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Tracing the origins and tracking the movements of invasive rubber vines (*Cryptostegia* spp., Apocynaceae)

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Abstract
Cryptostegia grandiflora and *C. madagascariensis* (Apocynaceae) are the only two species of this Madagascan plant genus. Both have been transported around the world as ornamentals due to their attractive flowers and based on a perceived potential as sources of rubber – hence, the common name rubber vine – because of their copious latex, which also contains toxic cardiac glycosides. As a result of their vigorous growth and ability to climb over and smother vegetation, both species have become invasive, posing an actual or potential threat to native ecosystems in many tropical and sub-tropical countries, as well as to human and animal health. Classical biological control (CBC), or the introduction of co-evolved natural enemies to control an invasive alien species in its exotic range, has successfully been used to tackle *C. grandiflora* in northern Queensland, Australia. This strategy is currently being evaluated for its suitability to manage *C. madagascariensis* in north-eastern Brazil using the same Madagascan rust fungus, *Maravalia cryptostegiae*, released as a CBC agent in Australia. For CBC to be successful, it is critical to understand the taxonomy of the invader as well as the origin(s) of its weedy biotype(s) in order to select the best-matched co-evolved natural enemies. Based on an exhaustive search in published and unpublished sources, we summarise the taxonomy and uses of these rubber vines, follow their historical movements and track their earliest records and current weed status in more than 80 countries and territories around the world.

Keywords
Cardiac glycosides, classical biological control, poisonous plants, taxonomy, uses, weed status

Introduction

Cryptostegia (Apocynaceae, Periplocoideae) is a plant genus native to Madagascar with two accepted species: *Cryptostegia grandiflora*, commonly referred to as rubber vine and *C. madagascariensis*, alternatively named Madagascar rubber vine (Klackenberg 2001; Rojas-Sandoval and Acevedo-Rodríguez 2013a, 2013b; WFO 2022). These perennial woody vines have showy light-pink or purple-pinkish flowers, respectively and produce a milky poisonous latex containing cardiac glycosides. Being climbers, both species can grow up into adjacent taller vegetation, as seen particularly for *C. grandiflora* in riverine forests in Madagascar, but commonly also grow as sprawling shrubs along creeks and gullies, especially in disturbed habitats (Marohasy and Forster 1991). Due to their attractive appearance, as well as their latex, *C. grandiflora* and *C. madagascariensis* have been introduced as ornamentals and/or as potential sources of rubber into numerous countries around the world. In many of their introduced ranges, both species have subsequently become aggressive invaders; smothering native vegetation and threatening local biodiversity, as well as livelihoods (McFadyen and Harvey 1990; Rodriguez-Estrella et al. 2010; Sousa et al. 2016; Bekele et al. 2019; de Lucena et al. 2021). The extent of such invasions can be vast and include large conservation or environmentally-sensitive areas, rendering conventional methods of control by mechanical and/or chemical means inadequate and uneconomic. In these situations, classical biological control (CBC) – an environmentally benign and sustainable method, based on the use of co-evolved and highly specific natural enemies from the invader's native range for control in its introduced range – can offer a promising alternative method for control or form part of an integrated management strategy. Australia pursued this approach when embarking on a CBC programme to tackle the *C. grandiflora* invasion in tropical Queensland in the 1980s. This biocontrol initiative, based on the use of a rust fungus, is now considered to be one of the most successful ever implemented on this continent (Page and Lacey 2006; Palmer et al. 2010).

In order to achieve such success, it is fundamental to correctly determine the taxonomic position of an invasive plant species, as well as the biotype(s) present in the invaded country or region, in order to achieve a close match with its compatible natural enemies from the native range. This is especially critical when exploiting plant pathogens, such as rust fungi as biocontrol agents; typically, these are host specific at both the inter- and intra-species level. Where multiple or mixed introductions have taken place – particularly commonplace for plant species of horticultural or ornamental interest, such as *Lantana camara* (Verbenaceae) (Thomas et al. 2021) – it is crucial to establish such matches for all the invasive biotypes present. In the pre-molecular era, when field surveys searching for CBC agents in the native range had to rely solely on traditional plant taxonomic skills and herbarium records, identifying the area(s) in the centre of origin harbouring biotypes of the target plant species best-matched with the weed biotype(s) occurring in the invaded exotic range was inherently difficult. This is probably why a number of weed CBC programmes have been viewed as failures or only as partial successes – despite the fact that the natural enemy releases may have contributed to some degree of control of susceptible weed populations – because their impacts were cryptic and went unnoticed (Hoffman and Moran 2008; Barton 2012; Schwarzländer et al. 2018; Morin 2020).

A prime example of the complexity and problems involved when working with rust biocontrol agents is that of the invasive skeleton weed, *Chondrilla juncea* (Asteraceae), in Australia and its co-evolved rust, *Puccinia chondrillina* (Pucciniaceae), from the centre of origin in the Mediterranean Region. Following the initial release of a rust strain from Italy, populations of skeleton weed fell dramatically and this success has been well documented (Cullen et al. 1973; Burdon et al. 1981). However, the introduced rust strain or pathotype proved to be so specific that unrecorded resistant plant biotypes came to the fore and replaced the previously dominant rust-susceptible populations. Using isoenzyme techniques for biotype-pathotype matching, additional rust strains from both Italy and Turkey were released to achieve control of the emergent weed populations (Cullen and Hasan 1988). Similarly, the previously mentioned Australian biocontrol initiative against *C. grandiflora* became successful only following the release of a second strain of the host-specific Madagascan rust *Maravalia cryptostegiae*. Initial releases, undertaken with a strain sourced from *C. madagascariensis* in the northern region of Madagascar, proved to be ineffective against the congeneric target weed (Evans and Tomley 1996). In more recent times, molecular techniques have been adopted for CBC to better identify centres of origin of invasive alien plant species, as well as to pinpoint specific biotypes, thereby improving the chances of finding better-matched, co-evolved natural enemies. For example, a molecular analysis has been used recently to identify the biotypes of Himalayan balsam (*Impatiens glandulifera*, Balsaminaceae), an invasive weed in the British Isles, based on chloroplast DNA sequences (Kurose et al. 2020). The results indicated that at least three separate introductions of this ornamental plant were made and that those biotypes resistant to the two strains of a rust *Puccinia komarovii* var. *glanduliferae*, from north-west Pakistan and north-west India, released in the UK thus far, probably originated in the eastern Kashmir Region of the Himalayas. Further targeted surveys to collect and identify additional rust strains from this region have been initiated to address the problem.

Currently, a similar study is underway as part of a CBC project for Brazil aiming to match pathotypes of *M. cryptostegiae*, under evaluation as a biocontrol agent, with the biotype(s) of *C. madagascariensis* invading the north-eastern region of the country. Literature searches to establish the identity of these weed populations and to trace their origin have revealed a complex history of inter-continental transport of *Cryptostegia* species spanning centuries. In addition to summarising the taxonomic debate surrounding the genus *Cryptostegia*, we track the movements linked to its uses and assess the environmental impact of the two rubber vines from Madagascar in the countries and regions where they have been introduced.

Taxonomic history

The genus *Cryptostegia* was erected to accommodate the single species *C. grandiflora*, based on a specimen sent to the Royal Botanic Gardens (RBG) Kew from a hot-house plant cultivated in the English Home Counties: "where it flowered in summer, we believe, for the first time in Europe" (Brown 1820). Robert Brown was the botanical consultant at RBG Kew and Keeper of Botany at the British Museum (Desmond 1995) and "The name [*Cryptostegia*] was suggested to Mr. Brown by the circumstances of the enclosure of the five-scaled crown within the tube of the corolla and it not being exposed to view as in other bordering genera" (Brown 1820). In the absence of a holotype, the illustration of this specimen (Brown 1820: t. 435; see Fig. 1) was chosen by Marohasy and Forster (1991) as the lectotype.

The main description of *C. grandiflora* in Brown (1820) is actually by Roxburgh, under the name *Nerium grandiflorum*, based on a specimen collected in India and listed in Hortus Benghalensis (Roxburgh 1814), but only published posthumously, nearly two decades later, in Flora Indica (Roxburgh and Carey 1832). However, before Roxburgh left India in 1813, he appears to have sent the description – as well as a drawing, listed in Icones Roxburghianae (Sealy 1956; see Fig. 2) – to RBG Kew, which was used to complement Brown's type description of the genus *Cryptostegia*. The latter is brief and in Latin, preceding the body of the paper, which was written by the editors of the *Botanical Register* – a short-lived journal devoted to 'Exotic plants cultivated in British Gardens'. In this case, the exotic *C. grandiflora* had been grown by Sir Abraham Hume – on his estate at Wormleybury, Hertfordshire – who, as a director of the East India Company, maintained a large collection of rare Indian plants regularly sent to him by William Roxburgh from the Calcutta Botanic Garden (Harwood 2007; Kochhar 2013).

According to Roxburgh (1814), the collection of *N. grandiflorum* in the Botanic Garden at Calcutta was sent by Dr B. Heyne from southern India in 1804. Benjamin Heyne was a botanist employed by the East India Company who was variously based at botanical gardens in Bangalore and Mysore (Sikarwar 2020). The fall of the Mysore Sultanate in 1799 opened up access to the Western Ghats and the Malabar Coast, allowing plant collections to be undertaken in these areas (Heyne 1814). In the latter publication, Heyne devotes a section to latex-producing plants and *Nerium* is cited in the list. It is reasonable to suppose, therefore, that Heyne would have labelled the rubber-vine material that he despatched to Roxburgh in 1804 as an unknown and endemic species of *Nerium*. All the subsequent references quote *C. grandiflora* as being "A native of the Peninsula of India" (Brown 1820; Roxburgh and Carey 1832). This raises the further assumption that *C. grandiflora* had been present in south-west India for a considerable period of time, becoming naturalised and accepted locally as part of the native flora and not as an exotic species. There are several overriding questions: why did rubber vine not become invasive in the region; and who introduced it from Madagascar and when?

