Neglected plant parasites: Mitrastemonaceae

Teixeira-Costa, Luiza
Suetsugu, Kenji

(Citation)
Plants, People, Planet,5(1):5-13

(Issue Date)
2023-01
(Resource Type)
journal article
(Version)
Version of Record

Received: 9 June 2022 | Revised: 1 August 2022 | Accepted: 17 August 2022

DOI: 10.1002/ppp3.10322

FLORA OBSCURA

FLORA OBSCURA Plants People Planet PPP Open Access

Neglected plant parasites: Mitrastemonaceae

1 | INTRODUCTION

Mitrastemonaceae are a small, yet remarkable family of parasitic flowering plants. They are composed of a single genus, *Mitrastemon* Makino (sometimes misspelled as "*Mitrastema*" or "*Mitrastemma*"), for which a total of six taxa were described since the early 1900s (Meijer & Veldkamp, 1993). Most of these taxa have been synonymized and at present only two species are recognized: *Mitrastemon matudae* Yamam., known from Mexico, Central America, and Colombia; and *Mitrastemon yamamotoi* Makino, found across Southeast Asia, Taiwan, Japan, and parts of India (Nickrent, 2020). Both species are devoid of roots, stems, and regular leaves. They appear as cream-colored to whitish-pink, solitary, hermaphrodite flowers that form aggregated patches on the forest floor (Figure 1a–d). Their vegetative body is reduced to an endophyte ("endo" = internal + "phyte" = plant) that spreads within the roots of host trees, from which these achlorophyllous plants derive all their nutrients (Watanabe, 1936a).

This cryptic growth form in which the parasitic plant is entirely hidden within host tissues lasts for most of these plants' life cycle. Allied to this peculiar lifestyle, the muted colors and small flower size ranging from 3 to 5 cm tall (Makino, 1911; Meijer & Veldkamp, 1993) make these plants easy to overlook among the leaf litter (Jochems, 1928). This may explain the small number of herbarium records (<150 specimens) available online for both *M. matudae* and *M. yamamotoi* in collections worldwide (Teixeira-Costa et al., 2022). In turn, this scarcity of records could be why populations appear to be fragmented across the disjunct geographical distribution of the family (Figure 1e).

Difficulties in collecting and interpreting the morphology and development of *Mistrastemon* also led to long-standing challenges in resolving the phylogenetic position of the family. Associations with other parasitic plant families, such as Rafflesiaceae and Hydnoraceae, and even an affiliation with the Nepenthaceae, a tropical family of carnivorous pitcher plants, have been suggested (Makino, 1911). It was only in recent decades that Mitrastemonaceae were placed with confidence in the Ericales (Barkman et al., 2004; Nickrent et al., 2004), an order including commercially important species such as tea, persimmon, blueberry, and azalea. Later, Mitrastemonaceae were resolved as sister to the Lecythidaceae, the Brazil nut family, suggesting an ancient Neotropical origin for the clade (Rose et al., 2018).

These recent findings have advanced our understanding of historical biogeography for the family and prompted a reexamination of the ecology of Mitrastemonaceae. Here we review key aspects of the life cycle, reproductive ecology, and host relationships in Mitrastemonaceae to identify gaps in our current knowledge about the biology of one of the most overlooked families of parasitic flowering plants.

2 | LIFE CYCLE

The lifestyle in parasitic plants like Mitrastemonaceae, known as endoparasites, is associated with a series of developmental adaptations. In many parasitic plants, the absence of one or more organs is caused by processes of reduction or abortion at some stage during the course of development. In *Cuscuta* (Convolvulaceae) and *Cassytha* (Lauraceae), for instance, the rudimentary root system withers and dies once host attachment has been secured (Weber, 1981; Yuncker, 1932). On the other hand, roots, shoots, and expanded leaves are entirely absent in Mitrastemonaceae. Unlike other achlorophyllous root parasites, such as those in the family Balanophoraceae, no underground organs such as tuber or rhizomes are formed. The peculiar body plan of Mitrastemonaceae plants is likely to be due to abortion of the embryonic shoot apex soon after germination (Teixeira-Costa & Davis, 2021). This hypothesis is based on the biology of other endoparasitic plants, such as *Viscum minimum* (Viscaceae; Kuijt, 1986) and *Tristerix aphyllus* (Loranthaceae; Mauseth et al., 1985). Still, further confirmation is required for Mitrastemonaceae, as the initial phases in the life cycle of these plants have yet to be observed and described.

It is only at the onset of their reproductive development that *Mitrastemon* plants become externally visible (Figure 2a). This reproductive phase follows a long vegetative growth period that extends for 3 to 4 years (Watanabe, 1933a). During this initial period, the body of the parasite consists of a network of parenchymatous threads that grows exclusively within the host roots, ultimately colonizing the host bark (Figure 2b,c). This reduced vegetative body later differentiates

