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Evolutionary and ecological insights from *Cytinus*: A plant within a plant

1 | INTRODUCTION

The genus *Cytinus* L. is arguably one of the most enigmatic in the plant kingdom. It belongs to one of four families of parasitic plants, which grow embedded within the tissues of their hosts in a way similar to some fungi (Teixeira-Costa & Suetsugu, 2023; Thorogood et al., 2021). Due to a convergence in life history, the families Apodanthaceae, Cytinaceae, Mitrastemonaceae and Rafflesiaceae were long-thought to be monophyletic. However, molecular phylogenetic data have revealed their independent origins, placing Apodanthaceae in the order Cucurbitales, Mitrastemonaceae in Ericales, Rafflesiaceae in Malpighiales and Cytinaceae in the order Malvales, close to Neotropical Muntingiaceae (Filipowicz & Renner, 2010; Nickrent, 2007, 2020; Nickrent et al., 2004).

Cytinus shows an extreme reduction in morphological characters, lacking roots, with a stem reduced to the inflorescence axis beset with scale-like leaves, and flowering shoots only visible during the reproductive period when they emerge from the host (de Vega et al., 2009, 2007). The vegetative tissues are reduced to an endophytic system that lives entirely within the roots (rarely the stems) of the host. The endophyte inside host tissues forms filaments that anastomose, ultimately to generate bands of parasitic tissue, which forms sinkers with transfer cells. These facilitate the absorption of water and photoassimilates from host to parasite (de Vega et al., 2007). As non-photosynthetic angiosperms, the plastome of *Cytinus* is extremely reduced in size and gene content (Roquet et al., 2016); thus, the plants are completely dependent on their host for carbon nutrition and survival.

The genus *Cytinus* includes eight accepted species native to the Old World, with a striking distribution spanning the Mediterranean Basin, South Africa and Eswatini in southern Africa and Madagascar. Taxonomic boundaries are poorly delimited in the genus, owing to reduced morphological features, poor preservation as dried specimens and a dearth in herbarium records from some regions, for example, Madagascar, where we have identified putative taxa, which remain to be described. Even at the intra-specific level, phylogenetic studies indicate that evolutionary history of *Cytinus* is more complex than previously understood. Host-specific genetic races or ecotypes appear to have been overlooked because of cryptic morphology (de Vega et al., 2008; Martos et al., in press). *Cytinus* attract a diverse array of pollinators, including insects, birds and rodents (de Vega et al., 2009; Hobbhahn & Johnson, 2015; Johnson et al., 2011), but reproductive biology, including mode of seed dispersal, remains poorly understood for most species. Taken together, the genus *Cytinus* is a promising and largely untapped model system for exploring the genetics and evolution of parasitism, host-driven speciation and reproductive biology.

Here, we provide a brief review of the ecology and evolution of this neglected genus of endoparasites and present novel data on its remarkable diversity of pollinators and predators. We discuss potentially novel taxa and address taxonomic confusion in the genus and their implications for conservation and risk assessment.

2 | BIOGEOGRAPHY, TAXONOMY AND EVOLUTION

The family Cytinaceae contains two genera with a curiously disjunct distribution, spanning the New World (*Bdallophytum* Eichler, with four species from Mexico and Central America to Colombia; Alvarado-Cárdenas, 2009; Fernández-Alonso & Cuadros-Villalobos, 2012) and the Old World (*Cytinus*, Mediterranean Basin, Southern Africa, and Madagascar). Phylogenetic studies suggest a neotropical origin of the Cytinaceae in the late Cretaceous, with *Cytinus* highly supported as monophyletic and sister to *Bdallophytum* (Hernandez-Gutierrez & Magallon, 2019; Nickrent, 2007). The historical biogeographic reconstruction of *Cytinus* hypothesizes a divergence from the American ancestral lineages around 60 Myr and long-distance dispersal to tropical Africa (Martos et al., in press). Subsequent colonization of Madagascar (where the ancestors of *Cytinus* may have obtained climatic refuge), followed by expansion into warm temperate latitudes of South Africa and around the Mediterranean Basin, and eventual

FIGURE 1 Legend on next page.

speciation by host-specialization, may explain the unusual disjunct distribution of *Cytinus*. Genetic analyses support the monophyly of each biogeographical region, that is, a Mediterranean clade, a southern African clade and a Malagasy clade.