Historical events point to the Portuguese who colonised the area around Cochin on the Malabar Coast in the early 16th century and later established a viceroy ship there. Around this period, the first attempt at European colonisation of Madagascar was also by the Portuguese; although the first permanent settlement was not established until around 1615 at the behest of the Portuguese Viceroy of India. This colony in southern Madagascar, near Fort Dauphin (Taolagnaro), became pivotal in the transoceanic trade route between Portugal and India (Brown 2001). Plants from Portuguese

Figure 1. Lectotype of *Cryptostegia grandiflora* in Brown (1820), based on a flowering specimen donated by Sir Abraham Hume from his hot-house at Wormleybury Manor, Hertfordshire, England.

colonies in Africa and the Americas (Brazil) and, presumably, also from Madagascar, arrived in India via this route (Gavali and Lakhmapurkar 2018; Sikarwar 2020). *Cryptostegia grandiflora* is a common plant in the southern region of Madagascar (Marohasy and Forster 1991; Klackenberg 2001) and, thus, may have attracted the attention of the Portuguese colonists, either as an ornamental or for its purported local uses in making cloth and rope for fishing nets (Jumelle 1907; Klackenberg 2001).

The new species *C. madagascariensis*, in Bojer's (1837) Hortus Mauritianus – or, 'the exotic and indigenous plants cultivated in Mauritius' – was the first indication that *Cryptostegia* might not be native to India. Bojer recorded *C. madagascariensis* as present in botanical gardens on Mauritius, but gave its origin as Madagascar, specifically

Figure 2. Illustration of *Cryptostegia grandiflora* (as "*Nerium grandiflorum* Roxb."), from Icones Roxburghianae (Sealy 1956); drawings commissioned by William Roxburgh of plants in the Calcutta Botanical Garden and sent to RBG Kew together with specimens and descriptions, between 1793 and 1813.

as a coastal plant common around the Bay of Bombetok[a], which lies in north-west Madagascar close to the port of Majunga (Mahajanga). His view was reinforced by P. Koenig, a plant collector who sent specimens to Kew from Mauritius in 1907–1908 and who posited that *Cryptostegia* had already been introduced on to the island by the Malagasy people two to three centuries earlier (Klackenberg 2001). Bojer (1837) also listed *C. grandiflora* as growing in Mauritius, but still gave its origin as India. Decaisne (1844) gave a full description of the genus and both the species, *C. grandiflora* and *C. madagascariensis*; the former said to be from India, the latter from Madagascar. Amongst the critical distinguishing characters between the species, he noted the corona lobes as being bifid or bilobed in *C. grandiflora* and entire in *C. madagascariensis*, which has since been confirmed by others (Hemsley 1904, see Fig. 3; Jumelle 1908; Polhamus et al. 1934; Marohasy and Forster 1991; Klackenberg 2001). Costantin and Gallaud (1906) listed both *C. grandiflora* (local name: lombiri) and *C. madagascariensis* (local name: lombiro) from Madagascar, but described the former as exotic ("non indigène") and growing spontaneously. Furthermore, they named an indigenous variety from the Tulear (Toliara) Region, *C. grandiflora* var. *tulearensis* (local name: lombirivoharoto), distinguished by its smaller, more elongated leaves and smaller fruits (Costantin and Gallaud 1906).

Subsequently, Jumelle (1908, 1912) confirmed the presence of *C. grandiflora* in Madagascar – specifically, being confined to the southern region and reaching as far as Tulear in the south-west – but was unclear about its origin. He still appears to have included India within its natural range, describing it as common, whilst listing it as having been introduced into Mauritius and Réunion, as well as into Egypt,

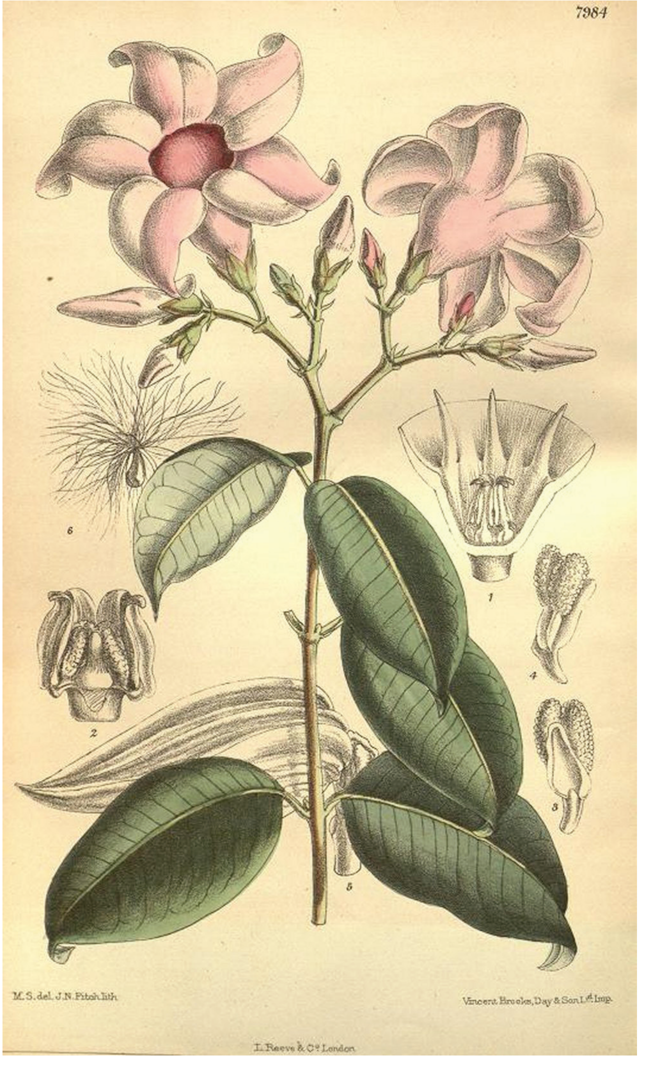

Figure 3. Illustration of *Cryptostegia madagascariensis* in Hemsley (1904), drawn from a plant grown at Royal Botanic Gardens, Kew.

Sudan, Java, Mexico and Cuba. Klackenberg (2001) considered that Jumelle (1908) was, in fact, the first to recognise that *C. grandiflora* is a Madagascan endemic – and, therefore, that it must have been introduced into India – but this interpretation is open to question and, from the literature review, it still remains unclear exactly when *C. grandiflora* was confirmed definitively as being indigenous to Madagascar and exotic in India. As late as 1975, it was still being described as native to India, whilst the Madagascan endemicity of *C. madagascariensis* was unambiguous (Spellman 1975). Nowadays, the Madagascan origin of both *Cryptostegia* species is undisputed (Ionta and Judd 2007).

Taxonomic status

The two species recognised in the most recent treatment of the genus (Klackenberg 2001) – *C. grandiflora* and *C. madagascariensis* – are morphologically separated as follows:

"Calyx lobes > 13 mm long; corona lobes bifid; spathe of translator orbicular, obtuse at apex; leaves always glabrous; follicles often more than 10 cm long.................... .... **1. *C. grandiflora***

Calyx lobes ≤ 13 mm long; corona lobes entire; spathe of translator ovate, acute at apex; leaves sometimes hairy; follicles shorter than 10 cm............**2. *C. madagascariensis***"

The flower main characteristics to separate the two species were illustrated by Curtis (1946; see Fig. 4).

Hochreutiner (1908) distinguished *Cryptostegia glaberrima* from *C. madagascariensis* using the lack of leaf indumentum as one criterion, while Marohasy and Forster (1991) delimited three varieties of *C. madagascariensis*: var. *madagascariensis*, with sparse to dense indumentum on both leaf surfaces; var. *glaberrima*, glabrous on both surfaces; and var. *septentrionalis*, with indumentum only on the upper surface. However, Klackenberg (2001) considered that this is "a taxonomically useless character in *Cryptostegia*", since he encountered varying degrees of leaf hairiness in the continuum of populations of *C. madagascariensis* along the west coast of Madagascar. While not having seen the type of *C. grandiflora* var. *tulearensis*, Klackenberg (2001) considered this as an uncertain taxon and likely a synonym of *C. grandiflora*.

Distribution and ecology in Madagascar

Marohasy and Forster (1991) were the first to map and interpret the distribution and ecology of the genus *Cryptostegia* in Madagascar, following extensive surveys from 1987–1988 by the former author. *Cryptostegia madagascariensis* was found to have a continuous distribution along the western coast, from Tulear in the south-west to Maromandia in the north-west, a distance of some 1600 km, occurring naturally in riverine and seasonally-flooded forests in areas with an annual rainfall between 600 and 1800 mm. However, they noted that it could be an aggressive invader in disturbed habitats and especially in secondary savannahs, where it grows in full sun (Fig. 5A). The geographically-isolated populations in the extreme north-west region around Diego Suarez (Antsiranana), with a monsoonal climate (1200–1800 mm per annum) – separated taxonomically as var. *septentrionalis* (Marohasy and Forster 1991) – occur in gullies and often form dense stands in coastal saltmarshes (Fig. 5B). They seem to have a distinct ecological niche and are possibly genetically isolated. Differences in populations like these may be relevant and could explain their ability (or not) to invade exotic ecosystems and, ultimately and critically, define the success of any biological control programme by using best-matched natural enemies.

