Revision of the genus *Cryptostegia* R. Br. (Apocynaceae, Periplocoideae)

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ABSTRACT
The Malagasy endemic but widely introduced tropical genus *Cryptostegia* is revised. Two species, *C. grandiflora* and *C. madagascariensis*, are accepted. Geographic distribution of some important characters is discussed and plotted on a map. Diagnostic characters, descriptions, drawings and distribution maps are presented. Typifications are discussed.

KEY WORDS
Cryptostegia,
Apocynaceae,
Periplocoideae,
Madagascar.

RÉSUMÉ
Révision du genre Cryptostegia R. Br. (Apocynaceae, Periplocoideae).
Le genre *Cryptostegia,* endémique de Madagascar mais dont les espèces ont été largement introduites en région tropicale, est révisé. Deux espèces, *C. grandiflora* et *C. madagascariensis,* sont acceptées. La distribution géographique de quelques caractères importants est discutée et indiquée sur une carte. Des caractères diagnostiques, des descriptions, des illustrations et des cartes de distribution sont présentés. Les typifications sont discutées.

MOTS CLÉS
Cryptostegia,
Apocynaceae,
Periplocoideae,
Madagascar.

INTRODUCTION

Cryptostegia is a small Malagasy periplocoid genus with showy white to pink flowers. It is endemic to West Malagasy phytogeographical Region. *Cryptostegia* is a liana or shrub with scrambling or self-supporting branches. The two most recent views presented on the taxonomy of *Cryptostegia* (MORAT 1973; MAROHASY & FORSTER 1991) express large discrepancies in the interpretation of important characters, and one or four taxa were accepted. However, relevant material was not all consulted in these treatments. Consequently, a new revision of the genus is justified.

Cryptostegia was described in 1819 by R. BROWN from a specimen collected in India, but it was mentioned even earlier in a manuscript of Flora Indica by ROXBURGH as *Nerium grandiflorum*. This manuscript was published, however, only in 1832. A second species, *C. madagas-*

cariensis, was added in 1844 by DECAISNE and was based on material from Madagascar distinguished mainly by its entire corona lobes, not bifid as in *C. grandiflora*. A third species, *C. glaberrima*, was described by HOCHREUTINER (1908), also from Malagasy material. It was characterized primarily by having completely glabrous leaves, compared to the supposedly more or less hairy ones of *C. madagascariensis*. The existence of *C. glaberrima* as a separate species has not been endorsed by subsequent authors, but has recently been accepted at infraspecific level by MAROHASY & FORSTER (1991). Variation in leaf pubescence was also discussed by JUMELLE (1907), who found a gradual variation and gave no taxonomic value to this character. JUMELLE (1908) maintained, however, the distinction between *C. grandiflora* and *C. madagascariensis* based on differences in calyx and corona morphology. CHOUX mentioned both *C. grandiflora* and *C. madagascariensis* in his "Index des Asclépiadacées de Madagascar", but later commented in the "Catalogue des Plantes de Madagascar" that the former probably only was a variation of the latter (CHOUX 1914; 1931). In contrast, POLHAMUS et al. (1934) in an article discussing a case of interspecific hybridization between *C. grandiflora* and *C. madagascariensis*, stated that "there appears to be no occasion for confusing the two species, since the essencial differences are outstanding and easily recognized". MORAT (1973), however, argued that the variation described between *C. glaberrima*, *C. grandiflora* and *C. madagascariensis* only represents variation within a single species. MAROHASY & FORSTER (1991) recently contradicted MORAT in a taxonomic revision of the genus. Based on Australian (i.e. introduced) material and their own Malagasy collections only, but with extensive field observations, MAROHASY & FORSTER accepted both *C. grandiflora* and *C. madagascariensis* at the species level, as well as HOCHREUTINER's glabrous taxon as a variety, *C. madagascariensis* var. *glaberrima* (Hochr.) Marohasy & P.I. Forst. Furthermore, a fourth taxon, *C. madagascariensis* var. *septentrionalis* Marohasy & P.I. Forst. was added, characterized by the leaves being hairy on their upper side but glabrous below. In the present study some of the morphological variation used in earlier classifications is shown to be unclear. However, important correlations between characters do exist and two species are recognized, but no useful infraspecific delimitations are found.

Anatomical features of *Cryptostegia* have been thoroughly discussed by ARTSCHWAGER (1946).