In the Mediterranean Basin, from Macaronesia to Asia Minor, *Cytinus* occurs in thermophilous, maquis-type vegetation where it parasitizes the roots of shrubs in the family Cistaceae exclusively (de Vega et al., 2008). Most taxonomic treatments recognize two species, *Cytinus hypocistis* (Figure 1a,b) and *C. ruber* (Figure 1c) (Table 1), which are distinguished mainly by flower colour (yellow-orange and pale pink, respectively) and by the identity of the host, the former parasitizing white or yellow-flowered *Cistus* (including *Halimium*) and *Helianthemum*, and the latter occurring on pink-flowered *Cistus* (Villar, 1997; Webb, 1993). Based on measures of subtle floral traits, several subspecies have been recognized including: *C. hypocistis* subsp. *hypocistis*, *C. hypocistis* subsp. *macranthus* Wettst., *C. hypocistis* subsp. *orientalis* Wettst. (ex Hayek), *Cytinus hypocistis* subsp. *pityusensis* Finschow, and *Cytinus hypocistis* subsp. *subexsertum* Finschow ex G. Kunkel for the yellow-flowered plants and also *C. hypocistis* subsp. *kermesinus* (Guss.) Arcang. and *C. hypocistis* subsp. *clusii* Nyman (both synonyms of *C. ruber*). More recently, genetic data have revealed that Mediterranean *Cytinus* can be separated into well-characterized genetic races or cryptic species associated respectively with different host lineages and that *C. ruber* is not more genetically differentiated from *C. hypocistis* than is the case among races of the latter (de Vega et al., 2008; Martos et al., in press). Such studies prompts a re-evaluation of the taxonomy of Mediterranean species. A more detailed examination over years of *C. hypocistis* populations has revealed that the number of flowers produced, morphological traits, floral rewards and flowering phenology is significantly influenced by the host species (de Vega, 2007; de Vega et al., unpublished). Thus, the distinction of races is supported not only by molecular data but also on phenotypic data. Again, this points to host specificity as an underestimated driver of speciation in the genus *Cytinus*.

Three endemic taxa have been described for Southern Africa: *Cytinus sanguineus* (Thunb.) Fourc. (synonym *Cytinus dioicus* Juss.) (Figure 1d,e), *Cytinus capensis* Marloth (Figure 1f) and the recently described *Cytinus visseri Burgoyne* (Figure 1g,h) (Table 1), the former two found in the Cape floristic Region (in Renosterveld, Cape Flats Dune Strandveld, and fynbos) and the latter in rocky sandstone outcrops of the northern South African Provinces and Eswatini ~1,400–2,000 m (Burgoyne, 2006; Smithies & Burgoyne, 2010). However, the recent discovery of numerous additional *Cytinus* populations that are likely taxonomically different from the above (Hobbhahn, unpublished; Burgoyne, unpublished) indicate that South Africa is likely richer in *Cytinus* species. *Cytinus capensis* has been synonymized under *C. sanguineus* (Goldblatt & Manning, 2000); however, differences in several floral features, pollination syndromes, flowering time and genetic data (Hobbhahn & Johnson, 2013, 2015; Martos et al., in press) all support the recognition of several phylogenetic species in this clade. In South Africa, *Cytinus* are specialized on Asteraceae and, to a lesser extent, Thymelaeaceae and Rutaceae (Burgoyne, 2006; Martos et al., in press). As noted for the Mediterranean taxa, Southern African *Cytinus* can be separated into races associated with specific host taxa, including *Helichrysum*, *Metalasia*, *Anaxeton*, *Oedera* and *Elytropappus* (Asteraceae) and *Passerina* (Thymelaeaceae) (Martos et al., in press). A thorough investigation of reliable and meaningful phenotypic and genetic parameters for defining cryptic taxa and the evolution of host races in southern African *Cytinus* is necessary to inform taxonomy and conservation.

