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Prosopanche: A remarkable genus of parasitic plants

1 | INTRODUCTION

Prosopanche de Bary (Hydnoraceae) is a remarkable genus of subterranean holoparasitic plants native to South America and Costa Rica (Figure 1). There are currently seven recognised species (Figure 2), three of which were described in the last 4 years (de Carvalho et al., 2021). All seven species have highly reduced vegetative bodies and have lost leaves and functional roots completely. Each individual consists of an underground network of vegetative branching rhizomes lined with rows of meristematic tubercles. These tubercles can either remain dormant, develop into substantial fleshy flowers that breach the soil surface or form a haustorial connection upon contact with a host root (Musselman & Visser, 1989). Some *Prosopanche* are harvested and sold for their edible fruits, or their rhizomes, which are purported to have anti-asthmatic properties or are used as an expectorant (Cocucci, 1965; Cocucci & Cocucci, 1996).

The last comprehensive monograph of *Prosopanche* was written in 1965 by A. Cocucci, in which he concluded there were just two species in the genus. Recent work has focused on their ecology, for example, interactions between *Prosopanche* and the associated specialist *Hydnorobius* weevils that interact with them (Ferrer & Marvaldi, 2010; Sequeira et al., 2018), or the discovery of new species; otherwise, *Prosopanche* has received very little attention in the literature in the last 60 years (de Carvalho et al., 2021). Furthermore, *Prosopanche* has never been cultivated outside of its native range (Thorogood et al., 2022). Here, we provide an up-to-date revision of the current state of understanding of *Prosopanche* and make recommendations for future research in this enigmatic genus.

2 | TAXONOMY

The entirely holoparasitic family Hydnoraceae contains just two genera, with a disjunct distribution spanning South and Central America (*Prosopanche*: seven species; de Carvalho et al., 2021) and Africa and the Arabian Peninsula (*Hydnora*: eight species; Bolin et al., 2018). Both genera share the same basic body plan and holoparasitic habit but vary in certain morphological and ecological characters, including host preference. The genera are interpreted to have diverged at least

55 MYA (Naumann et al., 2013). Plants of *Prosopanche* species are generally smaller in stature than those of *Hydnora* and differ in having interstaminal appendages and fused polythecous anthers (Cocucci, 1965, 1975; Cocucci & Cocucci, 1996). Initially thought to be closely related to *Rafflesia* (Rafflesiaceae), early DNA sequencing analyses placed the two genera in the family Aristolochiaceae (Piperales) (Cronquist, 1981; Naumann et al., 2013). However, recent phylogenomic analyses show that the two genera lie sister to the Aristolochiaceae, leading authors to treat the Hydnoraceae as a distinct family (Jost et al., 2021). The Hydnoraceae are also remarkable for being the only entirely holoparasitic angiosperm family outside the eudicots, and, together with the unrelated genus *Cassytha* (Lauraceae), they comprise one of the earliest diverging parasitic lineages (Nickrent, 2020).

The first reference made to *Prosopanche* appears in the literature in 1845, cited as *Hydnora americana* R. Br., from a single collection from South America housed at the Kew Herbarium (then Hooker's Herbarium) (Brown, 1845). Heinrich de Bary (1868) described the genus *Prosopanche*, with a single species, *Prosopanche burmeisteri* (synonym of *Prosopanche americana*). In the following century, new species and varieties were described across Argentina and Paraguay, all of which were later synonymised under *Prosopanche bonacinae* and *P. americana* by Cocucci in 1965. Since then, five new species have been described across Central and South America: *Prosopanche costaricensis* (Gómez & Gómez-Laurito, 1981), *Prosopanche caatingicola* (Machado et al., 2012), *Prosopanche panguanensis* (Martel et al., 2018), *Prosopanche demogorgoni* (Funez et al., 2019) and *Prosopanche cocuccii* (de Carvalho et al., 2021).