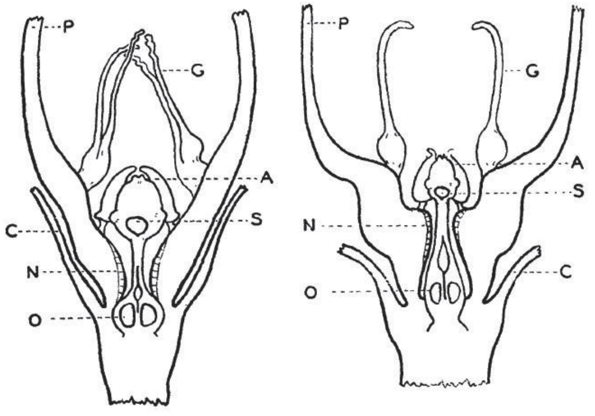

Figure 4. Diagram of a longitudinal section of *Cryptostegia grandiflora* (left) and *C. madagascariensis* (right) flowers; showing the corolline corona (G) in *C. grandiflora*, with bifid lobes converging at the tips and hiding the anthers (A) and stigma (S) – hence the generic descriptor – whilst those of *C. madagascariensis* are entire and separate. C = calyx, N = nectary, O = ovary, P = corolla lobes; ex Curtis (1946).

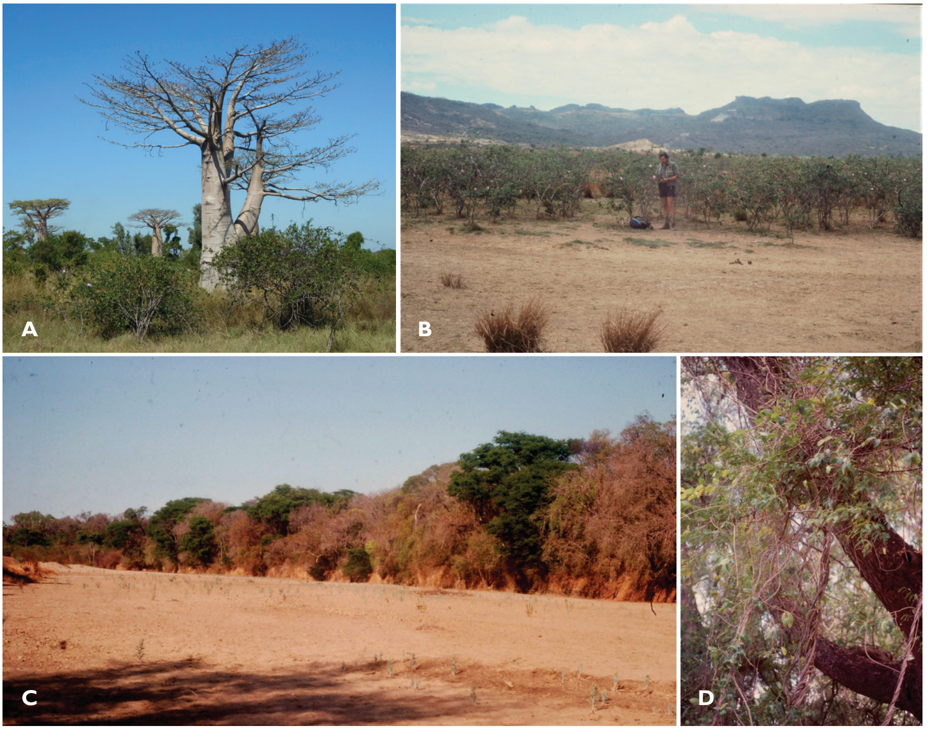

Figure 5. Habitats of *Cryptostegia* in Madagascar **A** *C. madagascariensis* forming low shrubs in savannah with typical baobab vegetation, Morondava-Manja area, west-central Madagascar **B** *C. madagascariensis*, in littoral locality forming dense, low stands on compacted sand, Ramena beach, Diego Suarez, northern Madagascar **C** gallery-forest habitat of *C. grandiflora* in south-west Madagascar, along dry river bed **D** lianas of *C. grandiflora* growing into the canopy of tamarind trees within gallery forest, Betioky, south-west Madagascar.

Cryptostegia grandiflora has a narrower distribution in Madagascar, being restricted to the dry south-west region, some 600 km distance between Tulear and Fort Dauphin, with an annual rainfall of less than 600 mm. It is a vigorous climber in gallery or riverine forests (Fig. 5C, D) and common in disturbed habitats, occurring along river beds, creeks and gullies, from sea level to ca. 500 m.a.s.l. The two species are sympatric between the Fiherenana and Onilahy Rivers, north of Tulear, from where putative hybrids have been reported (Marohasy and Forster 1991).

Uses

Morais et al. (2021) reviewed the plant chemistry of the genus *Cryptostegia* in relation to its biological activities and industrial applications. Here, we examine more critically the attempts to utilise the genus as a crop and as a source of medicinal products.

Rubber

Danthu et al. (2016) charted the history of rubber production in Madagascar, which was based on crude extractions from the logged stems of various members of the Euphorbiaceae and Apocynaceae. They included both species of *Cryptostegia*, in which the quality of rubber from *C. grandiflora* had previously been noted by Jumelle (1912) as being superior to that from *C. madagascariensis*. The use of latex, or gum elastic, by the indigenous peoples had been recorded as long ago as the end of the 18th century (Danthu et al. 2016). However, it was not until the latter part of the 19th century that exports of rubber to Europe commenced and by the end of this and the early 20th century that it formed the major export from Madagascar. Palay rubber – as the product from *Cryptostegia* was known on the international commodity market, although this name has its origin in India and is probably derived from the Tamil word, palai – occupied around 20–30% of the total rubber exports; the greater percentage coming from the Euphorbias (Danthu et al. 2016). As these authors highlighted, this came at great cost to the different forest ecosystems from where the plants were extracted and the increasing scarcity of raw material plus the rise of the superior *Hevea* rubber led to the decline of rubber production in Madagascar after the First World War. However, during the Second World War – as Madagascar passed into Allied hands – there was a concerted, but short-lived effort (1943–1945) to resuscitate the rubber industry in order to secure the world demand following the Japanese occupation of the *Hevea* plantations in Asia (Danthu et al. 2016).

These events also led the USA to invest more heavily in alternative sources of rubber, including *Cryptostegia*, through the Emergency Rubber Project. Experimental plantations were initiated or revived in various tropical countries of the Americas, especially in Haiti (Knight 1944; Finlay 2009). Based on previous post-war research, Palay rubber was considered to be equivalent or even superior to *Hevea* rubber and high-yielding hybrids had been developed in the USA (Polhamus et al. 1934). This *Cryptostegia* material formed the basis of the multi-million dollar rubber project initiated in Haiti in 1943, with over 60,000 acres being commandeered and cleared for planting (Symontowne 1943). However, a combination of various factors hampered the initiative, including: devastating insect attacks (Knight 1944), drought, difficulties in harvesting and, more critically, poor yields due to the technical problems involved with latex extraction (Stanton 1944). This resulted in "The embarrassing collapse of *Cryptostegia*" (Finlay 2009), with serious socio-economic and political ramifications in both Haiti and the USA. These historical failings with rubber-vine cultivation were not addressed by Augustus et al. (2000) who explored the potential of *C. grandiflora* as a multi-purpose crop in India, particularly as an alternative source of biofuel. They noted that "It grows profusely without agronomic management": one of the reasons that it failed in Haiti was because of harvesting logistics (Finlay 2009) and, of course, a trait that makes rubber vine such an aggressive weedy invader.

Fibre

Jumelle (1907) gave a detailed account of the production of fibre from *C. madagascariensis* in north-west Madagascar, which was used to make textiles, rope and fishing nets. However, there are no reports of its current exploitation as a fibre crop in Madagascar or elsewhere, except perhaps for Papua New Guinea (fide Herb K annotation).

Medicinal

There are various reports in the literature of the anti-tumour and anti-microbial potential of bioactive extracts of *C. grandiflora*, as well as analgaesic properties (Doskotch et al. 1972; Mukherjee et al. 1999; El Zalabani et al. 2003; Singh et al. 2011; Hanumanthappa et al. 2012; Morais et al. 2021). Castro et al. (2014) reported that *C. grandiflora* was widely used in folk medicine on the Caribbean coast of Colombia – particularly, as an anti-inflammatory – and identified metabolites in the leaves that proved to have anti-inflammatory properties in both *in vitro* and *in vivo* experiments. Similar ethnobotanical surveys in India also revealed that leaf decoctions of *C. grandiflora* were used to treat liver and nervous disorders (Wagh and Jain 2018).

Conversely and somewhat ironically, in their Madagascan centres of origin, the two rubber-vine species have limited medicinal uses, although Jumelle (1907) did note that the Sakalava tribe of western Madagascar prepared root decoctions of *C. madagascariensis* to cure chronic gonorrhoea. In fact, these vines are avoided by most ethnic groups who often warn travellers about the toxic dangers of the latex (Evans HC, pers. obs. 1988) – which contains glycosides that affect cardiac systems – and *C. grandiflora* has been linked with both animal and human deaths in Australia (McFadyen and Harvey 1990). In Madagascar, *C. madagascariensis* has been traditionally used as a poison to commit suicide or against enemies (Jumelle 1907), especially by 'wronged' wives. Ironically, in its exotic range, it is also known as 'flor de muerto' (death flower) in Colombia (Castro et al. 2014) and as 'viuvinha' (small widow) or 'viúva-alegre' (happy widow) in north-east Brazil (Sousa et al. 2016; Morais et al. 2021).