When described by BROWN (1819), *Cryptostegia* was thought to be a native of the Indian peninsula, represented by the single species *C. grandiflora*. In contrast, DECAISNE's (1844) *C. madagascariensis* was thought to be endemic to Madagascar. Later COSTANTIN & GALLAUD (1906) reported *C. grandiflora* from SW Madagascar for the first time and this species was then supposed to be indigenous in both Asia and Madagascar. Only a couple of years later, however, JUMELLE (1908) proposed that both *C. grandiflora* and *C. madagascariensis* were in fact endemic to Madagascar and explained the pantropical distribution of *C. grandiflora* as introductions. *Cryptostegia* was introduced first in the adjacent areas in the Indian Ocean, and later to the Americas, both for its rubber content and as an ornamental (see POLHAMUS et al. 1934). An early introduction was reported by P. KOENIG, who collected cultivated plants at Mauritius 1907-1908. He annotated in schedae (*P. Koenig s.n.,* Mauritius, K) that this plant was introduced to this island two or three centuries earlier by the Malagasy people who settled at the foot of the Signal Mountain. *Cryptostegia* is today known from many parts of the tropics, often naturalized. Both *C. grandiflora* and *C. madagascariensis* have been used for introduction, with *C. grandiflora* probably being the more frequently introduced of the two as estimated by collections made from outside Madagascar.

The latex of *Cryptostegia* has been used for production of rubber in India and Madagascar, for example (JUMELLE 1908; POLHAMUS et al. 1934), hence the English names "Indian"or "Madagascar rubber vine". The hybrid between the two species yields twice as much latex as either of the parent species (POLHAMUS et al. 1934). In Madagascar the fibers also have been utilized for making threads and ropes, mostly for manufacturing nets and fishing lines (JUMELLE 1907). Its poisonous properties have sometimes been utilised for

committing suicide for religious reasons (CHOUX 1931). It has also been taken as a medicine to cure gonorrhoea (JUMELLE 1907), as well as a cardiotonic (BOITEAU 1986).

MATERIALS AND METHODS. — This study is based on dried specimens of native Malagasy material from the following herbaria: BM, G, K (also introduced material), MO, P, S and WAG (abbreviations according to HOLMGREN et al. 1990).

DISCUSSION

Delimitation of species

Most authors (DECAISNE 1844; JUMELLE 1908; CHOUX 1914; MAROHASY & FORSTER 1991) have recognized two separate species within *Cryptostegia*, *C. grandiflora* and *C. madagascariensis*, and only one, HOCHREUTINER (1908), has argued for a third species, *C. glaberrima*. CHOUX (1931) and particularly MORAT (1973) have proposed to include the morphological variation within a single species, *C. grandiflora*.

POLHAMUS et al. (1934) presented a study on hybridization between *Cryptostegia grandiflora* and *C. madagascariensis* and their content of latex, based on cultivated material in a botanic garden in Florida, U.S.A. A host of distinguishing characters between the parent species were given, and the authors excluded all doubt on the specific distinctness of these two taxa. The distinguishing characters presented included most parts of the plant, e.g. habit of growth, stem colour and texture, shape of nodes, length of internodes, number and size of lenticels, length of pedicels, colour, size and shape of corolla, size and shape of calyx, shape of corona lobes, shape of translator spathes, colour of venation on young leaves, texture and colour and shape of leaf lamina, colour and length of petioles, and size and shape of follicles. Many of these characters have been discussed by later taxonomists, most extensivly so by MAROHASY & FORSTER (1991). Unfortunately it is difficult to evaluate the reliability of this study from a taxonomic point of view, as the actual number of individuals, or how many different genetic sources they represented, were not given. Presumably, however, only a fraction of the natural variation seen in Madagascar was studied. Table 1 shows that the range of variation of POLHAMUS et al. (1934) is limited when

Table 1. — Measurements of ***Cryptostegia*** presented by POLHAMUS et al. (1934) (**1**), MAROHASY & FORSTER (1991) (**2**) and the present study (**3**) in this order from top to bottom within each category, respectively.

