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Langsdorffia: Creatures from the deep?

1 | INTRODUCTION

Langsdorffia Mart. (family Balanophoraceae) is a genus of flowering plants unlike any other in appearance. Four species are recognized currently, with disjunct distributions: *L. hypogaea* Mart., which is widespread across Central and South America; *L. malagasica* (Fawc.) B. Hansen, which is endemic to Madagascar; *L. papuana* Geesink in Papua New Guinea; and the recently described *L. heterotepala* L.J.T. Cardoso, R.J.V. Alves J.M.A. Braga, which is restricted to just a handful of forests in the south and southeast of Brazil (Figure 1) (Cardoso, 2020; Cardoso, Alves, & Braga, 2011). All are highly derived root holoparasites that are devoid of chlorophyll and are dependent entirely on their host plants for their nutrition (Kuijt, 1969). Their scaly, often brightly colored inflorescences erupt from ascending subterranean branches on the dingy forest floor, and superficially resemble deep sea creatures, rather more than they do flowering plants (Figure 2).

The family Balanophoraceae is in the sandalwood order (Santalales), which is the largest order of parasitic plants with 179 genera and 2,460 species. This family comprises 18 genera and over 40 species, and is a family replete with bizarre-looking holoparasites. The exact evolutionary origins of the Balanophoraceae were unclear until the introduction of molecular data. Su, Hu, Anderson, Der, and Nickrent (2015) used nuclear, plastid, and mitochondrial sequence data to resolve its position in the sandalwood order. The authors demonstrated that the family in fact comprises one slow-evolving clade that includes the genera *Dactylantus*, *Hachettea*, and *Mystropetalon* in the family Mystropetalaceae, and a relatively rapidly evolving clade comprising the remaining Balanophoraceae s.str., that includes the genus *Langsdorffia*. These data help to explain why morphology-based classifications of this family varied historically. Several new species have been described in the family, some very recently, such as *Ombrophytum chilensis* in Chile (Kuijt & Delprete, 2019), and *O. villamariensis* in Colombia (Guzmán-Guzmán, 2019). Meanwhile, *Balanophora papuana* was rediscovered recently in North Sumatra after 39 years without detection (Damayanto & Riastiwi, 2019). The scarcity, elusive nature, and remote locations of known Balanophoraceae indicate that further species may await discovery. Furthermore, little is understood about the biology of most of the species already known to science. Here we provide a brief review of the ecology and reproductive biology of one of the least examined genera in the family, *Langsdorffia*, and place emphasis on this highly unusual genus as a candidate for further research and conservation focus.

2 | LIFE HISTORY AND ECOLOGY

The family Balanophoraceae comprises predominantly tropical subterranean root parasites of shrubs, herbs, and trees that are seldom encountered or collected, and generally preserve poorly (Hsiao, Mauseth, & Gomez, 1994). Little is known about the life history and ecology of most species in the family. All species of *Langsdorffia* are highly modified parasites comprising just a series of tubers and inflorescences, and lack an ordinary stem structure and all trace of functional apical meristems (Hsiao et al., 1994). The Balanophoraceae more broadly feature a particularly complicated host-parasite vascular interface, in which the parasitic tuber appears to engulf the host plant's roots (Figure 2d) (Santos, Nascimento, Marzinek, Leiner, & Oliveira, 2017), the vascular tissues of which infiltrate the parasite tissue extensively (Hsiao, Mauseth, & Peng, 1995). Interestingly, all Balanophoraceae appear to lack stomata entirely, which is highly unusual in the plant kingdom beyond submerged aquatics (Kuijt & Dong, 1990).

Little research has been carried out to examine the host specificity of *Langsdorffia*. While holoparasites are generally host specific, *L. hypogaea* (Figure 2) has been shown to parasitize over 20 host species including shrubs, trees, lianas, and even a cactus, from 16 families; however, an apparent preference for *Miconia albicans* (Melastomataceae) indicates at least a degree of specificity (Santos et al., 2017). This species occurs in various habitats including neotropical savanna and tropical rainforest, each with a very different assemblage of plants. It is possible that populations of *L. hypogaea* are locally adapted to hosts with distinct ecologies, and underlying genetic divergence is obscured by their reduced morphological features. This has been shown in other parasitic plants (Thorogood, Rumsey, Harris, & Hiscock, 2008). Reciprocal crosses on different host species, combined with population genetics-based analyses could reveal cryptic host-defined taxa in *Langsdorffia* which would inform conservation practice. Extensive data on the host range of other species of *Langsdorffia* have not been published. Various species including *Eugenia* spp., *Meliosma pinnata*, *Metrosideros eugenioides*, and *Vaccinium* spp. were suggested to be the hosts of *L. papuana* in Papua New Guinea when it was first described (Geesink, 1972),