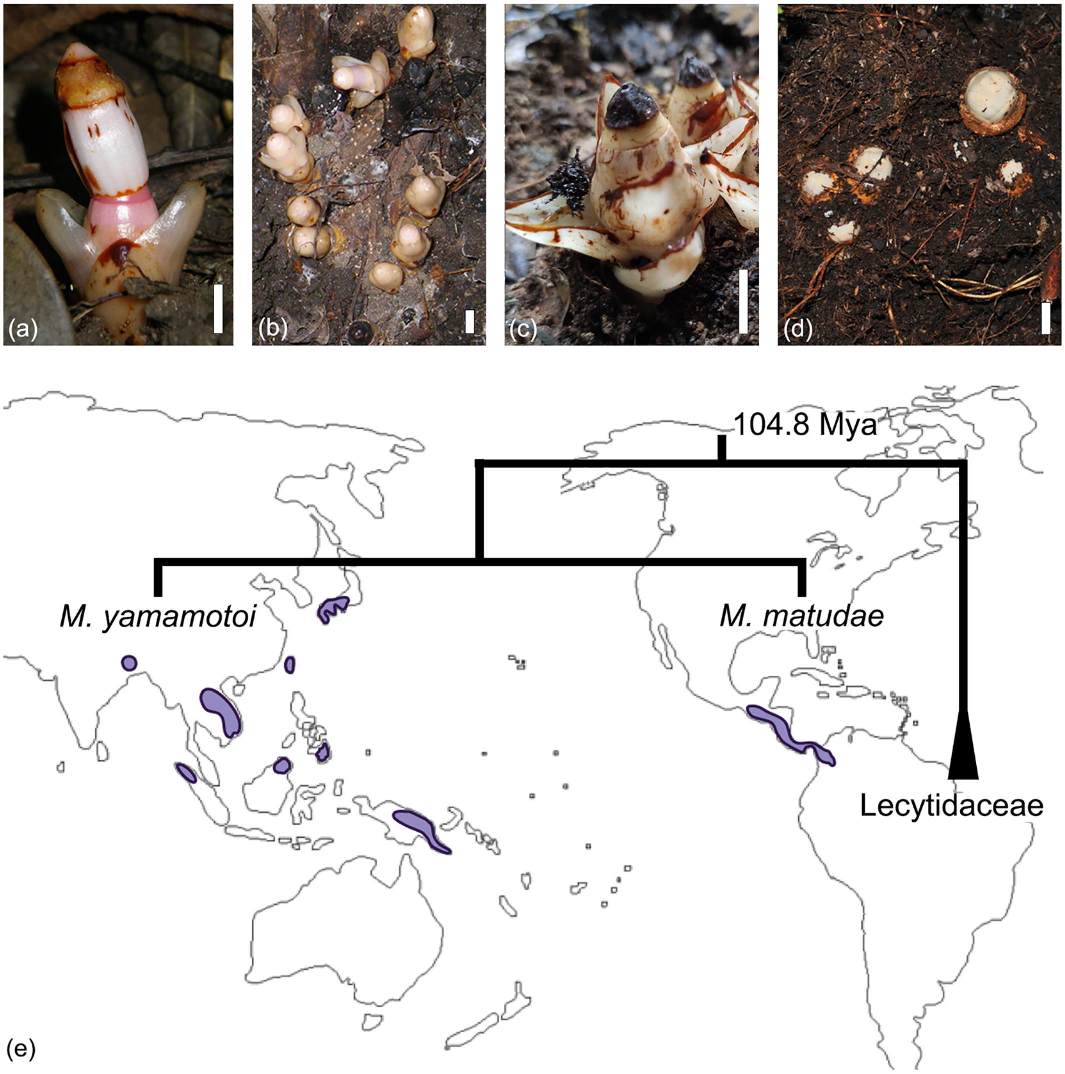

FIGURE 1 Mitrastemonaceae species distribution. The family is composed of only two species, (a, b) *Mitrastemon yamamotoi* and (c, d) *Mitrastemon matudae*, which are distributed (e) across Southeast Asia, Taiwan, Japan, and parts of India, and from Mexico, Central America, and Colombia, respectively. Scale bars = 2 cm. Photographs: (a, b) K. Suetsugu; (c) Aureliano Argüello Figueroa; (d) L. Teixeira-Costa

vessel elements that establish vascular connections with the host wood (Figure 2d; Teixeira-Costa et al., 2021). These direct, vessel-to-vessel connections provide an abundant supply of water, nutrients, and host-derived chemicals, which, in turn, may allow the parasite to undergo faster cell proliferation and differentiation. As flower buds develop, they appear on the host root as small knobs, which continue to grow for approximately 5 months until they eventually break through the host bark and become exposed (Watanabe, 1936b). Multiple flower buds can sprout in proximity (Figure 2e) due to the frequent anastomosing of individual endophyte clusters (Figure 2f; Watanabe, 1936a, 1936b). Nevertheless, not all flower buds mature simultaneously, and neighboring host roots often bear plants at different developmental stages (Jochems, 1928). This strategy might contribute to offering resources to pollinators and seed dispersers over a longer period.

It is noteworthy that the extensive proliferation of parasite endophytic tissue within the host bark can lead to severe modifications of the root structure. In infested hosts, high vessel density and reduced vessel lumen size is apparent, especially in the area promoting an intersection between the parasite flower buds and the host wood (Teixeira-Costa et al., 2021). An increase in vessel proliferation could then induce the initiation of multiple lateral roots (Aloni, 2021), leading to a bifurcated branching pattern with roots that run closer to soil surface (Suetsugu & Yamashita, in press; Watanabe, 1933b, 1934a). In other host–parasite systems, structural modifications have been related to changes in host cambial activity promoted by the parasite (Aloni, 2015; Spallek et al., 2017; Teixeira-Costa & Ceccantini, 2015), which appears to be a common feature of host–parasite interactions (Teixeira-Costa, 2021). Despite of these structural alterations, no significant pathogenicity is reported in the association between *Mitrastemon* species and their hosts. Moreover, considering the slow and prolonged life cycle of these parasites, it is unlikely that severe damaged is caused to the host.

