrestrial plants form mycorrhizal mutualisms in which plants provide carbon to fungi in exchange for minerals. However, in some non-photosynthetic plants called mycoheterotrophic plants, the usual polarity of carbon movement from plant to their mycorrhizal fungi is reversed, and these mycoheterotrophic plants exploit all the nutrition from the fungi (Leake, 1994). Mycoheterotrophic plants typically remain below-ground most of the time in the dark forest understory, and their aboveground organs appear through the leaf litter only during the short flowering and fruiting period (Leake, 1994; Thorogood, 2019; Thorogood & Mat Yunoh, 2021). A prime example of this is the leafless orchid genus *Gastrodia* with more than 100 species distributed throughout the temperate and tropical regions of Asia, Oceania, Madagascar, and Africa (Suetsugu, 2019, 2021). *Gastrodia* is an essential taxon to understand the mechanism of species diversification in mycoheterotrophs because it is the most species-rich genus among mycoheterotrophic plants.

In Asia and the Pacific, *Gastrodia* species are used as medicine and food—*Gastrodia elata* was used as a traditional Chinese medicine for dizziness and neuralgia as early as 100 AD, while *Gastrodia cunninghamii* rhizomes are regarded as a delicacy by the Māori of New Zealand (Liu et al., 2021). *Gastrodia* sepals and petals are fused into a flower tube expanded basally to accommodate a basal platform between the column and the lip; this gives the flowers a rather unappealing stomach-like appearance that explains the Greek derivation of the name *Gastrodia*, which means “like a stomach” (Liu et al., 2021). Recently, several *Gastrodia* species with unappealing and easily overlooked but ecologically and evolutionarily intriguing floral morphology have been described in Ryukyu Islands (Japan) and Taiwan (Hsu et al., 2012; Suetsugu, 2013b, 2014, 2016, 2019). Some species of *Gastrodia*, such as *G. elata*, reach 60–100 cm in height during flowering period. In contrast, the inflorescences of these recently described *Gastrodia* species are only 3–15 cm long (Figure 1). After emerging from the leaf litter in the spring, their flowers remain closed throughout their approximately 1-month flowering period. This

trait called cleistogamy, in which plants produce only closed and self-pollinating flowers, has evolved in more than 30 angiosperm lineages (Culley & Klooster, 2007). However, complete cleistogamy—the absolute absence of open flowers—has been rarely recognized, consistent with Darwin's doubts about its existence (Pannell, 2009). Thus, *Gastrodia* is probably the only genus that contains species with completely cleistogamous flowers as confirmed by intensive monitoring. An overview of *Gastrodia* biology is presented here, emphasizing the reproductive biology of these recently described species that neither photosynthesize nor bloom.

2 | FUNGAL ASSOCIATIONS: INDIRECT SAPROPHYTES

Despite being achlorophyllous, mycoheterotrophic plants do not directly parasitize other plants, or obtain carbon from decaying plant or animal matter (Leake, 1994). Therefore, these organisms are now referred to as mycoheterotrophs rather than saprophytes, a term that was once widely used, because this better reflects their unique nutritional dependence on fungal carbon (Leake, 1994). Most mycoheterotrophic plants obtain carbon from photosynthetic plants via shared mycorrhizal networks (Leake, 1994). However, some mycoheterotrophic orchids depend on saprotrophic fungi, which decompose dead wood and decaying litter (Martos et al., 2009; Ogura-Tsujita et al., 2009; Suetsugu et al., 2020). For example, *G. elata* has been found to exploit carbon that was fixed in the past from deadwood (Suetsugu et al., 2020). Atmospheric nuclear bomb testing during the mid-20th century increased the ^{14}C concentration. However, the atmospheric ^{14}C concentration gradually decreased after the ban on atmospheric nuclear testing in 1963. Therefore, the carbon age (the time since carbon was fixed from atmospheric CO_2 by photosynthesis) can be estimated by measuring the concentration of ^{14}C . Suetsugu et al. (2020) concluded that *G. elata* acquired ^{14}C -enriched bomb carbon from deadwood via saprotrophic fungi because it contained high concentrations of ^{14}C , dating from over 10 years before the sampling period. Although no plants directly consume dead organic