Weed status

This section covers those continents or geographic regions for which data regarding the presence and status of the two *Cryptostegia* species exist. Data were gathered from both published and unpublished sources, i.e. reports and herbaria records, as well as from web-based sources: namely, the Global Biodiversity Information Facility (GBIF), the Germplasm Resources Information Network (GRIN) and the databases Tropicos, the Global Invasive Species Database (GISD), Pacific Islands Ecosystems at Risk (PIER) and Plants of the World online (POWO). All herbaria consulted are referred to with their acronyms according to Thiers (2022). Identification of individual *Cryptostegia* species from herbarium specimens could not always be confirmed, as online images were often not available or specimens were not well preserved. Thus, in most cases, the species identification given on the respective labels and in the databases was accepted. Table 1 lists occurrences of *C. grandiflora* and *C. madagascariensis* for individual countries and territories with earliest records, where known and additional information. Those for which more detailed information is available – concerning the history of introduction, the use and current status of the species – are discussed below. The situation in Australia is treated in depth because it is where *Cryptostegia* was first identified as a major invasive weed and a management strategy for its control was pioneered.

Asia

China (Hong Kong)

A specimen of *C. madagascariensis* in Herb K from the Hong Kong Botanical Garden dated 1879 indicates that the species must have been introduced from another British colonial botanical garden.

India

The history of *C. grandiflora* in India has already been discussed at length. Suffice to say that there are few publications of it as a problematic or invasive weed. In the invasive alien flora of India (Srivastava et al. 2014), *C. grandiflora* is described as an “aggressive coloniser” and “occasional in forests”, but quantitative data are lacking. It is also listed in the invasive alien species of Uttar Pradesh – with its weedy status described as “interfering” – but it is not included in the list of India’s most noxious weeds (Reddy et al. 2008). Similarly, it is included under its native name, ‘rubber-bel’, in a study of the plant composition of a conservation area in Rajasthan, but with no indication of its invasive or alien status in the comments on invasive alien weeds (Chaudhary and Shringi 2017). The earliest Herb K record is from January 1804, labelled “*Echites-Apocynum*, from the Governor’s garden” (Fig. 6). Exactly from which city or region is unknown, but this coincides with the date when a collection labelled *N. grandiflorum* was sent from southern India to the Botanic Garden at Calcutta, as discussed earlier. The oldest specimen of *C. grandiflora* for which a locality is documented was collected by Herbert Wight in the southern State of Tamil

Table 1. Occurrences, earliest records and current status of *Cryptostegia grandiflora* and *C. madagascariensis* by individual countries.

Country/ Region	*Cryptostegia grandiflora*			*Cryptostegia madagascariensis*			References[c]
	Presence[a]	Earliest record[b]	Notes	Presence	Earliest record	Notes	
Asia							
Bangladesh	+	u	–	-	–	–	POWO (2022)
China: Hong Kong	-	–	–	+	1879 (Herb K)	–	Herbarium record
India	+	1804 (Herb K)	cultivated, established	+	u	established	Chaudhary and Shringi (2017); POWO (2022); Srivastava et al. (2014)
Indonesia	+	1897 (Herbs LD, UPS)	cultivated, not naturalised	-	–	–	Setyawati et al. (2015)
Pakistan	+	1962 (Herb SINDH)	cultivated	-	–	–	Flora of Pakistan (2022)
Philippines	+	u	cultivated, Merrill (1912) states introduction as recent	+	1955 (Herb US)	garden record	Herbarium record (*C. madagascariensis*); Merrill (1912); Razon (2008)
Saudi Arabia	+	1893 (Herb L)	–	-	–	–	Herbarium record
Singapore	+	u	cultivated	-	–	–	Chong et al. (2009)
Taiwan	-	–	–	+	1971 (Herb TAI)	–	GBIF (2021)
Yemen	+	–	cultivated	-	–	–	Alasbahi and Al-Hawshabi (2021)
Africa							
Angola	+	–	as *Cryptostegia* sp. in Herb LISU, Herbario Angola	+	–	as *Cryptostegia* sp. in Herb LISU, Herbario Angola	GBIF (2021)
Botswana	+	u	naturalised	-	–	–	Witt and Beale (2018)
Burkina Faso	+	u	–	-	–	–	POWO (2022)
Comoros	+	u	–	-	–	–	POWO (2022)
Congo	-	–	–	+	u	–	POWO (2022)
Cote d'Ivoire	+	1995 (Herb UCJ)	–	-	–	–	GBIF (2021)
Egypt	+	1904 (Herbs S, UPS)	cultivated	-	–	–	El Zalabani et al. (2003)
Ethiopia	+	1972 (Herbs MO, WAG in L)	invasive in the Afar and Shewa regions	-	–	–	Bekele et al. (2019); Luizza et al. (2016); Witt and Luke (2017); Witt et al. (2018)
Gambia	+	u	–	-	–	–	POWO (2022)
Ghana	+	1927 (Herb GC)	–	+	1932 (Herb K)	–	Asase (2021); Herbarium record (*C. madagascariensis*)
Guinea	+	u	–	-	–	–	POWO (2022)
Kenya	+	u (Herb US)	–	+	1970 (Herb K)	cultivated, established, record of the rust *M. cryptostegiae* from 1950	Herbarium record (*C. grandiflora*); Witt and Beale (2018); Witt and Luke (2017)
Madagascar	+	1879 (Herb MO)	endemic	+	1911 (Herbs MO, S)	endemic	Costantin and Gallaud (1906); Jumelle (1908, 1912); Klackenberg (2001); Marohasy and Forster (1991)
Malawi	-	–	–	+	–	naturalised	Witt and Beale (2018)

Country/ Region	*Cryptostegia grandiflora*			*Cryptostegia madagascariensis*			References[c]
	Presence[a]	Earliest record[b]	Notes	Presence	Earliest record	Notes	
Mali	+	u	–	-	–	–	POWO (2022)
Mauritius	+	1867 (Herb K)	record from Hooker herbarium at Herb K, established	+	1867 (Herb K)	specimen from Hooker herbarium at Herb K, naturalised, recorded as native in GISD and PIER (referencing outdated version of GRIN)	Bojer (1837); GRIN (2022)
Mayotte	+	u	cultivated	+	–	undated record in Herb P	GISD (2022); Herbarium record (*C. madagascariensis*); PIER (2022)
Morocco	+	u	–	-	–	–	Rojas-Sandoval and Acevedo-Rodríguez (2013a)
Mozambique	+	u	–	+	u	–	POWO (2022)
Namibia	+	1958 (Herbs MO, US)	–	-	–	–	Brain and Fox (1994); Ranwashe (2022)
Nigeria	+	1966 (Herb WAG in L)	–	-	–	–	Herbarium record
Réunion	+	u	naturalised, potentially invasive	-	–	–	Comité Français de L' UICN (2022); Groupe Espèces Invasives de La Réunion (2022)
Senegal	+	1960 (Herb IFAN)	–	-	–	–	GBIF (2021); POWO (2022)
Seychelles	+	u	–	+	u	naturalised, recorded as native in GISD	GRIN (2022); POWO (2022); Robertson and Todd (1983)
Somalia	-	–	–	+	1989 (Herb UPS)	–	Thulin (2006)
South Africa	+	1943 (Herb K)	invasive in Limpopo, Mpumalanga and North–West Provinces	+	1860s (Bot. Garden Cape Town)	invasive in Limpopo and North–West Provinces	Invasives South Africa (2022); Sztab and Henderson (2015a, b)
Tanzania	+	u	–	+	1929 (Herb EA)	cultivated	Witt and Beale (2018); Witt and Luke (2017); Witt et al. (2018)
Zambia	+	u	naturalised	+	–	naturalised	Witt and Beale (2018); Witt and Luke (2017)
Zimbabwe	+	1976 (Herb K)	cultivated	+	–	–	POWO (2022)
North America							
Mexico	+	1897 (Herb US)	invasive in Baja California, Chiapas, Tabasco, Yucatan	+	1930 (Herb NY)	recorded from Baja California, Tabasco, Yucatan	Davidse et al. (2009); Patterson and Nesom (2009); Rodriguez-Estrella et al. (2010); Rojas-Sandoval and Acevedo-Rodríguez (2013a, b)
USA	+	Mainland 1905 (Herb NY), Hawaii 1930 (Herb BISH)	mainland record from New York Botanical Garden, possibly invasive in Texas, Florida	+	Mainland 1905 (Herb NY), Hawaii 1906 (Herb BISH)	mainland record from New York Botanical Garden, invasive in Florida, Hawaii	Patterson and Nesom (2009); Polhamus et al. (1934); Witt and Luke (2017)