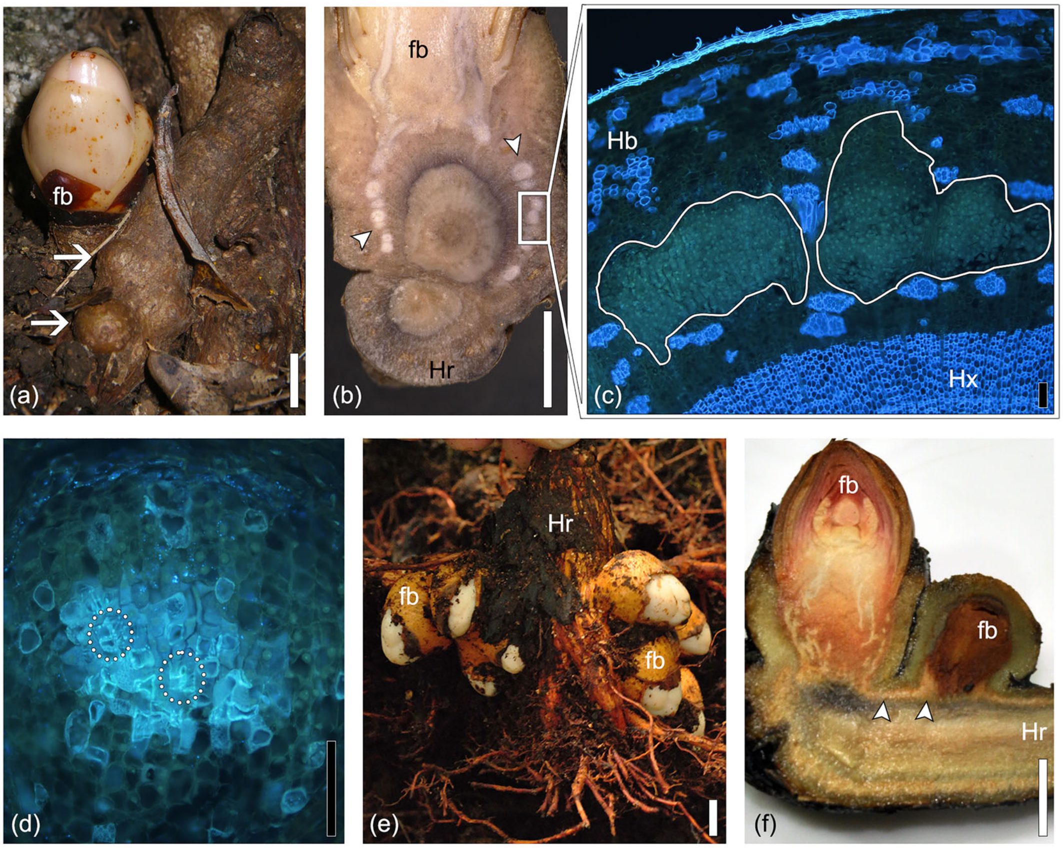

FIGURE 2 Early developmental stages of *Mitrastemon* spp. Mitrastemonaceae spend most of their life cycle inside the roots of host plants, becoming visible aboveground only at (a) the onset of flower bud development. Prior to this stage, the parasite grows as a (b, c) network of parenchyma cells embedded in the host phloem, later forming a vascular connection with the host wood via (d) vessel elements. As growth progresses, (e) multiple flower buds emerge from the host root, which acquires a hypertrophied appearance due to (f) the anastomosing of individual endophyte clusters. fb: exposed flower buds; Hr: host root; Hb: host bark; Hx: host xylem; arrows: flower buds within the host root; arrowhead: endophytic tissue. White scale bars = 2 cm; black scale bars = 100 μm. Photographs: (a–d) K. Suetsugu; (e, f) L. Teixeira-Costa

3 | REPRODUCTIVE ECOLOGY

The flowers of both species of Mitrastemonaceae are similar regarding their morphology and development. Differences between the two species relate mainly to size, with *M. matudae* typically having longer and wider flowers (Meijer & Veldkamp, 1993). Additionally, differences between the two recognized varieties, *M. yamamotoi* Makino var. *yamamotoi* and *M. yamamotoi* var. *kanehirai* (Yamam.) Makino are attributed to the number of bracts per series (Flora of China Editorial Committee, 2003; Watanabe, 1934b), although intermediary forms have been described for the same area with no clear correlation to host identity or plant size (Meijer & Veldkamp, 1993). Like many plants in the Ericales, the androecium is particularly distinctive (Chartier et al., 2017). In both *Mitrastemon* species, flowers are protandrous, meaning that the androecium mature before the gynoecium. During the initial male phase, the connate stamens form a miter-shaped tube (Figure 3a), which caps the style and stigma (Nickrent et al., 2004). This characteristic staminal tube gives the genus its name (Meijer & Veldkamp, 1993). As development progresses, the flower enters an intermediary stage marked by the circumscissile rupture of the deciduous tube (Figure 3b). This leads to the female phase of the flower, as the dehiscence of the androecial tube reveals the mature gynoecium (Figure 3c). Nectaries can be found across the flower during both stages, being present on the ovary wall, on outer surface of the tepal tube, and at the base of the uppermost pair of scale leaves, which store most of the nectar due to their cistern-like shape (Watanabe, 1934c). A large volume of nectar is produced (~600 μl in 20 h per flower, according to Watanabe, 1934b), which attracts a variety of animals.

Atypical flower morphology, combined with the non-photosynthetic habit, which allows *Mitrastemon* to thrive in the shaded forest floor, suggests that these species may rely on unusual pollinators. Indeed, the dark environment inhabited by these plants is rarely visited by typical pollinators such as bees and butterflies (Suetsugu, 2015, 2018). Nevertheless, a wide diversity of animals ranging from flies (*Drosophila* sp. and *Chrysomyia* sp.) to a bee (*Apis* sp.) and a bird species (*Zosterops* sp.) have been occasionally reported to forage for nectar among *M. yamamotoi* flowers (Matuda, 1947; Watanabe, 1934a). It was only recently that Suetsugu (2019) unequivocally showed that hornets (Figure 3d), crickets (Figure 3e), and cockroaches (Figure 3f) effectively pollinate *Mitrastemon*. The investigated population of *M. yamamotoi* in southern Japan was observed to be

FIGURE 3 Reproductive ecology of *Mitrastemon yamamotoi*. Flowers have an initial (a) male phase, characterized by a miter-shaped staminal tube, which (b) senesces later in the development to expose (c) the mature gynoecium characteristic of the female phase of the flower. Insects such as hornets (including *Vespa mandarinia*; d), crickets (including *Diestrammena yakumontana*; e), and cockroaches (*Opisthoplatia orientalis*; f) pollinate the flowers leading to the formation of (g) berry-like fruits. Seed dispersal is likely carried out by birds, as (h, i) many small seeds have been observed in the droppings defecated by the bulbul *Hypsipetes amaurotis*. White scale bars = 2 cm; black scale bar = 100 μm. Photographs: (a–i) K. Suetsugu

diurnally pollinated by hornets (*Vespa* sp. and *Vespula* sp.), while cockroaches (*Opisthoplatia* sp. and *Onychostylus* sp.) and a cricket species (*Diestrammena* sp.) were among the most frequent nocturnal floral visitors, carrying pollen grains on their legs, heads, and mouthparts (Suetsugu, 2019). Suetsugu (2019) also showed that *M. yamamotoi* is a self-compatible species; crickets and cockroaches contribute to its geitonogamous pollination, whereas hornets facilitate outcrossing. No data on the pollination of *M. matudae* appear to be available. Contrary to anecdotal reports (e.g., Matuda, 1947), birds were rarely seen visiting *M. yamamotoi* flowers for nectar (Suetsugu, 2019). On the other hand, species such as *Zosterops palpebrosus* have frequently been suggested to forage the berry-like fruits of *Mitrastemon* species (Figure 3g; Watanabe, 1936c). Indeed, several of the minute *Mitrastemon* seeds have been observed in bird droppings (Figure 3h,i), indicating that birds do act as seed dispersers at least for *M. yamamotoi* (Suetsugu, unpublished data).

