

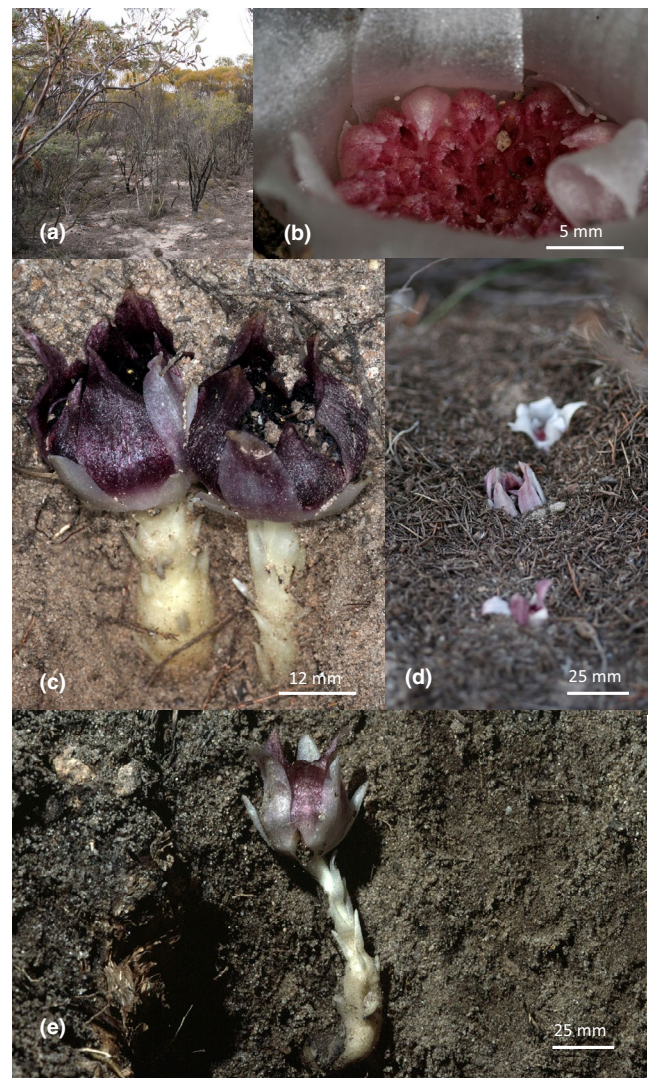
# Rhizanthella: Orchids unseen

## 1 | INTRODUCTION

The author and naturalist, W. H. Hudson, wrote of an atheist who went to an orchid show and left believing in the devil (Young, 1947). For centuries, orchids have captured the imagination like no other plants. These are the masters of deception. From manipulating insects with pollination “obstacle courses”, to stealing food from other plants via parasitic associations with fungi, their extraordinary biology can excite and inspire—orchids are an antidote to plant blindness. Here we place focus on some of the most obscure and enigmatic plants in this fascinating family, belonging to the genus *Rhizanthella*: the world's only underground flowers (see Movie S1).

Many orchids have evolved a mycoheterotrophic life history, a form of parasitism that is both elusive and poorly understood. Mycoheterotrophic plants obtain carbon from other photosynthetic plants through a shared mycorrhizal fungal network, rather than by photosynthesis. Some are very rare, grow in deep shade under leaf litter, and are easily overlooked (Thorogood, 2019). None more so, than the Australian underground orchids of the genus *Rhizanthella*, in which three of the four recognized taxa, remarkably, do not even emerge above the surface of the soil when flowering (Figure 1). The discovery of this remarkable genus in Western Australia in 1928 was an international sensation (Dixon, 2003; Dixon & Christenhusz, 2018) and underground orchids remain unique among flowering plants. All discoveries of *Rhizanthella gardneri* up to 1979 were accidental and resulted from clearing or farming activities (Hågsater & Dumont, 1996). In the absence of phylogenetic data, the taxonomy of the genus is tentative (Figure 2). Until recently, the genus *Rhizanthella* was considered, generally, to comprise three rare and local species in Australia: the eastern underground orchid, *Rhizanthella slateri* in New South Wales (Clements & Cribb, 1984; Rupp, 1932); the western underground orchid, *R. gardneri* in the central Wheatbelt (Rogers, 1928) and the poorly circumscribed Lamington underground orchid, *Rhizanthella omissa* on the Lamington Plateau (Jones & Clements, 2006). Very recently, *Rhizanthella johnstonii*, known only from near the southern coast of Western Australia, was described as distinct from *R. gardneri* (Dixon & Christenhusz, 2018), resolving what was long considered to be a disjunct distribution of this species across Western Australia (Rogers, 1928; Dixon & Christenhusz, 2018). Notwithstanding this discovery, the spatial separation of the genus *Rhizanthella* several thousand kilometers from east to west suggests

that extant taxa may be relict species from a time before central Australia became arid (Delannoy, Fujii, Colas des Francs-Small, Brundrett, & Small, 2011). Research into the habitat characteristics of *R. gardneri* suggest that this species tolerates a range of conditions