	C. grandiflora	***C. madagascariensis***
Leaf		
lamina length	10-12 cm[1]	7-9 cm[1]
	up to 10 cm[2]	up to 9.2 cm[2]
	6-9 cm[3]	2-11 cm[3]
lamina width	5-7 cm	4-6 cm
	up to 6.3 cm	up to 5.2 cm
	3-5 cm	1.5-5.5
petiole length	10-14 mm	5-7 mm
	7-20.8 mm	3.7-16.6 mm
	5-15 mm	3-10 mm
Pedicels	8-9 mm	7-8 mm
	4.2-8.5 mm	3.1-7.7 mm
	3-7 mm	3-7 mm
Calyx		
lobe length	13-15 mm	7-8 mm
	11.9-18.7 mm	9-14 mm
	14-20 mm	5.7-12.8 mm
lobe width	6-7 mm	3-4 mm
	5.6-9.8 mm	3.5-6.9 mm
	4.2-8.8 mm	2.7-5.4 mm
Corolla		
total length	70-75 mm	55-60 mm
	50-60 mm	30-40 mm (probably not flattened)
	48-70 mm	(29-)42-64 mm
tube length	45-50 mm	25-30 mm
	19-45 mm	12-23 mm
	18-30 mm	(9-)15-25 mm
lobe length	45-50 mm	35-40 mm
	21-43 mm	24-41.4 mm
	32-56 mm	(20-)25-44 mm
lobe width	25-28 mm	18-22 mm
	13-22.5 mm	12-24.6 mm
	15-30 mm	(8-)14-26 mm
Corona length	12-13 mm	8-9 mm
	c. 10 mm	6-8.5 mm
	8-11 mm	6-9 mm
Follicle length	11-12.5 cm	7.5-9 cm
	10-15.4 cm	5.8-9.9 cm
	8-13.5 cm	(5-)7-9 cm

compared with MAROHASY & FORSTER (1991) and the present study, both based on wild material. For example, the differences given by POLHAMUS et al. for petiole and pedicel lengths and leaf lamina sizes, are not confirmed from wild, native material. It is also seen that cultivated material seems to have larger corollas, compared to wild material. Both MAROHASY & FORSTER (1991) and the present study show smaller figures for all parts of the corolla. Nevertheless, some of the clear-cut distinguishing characters of POLHAMUS et al. have a bearing on the taxonomy in a wider perspective. The following discussion will concentrate, however, on the findings of MAROHASY & FORSTER (1991) as they used a larger sample of wild Malagasy material.

MAROHASY & FORSTER (1991) found *Cryptostegia grandiflora* to be characterized by having leaves with 11-13 secondary veins and *C. madagascariensis* with 14-16 veins. I can see no difference between the southern (only *C. grandiflora* present), western or northern (only *C. madagascariensis* present) populations of *Cryptostegia* in this respect. The number of secondary veins varies between individuals within each geographical area. Furthermore, it is difficult to decide what veins should be counted, as several diverge from the mid-nerve but not always or only faintly reach the margin.

Another character, observed by POLHAMUS et al. (1934) on cultivated material and later corroborated by MAROHASY & FORSTER (1991) on wild material, was stems with numerous, small lenticels in *Cryptostegia grandiflora* but with few, prominent lenticels in *C. madagascariensis*. This is in general confirmed in the present study, although exceptions are found, e.g. large differences within branches or parts of branches within a single individual are sometimes present, and the character is not always easy to discriminate. Larger lenticels in the north and smaller in the south could possibly also be due to a climate gradient. This idea is, however, not supported by data from other widely distributed Malagasy Periplocoideae, e.g. *Pentopetia androsaemifolia* Decne. and *Pentopetia graminifolia* (Costantin & Gallaud) Klack., where the number of lenticels seems to vary between or within individuals but not geographically. Furthermore, it is interesting to note that this character was also used by HOCHREUTINER (1908) to distinguish between *C. madagascariensis* and his new species *C. glaberrima* (= *C. madagascariensis* var. *madagascariensis* and var. *glaberrima* of MAROHASY & FORSTER), i.e. between hairy and glabrous specimens within *C. madagascariensis*.

MAROHASY & FORSTER (1991) observed a distinct difference in corolla length between *Cryptostegia grandiflora* (5-6 cm long) and *C. madagascariensis* (3-4 cm long). The accompanying photograph, however, of (typical?) corollas (MAROHASY & FORSTER 1991, fig. 2C) shows one of *C. madagascariensis* c. 5 cm long and one of *C. grandiflora* c. 6 cm long, hardly distinguishable one from another. Neither can a distinct gap in corolla length between the two taxa be derived from the species descriptions (MAROHASY & FORSTER 1991). Figure 1 illustrates the variation in length of the corolla of some of the material used in the present study. The length has been measured with the corolla flattened, i.e. equalling the tube and lobe lengths added together. Although large corollas are common in the southwestern part of Madagascar, i.e. in the distribution area of *C. grandiflora*, no distinct geographical limit can be drawn between small and large flowers. This is also in accordance with the observations of JUMELLE (1908), who stated that the shape and size of the corolla of *C. grandiflora* and *C. madagascariensis* are more or less the same. The difference in length of the corolla tubes (12-23 mm vs. 19-45 mm) that could be deduced from the measurements of MAROHASY & FORSTER (1991), could not be observed in the material used in the present study. Furthermore, very large corolla tubes (c. 45 mm long) stated by POLHAMUS et al. (1934) and MAROHASY & FORSTER (1991) to be present in *C. grandiflora*, have not been found. In the present study no specimens were observed with tubes longer than 30 mm.