Regarding seed fate, initial research by Watanabe (1933a) remarked on the low seed germination rate of *M. yamamotoi* and suggested asexual reproduction should play a larger role in the effective propagation at a local scale. Years later, this hypothesis was strengthened after a series of careful germination experiments yielded no positive results (Watanabe, 1936c, 1937a). In some parasitic plants, *Mitrastemon* species included, mycobionts have been suggested to play a role in the process of germination (Baird & Riopel, 1986; de Vega et al., 2010; Watanabe, 1936c; Wicaksono et al., 2021; Williams & Zuck, 1986). If so, both root exudates from Fagaceae hosts, as well as fungal-specific molecules might be necessary as germination cues. These hypotheses remain untested, however, and no record of successful ex situ germination is available for *Mitrastemon* species (Baskin & Baskin, 2022).

4 | PHENOLOGY

Mitrastemonaceae are distributed across a wide geographical area, occurring in tropical and subtropical forests with equatorial or warm-temperate climates with fully humid to winter-dry precipitation regimes (FAO, 2020; Kottek et al., 2006). In populations located in areas with more seasonality, *Mitrastemon* is generally observed to flower during the dry season (Meijer & Veldkamp, 1993). However, these observations lack quantitative details and often contradict each other. In the same locality in India, for instance, *M. yamamotoi* is recorded to have been collected in different seasons (Rao & Balakrishnan, 1972), or to occur only during the dry season (Mir et al., 2016). In southern Taiwan, *M. yamamotoi* var. *kanehirai* is reported to flower from February to April and produce fruits in October (Flora of China Editorial Committee, 2003; Matuda, 1947), while video recordings for the same variety growing in central Taiwan show that flowering occurs from October to November and seed dispersion occurs from early December to February (Jeng et al., 2017). On the other hand, observations from southern Japan appear to be more consistent, indicating that the flowering season extends from late October to December (Matuda, 1947; Suetsugu, 2019; Watanabe, 1936b). Finally, in North Sumatra and in southern Mexico, flowering and seed dispersion are reported to occur all year round for both *M. yamamotoi* and *M. matudae* (Jochems, 1928; Matuda, 1947).

In at least some of the conflicting cases mentioned above, discrepancies can be related to factors such as differences in elevation or even recent climatic changes. It is, however, more likely that fluctuations in the parasite reproductive phenology are correlated or influenced by host identity and biology. Recently, the parasitic vine *Cuscuta australis* (Convolvulaceae) was shown to lack autonomous flowering and to use host-derived signals to regulate its own reproduction (Shen et al., 2020). Considering that flowering signals are mobile proteins transported through the phloem (Kondhare et al., 2021), a similar mechanism could have evolved in *Mitrastemon*. At the same time, asynchronous flower production has also been reported in other endoparasitic species, such as *Rafflesia* spp. (Rafflesiaceae; Beaman et al., 1988) and *Bdallophytum bambusarum* (Cytinaceae; García-Franco & Rico-Gray, 1996). In these endoparasites, population genetics revealed that multiple individuals of the same parasite species can infest a single host and that the endophytic tissue of these plants can extend for up to 14 m within host tissues in the case of Rafflesiaceae (Barkman et al., 2017; García-Franco et al., 1998). Therefore, additional factors beyond the influence of host phenology could be involved in controlling flowering time in *Mitrastamon* and other endoparasites.

5 | HOST RANGE

Host range can be defined as the diversity of species effectively used by a parasitic plant throughout its geographical distribution (Heide-Jørgensen, 2008). For many parasitic species, this topic has received renewed attention in recent decades. *Mitrastemon yamamotoi* and *M. matudae* were originally described from Southern Japan and Southern Mexico as parasites growing on *Quercus cuspidata* and *Quercus boqueronae* (Fagaceae), respectively (Makino, 1909; Yamamoto, 1936). Years later, as both species were collected in several new localities, *M. matudae* was consistently observed only on *Quercus* spp. (Meijer & Veldkamp, 1993) while additional hosts were reported for *M. yamamotoi*, including *Castanopsis*, *Lithocarpus*, and *Trigobalanus* (Fagaceae; Matuda, 1947; Togashi, 1974; Watanabe, 1937b). Since then, Mitrastemonaceae have been traditionally interpreted to be a family of host-specialist parasites restricted to the Fagaceae. This form of strict host specificity is also reported for other endoparasites, such as Rafflesiaceae and Apodanthaceae (Teixeira-Costa & Davis, 2021). More recently, however, a wide variety of other species have also been claimed to be hosts for *M. yamamotoi*, including Asteraceae, Fabaceae, and Myrtaceae plants (Amoroso et al., 2018; Mir et al., 2016; Rao & Balakrishnan, 1972). These observations have then raised questions regarding the host range of Mitrastemonaceae.

Host specificity is crucial for understanding many aspects of the natural and evolutionary history of parasitic plants, including diversification, historical biogeography, and conservation (Schneider et al., 2016). Therefore, we analyzed herbarium specimens of *M. yamamotoi* indicated to be growing on *Elaeocarpus lanceifolius* (Elaeocarpaceae; ASSAM 38224), *Eugenia* sp. (Myrtaceae; L 1666884), and *Vernonia volkameriifolia* (Asteraceae; ASSAM 38225). For each specimen, a segment of the host root at some distance of the parasite reproductive structures was sampled, rehydrated, manually sectioned, and prepared for anatomical analysis (for methodological details, see Smith & Smith, 1942; Ruzin, 1999). In all three cases, the structure of the roots was clearly consistent with the wood anatomy of most *Quercus* and *Castanopsis* species (Fagaceae), which is remarkably different from the wood anatomy of the plants indicated in the specimen labels. Thus, despite including a limited number of samples, our analysis corroborates the interpretation of Mitrastemonaceae as specific to hosts in the Fagaceae. Future analyses using methods such as DNA barcoding will be especially useful in cases where host identity is uncertain due to insufficient collection of host material (Pelser et al., 2016; Teixeira-Costa et al., 2022). These methods are of increasing importance in the case of parasite species associated with the roots of their host plants, including not only Mitrastemonaceae but also euphytoid or obligate root parasites, for which careful examination and extensive excavation of roots are required for the correct host identification. As shown by the examination of haustorium connections, nearly 40% of the species occurring in close proximity to the euphytoid parasite *Thesium chinense* (Thesiaceae) did not serve as host plants (Suetsugu et al., 2008).