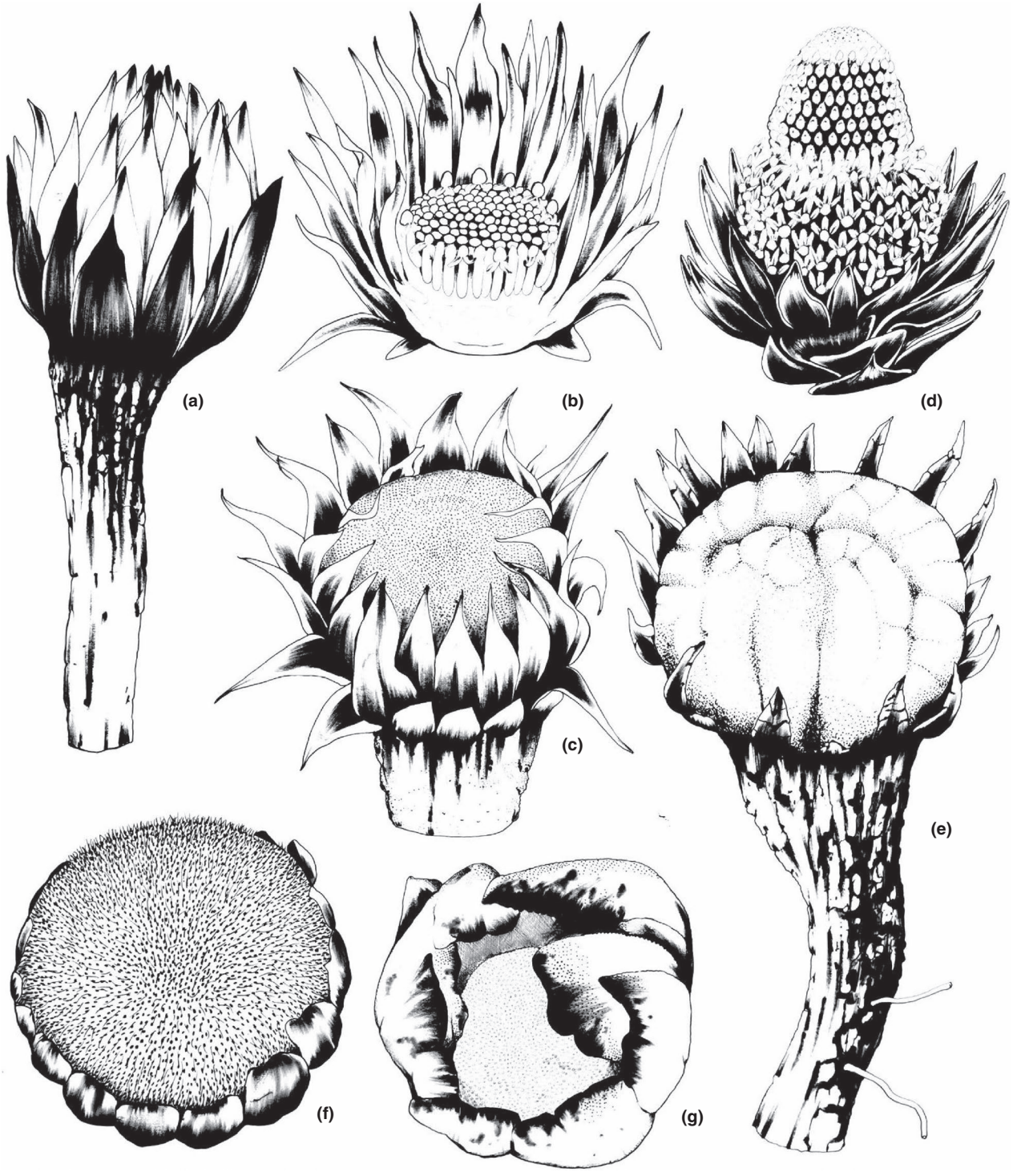

FIGURE 1 The four known species of *Langsdorffia*: (a) *L. papuana* (male inflorescence, 3.5–5 cm); (b) *L. heterotepala* (section through male inflorescence, 2–4 cm); (c) *L. heterotepala* (infructescence); (d) *L. hypogaea* (male inflorescence, 1–3 cm); (e) *L. hypogaea* (infructescence); (f) *L. malagasica* (infructescence); (g) *L. malagasica* (inflorescence, 3 cm). Images not to scale; approximate dimensions of the longest axes are indicated. Illustration: Chris Thorogood

but this has not been revisited or confirmed to our knowledge. The host range of *L. malagasica* and the recently described *L. heterotepala* (Cardoso et al., 2011) have not been assessed in detail either. Given the dependency of these parasites on their host plants, an assessment of the host range of all species of *Langsdorffia* will be an essential next step in their conservation.