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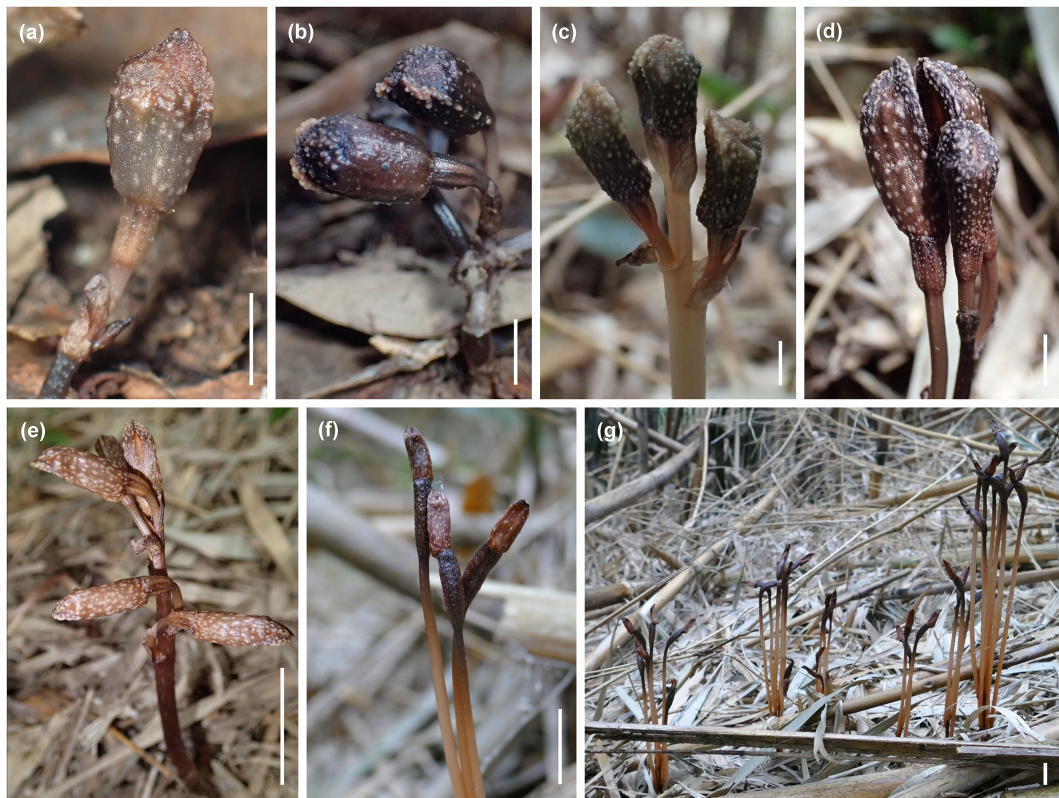


FIGURE 1 Flowers and fruits of completely cleistogamous *Gastrodia* species recently described from Japan and Taiwan. (a) *Gastrodia clausa*. (b) *Gastrodia amamiana*. (c) *Gastrodia takeshimensis*. (d–g) *Gastrodia flexistyloides* at the flowering (d) and fruiting (e–g) stages. (g) Although elongated pedicels are present to facilitate seed dispersal by wind, their perianth tubes remain enclosed, indicating they were unopened throughout their flowering season. (a)–(d) Scale bar, 5 mm. (e–g) Scale bar, 2 cm. Photographs: Kenji Suetsugu

matter, these findings indicate that some mycoheterotrophic orchids are indirectly saprophytic, utilizing wood debris in the forest carbon cycle.