Three accepted species are endemic to Madagascar: *Cytinus malagasicus* Jum. & H. Perrier (Figure 1i) known solely from the type specimen collected in 1912 (Jumelle & Perrier de la Bâthie, 1915), *Cytinus baronii* Baker f. (Figure 1j–l) and *Cytinus glandulosus* Jum. (Table 1). All occur in primary, humid forests. *Cytinus baronii*, found exclusively on the Masoala peninsula, and *C. glandulosus* on the Massif du Tsaratanana (NE Madagascar) appear to specialize on *Croton* (Euphorbiaceae); however, *C. baronii* was first described as potentially parasitising *Dicoryphe* (Hamamelidaceae), and *C. malagasicus*, found in the Analamazaotra forest (Centre-East Madagascar), was described parasitising *Dombeya* (Malvaceae) (Baker, 1888; Jumelle & Perrier de la Bâthie, 1915). The host identification in these cases is dubious.

More recent field observations in remote locations suggest that further Malagasy *Cytinus* taxa may await discovery. Based on morphological, biogeographical and phenological data, we propose at least four Malagasy *Cytinus* taxa remain unreported (Table 1; Figure 2). Here, we present imagery and morphological and ecological information on these taxa for the first time (see Section 3). The first undescribed taxa (*Cytinus* sp1) blooms in November and has been observed at the Masoala Peninsula (NE Madagascar) at 0–100 m parasitizing *Croton* sp., forming a population of ~100 individuals (year 1996; Schatz, personal communication). In the year 2015, the population was observed again, and a high density of flowers was observed (Figure 2a,b). *Cytinus* sp2 (Figure 2c–e) flowers in August and occurs in the Tsinjoarivo-Ambalaomby protected area (Central-East Madagascar), at 1,400–1,600 m. In this area, two populations have been found 13 km apart, one with male and one with female flowers; until genetic data are available, we tentatively consider these to correspond to the same taxon. In this region, its vernacular name is 'Atoditany', meaning 'egg of the earth'. A morphologically similar taxon, also flowering between August and September, and showing relatively similar female and male flowers, occurs in NE Madagascar at Marojejy National Park, more than 650 km away (Figure 2f–h). However, the relatedness of these taxa and the associated host species require

FIGURE 1 Accepted species in the genus *Cytinus* and associated pollinators. (a) *C. hypocistis*, (b) *Crematogaster auberti* ants pollinating *C. hypocistis*, (c) *C. ruber*, (d) *C. sanguineus*, (e) Malachite sunbird *Nectarinia famosa* probing flower of *C. sanguineus*, (f) *C. capensis*, (g) *C. visseri*, (h) *Elephantulus brachyrhynchus* feeding on nectar in *C. visseri*, (i) *C. malagasicus*, (j and k) *C. baronii* and (l) *Nesomis audeberti* feeding on nectar in *C. baronii*. Photos (a)–(c) by R. G. Albaladejo; photos (d)–(f) and (j)–(l) by N. Hobbhahn; photos (g) and (h) by S. D. Johnson; photo (i) from original description.

TABLE 1 Characteristics of *Cytinus* taxa.

Species	Area	Sexualsystem	Flower production	Flower colour	Tepals	WC	FP
C. hypocistis	MED	Mon	Inf (1–26)	Yellow-orange	4	1.3	Mar–Jun
C. ruber	MED	Mon	Inf (1–20)	White-pinkish	4	1.4	May–Jun
C. capensis	SAF	Dio	Inf (1–14)	Deep wine-red	4 (5,6)	1.7	July–Sep
C. sanguineus	SAF	Dio	Inf (1–4)	Deep crimson	6 (5)	2.2	Aug–Sep
C. visseri	SAF	Dio	Inf (1–21)	Dark maroon	6 (5)	1.6	Jan–May
C. baronii	MAD	Dio	Inf (1–4)	White	6	4.5	Oct
C. glandulosus	MAD	Dio	Inf (5–16)	Brownish	5	4	Oct–Dec
C. malagasicus	MAD	Dio	Inf (3)	Brownish	6	4	?
C. sp1	MAD	Dio	Sol	White	4	6	Nov
C. sp2	MAD	Dio	Sol	White-brownish	4	6	Aug–Sep
C. sp3	MAD	Dio	Inf (?-15)	Yellow	6?	4	Nov
C. sp4	MAD	Dio	Inf (4–8)	White	6	6	Oct–Nov