Finally, it is worth noting that while Mitrastemonaceae have been estimated to have diverged from their sister lineage around 104 million years ago (Rose et al., 2018), the stem-age of Fagaceae is estimated at around 99.3 million years (Xiang et al., 2014). Given that branching age estimation is subject to blurring due to age calibration and other factors (Arbogast et al., 2002), it is reasonable to assume that the branching age estimates of the two lineages are in close agreement. In this case, it is possible that the Mitrastemonaceae have evolved in parallel with the Fagaceae since their divergence. On the other hand, this slight discrepancy in the estimated ages of parasite and host lineages might indicate that Mitrastemonaceae might have been associated with other host plants during their evolutionary history. This apparent contradiction has also been observed for other parasite lineages with high host specificity, leading to the hypothesis of temporal specialization, whereby parasitic plants evolved to become more efficient in infesting a narrow range of hosts while losing the genetic information required for successful infestation of rarely encountered host species (Naumann et al., 2013). Host range expansion is also possible, and it has been reported to take place over shorter time frames (Bruce & Gressel, 2013). Continued research and careful analyses are needed, however, to determine if that is the case for Mitrastemonaceae. Furthermore, once the entire genome of *Mitrastemon* is sequenced and analyzed, past host association will likely be elucidated by detecting any additional horizontal gene transfers (Cai et al., 2021) beyond what has been suggested between *Mitrastemon* and Fagaceae (Barkman et al., 2007; Nickrent et al., 2004).

6 | FUTURE RESEARCH

Several aspects of the biology of Mitrastemonaceae remain unknown. As with most endoparasitic lineages, seed germination and initial host penetration have yet to be documented. Similarly, the processes of nutrient uptake by the parasite during the early stages of its development remain undescribed. Penetration of the host xylem, as well as vessel element differentiation are only observed in the parasite endophytic tissue upon the initiation of flower bud development (Teixeira-Costa et al., 2021). In this scenario, host-derived nutrients are hypothesized to enter the parasite endophyte via either symplast or apoplast pathways. The former implicates the formation of secondary plasmodesmata, complex structures connecting the protoplast of cells derived from different origins. On the other hand, capturing nutrients via the apoplast would require the presence of specialized transmembrane transporters in the cells of the parasite endophyte. Both processes have been documented in the interactions between other parasite species and the phloem of their hosts (Fischer et al., 2021; Péron et al., 2017). Thus, elucidating the resource uptake mechanisms in plants like *Mitrastemon* will not only advance the knowledge about these peculiar species but also shed light into the dynamics of the intimate association between endoparasitic plants and their hosts.

In the context of their reproductive ecology, the interactions between *Mitrastemon* and its pollinators and seed dispersers also warrant further investigation. For instance, the way in which *M. yamamotoi* attracts its insect pollinators remains untested. One hypothesis is that as insects like hornets, crickets, and cockroaches usually forage fermented sap, the unique assemblage of *M. yamamotoi* pollinators could be attracted by volatiles produced by nectarivorous yeasts (Suetsugu, 2019). This would explain the sour, fermented-like smell reported for the nectar of *M. yamamotoi* flowers (Jochems, 1928). The discovery made by Suetsugu (2019) also suggests that pollination systems involving unusual and unexpected taxa might be more widespread than previously thought, especially in non-photosynthetic plants with highly modified floral morphology. It is noteworthy that reproductive systems can differ among populations, even within the same species (Whitehead et al., 2018), and the population studied by Suetsugu (2019) is near the northern limit of its distribution. Moreover, specific information on pollination and seed dispersal interactions in *M. matuade* remain unavailable. Therefore, further research is needed to clarify the reproductive biology of the genus *Mitrastemon* as a whole.

Data on interactions between Mitrastemonaceae and non-host species, including mutualists, competitors, and herbivores, is also critical for conservation efforts. Both *M. matudae* and *M. yamamotoi* inhabit forest areas considered as global biodiversity hotspots (Figure 1e), but which are also severely threatened by land-use and climate changes, as well as over-exploitation (Dinerstein et al., 1995; Hughes, 2017). In fact, *M. yamamotoi* has already been reported as threatened in parts of India and China (Botanic Gardens Conservation International, 2022; Mir et al., 2016). Future research focusing on seed dormancy, germination, and initial host penetration in Mitrastemonaceae should provide important information also to ex situ cultivation efforts carried out by institutions with prominent roles in conservation and public engagement, such as botanical gardens (Primack et al., 2021; Thorogood et al., 2022).

KEYWORDS

endoparasite, endophyte, host range, life history, parasitic plants, pollination

ACKNOWLEDGEMENTS

Herbarium specimens used for the analysis of host specificity in *Mitrastemon yamamotoi* were provided by the Botanical Survey of India, Eastern Regional Centre (ASSAM 38224, 38225) and the Naturalis Biodiversity Center (L 1666884). The authors are grateful to the curators and staff members at these institutions, as well as to Anthony Brach and Michaela Schmull (Harvard University Herbaria), for their valuable support. LTC acknowledges Alexander Vázquez, Daniel

Gómez, Fernando Vázquez, Juan Martínez, Juvenal Hernández, and Martín Castillo who greatly helped collecting *Mitrastemon matudae* at the Reserva Biológica La Sepultura, in Mexico. Figure 1c is under a Creative Commons license type Attribution Non-Commercial 4.0 International (creativecommons.org/licenses/by-nc/4.0/). LTC was supported by a postdoctoral fellowship from the Harvard University Herbaria, and a junior fellowship from the Hanse Wissenschaftskolleg - Institute for Advanced Studies. KS is supported by PRESTO from Japan Science and Technology Agency (JST) (JPMJPR21D6).

CONFLICT OF INTEREST

The authors have no conflict of interests to disclose.

AUTHOR CONTRIBUTIONS

L.T.C. led the writing of the manuscript, prepared the figures, and carried out the analysis of herbarium specimens. K.S. provided most of the photographs, contributed significantly to the development of the manuscript, and wrote most sections on reproduction ecology. Both authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

FUNDING INFORMATION

Japan Science and Technology Agency, Grant/Award Number: JPMJPR21D6; Hanse Wissenschaftskolleg - Institute for Advanced Studies; Harvard University Herbaria

Luiza Teixeira-Costa[1,2]
Kenji Suetsugu[3]

[1]*Harvard University Herbaria, Cambridge, Massachusetts, USA*
[2]*Hanse-Wissenschaftskolleg-Institute for Advanced Study, Delmenhorst, Germany*
[3]*Department of Biology, Graduate School of Science, Kobe University, Kobe, Japan*

Correspondence
Luiza Teixeira-Costa, Harvard University Herbaria, Cambridge, MA, USA.
Email: luiza.teixeirac@gmail.com

Kenji Suetsugu, Department of Biology, Graduate School of Science, Kobe University, Kobe, Japan.
Email: kenji.suetsugu@gmail.com

ORCID

Luiza Teixeira-Costa https://orcid.org/0000-0002-1405-8567
Kenji Suetsugu https://orcid.org/0000-0002-7943-4164

REFERENCES

Aloni, R. (2015). Ecophysiological implications of vascular differentiation and plant evolution. *Trees*, *29*, 1–16. https://doi.org/10.1007/s00468-014-1070-6

Aloni, R. (2021). Can a differentiating vessel induce lateral root initiation? In R. Aloni (Ed.), *Vascular differentiation and plant hormones* (pp. 177–184). Springer Nature Switzerland AG, Cham.