JUMELLE (1908), not observing any significant difference in size of corolla between *Cryptostegia grandiflora* and *C. madagascariensis*, pointed instead at the broader and more broadly ovate calyx lobes as well as the deeply bifid corona lobes as diagnostic characters for *C. grandiflora*. The supposedly more broadly ovate calyx lobes are not, however, confirmed in this study. The length to width propor-

tion of calyx lobes longer than 13 mm, i.e. mostly in southwestern Madagascar, is 2.2-3.4 and that of lobes shorter than 13 mm, i.e. mostly in the northern and western parts of the island, is 1.9-3.4, i.e. ovate to narrowly ovate in both cases.

Instead of different shapes, POLHAMUS et al. (1934) found a large gap in the length of the calyx between *C. grandiflora* (13-15 mm long lobes) and *C. madagascariensis* (7-8 mm). This gap was not confirmed by MAROHASY & FORSTER (1991). The length of the calyx lobes varies from 5.7 mm long, measured on a specimen from Tsingy de Bemaraha, to 20 mm, measured on a specimen from the south. At first glance there seem to be a north-south gradient in size, similar to a subspecific pattern with a rather wide transition zone between Morondava and the Toliara area (Fig. 1). However, if analysing the calyx length together with the corona lobes, a correlation between long calyx lobes (> 13 mm) and more or less bifid corona lobes are found. Furthermore, long calyx lobes have reflexed margins (Fig. 3A).

Bifid corona lobes (Fig. 3B) have been considered by several authors to be a distinct character for *C. grandiflora*. This feature was pointed out in the protologue by BROWN (1819), and mentioned by DECAISNE (1844) as one of the distinguishing characters between *C. grandiflora* and his new species *C. madagascariensis*. Subsequent authors such as JUMELLE (1908) and MAROHASY & FORSTER (1991) have agreed. CHOUX (1931) and MORAT (1973), however, stated that all intermediate stages between entire and bifid corona lobes exist, and argued that this character was of limited taxonomic value. The same opinion was held by PERRIER DE LA BÂTHIE according to in schedae notes. Figure 1 presents the variation of the corona lobe, its length and degree of bifurcation. In fact a large variation from slightly to deeply bifid lobes can be seen. Bifid corona lobes are mainly found in the southwest, but reach north to the Morondava area.

Almost all specimens with at least slightly bifid corona lobes and long calyx lobes with reflexed margins also have rounded and obtuse translator spathes (Fig. 3C), contrary to the ovate and acute spathes (Fig. 4D) found in specimens with short calyx lobes with more or less flat margins, and entire corona lobes (Fig. 4C). In addition, both POLHAMUS et al. (1934) and MAROHASY & FORSTER (1991) observed on living material pale yellow-green petioles to be characteristic of *C. madagascariensis* and reddish purple ones of *C. grandiflora*. Consequently, a good correlation between at least four characters is present, mostly allopatric but with a fairly large area of sympatry. This pattern is interpreted as a presence of two separate species (Figs. 1, 2).

It has also been proposed (JUMELLE 1908; POLHAMUS et al. 1934; MAROHASY & FORSTER 1991) that the follicles in *Cryptostegia grandiflora* are 10 cm or longer, and in *C. madagascariensis* shorter than 10 cm. In fact, all follicles of 14 studied fruiting specimens north of Morondava (only *C. madagascariensis* known from this area) were shorter than 10 cm, and all of five available specimens from the far south (only *C. grandiflora* known) were longer than 10 cm. There is a rather broad transition zone around Toliara, where both longer and shorter follicles are present. There is a problem in correlating this character with the floral ones, as flowers and fruits are only rarely present at the same time. However, in e.g. specimen U of Figure 1 with all floral characters corresponding to *C. grandiflora*, the mature follicle is only eight cm long. Also specimens with both longer and shorter mature follicles present on the same individual are found (Fig. 3E). Consequently, there is no absolute correspondence between follicle length and taxon, but on the other hand follicles longer than 10 cm has never been seen on individuals of *C. madagascariensis*.