It is a great mystery why saprotrophic fungi, which usually gain their nutrition from organic matter (but also see Thoen et al., 2020), form symbiotic relationships with mycoheterotrophic plants. Nevertheless, because mycoheterotrophic plants rely entirely on their mycorrhizal fungi for carbon, adaptation to different fungal associates can result in isolation, leading to speciation in mycoheterotrophic plants (Merckx & Bidartondo, 2008; Taylor et al., 2003). For instance, *Gastrodia confusa* is predominantly associated with species of *Mycena* that are found only in bamboo thickets and is potentially restricted to the dense bamboo understory as a consequence of this specialized partnership (Kinoshita et al., 2016). Adaptation to vegetation-specific fungal communities may have triggered habitat differentiation and subsequent speciation across the genus *Gastrodia*.

3 | REPRODUCTIVE BIOLOGY

Their exclusive reliance on fungi for nutrition allows mycoheterotrophic plants to colonize shady areas, thereby avoiding competition with green plants (Bidartondo, 2005). Plants that thrive in such low-light environments are less attractive to potential pollinators,

such as bees, which prefer brightly lit, green plant-filled areas (Herrera, 1995, 1997). Therefore, although interactions with pollinators are considered to be the driving force behind the astonishing diversification of orchids (Nilsson, 1992), autonomous self-pollination is relatively widespread for mycoheterotrophic orchids (Leake, 1994; Suetsugu, 2013a, 2015; Zhou et al., 2012). Self-pollination might be an adaptation to ensure reproduction, compensating for the deficiency of pollinators in the habitat.

Although some *Gastrodia* species depend on specialized pollinators for reproduction (Martos et al., 2015; Suetsugu, 2018), many, including *Gastrodia confusoides*, *Gastrodia damingshanensis*, *Gastrodia nipponicoides*, and *Gastrodia okinawaensis*, have an autonomous selfing strategy, albeit they only bear open flowers (Hsu et al., 2012; Hu et al., 2014; Suetsugu, 2017b). Furthermore, complete cleistogamy, in which plants produce only closed and self-pollinating flowers, has been reported in five *Gastrodia* species: *Gastrodia clausa* (Hsu et al., 2012; Suetsugu et al., 2013), *Gastrodia takeshimensis* (Suetsugu, 2013b), *Gastrodia flexistyloides* (Suetsugu, 2014), *Gastrodia kuroshimensis* (Suetsugu, 2016), and *Gastrodia amamiana* (Suetsugu, 2019) (Figure 1). In all *Gastrodia* species, the sepals and petals are partially fused, forming a five-lobed perianth tube. In the species with chasmogamous (open, typically insect-pollinated) flowers, the dehiscence zone at the free portion of the sepals splits open during flowering (Figure 2), whereas in the cleistogamous species, it remains incomplete and fused