Amoroso, V. B., Mendez, N. P., & Lagunday, N. E. (2018). Mitrastemonaceae: A new family record for the Philippines. *The Philippine Journal of Science*, *147*, 775–779.

Arbogast, B. S., Edwards, S. V., Wakeley, J., Beerli, P., & Slowinski, J. B. (2002). Estimating divergence times from molecular data on phylogenetic and population genetic timescales. *Annual Review of Ecology and Systematics*, *33*, 707–740. https://doi.org/10.1146/annurev.ecolsys.33.010802.150500

Baird, W. V., & Riopel, J. L. (1986). Life history studies of *Conopholis americana* (Orobanchaceae). *American Midland Naturalist*, *116*, 140–151. https://doi.org/10.2307/2425946

Barkman, T. J., Klooster, M. R., Gaddis, K. D., Franzone, B., Calhoun, S., Manickam, S., Vessabuts, S., Sasirat, S., & Davis, C. C. (2017). Reading between the vines: Hosts as islands for extreme holoparasitic plants. *American Journal of Botany*, *104*, 1382–1389. https://doi.org/10.3732/ajb.1700117

Barkman, T. J., Lim, S.-H., Salleh, K. M., & Nais, J. (2004). Mitochondrial DNA sequences reveal the photosynthetic relatives of Rafflesia, the world's largest flower. *PNAS*, *101*, 787–792. https://doi.org/10.1073/pnas.0305562101

Barkman, T. J., McNeal, J. R., Lim, S.-H., Coat, G., Croom, H. B., Young, N. D., & DePamphilis, C. W. (2007). Mitochondrial DNA suggests at least 11 origins of parasitism in angiosperms and reveals genomic chimerism in parasitic plants. *BMC Evolutionary Biology*, *7*, 248. https://doi.org/10.1186/1471-2148-7-248

Baskin, J. M., & Baskin, C. C. (2022). Germination and seed/embryo size in holoparasitic flowering plants with "dust seeds" and an undifferentiated embryo. *Botanical Review*, *88*, 1–49. https://doi.org/10.1007/s12229-020-09242-y

Beaman, R. S., Decker, P. J., & Beaman, J. H. (1988). Pollination of Rafflesia (Rafflesiaceae). *American Journal of Botany*, *75*, 1148–1162. https://doi.org/10.1002/j.1537-2197.1988.tb08828.x

Botanic Gardens Conservation International. (2022). Threat Search online database. Available online: https://tools.bgci.org/threat_search.php (accessed July 2022).

Bruce, T. J. A., & Gressel, J. (2013). Changing Host Specificities: By Mutational Changes or Epigenetic Reprogramming? In D. M. Joel, J. Gressel, & L. J. Musselman (Eds.), *Parasitic Orobanchaceae* (pp. 231–241). Springer-Verlag.

Cai, L., Arnold, B. J., Xi, Z., Khost, D. E., Patel, N., Hartmann, C. B., Manickam, S., Sasirat, S., Nikolov, L. A., Mathews, S., Sackton, T. B., & Davis, C. C. (2021). Deeply altered genome architecture in the endoparasitic flowering plant *Sapria himalayana* Griff. (Rafflesiaceae). *Current Biology*, *31*, 1–10. https://doi.org/10.1016/j.cub.2020.12.045

Chartier, M., Löfstrand, S., von Balthazar, M., Gerber, S., Jabbour, F., Sauquet, H., & Schönenberger, J. (2017). How (much) do flowers vary? Unbalanced disparity among flower functional modules and a mosaic pattern of morphospace occupation in the order Ericales. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20170066. https://doi.org/10.1098/rspb.2017.0066

de Vega, C., Arista, M., Ortiz, P. L., & Talavera, S. (2010). Anatomical relations among endophytic holoparasitic angiosperms, autotrophic host plants and mycorrhizal fungi: A novel tripartite interaction. *American Journal of Botany*, *97*, 730–737. https://doi.org/10.3732/ajb.0900147

Dinerstein, E., Olson, D. M., Graham, D. J., Webster, A. L., Primm, S. A., Bookbinder, M. P., & Ledec, G. (1995). *A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean*. The International Bank for Reconstruction and Development/The World Bank.

FAO. (2020). *Global Forest Resources Assessment 2020: main report*. Food and Agriculture Organization of the United Nations.

Fischer, K., Lachner, L. A.-M., Olsen, S., Mulisch, M., & Krause, K. (2021). The enigma of interspecific Plasmodesmata: Insight from parasitic plants. *Frontiers in Plant Science*, *12*, 1–8. https://doi.org/10.3389/fpls.2021.641924

Flora of China Editorial Committee. (2003). Mitrastemon. In C. Y. Wu, P. H. Raven, & D. Hong (Eds.), *Flora of China* (pp. 270–271). Science Press & Missouri Botanical Garden Press.

García-Franco, J. G., & Rico-Gray, V. (1996). Distribution and host specificity in the Holoparasite *Bdallophyton bambusarum* (Rafflesiaceae) in a tropical Decidous Forest in Veracruz, Mexico. *Biotropica*, *28*, 759–762. https://doi.org/10.2307/2389062

García-Franco, J. G., Souza, V., Eguiarte, L. E., & Rico-Gray, V. (1998). Genetic variation, genetic structure and effective population size in the tropical holoparasitic endophyte *Bdallophyton bambusarum* (Rafflesiaceae). *Plant Systematics and Evolution*, *210*, 271–288. https://doi.org/10.1007/BF00985672

Heide-Jørgensen, H. S. (2008). *Parasitic flowering plants*. Brill, Leiden. https://doi.org/10.1163/ej.9789004167506.i-438

Hughes, A. C. (2017). Understanding the drivers of southeast Asian biodiversity loss. *Ecosphere*, *8*, e01624. https://doi.org/10.1002/ecs2.1624

Jeng, M.-R., Chen, C.-W., Yeh, G.-F., Hsieh, C.-C., Chen, Y.-C., & Chang, L.-W. (2017). Observations of the phenology of *Mitrastemon kanehirai* and animals that visited it during the reproductive season with a network camera. *Taiwan Journal of Forest Science*, *32*, 251–257.