**FIGURE 1** (a) The habitat of *Rhizanthella gardneri* in Western Australia; (b) The capitulum of *R. gardneri*; (c) Excavated mature inflorescences of *R. gardneri*; (d) The exposed bracts of *R. gardneri*. (e–f) Excavated inflorescences of *R. gardneri* showing habit. Photographs (a–d) by Etienne Delannoy; (e) by Jeremy Bougoure

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and may be more widespread than previously thought, given that there are extensive areas of suitable habitat across Southern and Western Australia (Bougoure, Brundrett, Brown, & Grierson, 2008). The rarity and subterranean life history of *Rhizanthella* suggest that new taxa could await discovery. Exploration surveys and phylogenetic data from across populations are required to resolve better, this cryptic genus. Surveys are complicated by the need for excavation, which involves careful removal of the top centimeter of soil to reveal the tips of the bracts (Figure 1d; Dixon, 2003). Indeed, locating the orchids is established to be difficult and unpredictable: searches between 1980 and 1984, involving 3,000 person-hours by volunteers, identified orchids in fewer than 4% of likely habitats (Dixon, 2003).

## 2 | EVOLUTION AND LIFE HISTORY

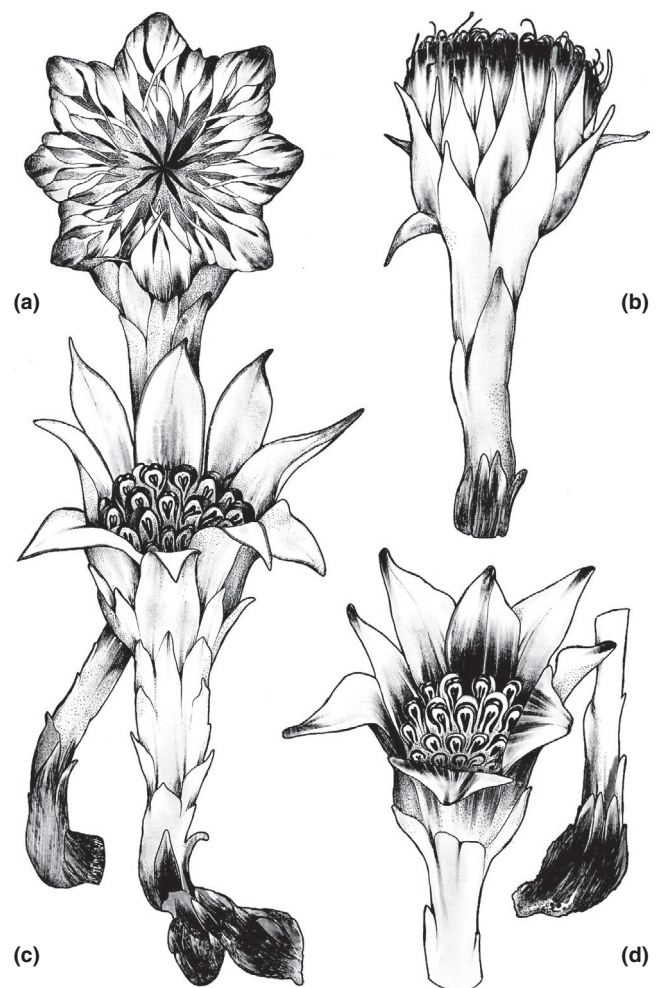
Mycoheterotrophy has evolved multiple times independently among flowering plants (Merckx, Bakkerb, Huysmansa, & Smets, 2009) and is particularly prominent among orchids (family Orchidaceae; Lam et al., 2018). Like other mycoheterotrophic orchids, *Rhizanthella* is parasitic, acquiring nutrients from a specific mycorrhizal fungus that forages for soil nutrients (i.e., Nitrogen) and at the same time, dependent on an autotrophic host for a continuous supply of carbon (Bougoure, Brundrett, & Grierson, 2010; Warcup, 1985). Thus, they are completely devoid of photosynthesis; indeed the plastid genome ("plastome") of *Rhizanthella* is established to be the smallest organelle genome described in land plants (Delannoy et al., 2011).