Country/ Region	*Cryptostegia grandiflora*			*Cryptostegia madagascariensis*			References[c]
	Presence[a]	Earliest record[b]	Notes	Presence	Earliest record	Notes	
Central America and the Caribbean							
Anguilla	-	–	–	+	u	cultivated	Varnham (2006)
Bahamas	+	1904 (Herb NY)	escape from cultivation	-	–	–	Britton and Millspaugh (1920)
Barbados	+	1906 (Herb US)	–	+	2007 (Herb US)	–	Orrell (2022)
Belize	+	1990 (Herb NY)	–	+	1970 (Herb MO)	cultivated	Balick et al. (2000)
Bermuda	+	u	escape from cultivation	-	–	–	Britton (1918)
British Virgin Isl[d]	+	u	recorded on Tortola Isl	+	u	invasive on Anegada Isl	GRIN (2022); McGowan et al. (2006)
Cayman Isl	+	u	cultivated, naturalised on all three islands	-	–	–	Varnham (2006)
Costa Rica	-	–	–	+	1966 (Herb MO)	Genus recorded at USDA Rubber Station since 1947 (Herb MO), but not identified at species level	Davidse et al. (2009)
Cuba	+	1895 (Herb NY)	invasive	+	1926 (Herb US)	–	González-Torres et al. (2012); Orrell (2022)
Dominica	-	–	–	+	u	–	GRIN (2022)
Dominican Republic	+	1910 (Herb US)	–	+	1977 (Herb MO)	–	POWO (2022)
El Salvador	+	u	–	+	1922 (Herb US)	–	Davidse et al. (2009)
Grenada	-	–	–	+	1924 (Herb US)	–	Orrell (2022)
Guadeloupe	+	1893 (Herb NY)	cultivated in Jardin botanique de la Basse–Terre	-	–	–	Herbarium record
Guatemala	+	2002 (Herb UVAL)	–	+	1994 (Herb UVAL)	–	Universidad del Valle de Guatemala (2022)
Haiti	+	u	not naturalised	+	1927 (Herb US)	not naturalised, identified as *C. grandiflora* in Herbs K and NY	Finlay (2009); Knight (1944); POWO (2022)
Honduras	+	1945 (Herbs F, MO)	invasive	+	1947 (Herb F)	–	Davidse et al. (2009)
Jamaica	+	1858 (Herb K)	not naturalised	+	u	–	POWO (2022)
Martinique	+	u	–	+	early 1900s	naturalised	Courty and Lasalle (2020)
Montserrat	+	1979 (Herb NY)	invasive	+	u	escape from cultivation, invasive	Varnham (2006); Young (2008)
Netherland Antilles	+	Curaçao 1913 (Herb US)	invasive on Curaçao, Aruba, Bonaire, naturalised on Saba, St Maarten/ St Martin, established on St Eustatius	+	Saba 2006 (Herb NY)	recorded on Saba, St Eustatius	Burg et al. (2012); Kairo et al. (2003); Mayfield-Meyer and Zhuang (2022)
Nicaragua	+	1987 (Herb WAG in L)	–	+	1923 (Herb MO)	–	Davidse et al. (2009); Herbarium record (*C. madagascariensis*)

Country/ Region	*Cryptostegia grandiflora*			*Cryptostegia madagascariensis*			References[c]
	Presence[a]	Earliest record[b]	Notes	Presence	Earliest record	Notes	
Panama	+	1977 (Herbs MEXU, MO)	recorded in Darién Province	+	1935 (Herb MO)	recorded in several provinces	Correa et al. (2004); Davidse et al. (2009)
Puerto Rico	+	1913 (Herb NY)	–	+	1915 (Herb US)	naturalised	Acevedo-Rodriguez (2005); Gann et al. (2022); Witt and Luke (2017)
St Lucia	+	1909 (Herb L)	–	+	u	cultivated, naturalised	Graveson (2021); Herbarium record (*C. grandiflora*)
Trinidad & Tobago	+	1909 (Herb L)	–	+	1933 (Herb MO)	–	Powo (2022)
US Virgin Isl	+	1923 (Herb NY)	herbarium record from St Croix, erroneously reported from St John	+	1970 (Herb MO)	naturalised on St Croix, St John, St Thomas	Acevedo-Rodriguez (1996); Acevedo-Rodriguez (2005); Orrell (2022)
South America							
Brazil	+	1906 as *C.* sp. (Herb P), 1916 as *C. grand.* (Herbs SP, IPA)	naturalised in Bahia, Mato Grosso do Sul, Pará, Piauí, Rio Grande do Norte	+	1906 as *C.* sp. (Herb P), 1930 as *C. madagascariensis* (Herb US)	invasive in Ceará, Pernambuco, Piauí, Maranhão, Rio Grande do Norte, recorded in Bahia	da Silva et al. (2008); Flora e Funga do Brasil (2022); Silva et al. (2018)
Colombia	+	1906 (Herb US)	–	+	1899 (Herb US)	–	Gracia et al. (2019)
Ecuador	+	1926 (Herb US)	herbarium record from mainland Bahia, cultivated on Santa Cruz Isl., Galapagos	-	–	–	Guézou et al. (2010)
French Guiana	+	1977 (Herb WAG in L)	–	+	2000 (Herb US)	–	Herbaria records
Guyana	-	–	–	+	1988 (Herb US)	escape from cultivation	Funk at al. (2007)
Suriname	+	1972 (Herb U in L)	–	-	–	–	Herbarium record
Peru	+	1959 (Herb F)	naturalised in Cajamarca	-	–	–	Herbarium record; GRIN (2022)
Venezuela	+	1922 (Herb US)	–	+	1939 (Herb US)	escape from cultivation, recorded in Amazonas, Aragua, Bolívar, Lara, Nueva Esparta, Sucre	Funk et al. (2007); Hokche et al. (2008); Herbarium record (*C. grandiflora*)
Oceania							
Australia	+	1875 (GISD)	invasive in Queensland, recorded in Northern Territory, Western Australia	+	1953 (Australia Virtual Herb)	naturalised, recorded in Queensland, Northern Territory, Western Australia	Atlas of Living Australia (2023a, b); Marohasy and Forster (1991); Tomley (1995)
Cook Isl	-	–	–	+	1993 (Herb CHR)	established, recorded from Isl of Rarotonga, Mangaia, 'Atiu, Penrhyn	McCormack (2007)
Fiji	+	u	established	-	–	–	Meyer (2000)
French Polynesia	+	1831 (Herb BISH)	cultivated on several Isl	+	1926 (Herb MO)–	treated as *C. grandiflora* in Herbs L, MIN, BISH	Florence et al. (2013); Herbarium record (*C. madagascariensis*)
Guam	+	1963 (Herb US)	cultivated, established	-	–	–	Fosberg et al. (1979)

Country/ Region	*Cryptostegia grandiflora*			*Cryptostegia madagascariensis*			References[c]
	Presence[a]	Earliest record[b]	Notes	Presence	Earliest record	Notes	
Marshall Isl	+	1965 (Herb BISH)	recorded on Kwajelein Atoll	-	–	–	Fosberg et al. (1979)
New Caledonia	+	1950 (Herb P)	invasive on New Caledonia Isl, Ile Grande Terre	-	–	–	Meyer (2000)
Northern Mariana Isl	+	u	recorded on Saipan Isl, established	-	–	–	Fosberg et al. (1979)
Palau	-	–	–	+	u	cultivated on Babeldaob, recorded on Koror	Space et al. (2003)
Papua New Guinea	+	1936 As *C.* sp. (Herb K)	cultivated on Bismarck Archipelago	-	–	–	Herbarium record; Peekel (1984)

[a]Presence: + = present, - = not recorded
[b]Earliest record: u = unknown, Herb (herbarium) acronyms according to Thiers (2022)
[c]References: source databases used, quoted where exclusive reference for *C. grandiflora* and/or *C. madagascariensis:* GBIF=Global Biodiversity Information Facility; GISD=Global Invasive Species Database; GRIN=Germplasm Resources Information Network, USDA; PIER=US Forest Service, Pacific Island Ecosystems at Risk; POWO=Plants of the World, Kew Science, UK; Tropicos=Botanical Database Missouri Botanical Garden, USA; full references given in manuscript
[d]Isl = island/islands

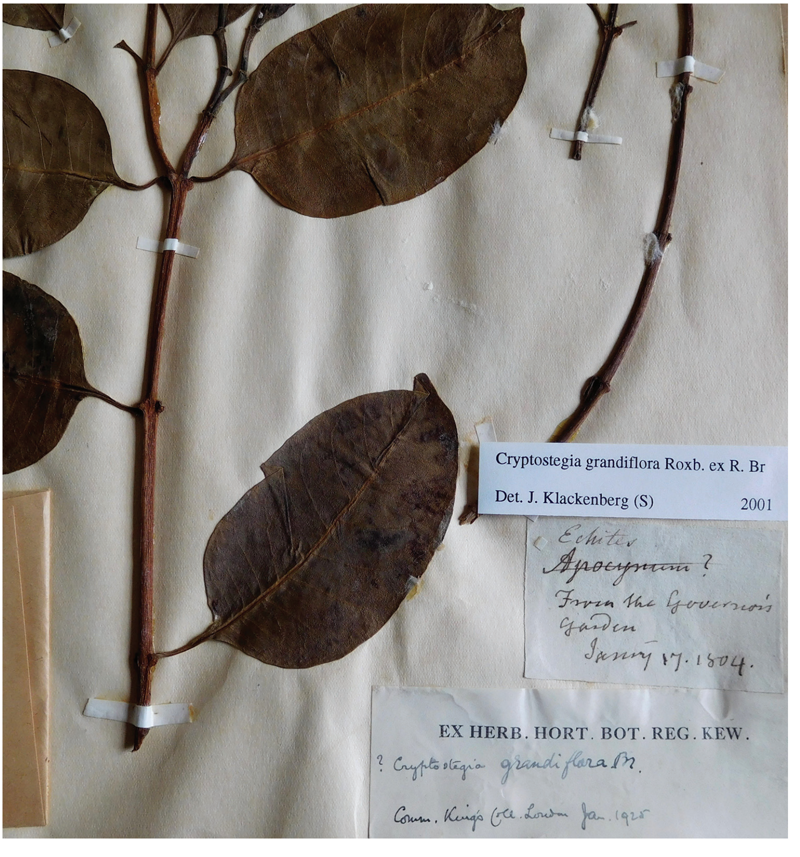

Figure 6. Herbarium specimen of *C. grandiflora* from India deposited at the Royal Botanic Gardens Kew (Herb K), collected in 1804 and originally identified as a species of *Echites* or *Apocynacum*; making it the earliest recorded collection of the genus *Cryptostegia*.