Jochems, S. C. J. (1928). Die Verbreitung der Rafflesiaceen-Gattung Mitrastemon. *Recueil Des Travaux Botaniques Néerlandais*, *25A*, 203–207.

Kondhare, K. R., Patil, N. S., & Banerjee, A. K. (2021). A historical overview of long-distance signalling in plants. *Journal of Experimental Botany*, *72*, 4218–4236. https://doi.org/10.1093/jxb/erab048

Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, *15*, 259–263. https://doi.org/10.1127/0941-2948/2006/0130

Kuijt, J. (1986). Observations on establishment and early shoot emergence of *Viscum minimum* (Viscaceae). *Acta Botanica Neerlandica*, *35*, 449–456. https://doi.org/10.1111/j.1438-8677.1986.tb00484.x

Makino, T. (1909). Observations on the flora of Japan. *Botanical Magazine Tokyo*, *23*, 325–327.

Makino, T. (1911). Observations on the flora of Japan. *The Botanical Magazine*, *25*, 252–257.

Matuda, E. (1947). On the genus Mitrastemon. *Bulletin of the Torrey Botanical Club*, *74*, 133–141. https://doi.org/10.2307/2481465

Mauseth, J. D., Montenegro, G., & Walckowiak, A. M. (1985). Host infection and flower formation by the parasite *Tristerix aphyllus* (Loranthaceae). *Canadian Journal of Botany*, *63*, 567–581. https://doi.org/10.1139/b85-072

Meijer, W., & Veldkamp, J. F. (1993). A revision of Mitrastema (Rafflesiaceae). *Blumea*, *38*, 221–229.

Mir, A. H., Upadhaya, K., & Khonglah, C. G. (2016). A note on *Mitrastemon yamamotoi* (Mitrastemonaceae): A root parasite of rare occurrence in North East India. *Journal of Japanese Botany*, *91*, 179–183.

Naumann, J., Salomo, K., Der, J. P., Wafula, E. K., Bolin, J. F., Maass, E., Frenzke, L., Samain, M. S., Neinhuis, C., dePamphilis, C. W., & Wanke, S. (2013). Single-copy nuclear genes place haustorial Hydnoraceae within Piperales and reveal a Cretaceous origin of multiple parasitic angiosperm lineages. *PLoS ONE*, *8*, e79204. https://doi.org/10.1371/journal.pone.0079204

Nickrent, D. L. (2020). Parasitic angiosperms: How often and how many? *Taxon*, *69*, 5–27. https://doi.org/10.1002/tax.12195

Nickrent, D. L., Blarer, A., Qiu, Y. L., Vidal-Russell, R., & Anderson, F. E. (2004). Phylogenetic inference in Rafflesiales: The influence of rate heterogeneity and horizontal gene transfer. *BMC Evolutionary Biology*, *4*, 1–17. https://doi.org/10.1186/1471-2148-4-40

Pelser, P. B., Nickrent, D. L., & Barcelona, J. F. (2016). Untangling a vine and its parasite: Host specificity of Philippine Rafflesia (Rafflesiaceae). *Taxon*, *65*, 739–758. https://doi.org/10.12705/654.4

Péron, T., Candat, A., Montiel, G., Veronesi, C., Macherel, D., Delavault, P., & Simier, P. (2017). New insights into phloem unloading and expression of sucrose transporters in vegetative sinks of the parasitic plant *Phelipanche ramosa* L. (Pomel). *Frontiers in Plant Science*, *7*, 1–15. https://doi.org/10.3389/fpls.2016.02048

Primack, R. B., Ellwood, E. R., Gallinat, A. S., & Miller-Rushing, A. J. (2021). The growing and vital role of botanical gardens in climate change research. *New Phytologist*, *231*, 917–932. https://doi.org/10.1111/nph.17410

Rao, A. S., & Balakrishnan, N. P. (1972). Mitrastemon yamamotoi (Makino) Makino (Rafflesiaceae)—A unique root parasite new to the Indian flora. *Indian Forester*, *98*, 234–235.

Rose, J. P., Kleist, T. J., Löfstrand, S. D., Drew, B. T., Schönenberger, J., & Sytsma, K. J. (2018). Phylogeny, historical biogeography, and diversification of angiosperm order Ericales suggest ancient Neotropical and East Asian connections. *Molecular Phylogenetics and Evolution*, *122*, 59–79. https://doi.org/10.1016/j.ympev.2018.01.014

Ruzin, S. E. (1999). *Plant microtechnique and microscopy*. Oxford University Press, Oxford.

Schneider, A. C., Colwell, A. E. L., Schneeweiss, G. M., & Baldwin, B. G. (2016). Cryptic host-specific diversity among western hemisphere broomrapes (Orobanche s.l., Orobanchaceae). *Annals of Botany*, *118*, 1101–1111. https://doi.org/10.1093/aob/mcw158

Shen, G., Liu, N., Zhang, J., Xu, Y., Baldwin, I. T., & Wu, J. (2020). *Cuscuta australis* (dodder) parasite eavesdrops on the host plants' FT signals to flower. *Proceedings of the National Academy of Sciences of the United States of America*, *117*, 23125–23130. https://doi.org/10.1073/pnas.2009445117

Smith, F. H., & Smith, E. C. (1942). Anatomy of the inferior ovary of Darbya. *American Journal of Botany*, *29*, 464–471. https://doi.org/10.1002/j.1537-2197.1942.tb10236.x

Spallek, T., Melnyk, C. W., Wakatake, T., Zhang, J., Sakamoto, Y., Kiba, T., Yoshida, S., Matsunaga, S., Sakakibara, H., & Shirasu, K. (2017). Interspecies hormonal control of host root morphology by parasitic plants. *Proceedings of the National Academy of Sciences*, *114*, 5283–5288. https://doi.org/10.1073/pnas.1619078114

Suetsugu, K. (2015). Autonomous self-pollination and insect visitors in partially and fully mycoheterotrophic species of Cymbidium (Orchidaceae). *Journal of Plant Research*, *128*, 115–125. https://doi.org/10.1007/s10265-014-0669-4