Abbreviations: Dio, dioecious; FP, flowering phenology; Inf, flowers arranged in inflorescences (range of flowers per inflorescence); MAD, Madagascar; MED, Mediterranean Basin; Mon, monoecious; SAF, Southern Africa; Sol, solitary flowers; WC, mean width of the corolla (cm) (measures of novel taxa from MAD are approximate).

careful analysis. *Cytinus* sp3 blooms in November and has been observed in the summit of mountain Maromokotro, potentially parasitizing *Polyscias* (Araliaceae). The first known record of this taxa was in 2010 and was observed again in November 2022 (Figure 2i–k). Finally, *Cytinus* sp4 flowers from October to November and was observed in 2010 and also years later at Anjanaharibe-Sud Special Reserve (Figure 2l–n), forming a small population of 40 inflorescences in an area of 500 m^2 (P. Hošek, personal communication). A combination of herbarium vouchers, detailed morphological observations and genetic analyses is essential to confirm the identity of novel Malagasy taxa in the genus *Cytinus*.

3 | FLORAL BIOLOGY, POLLINATION SYNDROMES AND ECOLOGY

All *Cytinus* taxa produce unisexual fleshy flowers (Figure 3), but there exists an astonishing geographical variation in sexual systems (monoecy and dioecy) and floral traits, including flower colour, size, scent and rewards, that are suggestive of multiple pollinator shifts.

Mediterranean *Cytinus* species are monoecious, and the inflorescence comprises a single, short spike with lateral female flowers and central male flowers. On a given host root, clusters of up 20 inflorescences may appear, which are usually produced by the same endophyte; in some cases, these can be genetically distinct, suggesting multiple infections of the same host may occur (de Vega, 2007). The tetramerous yellow (*C. hypocistis*) or white-pinkish (*C. ruber*) flowers (female wider and longer that males), secrete relatively limited nectar (c. 1 μl/24 h) and a scent dominated by a few aromatics compounds and irregular terpenes (mainly 4-oxoisophorone, (E)-cinnamaldehyde and (E)-cinnamyl alcohol) attract several ant species (Figure 1b). While seeking nectar, ants consistently touch the reproductive organs and carry large pollen loads (each male flower produce high amounts of pollen, up to 2.5×10^6 grains/flower), acting as the most effective and abundant pollinators (de Vega et al., 2009, 2014).

South African species are dioecious, with flowers either solitary or in short, few-flowered spikes protruding from the host root (Table 1). *Cytinus sanguineus* produces hexamerous (occasionally pentamerous), vermillion, scentless, easily accessible flowers which offer copious, diluted nectar (40 μl/24 h) from narrowly tubular floral nectaries (Hobbhahn & Johnson, 2015; Visser, 1981). This combination of floral adaptations conforms to the bird pollination syndrome and field observations have confirmed that this species is pollinated by Malachite Sunbirds (*Nectarinia famosa*) that, while visiting the flowers to forage for nectar, transfer efficiently copious amounts of pollen on their beaks between male and female inflorescences (Figure 1e) (Hobbhahn & Johnson, 2015). In contrast, *C. capensis* (with four, seldom more tepals, dark maroon and blooming from July to September), *C. visseri* (with five [six] tepals, scarlet and blooming from January to May), and most of the recently discovered populations possess characteristics consistent with the floral syndrome of plants pollinated by small, ground-dwelling mammals. *Cytinus capensis* and *C. visseri* have dark maroon unusually robust flowers, which contain copious (up to 130 μl) amounts of concentrated nectar (Hobbhahn et al., unpublished; Johnson et al., 2011). The densely hairy tepals remain tightly infolded, so that the flowers appear closed throughout anthesis (Hobbhahn et al., unpublished; Johnson et al., 2011). The flowers of *C. capensis* emit a strong, vanilla-like scent, while those of *C. visseri* produce a pungent scent reminiscent of nail-polish remover, dominated by two aliphatic ketones (3-hexanone and 1-hexen-3-one). Floral scent has been suggested to play an important role for both species in the attraction of small ground-dwelling mammals, *Aethomys* sp. (Muridae) in the case of *C. capensis*, and *Rhabdomys pumilio*, *Mus minutoides* (Muridae) and *Elephantulus brachyrhynchus* (Macroscelididae) (Figure 1h) in *C. visseri*, that efficiently open the flowers and transfer pollen from male to