The extreme morphological reduction of *Prosopanche* has deprived taxonomists of meaningful morphological characters to discriminate species. Key characters include the flower size, rhizome angle merosity, number of thecae on the synandrium, staminode type and flowers borne solitary or grouped in fascicles (Cocucci, 1965). A formal subgeneric classification has never been published, although more recent species protologues do contain scattered speculations on species relationships. Based on morphology, *P. bonacinae*, *P. caatingicola*, *P. demogorgoni* and *P. cocuccii* appear to be related; all are united by having smaller flowers than the other species in the genus and by their mostly trigonous rhizomes (de Carvalho

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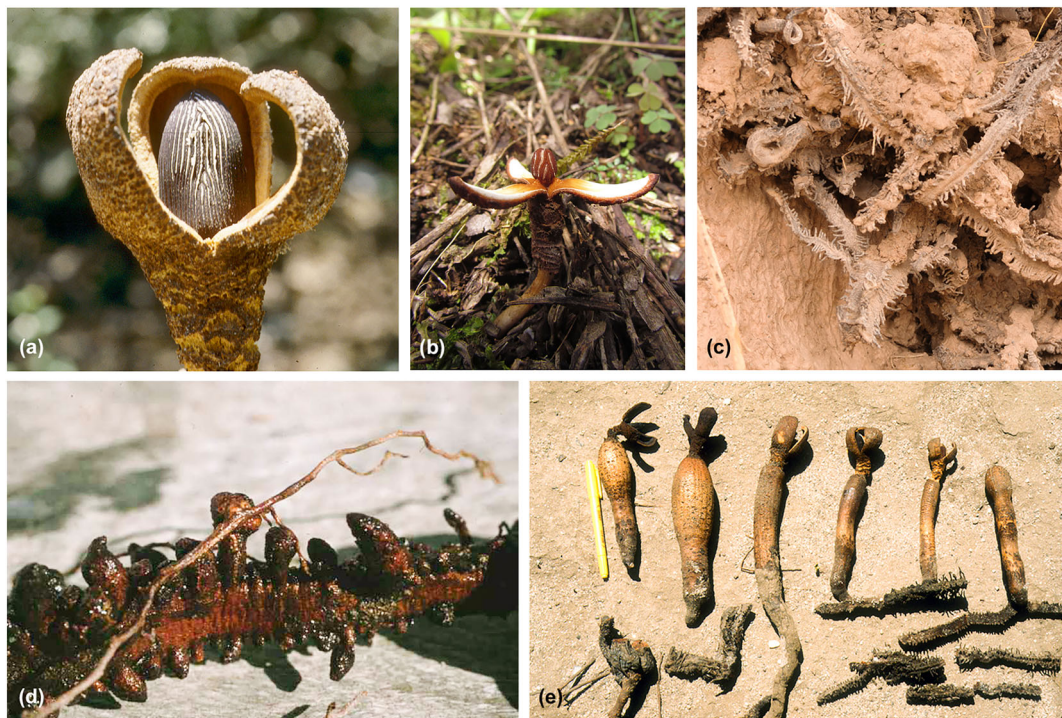


FIGURE 1 *Prosopanche* morphology. (a) *P. americana* open flower, (b) *P. demogorgoni* open flower, (c) *P. americana* underground rhizome system, (d) *P. bonacinae* rhizome and attached host root and (e) *P. americana* different developmental phases, from bud to fruit (right to left). Photographs (a, d, e) by Lytton J. Musselman, (b) by Luís A. Funez and (c) by Andrea A. Cocucci

et al., 2021). *P. panguanensis* bears some resemblance to *P. costaricensis*, which is in turn similar to *P. americana*, all three of which parasitise Fabaceae exclusively. This is supported by a recent phylogenetic tree reconstruction for the Hydnoraceae including three species of *Prosopanche*, in which *P. americana* and *P. panguanensis* form a clade that is sister to *P. bonacinae* (Jost et al., 2022). Extensive sampling is now needed to resolve relationships in the genus.

3 | BIOGEOGRAPHY

Prosopanche occurs across South and Central America (Figure 3). The two most widespread and frequently encountered species are *P. americana* and *P. bonacinae* which occur across most of Argentina, with scant records from Bolivia and Paraguay (Cocucci, 1965). Two species, *P. cocuccii* and *P. demogorgoni*, are found in the coastal Atlantic Forest region of southern Brazil, although each species is known only from a very small, localised area or, indeed, a single population (de Carvalho et al., 2021; Funez et al., 2019). *P. caatingicola* is known from an isolated population in the seasonally dry forests of north-eastern Brazil (Machado et al., 2012). *P. panguanensis* is known from the rainforests of central Peru, and *P. costaricensis* is reported only in the rainforests of Costa Rica (Gómez & Gómez-Laurito, 1981; Martel et al., 2018). These two species are the only known Hydnoraceae to occur in humid, tropical habitats.