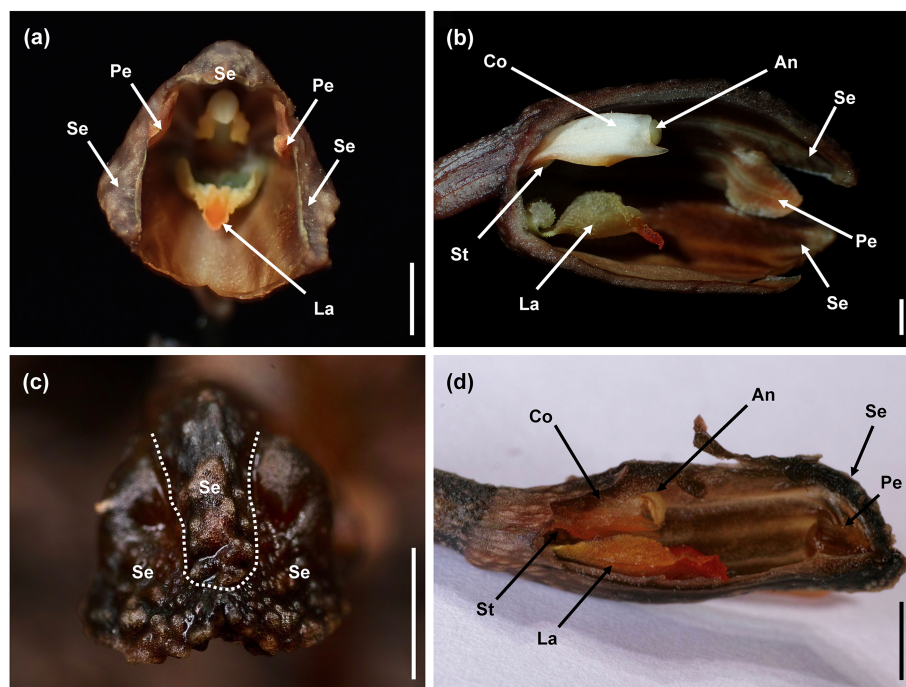


FIGURE 2 Comparative floral morphology of chasmogamous and completely cleistogamous *Gastrodia* sister species. (a, b) *Gastrodia nipponica*. (c, d) *Gastrodia takeshimensis*. The incomplete dehiscence zone at the free portion of the sepal in *Gastrodia takeshimensis* is indicated by dashed lines. Se, sepal; Pe, petal; La, labellum; An, anther cap; Co, column; St, stigma. Scale bar, 3 mm. Photographs: (a) Kenji Suetsugu and (b–d) Hiroaki Yamashita

even after flowering (Figures 1 and 2). Self-pollination in the cleistogamous species is facilitated by the loss of the rostellum, a physical barrier between the male and female parts, whereas in their chasmogamous sister species, the beak-like rostellum can act as a barrier preventing autonomous self-pollination. However, most cleistogamous plants, such as *Viola*, also produce normal open flowers. Therefore, notably, although hundreds of individuals of these cleistogamous *Gastrodia* species have been observed on multiple islands, no plants with open flowers were observed (Suetsugu, 2017a).

Reproductive barriers are required to isolate populations by preventing gene exchange, which results in accumulation of differences in phenotypic traits, leading to speciation (Rundle & Nosil, 2005). Complete cleistogamy can be an ultimate cause of reproductive isolation from other individuals as it physically blocks the potential gene flow between closely related species. Intriguingly, the range of completely cleistogamous taxa is generally nested within that of their outcrossing sisters (Kishikawa et al., 2019; Suetsugu, 2013b, 2016, 2017a). The coexistence among cleistogamous species and their outcrossing relatives strongly suggests that complete cleistogamy has arguably driven speciation, contributing to the maintenance of their reproductive integrity (Kishikawa et al., 2019; Ogaki et al., 2019).

4 | THE ABSOLUTE ABSENCE OF BLOOMING

Unreliable pollinator services and the cost of maintaining open flowers probably drove the completely cleistogamous *Gastrodia* species to abandon insect-mediated pollination (Suetsugu, 2014, 2016). However, complete cleistogamy can be a risky strategy, as the progeny will be less adaptive to changes in spatially and temporally

heterogeneous habitats (Culley & Klooster, 2007; Pannell, 2009). Darwin (1877) was skeptical about reported cases of complete cleistogamy, recommending further study under natural conditions to verify that no open flowers are produced. Nonetheless, it has since been observed in several species other than *Gastrodia*, including some other orchids and grasses (Culley & Klooster, 2007). However, most reports of complete cleistogamy are based on only a few individuals. This is especially true for orchids often grown in artificial environments such as greenhouses (Culley & Klooster, 2007). Based on recent reviews, the existence of species with no open flowers remains elusive (Culley & Klooster, 2007; Pannell, 2009), consistent with Darwin's doubts.