Interspecific hybrids between *Cryptostegia grandiflora* and *C. madagascariensis* were studied on cultivated material by POLHAMUS et al. (1934). The hybrid plants exhibited an exceptional vegetative vigour. It furthermore showed several intermediate character states, e.g. in node and internode structure as well as in number and size of lenticels, in degree of bifidity of the corona lobe, the shape of the translator spathe, and follicle morphology. POLHAMUS et al. (1934) also showed that the hybrid had a more than doubled content of latex. These findings also point at the existence of two species.

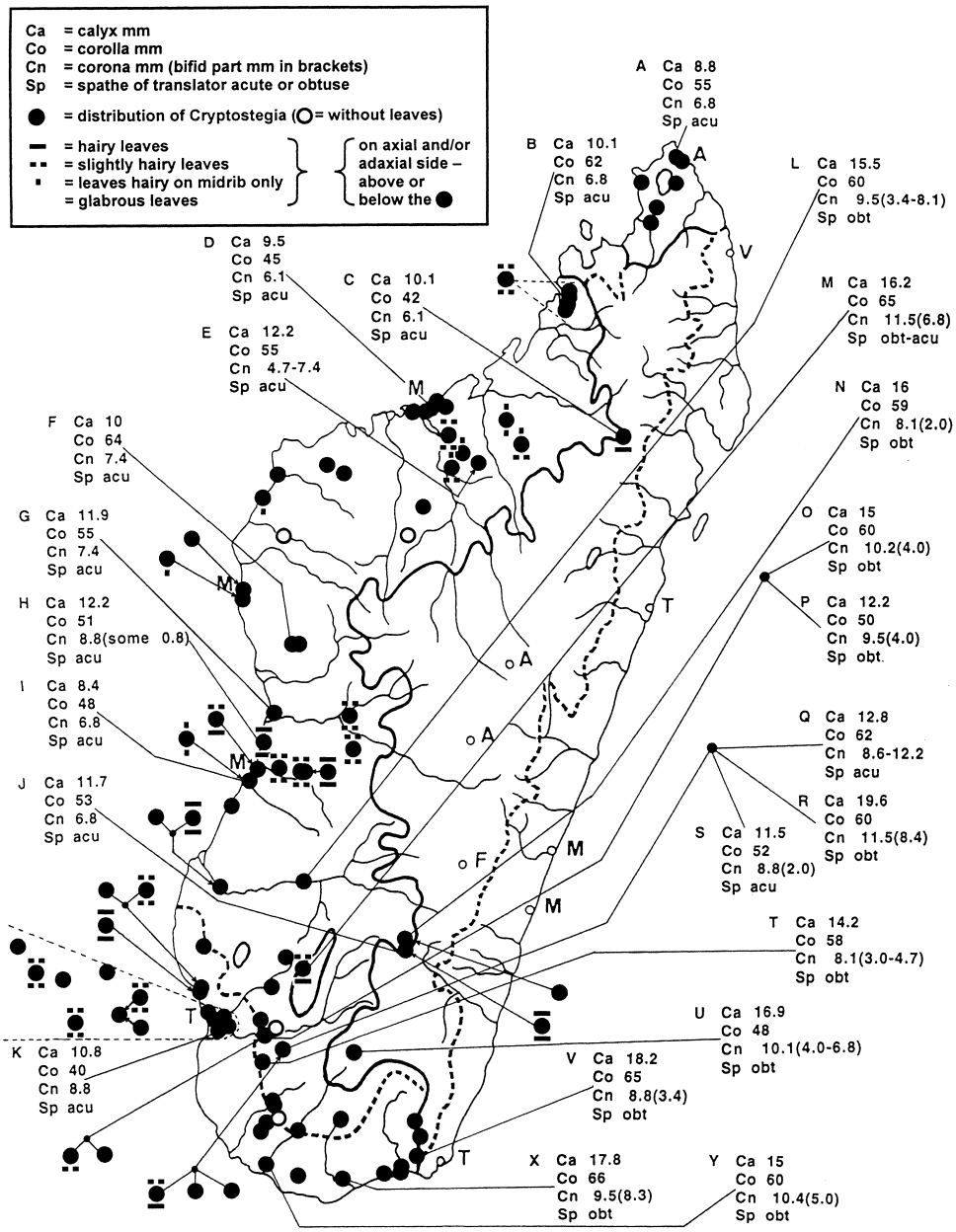

Fig. 1. — Distribution of some characters in ***Cryptostegia***. On left side (A-K) and Q are all *C. madagascariensis*, on right side (L-Y) *C. grandiflora* except for P, Q and S. A typical *C. grandiflora* (O) has been collected alongside a putative hybrid (P) with mixed characters (calyx and hairy leaves as *C. madagascariensis*). In Beza Mahafaly (Q, R, S) both species are present as well as a putative hybrid. Note also J and M. See further discussion in text. **A**, *Service Forestier: SF-1287*; **B**, *Marohasy C29*; **C**, *Réserves Naturelles: RN-2131*; **D,** *Marohasy C 21*; **E**, *Réserves Naturelles: RN-1109*; **F**, *Villiers et al. 4857*; **G**, *Marohasy C18*; **H**, *Omlor 12*; **I**, *Bosser 9714*; **J**, *Bernardi 11240*; **K**, *Turnour 4*; **L**, *Marohasy C15*; **M**, *Perrier de la Bâthie 16584*; **N**, *Service Forestier: SF-4740;* **O**, *Marohasy C2*; **P**, *Marohasy C65;* **Q**, *Phillipson 2622*; **R**, *Phillipson 2532*; **S,** *Phillipson 2594*; **T**, *Marohasy C8*; **U**, *Boiteau 363B*; **V**, *Alluaud 53*; **X**, *Marohasy C9*; **Y**, *Marohasy C6*.

Hybrids were also studied in wild material by MAROHASY & FORSTER (1991), and hybridization was said to occur rarely in a narrow zone where the two species are sympatric, specifically in the Toliara region. An area of sympatry between *Cryptostegia madagascariensis* and *C. grandiflora* is confirmed in this study, although this zone seems to be somewhat broader than earlier thought (Fig. 2). A couple of intermediate specimens have been found east of Toliara that lack the correlation usually seen between the bifid corona lobes, obtuse translator spathes and long calyx lobes (Fig. 1P,S). However, the pattern is not one of two subspecies as there is no distinct transition zone, but one of two species with a broad overlapping distribution and only a few scattered intermediate individuals.

Delimitation of varieties