FIGURE 2 Legend on next page.

female inflorescences while consuming nectar (Hobbhahn & Johnson, 2013; Johnson et al., 2011).

The pollination of Malagasy species remains a mystery, but floral features suggest most taxa are adapted to pollination by rodents or other small mammals (hinted at by Burgoyne, 2011). Like their counterparts on the African mainland, Malagasy *Cytinus* species are dioecious, with flowers borne solitary or arranged in inflorescences (Baker, 1888; Jumelle, 1923; Jumelle & Perrier de la Bâthie, 1915) (Table 1). *Cytinus baronii* is the only species that grows on the host trunks (Figure 1j), producing clusters of flowers surrounded by numerous orbicular scale leaves. The large male and female flowers are hexamerous, white and scented and offer copious nectar (Figure 1k). Recent field observations using motion-sensor camera recordings have revealed visitation in *C. baronii* by Malagasy endemic rodents genus *Eliurus* and *Nesomys* (Nesomyidae) that visit several flowers while seeking for nectar (Hobbhahn & Johnson, unpublished; Figure 1l). This is potentially the first report of pollination of *Cytinus* in Madagascar. To date, virtually nothing is known about the biology and ecology of the other two accepted species. The large size of the flowers and nectar chambers of *C. malagasicus* (hexamerous, brown, glabrous and arranged in an inflorescence, with aestivation arranged in a spiral) (Figure 1i) and of *C. glandulosus* (large conical inflorescence up to 15 cm across, with 5–16 brownish pentamerous, hairy flowers with five big nectar chambers) (Table 1) suggests pollination by small ground-dwelling mammals.

The size and morphological characters of the undescribed Malagasy taxa also point to small mammal pollination. *Cytinus* sp1 has large, solitary, tetramerous white flowers (Table 1; Figure 2a), with four large nectar chambers and a sweet fragrance resembling a tropical fruit with a slight fermentation odour. Although it bears some resemblance to *C. baronii*, *Cytinus* sp1 is tetramerous with thicker, fleshier and somewhat waxy tepals; the flowers are solitary, and the plant parasitizes roots rather than host stems. *Cytinus* sp2 bears solitary, tetramerous white-brownish flowers, showing a marked sexual dimorphism, with globose whitish female flowers with a black stigma (Figure 2c) and brownish, large male flowers, with an inflorescence axis bearing few scale-leaves (Figure 2d,e). Both male and female possess greatly enlarged nectar chambers. The form occurring in the north at Marojejy possesses similar female flowers (Figure 2f); however, the male flowers are smaller with shorter and rounder perianth lobes (Figure 2g). *Cytinus* sp3 is the only yellow-flowered *Cytinus* in the Southern hemisphere (Figure 2i–k). This taxon produces a very large and globose inflorescence of ~14 cm diameter, with up to 15 flowers with distinctly hairy tepals. Only female inflorescences have been observed. *Cytinus* sp4 is distinguished by its large, white, globose inflorescence up to 20 cm, covered with conspicuously densely imbricate, obovate white scales (Figure 2l,m). The inflorescence contains four to eight flowers, with usually six wide nectar chambers (Figure 2n). Scales and tepals turn rapidly brownish when inflorescence open, emitting a fragrance like honeydew melon (S. Goodman, personal communication). Virtually nothing is known about the biology and ecology of these potential new taxa. *Cytinus* sp2 (and the morphologically similar taxa observed at Marojejy) and *Cytinus* sp4 have been reported to be occasionally consumed by some lemur species (*Propithecus* sp.) (Irwin et al., 2007, E. Patel and R. Desiré, personal communication) (Figure 2h, note the sifaka holding a *Cytinus* flower in the hand), but the role of sifakas as potential pollinators cannot be ruled out.