Therefore, *Gastrodia* is probably the sole genus that contains the completely cleistogamous species, which has been verified by a decade of monitoring hundreds of individuals. Preliminary microsatellite analysis has also supported the cleistogamous status of some *Gastrodia* species (Kishikawa et al., 2019; Ogaki et al., 2019). There were no polymorphic loci observed from the microsatellites of *G. takeshimensis* individuals collected in a locality, despite several polymorphic loci in its sister species *Gastrodia nipponica* in another locality; the allelic fixation in *G. takeshimensis* reflects repeated selfing over many generations, entirely eradicating polymorphic loci (Kishikawa et al., 2019). Although most cases of cleistogamy are not truly “closed” marriage, given that they include some open flowers (Pannell, 2009), these *Gastrodia* species illustrate that complete cleistogamy—the absolute absence of open flowers—does exist in plants. Given that complete cleistogamy has evolved independently in this genus (Ogaki et al., 2019), the genus *Gastrodia* provides a unique opportunity to investigate the ecological significance, evolutionary history, and genetic mechanisms underlying the evolution of complete cleistogamy.

5 | CONCLUDING REMARKS

The absence of blooming and photosynthesis, which are fundamental to the common understanding of plants, forces us to think about what defines a plant. Selfing lineages tend to suffer a higher extinction risk, due to their accumulated deleterious mutations and slower rate of evolution (Wang et al., 2021; Wright et al., 2013). Although the transition from outcrossing to selfing is one of the most common evolutionary changes in plants, estimates of self-fertilization rates based on genetic markers indicate that very few plant species, if any, are completely selfing (Wright et al., 2013). Darwin could not believe that complete selfing could be maintained in the long term (Pannell, 2009), and his intuition is partially supported by the fact that even predominant selfers like *Arabidopsis thaliana* rarely outcross and exhibit genomic evidence of recombination (Pannell, 2009; Wright et al., 2013). This low level of outcrossing is probably enough to overcome the adverse consequences of an absence of effective recombination, including deleterious mutations and slower adaptation (Wright et al., 2008).

Consequently, completely cleistogamous *Gastrodia* species might be at an evolutionary cul-de-sac, being observed by chance before going extinct. The repeated emergence of completely cleistogamous taxa might be explained by a trade-off of short-term and long-term fitness (e.g., pollination limitation due to heterotrophic lifestyle, such as resource limitation and pollinator-hostile shaded habitat vs. maintenance of genetic diversity). Noteworthy, many of the autogamous or cleistogamous taxa were discovered from small islands, such as Ryukyu Islands (Hsu et al., 2012; Suetsugu, 2017a). Island populations are typically characterized by low genetic diversity due to population foundation (i.e., founder effect), geographical isolation from mainlands (i.e., limited immigration), and small population size (Jamieson, 2011). In fact, little genetic diversity is detected even in chasmogamous *Gastrodia* species on small islands harboring their cleistogamous sisters (Kishikawa et al., 2019; Ogaki et al., 2019). The low genetic variation decreases the value of cross-pollination because pollination from other genetically identical individuals is essentially the same as self-pollination. Therefore, island colonization may be one of the factors of evolution of complete cleistogamy.

To gain further insights into the evolution of complete cleistogamy, it will be fascinating to determine the evolutionary scale at which the trait persists in *Gastrodia*. Genome-wide genetic analysis methods, such as restriction site-associated DNA sequencing (RAD-seq), may assist in identifying the evolutionary stability of cleistogamy, by quantifying, for instance, the numbers of generations of repeated selfing and the accumulation of deleterious mutations. Focusing on non-blooming and non-photosynthetic *Gastrodia* species, which do not conform to the conventional image of plants, will paradoxically help to improve our understanding of plants more broadly.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS CONTRIBUTION

KS designed and performed the research, collected, and interpreted the data, and wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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achlorophyllous plant, breeding system, complete cleistogamy, mycoheterotroph, pollination biology, reproductive assurance, saprophyte, speciation

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