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Hydnora: The strangest plant in the world?

1 | INTRODUCTION

Hydnora is a remarkable, yet poorly known genus of parasitic plants which occur in the semi-arid regions of Africa, Madagascar and southern Arabia. An extreme reduction in morphological features, including the complete lack of leaves, has led to *Hydnora's* reputation as "the strangest plant in the world." Although it is one of the earliest branching parasitic plants in the flowering plant phylogeny, little work has been carried out on the genus and it remains virtually unknown in cultivation (see Movie S1 and Infographic S1). This holoparasitic (non-photosynthetic) plant, only emerges above ground to flower, can damage infrastructure by bursting through pavements (Maass & Musselman, 2001), and scarcely resembles any other flowering plant. Eight species of *Hydnora* are now recognized (Figure 1), of which one (*H. visseri*) was identified in 2011 in a market, advertised as a traditional medicine, in Johannesburg (Bolin, Maass, & Musselman, 2011; Williams, Falcão, & Wojtasik, 2011), and another (*H. arabica*) was only described in 2018 (Bolin, Lupton, & Musselman, 2018). Their unpredictable and elusive flowering, together with their remote distributions, suggest more species await discovery. Local communities may be instrumental in identifying new *Hydnora* species, making it a good "target" species for ethnobotanical research. Indeed, *Hydnora abyssinica* was discovered recently in Mozambique, following an ethnobotanical study conducted after rhizomes of *Hydnora* were found at the stalls of traditional medicine sellers (Williams et al., 2011).

2 | EVOLUTION AND LIFE HISTORY

The extreme reduction in morphological features of *Hydnora*—which is one of the few plants to lack all trace of leaves—has long obscured its evolutionary origins. Cronquist (1981) placed the Hydnoraceae within the Rafflesiales—a lineage famous for the largest flowers in the world (*Rafflesia* spp.). DNA sequence data have revealed that *Hydnora* is in fact placed with the family Aristolochiaceae in the order Piperales (Naumann et al., 2013; Nickrent et al., 2002), meaning their closest relatives are among the first divergent lineages of flowering plant—the so-called "basal angiosperms" (Jansen et al., 2007). Thus, with the exception of one known parasitic gymnosperm (*Parasitaxus*), and *Cassytha*—a genus of parasitic vines in the Lauraceae, the Hydnoraceae (comprising two genera: *Hydnora* in the Old World and *Prosopanche* in the New World), are the most basal parasitic plants known to science.

Hydnora has a narrow host range, and is parasitic upon the roots of host plants in the spurge (Euphorbiaceae), legume (Fabaceae), and torchwood (Burseraceae) families (Bolin et al., 2011; Bolin et al., 2018; Musselman & Visser, 1989). Host specificity can act as a catalyst for speciation in parasitic plants, in which cryptic species can be overlooked because of their reduced morphological features (Thorogood, Rumsey, Harris, & Hiscock, 2008). Because of their furtive life histories, poor representation in herbaria, and