The *Cytinus* species examined to date produce berry-like fruits containing many thousands of dust-like seeds with undifferentiated embryos (Bouman & Meijer, 1994; de Vega et al., 2011; de Vega & de Oliveira, 2007). Ants and rodents are efficient seed dispersers of Mediterranean *Cytinus* (de Vega, 2007). In the populations of *C. hypocistis*, the mice *Apodemus sylvaticus* and to a lesser extent the rabbit *Oryctolagus cuniculus* consume a large quantity of fruits during the night. They defecate droppings containing hundreds of viable *Cytinus* seeds right next to where they eat, so the dispersed seeds remain very close to the roots of the hosts. Ants (genus *Aphaenogaster*, *Crematogaster*, *Pheidolle*, *Tetramorium* and *Tapinoma*) also disperse large quantities of seeds of *C. hypocistis* during the day and carry them to ant hills, which are often very close to the roots of Cistaceae, even being observed at the base on the host trunks. Additionally, for Mediterranean *Cytinus*, a new type of dispersal, endozoochory by beetles, has been described (de Vega et al., 2011). The behaviour of the dispersers of *C. hypocistis*, placing dispersed seeds near host roots, may facilitate establishment in new host plants and even re-infection of natal hosts. Fine-scale genetic analyses in the Mediterranean *C. hypocistis* suggest that most seed dispersal events occur at short distances (de Vega et al., unpublished).

In southern Africa, rodents and even lizards have been suggested as potential seed dispersers of *C. visseri* (Smithies & Burgoyne, 2010); rats have been observed consuming the dry fruits of *C. glandulosus* (Perrier de la Bâthie, 1923). Foraging sifakas are attracted by the scent of the inflorescences of some of the Malagasy *Cytinus*, and predate them (Irwin et al., 2007), but these lemurs have been also observed consuming mature fruits (R. Desiré, personal communication), acting as potential dispersers. Details of seed germination and infection of host tissues remain a mystery, despite extensive attempts to germinate *Cytinus* seeds (de Vega et al., 2011). It is almost certain that *Cytinus* seeds require exposure to host-derived stimulants or require passage through the intestinal system of a disperser in order to germinate, as in other holoparasitic plants.

FIGURE 2 Potential new taxa in Malagasy *Cytinus*. (a) *Cytinus* sp1, (b) high density of *Cytinus* sp1 flowers bursting through host roots, (c) *Cytinus* sp2 female flower, (d and e) *Cytinus* sp2 male flowers, (f) *Cytinus* sp2 female flower of the population at Marojejy National Park, (g) *Cytinus* sp2 male flower of the population at Marojejy National Park, (h) *Propithecus candidus* eating a *Cytinus* sp2 flower (note the right hand of the sifaka), (i) group of inflorescences of *Cytinus* sp3, (j) immature inflorescence of *Cytinus* sp3, (k) detail of a female flower of *Cytinus* sp3, (l and m) inflorescences of *Cytinus* sp4 and (n) detail of female flowers of *Cytinus* sp4. Photos (a) and (b) by William J. Baker, RBG Kew; photos (c)–(e) by M. Irwin; photos (f)–(h) by E. Patel; photo (i) by C. Martin; photos (j) and (k) by F. Rakotonasolo; photos (l)–(n) by P. Hošek.