COSTANTIN & GALLAUD (1906) described *Cryptostegia grandiflora* var. *tulearensis* based on observations by the Sakalavas that some individuals of this species have smaller follicles as well as smaller and more elongate leaves. As already discussed under "Delimitation of species", single individuals of *C. grandiflora* occasionally are furnished with shorter follicles, sometimes together with longer ones. This variety has not been accepted by subsequent authors. The type material has not been found.

MAROHASY & FORSTER (1991) recognized three infraspecific taxa of *Cryptostegia madagascariensis* based on variation in leaf hairiness, viz. 1) var. *madagascariensis* which was characterized by having sparse to dense indumentum on both leaf surfaces; 2) var. *glaberrima* which was characterized by entirely glabrous leaves, both distributed in western and north-western Madagascar; 3) var. *septentrionalis* which was said to have leaves pubescent only on adaxial surface but abaxially glabrous and restricted to the northernmost part of the island.

Leaf pubescence is considered in Figure 1. Specimens with entirely glabrous leaves seem to be totally prevailing in some areas, e.g. in the far north, the far south (*Cryptostegia grandiflora*), and in west-central Madagascar between Mahajanga and Morondava. On the other hand only hairy leaves are seen in the Morondava area and south of Sambirano. Especially in the Toliara and Mahajanga areas, both entirely glabrous and hairy specimens are found. This same pattern is illustrated by MAROHASY & FORSTER (1991, fig. 1). However, hairy or glabrous leaves are not two distinct characters. The leaves can be hairy only on the mid-nerve below or on both sides of the mid-nerves, sometimes also on the secondary veins, or more or less hairy all over one or both leaf surfaces. This is in accordance with field observations by JUMELLE (1907) and JUMELLE & PERRIER DE LA BÂTHIE (1908) from north-western Madagascar (Mahajanga area), who found the character to be of no taxonomic value. This was contested, however, by HOCHREUTINER (1908), who stated differences in several characters, as size, shape and number of flowers, and shape and particularly in the pubescence of the leaves, between *C. madagascariensis* and *C. glaberrima*. The observations of HOCHREUTINER were based on a single herbarium sheet of each taxon, however, and the supposed differences have not been confirmed by other studies, except for the pubescent versus glabrous leaves that were confirmed and accepted by MAROHASY & FORSTER (1991) as the basis of two varieties of *C. madagascariensis*, viz. var. *madagascariensis* and var. *glaberrima*, respectively. The gradual transition in hairiness of the leaves makes the sorting out of different taxa difficult and meaningless. All specimens of *C. grandiflora*, however, are glabrous, i.e. all hairy specimens belong to *C. madagascariensis*. Otherwise pubescence is a taxonomically useless character in *Cryptostegia*.