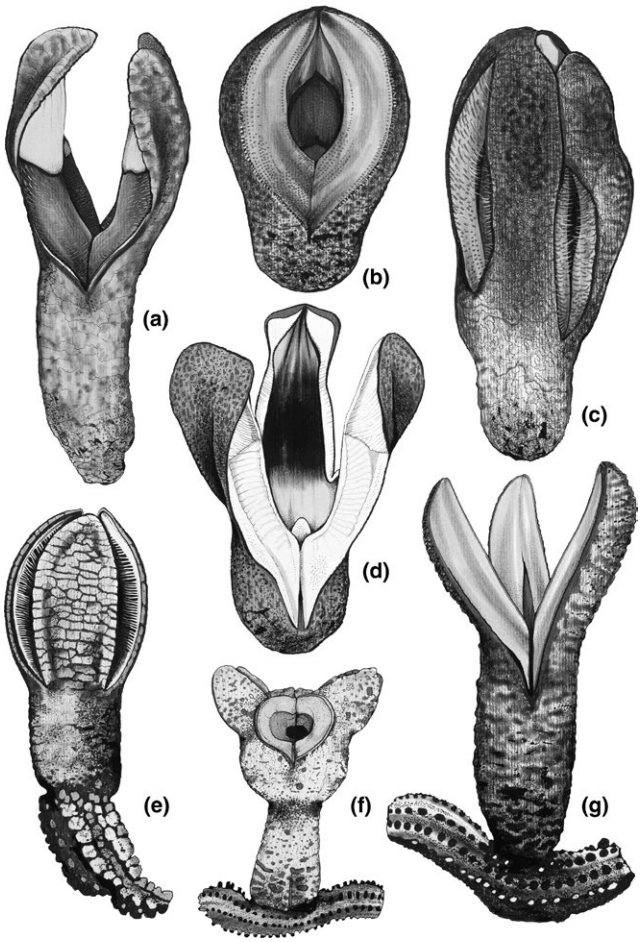

FIGURE 1 Diversity in the genus *Hydnora* (seven of the eight species known to science): (a) *Hydnora arabica*; (b) *H. visseri;* (c) *H. abyssinica;* (d) *H. esculenta;* (e) *H. africana;* (f) *H. triceps;* (g) *H. johannis*. Illustrations not to scale