Suetsugu, K. (2018). Achlorophyllous orchid can utilize fungi not only for nutritional demands but also pollinator attraction. *Ecology*, *99*, 1498–1500. https://doi.org/10.1002/ecy.2170

Suetsugu, K. (2019). Social wasps, crickets and cockroaches contribute to pollination of the holoparasitic plant *Mitrastemon yamamotoi* (Mitrastemonaceae) in southern Japan. *Plant Biology*, *21*, 176–182. https://doi.org/10.1111/plb.12889

Suetsugu, K., Kawakita, A., & Kato, M. (2008). Host range and selectivity of the hemiparasitic plant *Thesium chinense* (Santalaceae). *Annals of Botany*, *102*, 49–55. https://doi.org/10.1093/aob/mcn065

Suetsugu, K., & Yamashita, H. (in press). Host manipulation by a parasitic plant. *Frontiers in Ecology and the Environment*. PMID: in press.

Teixeira-Costa, L. (2021). A living bridge between two enemies: Haustorium structure and evolution across parasitic flowering plants. *Revista Brasileira de Botânica*, *44*, 165–178. https://doi.org/10.1007/s40415-021-00704-0

Teixeira-Costa, L., & Ceccantini, G. (2015). Embolism increase and anatomical modifications caused by a parasitic plant. *IAWA Journal*, *36*, 138–151. https://doi.org/10.1163/22941932-00000091

Teixeira-Costa, L., & Davis, C. C. (2021). Life history, diversity, and distribution in parasitic flowering plants. *Plant Physiology*, *187*, 32–51. https://doi.org/10.1093/plphys/kiab279

Teixeira-Costa, L., Davis, C. C., & Ceccantini, G. (2021). Striking developmental convergence in angiosperm endoparasites. *American Journal of Botany*, *108*, 1–13. https://doi.org/10.1002/ajb2.1658

Teixeira-Costa, L., Heberling, J. M., Wilson, C. A., & Davis, C. C. (2022). Parasitic flowering plant collections embody the extended specimen. *Methods in Ecology and Evolution*, 1–13. https://doi.org/10.1111/2041-210X.13866

Thorogood, C., Witono, J. R., Mursidawati, S., & Fleischmann, A. (2022). Parasitic plant cultivation: examples, lessons learned and future directions. *Sibbaldia: The International Journal of Botanic Garden Horticulture*, 1–27.

Togashi, M. (1974). Mitrastemon sp. found in North Borneo. *Journal of Japanese Botany*, *49*, 214–215.

Watanabe, K. (1933a). Ungeschlechtliche Fortpflanzung von *Mitrastemon yamamotoi*. *Proceedings of the Imperial Academy of Japan*, *9*, 412–415. https://doi.org/10.2183/pjab1912.9.412

Watanabe, K. (1933b). Ungeschlechtliche Fortpflanzung von *Mitrastemon yamamotoi*. *Proceedings of the Imperial Academy*, *9*, 412–415. https://doi.org/10.2183/pjab1912.9.412

Watanabe, K. (1934a). Biologie von *Mitrastemon yamamotoi* Makino (Rafflesiaceae). II. Vegetative Fortpflanzung. *Botany Magazine Tokyo*, *48*, 467–472. https://doi.org/10.15281/jplantres1887.48.467

Watanabe, K. (1934b). Abweichende Formen von *Mitrastemon yamamotoi*. *Proceedings of the Imperial Academy*, *10*, 600–603. https://doi.org/10.2183/pjab1912.10.600

Watanabe, K. (1934c). Uber die Flussigkeitsabsonderung der Bluten von *Mitrastemon yamamotoi*. *Proceedings of the Imperial Academy*, *10*, 507–508. https://doi.org/10.2183/pjab1912.10.507

Watanabe, K. (1936a). Morphologisch-biologische Studien uber die Gattung Mitrastemon (II). *Journal of Japanese Botany*, *12*, 698–711.

Watanabe, K. (1936b). Morphologisch-biologische Studien uber die Gattung Mitrastemon (III). *Journal of Japanese Botany*, *12*, 759–773.

Watanabe, K. (1936c). Morphologisch-biologische Studien uber die Gattung Mitrastemon (IV). *Journal of Japanese Botany*, *12*, 848–858.

Watanabe, K. (1937a). Morphologisch-biologische Studien uber die Gattung Mitrastemon (V). *Journal of Japanese Botany*, *13*, 14–24.

Watanabe, K. (1937b). Morphologisch-biologische Studien uber die Gattung Mitrastemon (VI). *Journal of Japanese Botany*, *13*, 75–86.

Weber, J. Z. (1981). A taxonomic revision of Cassytha (Lauraceae) in Australia. *Journal of the Adelaide Botanic Gardens*, *3*, 187–262.

Whitehead, M. R., Lanfear, R., Mitchell, R. J., & Karron, J. D. (2018). Plant mating systems often vary widely among populations. *Frontiers in Ecology and Evolution*, *6*, 1–9. https://doi.org/10.3389/fevo.2018.00038

Wicaksono, A., Mursidawati, S., & Molina, J. (2021). A plant within a plant: Insights on the development of the Rafflesia endophyte within its host. *Botanical Review*, *87*, 233–242. https://doi.org/10.1007/s12229-020-09236-w

Williams, C. E., & Zuck, R. K. (1986). Germination of seeds of *Epifagus virginiana* (Orobanchaceae). *The Michigan Botanist*, *25*, 103–106.

Xiang, X. G., Wang, W., Li, R. Q., Lin, L., Liu, Y., Zhou, Z. K., Li, Z. Y., & Chen, Z. D. (2014). Large-scale phylogenetic analyses reveal fagalean diversification promoted by the interplay of diaspores and environments in the Paleogene. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 101–110. https://doi.org/10.1016/j.ppees.2014.03.001

Yamamoto, Y. (1936). Species nova Mitrastemonacearum (Rafflesiacearum) ex México. *Botanical Magazine Tokyo*, *50*, 539–541. https://doi.org/10.15281/jplantres1887.50.539

Yuncker, T. G. (1932). The genus Cuscuta. *Memoirs of the Torrey Botanical Club*, *18*, 113–331.

How to cite this article: Teixeira-Costa, L., & Suetsugu, K. (2022). Neglected plant parasites: Mitrastemonaceae. *Plants, People, Planet*, 1–9. https://doi.org/10.1002/ppp3.10322