Cryptostegia madagascariensis var. *septentrionalis* was characterized in the protologue by the single character of having leaf lamina with dense indumentum on the adaxial surface, but glabrous abaxially. All specimens found in northernmost Madagascar (N of Sambirano Domain) were said to belong to this variety (MAROHASY & FORSTER 1991). The type material (*Marohasy C52*, isotypes at K and MO studied), however, as well as all the paratypes given (*Marohasy C51, C53, C54, C55*) (MAROHASY & FORSTER 1991) are completely glabrous, except for one specimen which is furnished with sparse hairs along the mid-nerve

abaxially. In fact, not a single hairy specimen has been observed among the herbarium specimens studied from this area and I cannot see any foundation for this taxon (see also below, "Nomenclatural note").

In addition to the variation of hairiness of the leaves, the corolla is sometimes hairy outside at the tube and/or part of the corolla lobes. This pubescence is not always correlated to the leaf pubescence and more or less hairy corollas might also occur on specimens with glabrous leaves. Also, this pubescence varies from being glabrous to slightly to distinctly hairy and is likewise of no taxonomic value.

TAXONOMY

CRYPTOSTEGIA R. Br.

Bot. Reg. 5: 742, t. 435 (1819). — Type: *Cryptostegia grandiflora* R. Br.

Woody liana to shrub with scrambling branches, usually 2-3 m high and self-supporting but sometimes climbing up to 10 m high; branches glabrous to hairy, with lenticels. Leaves decussate, somewhat coriaceous; blade usually oblong or elliptic to ovate, almost truncate to usually tapering at base into a distinct glabrous to hairy petiole, usually acuminate at apex, glabrous to hairy; venation looped, with finely reticulate and distinctly visible veinlets below when dry; mid-rib when dry ± even with leaf surface above to slightly impressed, raised below.

Inflorescences in terminal, mono- to dichasially branched, usually hairy cymes. Flowers 1-5 but sometimes up to 9, c. 3 cm long or more; bracts narrowly triangular, caducous, usually hairy. Calyx lobes narrowly ovate to elliptic, acute to usually acuminate, shorter than the corolla tube, hairy; margins sometimes reflexed. Corolla slightly twisted in bud, with the lobes fused for (1/4-)1/3-2/5(-1/2) of their length into a tube, campanulate to salverform, glabrous to hairy outside, glabrous inside, white to pink; tube ± cylindric, slightly widening towards the mouth, glabrous inside; lobes narrowly ovate to elliptic, acute to rounded at apex, erecto-patent or bent outwards. Corona lobes inserted in the tube below the sinuses of the corolla lobes, free, entire to bifid, filiform, ± straight, covering the staminal cone, glabrous. Stamens inserted at the base of the corolla tube, included, glabrous; filaments short, inserted at a distance below the corona lobes; anthers with distinct and narrow protruding connective up to 1.5 mm long. Translators placed in 5 cavities at the style head; spathe rounded to ovate, obtuse to acute at the apex; stipe present; viscidium flat. Style disinct, glabrous.

Follicles narrowly ovoid to fusiform, straight to boat-shaped, ± triangular with 3 longitudinal wings, acute at apex and often with a small hook, thick-walled, recurved 90° at base, glabrous to finely pubescent. Seed surface tuberculate or with shorter ridges.

Key to the species

1. 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**
1'. 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**

1. Cryptostegia grandiflora Roxb. ex R. Br.

Bot. Reg. 5: t. 435 (1819). — Type: Bot. Reg. 5: t. 435 (1819) (lectotype, fide MAROHASY & FORSTER 1991).

Nerium grandiflorum Roxb., Fl. Ind., ed. 2, 2: 10 (1832). — Type: not designated.