Nadu in 1849 (Herb S). *Cryptostegia madagascariensis* is also reported as established in India, but without information when it was first recorded (GISD 2022; POWO 2022).

Indonesia

The first herbarium specimen of *C. grandiflora* dates from 1904 (Herb L), although records document that the species has been present at Bogor Botanical Garden, Java since at least 1897 (Herbs LD, UPS). While *C. grandiflora* is included in a guide book to the invasive alien plants of Indonesia (Setyawati et al. 2015), it is described as rare and an ornamental with no indication that it has become naturalised.

Pakistan

Whilst the earliest herbarium specimen of *C. grandiflora* from Pakistan dates from 1962 (Herb SINDH), a new fungus, *Pleosphaeropsis* (now *Aplosporella*) *cryptostegiae*, was described from dead twigs of rubber vine, collected in 1939 from Lahore – then part of India (Chona and Munjal 1950). Presumably, this was from a cultivated plant and there are no reports of *C. grandiflora* as an invasive species. According to Index Fungorum (2023), there are 12 confirmed fungal taxa bearing the species epithet '*cryptostegiae*', three of which are from the Lahore Region of Pakistan and six from India, all on *C. grandiflora*, as well as two from Brazil. Ironically, there is only a single validated species with this epithet, the rust *M. cryptostegiae*, listed in the Index from Madagascar. This would give the impression that *C. grandiflora* is, indeed, native to the Indian subcontinent: in reality, however, it is more a reflection of the historical dearth of mycologists in Madagascar compared to both India and Brazil.

Yemen

Alasbahi and Al-Hawshabi (2021) reported *C. grandiflora* as present throughout Yemen and cultivated as an ornamental. Its poisonous properties were highlighted, but with no mention of the plant being invasive.

Africa

Egypt

There are no indications that *C. grandiflora* is weedy in Egypt (El Zalabani et al. 2003), although herbarium records in Herbs S and UPS show that it has been cultivated in Cairo since at least 1904.

Ethiopia

Witt et al. (2018) reported *C. grandiflora* as being problematic and invasive in the Awash National Park: "smothering native *Acacia* species and displacing valuable forage species"; which is based on an earlier study in the Afar Region of north-eastern Ethiopia (Luizza et al. 2016). This was subsequently reinforced by Bekele et al. (2019), who undertook an impact assessment study in the East Shewa Zone of the Oromia Region and concluded that *C. grandiflora* is a major driver of biodiversity loss, as well as posing a threat to the agro-economy because of its impact on pastoralists. First reported in 1972 (Herbs MO, WAG in L), records in Herb K from Ethiopia dating from the same time describe *C. grandiflora* as "rare" to "quite frequent" in the Awash area of the central Highlands, giving no indication that it was problematic or invasive at that time.

Ghana

The presence of *Cryptostegia* was first reported as *C. grandiflora* from Accra in 1927 (Asase 2021), whilst Herb K has a record of *C. madagascariensis* from 1932 with the annotation: "Introduced from Victoria Botanical Gardens" – presumably, in nearby Cameroon, now Limbe Botanical Gardens. There is no indication that either species has become naturalised or invasive in any of the West African countries.

Kenya

Witt and Luke (2017) stated that *C. madagascariensis* is a garden ornamental which has not naturalised in Kenya and Herb K collections from the early 1970s show *C. madagascariensis* being cultivated as an ornamental along the coast, north of Mombasa. However, there is a record in the fungarium of the Imperial Mycological Institute (IMI, now held at RBG Kew) of the rust *M. cryptostegiae* from the same area dating from 1950, with more records of heavily-rusted plants from the 1970s. It is tempting to speculate that the rust is keeping the vine in check by reducing its fitness and fecundity. Herb US holds undated records of *C. grandiflora*, based on images from Tsavo West National Park and the Mombasa Beach Hotel, where the species seems to be cultivated.

Namibia

Specimens at Herbs MO and US show records of *C. grandiflora* from the Namibian town of Karibib dating back to 1958. A Herb K record from the Etosha National Park in 2006 listed *C. grandiflora* as "fairly common"; whilst an earlier report from a game reserve bordering the Park described it as planted in "cultivated gardens", where it was linked to the poisoning and death of several elephants (Brain and Fox 1994).

South Africa

Henderson (2014) first highlighted the threat posed by *C. grandiflora* to grazing lands, riverine forests and woodlands in South Africa, subsequently detailing its escape from cultivation and the invasion of watercourses and pastoral land in the north-eastern Provinces of Limpopo and Mpumalanga (Sztab and Henderson 2015a). Equally, *C. madagascariensis* was listed as naturalised and potentially invasive (Sztab and

Henderson 2015b). Herb K records show the earliest collection of *C. grandiflora* from an arboretum in Pretoria in 1943; however, there are much earlier collections of *C. madagascariensis* from the botanic garden in Cape Town, dating from the 1860s and 1880s. Both *Cryptostegia* species are included on the 'Alien and Invasive Species List' of the National Environmental Management Biodiversity Act (NEMBA) and fall under environmental legislation for control (Government of South Africa 2020).

Tanzania

First collected in Tanga, north-east Tanzania, in 1929 (Herb EA), with early 1930s Herb K collections of *C. madagascariensis* (initially identified as *C. grandiflora*) from the nearby Moa District showing the annotation: "originally introduced as a rubber vine [presumably as a source of rubber] and now found in most gardens on the coast". However, there have been no reports of it as an invasive species (Witt et al. 2018). Similarly, *C. grandiflora* has also been recorded as an ornamental in Tanzania and is not listed as an invasive (Witt and Beale 2018).

Mascarenes

Mauritius

Bojer (1837) had listed *C. madagascariensis* as an exotic species in the flora of Mauritius and this is substantiated in an annotation by the botanist P. Koenig on a specimen in Herb K (originally from the Hooker Herbarium, deposited in 1867): "introduced here 2 or 3 centuries ago by the 'Malagasey' people who settled at the foot of the Signal Mountain, where it is most abundant". Whilst GISD and PIER (2022) list the species as native to Mauritius, referencing a 2013 version of GRIN, the latest version gives its status as naturalised (GRIN 2022). A record of *C. grandiflora* from the Hooker Herbarium in Herb K also documents this species as occurring in Mauritius. Neither species has been reported as invasive on the island.

Seychelles

Similar to Mauritius, GISD (2022) lists *C. madagascariensis* as native to the Seychelles, whilst other sources give its status as introduced and naturalised (Robertson and Todd 1983; GRIN 2022; POWO 2022). No further information is available for *C. grandiflora*, which is also recorded as being present.

Réunion

First introduced as an ornamental, *C. grandiflora* is now naturalised in the savannah areas. The species is listed as potentially invasive and as a threat to dry savannahs and pastures (Comité Français de L'UICN 2022; Groupe Espèces Invasives de La Réunion 2022).

North America

Mexico

Rodriguez-Estrella et al. (2010) indicated that *C. grandiflora* was introduced as an ornamental in the 1930s; however, a record in Herb US documents that the species has been present in Sinaloa, northwest Mexico, since the late 19th century. In 1924, it was reported to be naturalised in this Mexican state (Standley 1924) and recorded as invading dry rivers in Sonora in 1935, where it was said to be cultivated in gardens as an ornamental. In the early 1940s, *C. grandiflora* was also grown for research purposes as a source of rubber at the United States Cryptostegia Research Laboratory, Ciudad Victoria, Tamaulipas (Stewart et al. 1948). Present in at least 10 Mexican states (Patterson and Nesom 2009), investigations of the occurrence of *C. grandiflora* in natural oases in the dry region of the Baja California Peninsula found a high incidence, posing a significant threat to endemic species of oasis-dependent invertebrates and vertebrates (Rodriguez-Estrella et al. 2010). The species is now considered as invasive in Baja California as well as in Chiapas, Tabasco and Yucatan. Whilst *C. madagascariensis* is also known to be present in Baja California, Tabasco and Yucatan (Davidse et al. 2009), there is no reference to its being invasive.

USA

The earliest record for both *C. grandiflora* and *C. madagascariensis* is from the New York Botanical Garden in 1905. Both species are in cultivation in gardens and plant nurseries – especially in Florida, where they were introduced in the early 1900s (Polhamus et al. 1934) – and are usually marketed under the name purple allamanda. In Starr County, Texas, *C. grandiflora* has been reported to smother vegetation at sites along the Rio Grande (Patterson and Nesom 2009) and, based on climate matching, it has been classified as a high-risk invasive species in some southern states, notably Florida and Texas (Anon 2020). Considered by Meyer (2000) as a potential invader or a perceived threat to Hawaii, *C. grandiflora*, or more correctly, *C. madagascariensis* (fide Herb K), subsequently became invasive on several of the islands. The species was the subject of an apparently successful eradication campaign (Penniman et al. 2011), although this needs confirmation.