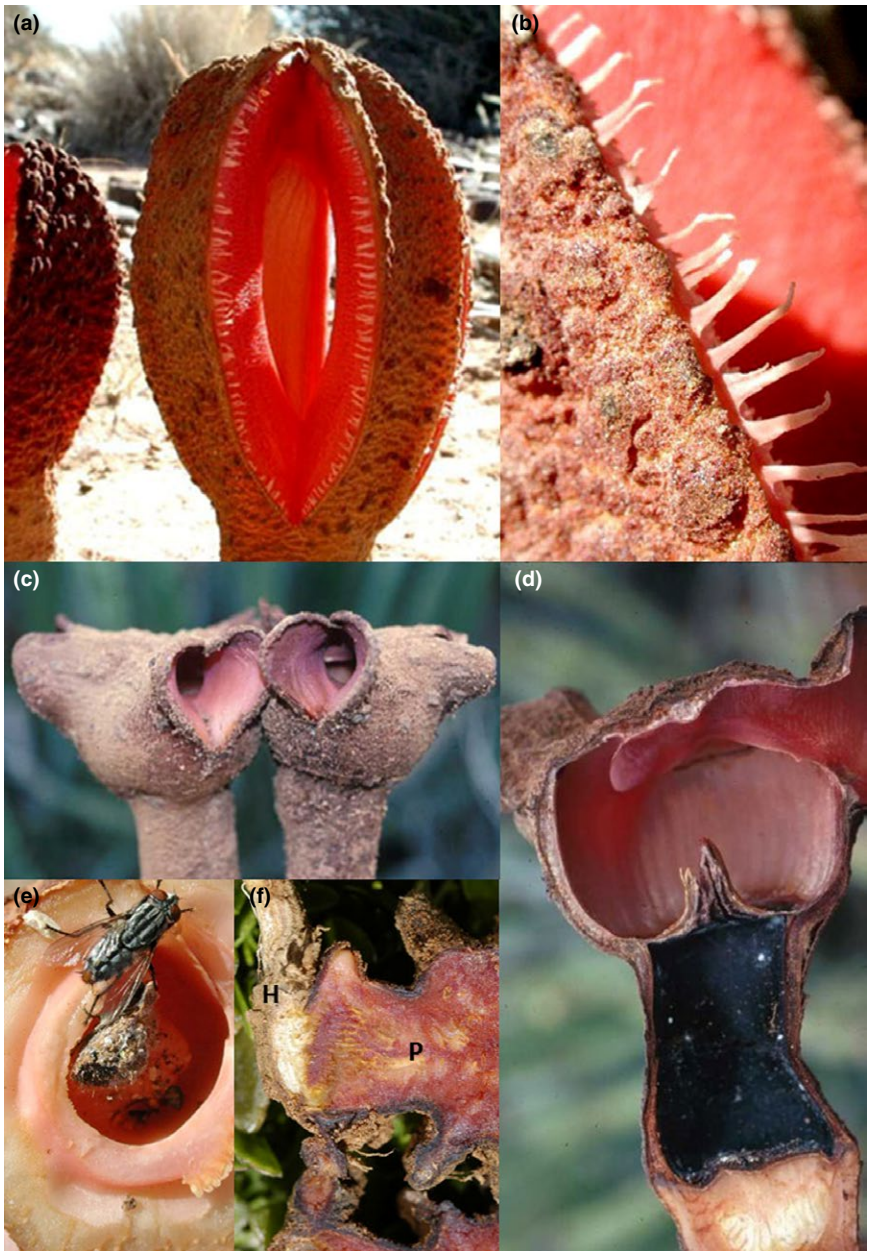

FIGURE 2 (a) Flowers of *Hydnora visseri*; (b) "Bait bodies" of *H. visseri*; (c) flowers of *H. triceps*; (d) cross section of *H. triceps* flower; (e) floral visitors in the floral chamber of *H. visseri*; (f) parasite tissue (P) of *H. triceps* attached to host root (H) of *Euphorbia dregeana*. Photographs by Lytton Musselman

recalcitrance to cultivation, empirical data and controlled experiments to test the host specificity of *Hydnora* are lacking. However the existence of distinct *Euphorbia*-parasitizing, and Fabaceae and Burseraceae-parasitizing lineages of *Hydnora*, respectively (Bolin et al., 2018), indicates that host specificity may have played a role in speciation.

3 | REPRODUCTIVE BIOLOGY

Of the few studies carried out on *Hydnora*, most have focused on reproductive biology. The pollination syndrome of *Hydnora* is classified as brood-site mimicry with imprisonment (Bolin, Maass, & Musselman, 2009). The peculiar flowers (Figure 2) attract insect pollinators (such as beetles) with a fetid smell, and possibly with slight heat production (Seymour, Maass, & Bolin, 2009), and temporarily imprison them in a floral chamber. Unusual tooth-like "bait bodies" (Figure 2b)—fetid bodies along the perianth lobe margins—are attractive to beetles in *H. africana* and *H. visseri*. Meanwhile peculiar *H. triceps* (Figure 2c–d) usually flowers beneath the soil surface, to which insects are apparently attracted through cracks in the ground (Musselman & Visser, 1989). The floral chamber of *Hydnora* comprises two parts: an androecial (male) chamber and a subtending gynoecial (female) chamber, connected by a central orifice that allows the passage of floral visitors between them (Figure 2e). A similar brood-site mimicry with imprisonment pollination syndrome is shared with *Aristolochia* spp. and may therefore be an ancestral state (Bolin et al., 2009).

4 | FUTURE WORK

Beyond reproductive biology, empirical studies on the *Hydnora* are scarce; however, recent research by Naumann et al. (2016) has put a spotlight on the genus *Hydnora* as a new model for understanding plastome evolution in parasitic plants. Interestingly, this work indicates that the plastome of *H. visseri*, while extremely reduced, is also likely to be functional, possibly relating to starch synthesis and storage (Naumann et al., 2016). In addition to its biology and life history, much further work is required to understand the diversity of the genus. Two of the eight known *Hydnora* species have been discovered only in the last decade and few botanists have ever encountered the genus. *Hydnora* is also virtually unknown in cultivation. *Hydnora africana* has been successfully cultivated just once outside its native range, on a host specimen of *Euphorbia caput-medusae*, in California. Attempts to cultivate *H. africana* from seed sown on pot-grown *Euphorbia tirucalli* (mislabeled as *E. mauritanica*) since 2008 in the University of Bristol Botanic Garden (UK), have failed (C. J. Thorogood, unpublished data). Cultivation trials will be important both in understanding the life history of this elusive genus, and for *ex situ* conservation. This will be particularly important for populations which are restricted to threatened habitats, such as *H. esculenta* in Madagascar.

5 | CONCLUDING REMARKS

Taken together, like so many parasitic plants, *Hydnora*, one of the "strangest plants in the world," remains elusive to science and cultivation. Even though about 1% of flowering plants are parasitic (Press & Graves, 1995), from an evolutionary perspective, parasitic plants are under-researched. As one of the earliest branching parasitic plants in the angiosperm phylogeny, *Hydnora* shows particular promise for investigating the evolutionary origins of parasitism in flowering plants.

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