The distribution of the genus is patchy and characterised by small, localised populations separated over great distances (Figure 3). This

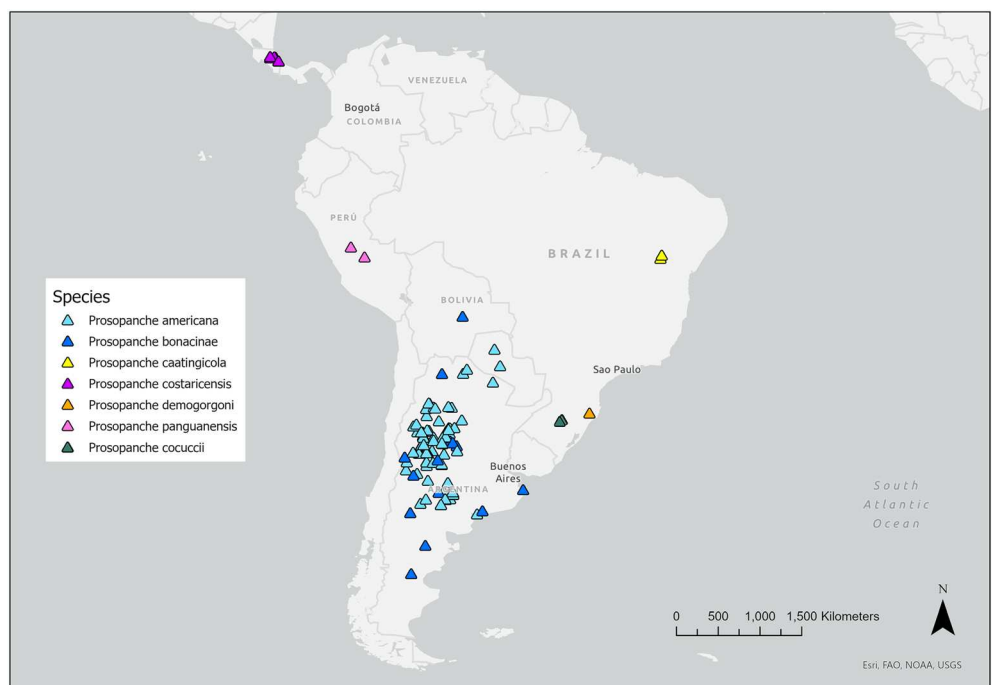
may be an artefact of poor sampling in remote areas. For example, there are no records of *Prosopanche* in Colombia, Ecuador and Panama; countries that lie between the known populations of *P. panguanensis* in Peru and *P. costaricensis* in Costa Rica. New populations of *Prosopanche* may be reported there in the future. Plants of *Prosopanche* tend to be inconspicuous and easily mistaken for fungi or tree roots and are collected or recorded infrequently. This may explain why new populations continue to be discovered. A similar trend is observed with *Hydnora* in Africa, where even as late as 2018, a population of *Hydnora abyssinica* was reported in Nigeria, over 1500 km from the nearest known population in Sudan (Agyeno et al., 2018). Interestingly, the plant was known to local communities in Nigeria and has been used in traditional medicine for centuries before it was reported formally to science (Agyeno et al., 2018). Given the number of recent species descriptions, it seems likely that additional populations of *Prosopanche* await discovery. Ethnobotanical research into the uses of *Prosopanche* by local communities may reveal new populations or taxa. For example, interviewing traders selling *Hydnora* rhizomes at traditional medicine markets in South Africa revealed new populations of *H. abyssinica* in Mozambique (Williams et al., 2011).