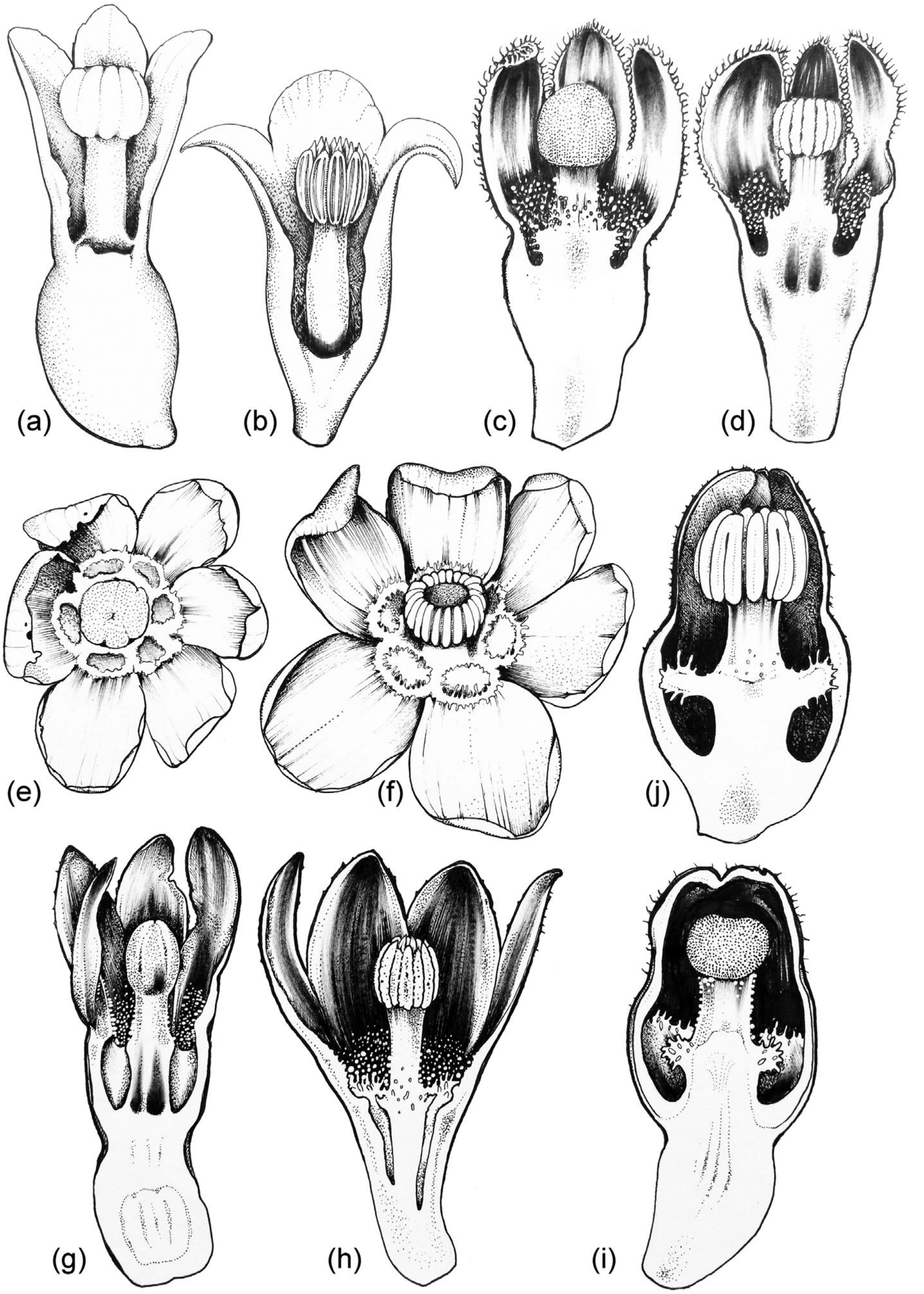

FIGURE 3 Floral morphology of some *Cytinus* species: (a) *Cytinus hypocistis* female; (b) *Cytinus hypocistis* male; (c) *Cytinus visseri* female; (d) *Cytinus visseri* male; (e) *Cytinus baronii* female; (f) *Cytinus baronii* male; (g) *Cytinus sanguineus* female; (h) *Cytinus sanguineus* male; (i) *Cytinus capensis* female; and (j) *Cytinus capensis* male. Illustrations not to scale. Drawn by Chris Thorogood.