3 | REPRODUCTIVE BIOLOGY

Little is known about the pollination biology, breeding systems, or seed dispersal of the Balanophoraceae (Kuijt & Delprete, 2019; Freitas et al., 2017), and in *Langsdorffia* in particular. All species in the family produce minute, unisexual flowers, borne in spike-like

FIGURE 2 *Langsdorffia hypogaea*: (a) Immature male inflorescence; (b) Male inflorescence in anthesis; (c) Female inflorescence in anthesis; (d) The host tissues (H) connected to the parasite tuber (P); E. Excavated specimens showing the extensive underground tuber system of the parasite

inflorescences on the dark forest floor; however, pollination mechanisms appear to be diverse (Goto, Yamakoshi, & Matsuzawa, 2012). Species in the genus *Balanophora* secrete nectar and are visited by ants, cockroaches, and moths in Japan (Kawakita & Kato, 2002) and *Lophophytum mirabile* is visited by beetles in the Ecuadorian Amazon (Borchsenius & Olesen, 1990). Here, *B. kuroiwai* appears to have evolved as a mutualistic pollination syndrome with pyralid moths, which use the plant as a brood site for their larvae to develop, like the better-known systems of fig–fig wasp and yucca–yucca moth (Kawakita & Kato, 2002). Brood-site pollination involving *Morellia* flies has also been observed in the related genus *Thonningia* in the rainforests of West Africa (Goto et al., 2012). Investigations into the reproductive biology of *Langsdorffia* are hampered by the rarity of the plants and a high rate of herbivory when they do appear (Freitas et al., 2017). Indeed, virtually nothing is known about the reproductive biology of *Langsdorffia* with the exception of *L. hypogaea*. The inflorescence of *L. hypogaea* comprises a fleshy, spadix-like structure that is covered with scales with hairy margins (Figure 2a–c); the male flowers are stalked, and the female flowers are sessile, and both have nectar-producing conical structures (Freitas et al., 2017; Hsiao et al., 1994; Santos et al., 2017). The flowers are brightly colored and sweetly scented during anthesis (Freitas et al., 2017), and 259 species of floral visitor have been observed from a diversity of orders including Hymenoptera, Hemiptera, Dermaptera, Blattodea, Araneae, and Coleoptera (Freitas et al., 2017). Ants (*Brachymyrmex*) are reported to visit this species most frequently; however, beetles (*Stelidota*) are suggested to be the principle pollinator in this species, and have been observed ovipositing in the flowers (Freitas et al., 2017). The white-naped jay (*Cyanocorax cyanopogon*) has also been observed visiting

the inflorescences of *L. hypogaea* in the Brazilian Cerrado region (Santos et al., 2017), but it is not known to what extent they effect pollination. Foraging primates (*Propithecus diadema*) are apparently attracted to the strong sweet smell of the inflorescences of *L. malagasica* in Madagascar (Irwin et al., 2007); pollination seems doubtful here. Together, the few data available suggest that *Langsdorffia* attract a diverse guild of floral visitors, including insects, birds, and mammals, and more broadly, that mutualistic pollination syndrome, involving moths, flies, and beetles, may be a common feature across the family Balanophoraceae.

4 | FUTURE WORK

Future work should focus on the effective propagation of *Langsdorffia*. The translocation and conservation of holoparasitic flowering plants are impeded significantly by the complete dependency on their host plants (Holzapfel, Dodgson, & Rohan, 2018). As a consequence of their difficulty of cultivation, parasitic plants seem to be underrepresented significantly in conservation collections. *Langsdorffia* is no exception and at present, none of the four known species exist in cultivation to our knowledge. This is concerning because all species occur in habitats under threat, and at least one species, *L. heteropetala*, may be classified as Critically Endangered in the future, because it has such a limited distribution (Cardoso, 2020; Cardoso et al., 2011). Even species that are widespread, such as *L. hypogaea*, which occurs across the Amazon, Caatinga, Cerrado, and Atlantic Forest eco-region, are considered at risk due to habitat loss (Felestrino et al., 2017). Placing emphasis on parasitic plants such as *Langsdorffia* in botanic gardens' conservation collections and seed-banking strategies will help safeguard the future of these extraordinary plants.

5 | CONCLUDING REMARKS

Langsdorffia is an extraordinary genus of plants unlike any other. Little is known about the biology of these plants beyond examinations of the pollination system and ecology of the most widespread species, *L. hypogaea*. A spate of recent species discovery in the family Balanophoraceae, coupled with the difficulty in encountering these unpredictable and elusive plants, suggest further *Langsdorffia* taxa may await discovery. Future work should focus on refining our understanding of their host specificity with a view to propagating them, and introducing them into botanic gardens' conservation collections.

KEYWORDS

Balanophoraceae, heterotrophic plant, holoparasite, *Langsdorffia*, parasitic plant

Chris Thorogood[1]
Jean Carlos Santos[2]

[1]*Department of Plant Sciences, Oxford University Botanic Garden, Oxford, UK*
[2]*Departamento de Ecologia, Universidade Federal de Sergipe, São Cristóvão, Sergipe, Brazil*

Correspondence
Chris Thorogood, Department of Plant Sciences; Oxford University Botanic Garden, Oxford, UK.
Email: chris.thorogood@obg.ox.ac.uk

ORCID
Chris Thorogood https://orcid.org/0000-0002-2822-0182
J.C. Santos https://orcid.org/0000-0001-6031-9193

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