Understanding the full extent of a species' distribution is critical for making informed conservation decisions (Guisan et al., 2013). Conservation data for *Prosopanche*, like for many holoparasitic plant species, are deficient, partly because population size is difficult to determine when the plants spend the majority of their life cycle underground and out of sight (Thorogood, 2019). Species distribution modelling may be useful to predict where *Prosopanche* occurs based



FIGURE 2 The genus *Prosopanche* comprises seven species: (a) *P. panguanensis*, (b) *P. americana*, (c) *P. costaricensis*, (d) *P. cocuccii*, (e) *P. bonacinae*, (f) *P. caatingicola* and (g) *P. demogorgoni*. Illustrations not to scale. Illustrations by Sebastian A. Hatt

FIGURE 3 Global distribution of the genus *Prosopanche*. Distribution map was generated using ArcGIS Pro 2.8 (Environmental Systems Resource Institute [ESRI], 2021), based on geographic coordinates extracted from Global Biodiversity Information Facility (GBIF, 2022).



on a set of known conditions and variables (Guisan et al., 2013). Shao et al. (2022) used Maxent modelling to identify suitable habitats in which to conserve the holoparasite *Cistanche deserticola* (Orobanchaceae) under predicted climate change regimes. One of the key variables used in the model is the distribution of its host species, *Haloxylon ammodendron*. In order to apply effective species distribution modelling to *Prosopanche* and influence conservation decisions, a clear understanding of host range and specificity is therefore critical (Giannini et al., 2012).

4 | PARASITISM AND HOST SPECIFICITY

All parasitic plants produce a specialised organ called a haustorium, which forms a cellular bridge that enables nutrient transfer from host to parasite (Teixeira-Costa, 2021). This structure has evolved independently at least 12 times across the angiosperms (Nickrent, 2020). Between and within these lineages, there is considerable variation in the mode and extent of host dependence, ranging from facultative hemiparasites to obligate holoparasites to endoparasites that spend their entire lifecycle within the host plant (Teixeira-Costa & Davis, 2021; Thorogood et al., 2021). Levels of specificity among parasitic plant families and genera vary considerably. *Prosopanche* are no exception (Cocucci, 1965; Cocucci & Cocucci, 1996; Okubamichael et al., 2016). *P. demogorgoni* and *P. cocuccii* have only been recorded to parasitise two host species, one in the Asteraceae and one in the Solanaceae (de Carvalho et al., 2021; Funez et al., 2019). *P. americana*, *P. caatingicola*, *P. panguanensis* and *P. costaricensis* have all been recorded to parasitise a handful of species in the Fabaceae (Gómez & Gómez-Laurito, 1981; Machado et al., 2012; Martel et al., 2018). Finally, *P. bonacinae* is a generalist and hosts are recorded from at least seven different families, though interestingly not from Fabaceae (Cocucci, 1965). It is important to note that records of host identification may be inaccurate. Host data are rarely recorded by field botanists or confirmed by excavation (M. Gilbert, 2021, pers. comm.; Teixeira-Costa et al., 2022). Often, the host is assumed to be the nearest plant to the parasite, which is not always the case.

Host specificity is controlled by a complex combination of host-parasite compatibility mechanisms. This has been explored widely in weedy species such as *Striga* (Rodenburg et al., 2017). Fewer studies have explored interactions in non-weedy species. Research into hemiparasitic *Rhinanthus* (Orobanchaceae) has revealed active defence mechanisms such as hypersensitive cell death at the haustorial interface to resist parasitic attack (Cameron & Seel, 2007); similarly, host specificity in wild populations of *Orobanche* (Orobanchaceae) is governed by compatibility interactions at the cellular level that manifest in a series of developmental checkpoints (Thorogood & Hiscock, 2010). However, the mechanisms driving host specificity are unknown in most parasitic plants, particularly holoparasites that are rare and recalcitrant to cultivation (Albert et al., 2021). Studies investigating host compatibility mechanisms in *Prosopanche* or indeed any Hydnoraceae are absent, despite the interesting patterns in host range observed across the family. It has been suggested that host

specificity may have played a role in speciation in the genus *Hydnora* (Thorogood, 2019) and this requires further work.