Central America and the Caribbean

Cryptostegia grandiflora and/or *C. madagascariensis* have been reported as present in all of the Central American countries, as well as on a number of the Caribbean islands; however, their respective status has been recorded as naturalised or invasive in less than half of the respective countries or territories (see Table 1).

Cuba

Records from the New York Botanical Garden (Herb NY) document that *C. grandiflora* was first collected in Cuba in the late 19th century; the species is now considered as invasive (González-Torres et al. 2012). There is no information about the status of *C. madagascariensis*, first recorded on the island in 1926 (Herb US).

Haiti

The history of *Cryptostegia* in Haiti has been detailed above, as have the failed attempts to cultivate it as a source of rubber in the 1940s. Records in Herb US show that *C. madagascariensis* was already present in 1927, but there are no reports of the species becoming naturalised or weedy. *Cryptostegia grandiflora* is also listed as present (POWO 2022) and specimens dating from 1927 were deposited in Herb K and Herb NY. Nonetheless, there is uncertainty about their correct identification as they are duplicates of the earliest collection made from Haiti by Ekmann (GBIF 2021), which have been reliably identified as *C. madagascariensis*. No specimens of the high-yielding, *Cryptostegia* hybrids, vegetatively reproduced and planted for rubber production, were deposited in public herbaria. The fact that, following the collapse of the rubber project neither of these hybrids, nor their parental species, have become invasive could point to environmental constraints, as yet poorly understood.

Martinique

Cryptostegia madagascariensis, or allamanda pourpre, was introduced in the early 1900s as an ornamental: now naturalised in the dry forests in the south of the island where it is perceived as a potential invasive threat (Courty and Lasalle 2020). However, the rider is added that *C. grandiflora* is also 'appreciated' and cultivated as a climbing ornamental.

Montserrat

The earliest record of *C. madagascariensis* in Montserrat is unknown, but the species is now regarded as one of the key alien plants on the island and is being closely monitored. It has been described as "covering large tracts of land in the Silver Hills where it grows almost as a monoculture at the expense of other species" (Young 2008). First recorded in 1979 (Herb NY), *C. grandiflora* is considered as equally invasive (Varnham 2006).

Netherland Antilles

Buurt (2010) was precise about how *C. grandiflora* arrived in Curaçao; reporting that "the plant was imported from the area near Tulear in Madagascar during the First World War", as a potential source of rubber, although a record in Herb US indicates that the species was present on the island as early as March 1913. The author considered that, although the species was invasive on the island, it was debatable if it had a detrimental impact on the ecosystem. However, in the Christoffel National Park, in the north of the island, there is no doubt that *C. grandiflora* is having a negative impact, smothering native vegetation, especially members of the Cactaceae (Evans HC, pers.

obs. 2005, see Fig. 7). *Cryptostegia grandiflora* is also reported as invasive on Aruba and Bonaire, as naturalised on Saba and St Maarten/St Martin and as present on St Eustatius (Arnoldo 1971; Kairo et al. 2003; Burg et al. 2012). *Cryptostegia madagascariensis* is also recorded as present on Saba and St Eustatius (Herb NY; Mayfield-Meyer and Zhuang 2022), but there are no reports of this species being invasive.

St Lucia

Unknown when first introduced, *C. madagascariensis* is now considered to be naturalised on the island and is commonly found in the dry savannah, especially around Micoud, Vieux Fort and Laborie (Graveson 2021). The species is also cultivated as an ornamental. There is a record of *C. grandiflora* in Herb L from 1909, but further information about the invasive status of this species is lacking.

Virgin Islands

Following its introduction as an ornamental, *C. madagascariensis* has become invasive on the British Virgin Island of Anegada, where it is posing a threat to the island's biodiversity (McGowan et al. 2006). The species is also reported as naturalised on each of the three main U.S. Virgin Islands, St Croix, St John and St Thomas (Acevedo-

Figure 7. *Cryptostegia grandiflora* over-growing native vegetation in Christoffel National Park, Curaçao, Lesser Antilles, 2005.

Rodríguez 2005). *Cryptostegia grandiflora* has been recorded on the islands of Tortola (British Virgin Islands) and St Croix (U.S. Virgin Islands), without further details about its invasive status (GRIN 2022). Though previously also reported from St John (Acevedo-Rodríguez 1996), this identification was subsequently corrected by the author to *C. madagascariensis* (Acevedo-Rodríguez 2005).

South America

Brazil

Two herbarium specimens collected in 1906 around Manaus, Amazonas and deposited in Herb P, are probably the oldest records of *Cryptostegia* in Brazil, indicating the presence of rubber vine in this region during the peak of the first Amazon rubber boom. In 1916, Pickel reported the cultivation of *C. grandiflora* in Olinda, Pernambuco, on the north-east coast of Brazil on the label of a herbarium specimen kept at Herb IPA, which possibly constitutes the second oldest collection of the genus in Brazil. The first record of *C. madagascariensis*, also from Pernambuco, dates from 1930 (Herb US). However, there is anecdotal evidence that the species might have been present in the region much earlier in the form of a painting by José dos Reis Carvalhoos from 1859 depicting a reddish-flowering vine, resembling *Cryptostegia* sp., climbing up a carnaúba palm (Fig. 8).

The first indication that rubber vine was problematic in Brazil came in a report from the north-east region entitled 'dangerous visitors' (Herrera and Major 2006), highlighting the invasion of *C.* "*grandiflora*" ("cipó-de-sapo" or toad creeper). The species was invading riverine forests and posing a threat to the forests of native carnaúba palm (*Copernicia prunifera*, Arecaceae). Subsequently, two of the present authors (Barreto

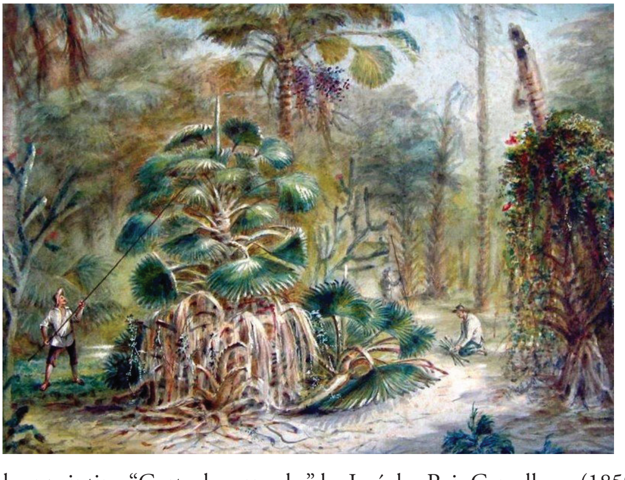

Figure 8. Watercolour painting "Corte de carnauba" by José dos Reis Carvalhoos (1859) depicting a red-purple flowering vine, potentially *Cryptostegia* sp., climbing up a carnaúba palm (right-hand side) (source: Wikimedia Commons, public domain).

RW and Evans HC) visited the region and confirmed these findings – in particular, its impact on the ecologically and economically important carnaúba or wax palm (Fig. 9A). However, the rubber vine species involved turned out to be *C. madagascariensis* (da Silva et al. 2008) and the plant was more commonly known as 'unha-do diabo'or devil's claw, due to the claw-like appearance of the fruits (Fig. 9B). It was posited that this material may have originated from the rubber-vine collection in the Rio de Janeiro Botanical Garden, which was misidentified as *C. grandiflora*, with the ubiquitous common name purple allamanda ('alamanda-roxa'; Fig. 9C). Molecular evidence corroborates this supposition (Authors, unpubl. data), although the oldest collections of *Cryptostegia* in the south-east region date from the 1940s, decades after the first records in the north and north-east of the country. While *C. grandiflora* has also been reported from several Brazilian states, listed as naturalised, but not yet invasive (Table 1), it is possible that these records are based on a misidentification of *C. madagascariensis*.

Studies show that *C. madagascariensis* is having a significant negative impact on the unique semi-arid Caatinga ecosystem in north-east Brazil, affecting the regeneration and ecological succession of native vegetation (Sousa et al. 2016), as well as altering the composition of arbuscular mycorrhizal communities (Souza et al. 2016). However, it is the socio-economic impact on the carnaúba palm that is the main cause of concern in the region since, as well being an emblematic and keystone species in the States of Ceará, Piauí and Rio Grande do Norte, *C. prunifera* is an important source of income and rural employment. In 2019, export of the high-quality wax obtained from the palm leaves was valued at over US$ 40 million to the Brazilian economy (IBGE 2019). This has been the main driver behind a collaborative project funded by private industry and the government of Ceará to assess the potential of the rust fungus *M. cryptostegiae* from Madagascar as a CBC agent, in an attempt to replicate the success of this strategy in managing the congeneric species *C. grandiflora* in Australia (Evans 2000, 2013). Within the scope of this Brazilian project, which commenced in 2018, surveys for fungal pathogens in the native Madagascan range of *C. madagascariensis* and subsequent screening in the UK under quarantine greenhouse conditions, identified a strain or pathotype of *M. cryptostegiae* highly virulent to the only known invasive biotype of *C. madagascariensis*. Host-specificity testing of the selected pathotype against 48 non-target plants representative of native Brazilian apocynaceous genera and species, as well as locally-important species from other plant genera, showed it to be specific to the genus *Cryptostegia*. In parallel, field studies were conducted in Ceará to collate data on *C. madagascariensis* populations and plant performance in order to establish a baseline against which future impacts of the rust can be assessed. If approved for release, *M. cryptostegiae* would be the first exotic weed biocontrol agent introduced into Brazil.