Underground orchid species appear to be ecologically distinct. For example *R. slateri* occurs in relatively moist, shady eucalypt woodland of central-eastern Australia (Jones, 2006) and flowers above ground; *R. omissa* is recorded to grow in casuarina forests and flowers underground, as do *R. gardneri* and *R. johnstonii*, which are associated with broom bush (*Melaleuca*) thickets (*M. scalene*, *M. hamata* and *M. uncinata*; family Myrtaceae; Bougoure et al., 2008; Dixon & Christenhusz, 2018; Warcup, 1985)—unusually for mycoheterotrophic plants which are typically associated with damp, shady habitats. There is also evidence that *Rhizanthella* shows extreme specificity for particular species of mycorrhizal fungi (Bougoure, Ludwig, Brundrett, & Grierson, 2009). Host specificity is suggested to drive speciation in autotrophic (parasitic plants) more broadly, in which host-defined cryptic taxa can be overlooked because of reduced morphological features such as functional leaves (Thorogood, Rumsey, & Hiscock, 2009; Thorogood, Rumsey, Hiscock, & Harris, 2008). Data on the population genetics across the genus *Rhizanthella* are lacking, however the presence of genetically distinct host specific taxa, obscured by cryptic morphology, should not be discounted.

## 3 | REPRODUCTIVE BIOLOGY

Very little is known about the reproductive biology of underground orchids, and for species besides *R. gardneri*, the pollinators are

virtually unknown. All species produce terminal capitula of small flowers enclosed by fleshy bracts. *Rhizanthella gardneri* is apparently clonal and persistent in a given location, and produces dormant daughter tubers (Dixon & Christenhusz, 2018; Hágstater & Dumont, 1996). Termites, fungus gnats, flies, and wasps have all been suggested to be pollinators of *R. gardneri* (George, 1980; Dixon, Pate, & Kuo, 1990; Dixon, 2003; Mursidawati, 2004; Swarts & Dixon, 2009). Interestingly, *Rhizanthella* is the only known angiosperm to be pollinated by termites (Dixon & Christenhusz, 2018). Ants are established to be the pollinators of the Mediterranean parasitic plant *Cytinus hypocistis* (de Vega, Arista, Ortiz, Herrera, & Talavera, 2009), which flowers at ground-level, and is also occasionally partially submerged by sand (CJ Thorogood & SJ Hiscock, pers. obs.). Meanwhile flies and fungus gnats are also known to pollinate other rare and inconspicuous mycoheterotrophic plants in the family Thismiaceae (Mar & Saunders, 2015; Woodward, Berry, Maas-van de Kamer, & Swing, 2007). The flowers of the parasitic plant *Hydnora triceps* also produces flowers beneath the soil surface from time to time, to which insects apparently are attracted through cracks in the ground (Musselman & Visser, 1989). Given that most species of *Rhizanthella* also bloom just below the soil surface, pollinators could access the



**FIGURE 2** The floral structures (capitula) of the four described species of *Rhizanthella*: (a) *R. slateri*; (b) *R. omissa*; (c) *R. johnstonii*; (d) *R. gardneri* (images not to scale)

capitula in a similar fashion. Clearly further work is required to understand better the pollination syndrome of this unique genus of orchids.



The seeds of *Rhizanthella* are produced in fleshy fruits which take several months to mature; seed dispersal has never been observed, although native fossorial (underground-dwelling) marsupial mammals are suggested to be likely dispersal agents for *R. gardneri* (Dixon & Pate, 1984; Hágsater & Dumont, 1996; Mursidawati, 2004); these animals are now extinct in the region where the plant occurs (Swarts et al., 2009).

#### 4 | CONCLUDING REMARKS

As orchids “unseen” *Rhizanthella* provides a fascinating narrative to engage people with plants. All species of *Rhizanthella* are scarce, have complex ecological dependencies and are of critical conservation concern. For example, just a handful of locations containing fewer than 20 individuals of *R. gardneri* exist, and the species is critically endangered (Delannoy et al., 2011; Swarts et al., 2009). Habitat fragmentation, reduced fire occurrence and the loss of seed dispersal agents all point to grave conservation concern for *R. gardneri*. Indeed, up to 95% of the probable range of the species has been cleared, and remnant bushland thickets containing the orchid are isolated, and in one case, privately owned (Hágsater & Dumont, 1996). Similarly, the newly described species *R. johnstonii* is known from just a single location, and is projected to decline in abundance (Dixon & Christenhusz, 2018). Climate change and soil salinization, together indicate a high level of extinction risk for *Rhizanthella* (Swarts et al., 2009). Taken together, these exceptionally unusual plants present a highly unusual challenge for conservation biologists, and their growth characteristics make it difficult to assign an accurate conservation status to them (Hágsater & Dumont, 1996). Botanic gardens have already played a major role in the conservation of *R. gardneri* to date through survey work and research into propagation and conservation management options (Swarts et al., 2009). However there are no conservation efforts in place currently, and the outlook for the survival of *R. gardneri*, at least, is precarious indeed. Further work should explore the population genetics, complex interdependencies, and the ecology and reproductive biology of the genus *Rhizanthella*. A combined approach of exploration surveys and *ex situ* conservation and re-introduction to suitable habitats should be an urgent priority to help conserve the world's only known underground flowers.

#### KEYWORDS

achlorophyllous, heterotrophic plant, mycoheterotroph, orchid, *Rhizanthella*

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