5 | POLLINATION ECOLOGY

Though pollination biology is unknown for most *Prosopanche* species, flower visitors were reported as early as 1868 by de Bary, who gave an account of observations of more than 50 Nitidulid beetles found inside the stigmatic chamber of flowers of *P. americana* collected in Andalgalá (Catamarca, Argentina). More accurate information was provided subsequently by Bruch (1923) who reported the association of two coleopteran species, *Neopocadius nitiduloides* (Nitidulidae) and *Hydnorobius hydnorae* (Curculionoidea: Belidae), with the flowers of *P. americana*. Only the Nitidulidae beetles carry pollen into the stigmatic chamber, while the Belidae weevils bore holes in the flower from the exterior and lay their eggs within, thus bypassing the pollen (Bruch, 1923). It was later realised that *Prosopanche* flowers are protogynous and that beetle pollinators are attracted to and temporarily imprisoned in the thermogenic and scented female phase flowers (Cocucci & Cocucci, 1996). Recent work has revealed that the Nitidulid beetles arrive at dawn during the stigmatic phase, when flowers heat up by ~8°C above air temperature and emit a pleasant fragrance reminiscent of overripe fruit (Rocamundi et al., in prep). The flowers function as a trap, in which beetle visitors fall into the stigmatic chamber during the female phase and are subsequently released at the beginning of the staminal phase, when the slippery inner chamber wall lining changes configuration. (Rocamundi et al., in prep.). The larger bodied *Hydnorobius* weevils are rarely involved in pollination and are attracted to the flower only by floral thermogenesis and not by the scent of female phase flowers (Rocamundi et al., in prep.). Both coleopterans complete their life cycles feeding on post floral tissues, which is not thought to impair plant fitness. Nitidulid beetles are also known to act as pollinators of *P. bonacinae* and *P. panguanensis*, the latter of which is known to produce the same Nitidulid-attracting scent constituent isolated from *P. americana* (Rocamundi et al., in prep.).

6 | CONCLUDING REMARKS

The genus *Prosopanche* is a remarkable genus that is poorly understood. Three of the seven known species were described only in the last 4 years, and significant gaps exist in their distribution data. Meanwhile, little or nothing is known about the ecology, distribution, life history, germination requirements and host specificity of most species; all of which are critical data for enabling effective conservation of these plants. Preliminary work is revealing interesting observations on these elusive plants' biology, for example, the intricate pollination mechanism of *P. americana* involving floral thermogenesis and pollinator imprisonment and the diverse range of host specificity across the genus (de Carvalho et al., 2021; Rocamundi et al., in prep). Now, we suggest further research should explore the evolutionary relationships

within the genus, using next generation sequencing and extensive sampling across its geographic range. Finally, we suggest that the long evolutionary history of holoparasitism in the Hydnoraceae makes this family an ideal candidate for exploring the evolutionary origins of parasitism among flowering plants.

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CONFLICT OF INTEREST

The authors have no conflict of interests to disclose.

AUTHORS CONTRIBUTIONS

S.A.H. wrote the manuscript and prepared the illustrations, figure and map, with edits from D.D.C., O.M.G., N.R., A.A.C., C.M. and C.J.T. The section on pollination ecology was written by N.R., A.A.C. and C.M.

DATA AVAILABILITY STATEMENT

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

KEYWORDS

evolutionary ecology, host specificity, Hydnoraceae, parasitic plant, parasitism, pollination, *Prosopanche*, taxonomy

Sebastian A. Hatt^{1,2} 
 Duncan D. Cameron² 
 Olwen M. Grace¹ 
 Nicolás Rocamundi³ 
 Andrea A. Cocucci³ 
 Carlos Martel¹ 
 Chris J. Thorogood^{4,5} 

¹Royal Botanic Gardens, Kew, London, UK

²Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

³Laboratorio de Ecología Evolutiva y Biología Floral, IMBIV, CONICET and Universidad Nacional de Córdoba, Córdoba, Argentina








⁴Department of Plant Sciences, University of Oxford, Oxford, UK

⁵University of Oxford Botanic Garden and Arboretum, Oxford, UK

Correspondence

Sebastian A. Hatt, Royal Botanic Gardens, Kew,
 London TW9 3AE, UK.
 Email: s.hatt@kew.org

ORCID

Sebastian A. Hatt  <https://orcid.org/0000-0003-4887-3508>
 Duncan D. Cameron  <https://orcid.org/0000-0002-5439-6544>
 Olwen M. Grace  <https://orcid.org/0000-0003-1431-2761>
 Nicolás Rocamundi  <https://orcid.org/0000-0003-0044-1722>
 Andrea A. Cocucci  <https://orcid.org/0000-0002-3464-3309>
 Carlos Martel  <https://orcid.org/0000-0001-9892-1999>
 Chris J. Thorogood  <https://orcid.org/0000-0002-2822-0182>

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