Colombia

Gracia et al. (2019) considered that *C. madagascariensis* was originally introduced into the resorts on the Caribbean coast of Colombia as an ornamental and described how it is now forming impenetrable thickets, covering trees and displacing indigenous dune

Figure 9. *Cryptostegia madagascariensis* **A** completely smothering native riparian vegetation and climbing up the endemic palm, *Copernicia prunifera* (Carnaúba or wax palm), Cruz, Acaraú River, Ceará, Brazil, 2007 **B** close-up of flowers and fruits; showing their claw-like nature, particularly of the opened fruits **C** in the Botanic Garden, Rio de Janeiro, with erroneous identification (inset), showing the characteristic whip-like shoots.

vegetation. Nonetheless, a record of *C. madagascariensis* in Herb US dates as early as 1899. The same herbarium also holds a record of *C. grandiflora* showing its presence in Colombia in 1906, while out of two authenticated *C. grandiflora* records in Herb K (Klackenberg 2001), the earlier one from Guajira near the Caribbean coast dates from

1917. It is likely, therefore, that multiple introductions of *Cryptostegia* species have taken place with the reported invasion of the dune ecosystem resulting from a more recent introduction event.

Ecuador

Gardener et al. (2010) discussed an eradication programme on the Galápagos Islands in which *C. grandiflora* was included, based on its past history as an invasive species elsewhere rather than on its spread within the islands. According to Guézou et al. (2010), the plant was detected only in gardens on Santa Cruz Island. Later, Buddenhagen and Tye (2015) discussed the programme and concluded that *C. grandiflora* had been "almost eradicated by 2007", although they noted that its management had since been abandoned. There is also a record of this species on mainland Ecuador from 1926 (Herb US), but there is no further information of its current presence or weed status.

Oceania

Australia

Tomley (1995) accessed published records from several botanical gardens in Brisbane and concluded that *C. grandiflora* was introduced into Australia as an ornamental in the late 19th century. It seems credible that it was sent from a botanical garden in India rather than arriving directly from Madagascar, although there is no evidence to support this supposition. Rubber-vine weed, as it became known, was reported as being weedy in Queensland some decades later, but it only became a problematic invasive weed following attempts to establish it as a source of rubber during the Second World War in the mining areas of central Queensland (Tomley 1995). By 1990, *C. grandiflora* was estimated to cover over 30,000 km^2 in tropical Queensland and was described as "the single greatest threat to biodiversity in tropical Australia" (Fig. 10A) (McFadyen and Harvey 1990). Based on climatic suitability, it was calculated

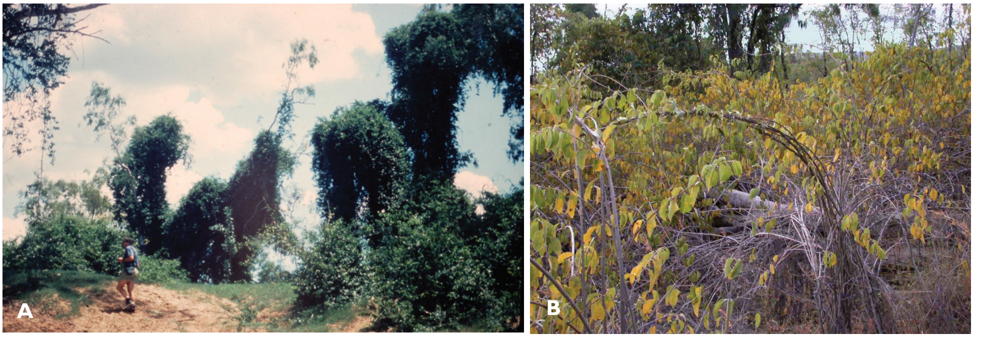

Figure 10. A *Cryptostegia grandiflora* climbing up into the canopy and smothering native *Eucalyptus* stands, northern Queensland, Australia **B** *C. grandiflora* thicket showing immediate impact of the rust, *Maravalia cryptostegiae*, with yellowing and falling leaves, three months after its release.

that the species had the potential to invade up to 160,000 km^2 (Tomley 1995), which has since been supported by CLIMEX modelling. This would put the whole of the Northern Territory and northern Western Australia at risk of invasion with severe implications for natural ecosystems, including World Heritage areas, such as Kakadu National Park (Kriticos et al. 2003).

This actual and potential threat to the ecosystems of tropical Australia was the catalyst for an integrated management strategy – including a CBC programme – implemented by the then Queensland Department of Lands. This was funded in part by the Australian Meat and Livestock Research and Development Corporation because of the impact of rubber-vine weed on the cattle industry due to loss of grazing and reduced access to water sources by weed infestations (McFadyen and Harvey 1990; Tomley 1995). Surveys in Madagascar for natural enemies of *Cryptostegia* identified several promising CBC agents; including the aforementioned damaging rust fungus, *M. cryptostegiae*. This rust has since been recognised as closely related to the genera *Elateraecium* and *Hemileia*, both phylogenetically distant from *Maravalia* and has temporarily been placed in the genus *Uredo* (Aime and McTaggart 2020). Thus, a new generic name will be needed to accommodate the rust species on *Cryptostegia* from Madagascar. It is also considered that this rust genus will prove to be unique to Madagascar; having co-evolved with its endemic plant host.

Following extensive safety testing, the Madagascan moth, *Euclasta whalleyi* (Pyralidae, Lepidoptera), as well as the rust fungus, were released in northern Australia in the late 1980s and early 1990s. Long-term monitoring studies of the rust have shown significant impacts on weed populations with much-reduced seedling recruitment (Fig. 10B) (Vogler and Lindsay 2002; Tomley and Evans 2004). An economic impact assessment put the net benefit of the project at over AU$ 230 million, with a benefit-cost ratio of 108:1 (Page and Lacey 2006), making it one of the most successful weed biocontrol programmes in Australia (Palmer et al. 2010; Evans 2013).

Cryptostegia madagascariensis is present in the Northern Territory, Queensland and Western Australia (Marohasy and Forster 1991; Atlas of Living Australia 2023a) but, to date, has not been reported as invasive in these States (Taylor D, pers. com. 2022).

Oceanian Islands

Cryptostegia grandiflora has been cultivated on a number of the islands. For Papua New Guinea, there is a Herb K record dated 1936 from the New Guinea Agricultural Department, labelled *Cryptostegia* sp., with the annotation: "from which fibre is prepared". Presumably, therefore, it was being grown as a crop for rope or similar products. While classed as established on several of the islands (see Table 1), *C. grandiflora* is described as a moderate invader only in New Caledonia (Meyer 2000). However, the same author considers the species also as a potential invader on Fiji. *Cryptostegia madagascariensis* has been reported only from the Cook Islands, French Polynesia and Palau – being less widely distributed in the region – and there are no reports of the species as an invasive.

Conclusions

The two representative species of *Cryptostegia* native to Madagascar are now present in most countries of the sub-tropics and tropics, including remote island systems. These species – commonly and collectively known as rubber vines – were introduced initially for their ornamental value, but later, prior to and during both World Wars, they were also cultivated as potential sources of rubber. In many, but not all countries, these two vines have become naturalised and, in several, they have assumed the status of an invasive weed posing a threat to indigenous ecosystems, as well as to agriculture. From the data available, the two rubber vines appear to be 'sleeper weeds' in the sense that many years may elapse from their escape and naturalisation to becoming invasive and problematic (Groves 2006). For example, *C. madagascariensis* has been cultivated in the north-east of Brazil since 1916, but it was a further 90 years before it was reported as invasive in this region. The reasons are unclear, but abiotic factors, such as soil type, climate change and/or habitat disturbance, may be involved. The weed status of *C. grandiflora* in India appears to be more complicated and difficult to interpret as there is no evidence to suggest that this species – several centuries since the first confirmed report of its presence – has become invasive or problematic, despite Kriticos et al. (2003) identifying extensive areas in southern India as being highly suitable for its growth, based on climatic data.

The Australian experience shows that CBC can be successful in controlling rubber vine invasions, provided the invasive *Cryptostegia* species and biotype is correctly matched with a respective pathotype of the rust *M. cryptostegiae*. Hopefully, this success can be replicated in Brazil and, potentially, other countries affected by invasive rubber vines should they embrace this control approach in the future. Nonetheless, the message would appear to be that, despite its attraction as an ornamental and perceived usefulness as a source of rubber, caution should be exercised concerning their potential to become invasive wherever the two species have been introduced, as well as posing a threat to human health, in addition to that of livestock and herbivores, in general, due to toxic glycosides in the latex (McFadyen and Harvey 1990; Brain and Fox 1994; Albuquerque et al. 2009; Alasbahi and Al-Hawshabi 2021). Their cultivation as ornamentals in public and private gardens must be discouraged and their commercialisation should be forbidden by law. At present, even in some places severely impacted by rubber vines, such as in north-east Brazil, it is still being deliberately cultivated which is likely to be contributing directly to the expansion of its distribution and the resulting negative impacts.

Author contributions

Marion Seier and Harry Evans conceptualised and put together the initial drafts of the manuscript. Alessandro Rapini, Marion Seier and Kate Pollard collated, validated and curated species distribution data. All authors reviewed, edited and approved the final manuscript.

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