4 | ETHNOBOTANY AND CONSERVATION

Mediterranean *Cytinus* have been used in traditional medicine since ancient times. More than 2,000 years ago, Hippocrates and Dioscorides recommended the juice of the inflorescences to treat a variety of disorders and since then has been used to treat indigestion, bleedings, dysentery, constipation and skin inflammation (Baumann, 1993; Lev & Amar, 2008; Sanna et al., 2006; Satil et al., 2017). Recent studies indicate the plants' hydrolysable tannins have cytotoxic activity against a broad spectrum of cancer cell lines (Magiatis et al., 2001) and that different extracts possess antimicrobial, antioxidant and anti-inflammatory activities (Maisetta et al., 2019; Silva et al., 2020), and, surprisingly, strong antiviral activity against the SARS-CoV-2 (de Araujo et al., 2023). The inflorescence axis and flowers have been traditionally consumed due to their nutritional properties (Satil et al., 2017; Tardío et al., 2006). We are unaware of any reports of the traditional uses of South African and Malagasy *Cytinus*.

Understanding the ecology, geographical distribution patterns, genetic structure of populations and host availability are critical for conservation planning involving parasitic plants (Barcelona et al., 2009; Marvier & Smith, 1997; Pelser et al., 2017). In the Mediterranean Basin, *C. hypocistis* is widespread and has not been evaluated in the IUCN list of endangered species. However, in some local areas, such as the eastern extreme of its distribution in Bulgaria (Petrova & Vladimirov, 2009), *C. ruber* has been included as species of ‘special interest’ (Boletin Oficial de la Región de Murcia (BORM), 2003) and evaluated as Critically Endangered (CR). In the Canary Islands, the status of some races of *Cytinus* on endemic *Cistus* requires assessment. In the Red list of South African plants, *C. sanguineus* is included in the Least Concern (LC) category, while *C. capensis* was considered critically endangered due to a limited number of collection records until recently, and in some places, it was even thought to have become extinct (Raimondo et al., 2009). *Cytinus visseri* was formerly evaluated as vulnerable with a limited distribution (Burgoyne, 2006), but its category reduced to LC in the Red List since it is not endemic to South Africa, also occurring in Eswatini. We suggest host identity should be considered in conservation planning, since cryptic host-defined races, comprising scarce and fragmented populations with unique genotypes may require additional management. Finally, the conservation status of Malagasy *Cytinus* has not been yet reviewed, but the numerous anthropogenic extinctions taking place in the island (Ralimanana et al., 2022) rapid habitat destruction, and small, fragmented and scarce populations advocate for their inclusion as CR taxa. Specifically, we suspect that *C. malagasicus* may already be extinct because it has not been recorded since its discovery in 1912. An urgent assessment of the biological and taxonomic diversity of Malagasy *Cytinus* will be crucial for their management and conservation.

5 | FUTURE RESEARCH

Extensive sampling combined with a detailed assessment of molecular, morphological and ecological data will be crucial to elucidate the evolutionary relationships within the genus *Cytinus*. With respect to sampling, we place particular emphasis on (1) host diagnosis, to identify potential host-specific races and cryptic taxa, which may have been neglected from taxonomic and conservation efforts, and (2) visiting remote locations of Madagascar to understand the life history and reproductive ecology of taxa from this poorly explored and rapidly changing geographic region. Given the marked diversity in pollination systems, we suggest further research could involve mapping floral traits and scent chemistry onto the *Cytinus* phylogeny to infer pathways of floral evolution. With respect to conservation, we recommend that seeds of all different races and taxa, as well as those of their host species, should be preserved in seedbanks, while the mechanisms of germination and initial processes of host infection also warrant urgent investigation (Thorogood et al., 2022). A combination of these data will be critical for ex situ conservation, particularly for taxa under threat. The unique combination of unusual biogeography spanning three major centres of diversification, complex floral traits and host specialization makes *Cytinus* a model system for exploring evolutionary diversification in parasitic plants.

KEYWORDS

Cytinaceae, endoparasite, host specificity, Madagascar, Mediterranean Basin, parasitic plant, pollination, South Africa

AUTHOR CONTRIBUTIONS

Clara de Vega and Chris J. Thorogood conceived the manuscript. Clara de Vega led the writing and prepared the figures. Chris J. Thorogood made the drawings. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

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

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