ILLUSTRATIONS: Figs. 2A (map), 3. — SCHUMANN 1895, fig. 63: Q-S; JUMELLE 1908,

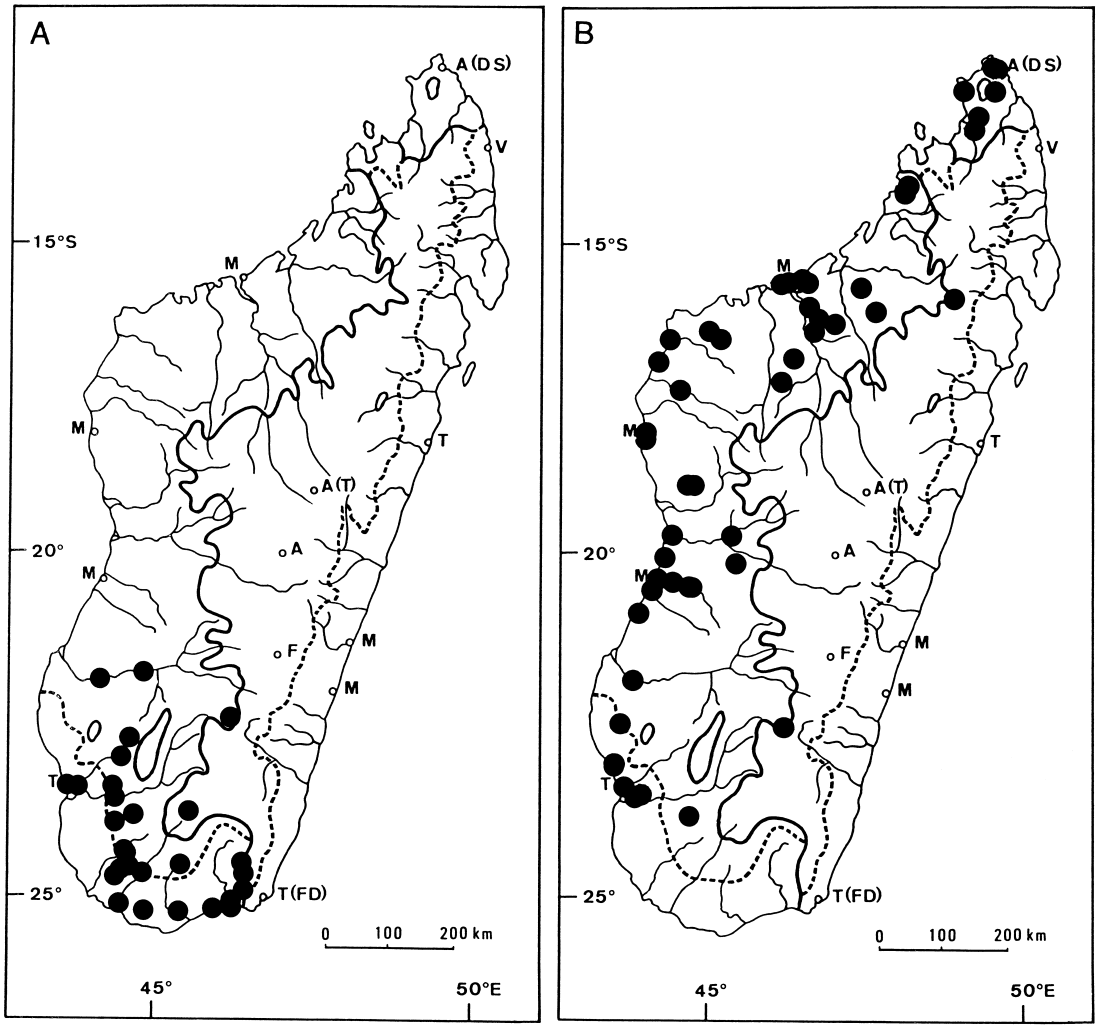

Fig. 2 — Distribution of ***Cryptostegia***: **A**, *C. grandiflora*; **B**, *C. madagascariensis*.

fig. 1; POLHAMUS et al.: 1934, pl. 2A, 4A, 5A; ARTSCHWAGER 1946 (several anatomical pictures); MAROHASY & FORSTER 1991, figs. 1, 2.

Branches glabrous, usually with numerous small lenticels. Leaf blade elliptic to ovate, 6-9 × 3-5 cm, cuneate to tapering at base, usually acuminate at apex, glabrous; petiole 5-15 mm long, glabrous to rarely slightly hairy.

Internodes of cymes 5-15 mm long; pedicels 3-7 mm long, usually hairy; bracts 2-7 mm long. Calyx lobes narrowly ovate to ovate, 14-20 × 4.2-8.8 mm, with reflexed margins. Corolla tube 18-30 mm long; lobes 32-56 × 15-30 mm. Corona lobes 8-11 mm high, bifid near apex only or cleft almost to the base. Staminal cone 3-4.5 mm high; anthers 2.7-4.5 mm. Translator spathe rounded, 1.5-1.9 mm long, obtuse at the apex. Style 1.3-3.4 mm long; style including style head 4.8-6.8 mm long.

Follicles 8-13.5 × 2-3.5 cm, glabrous. Seeds 5-8 mm long; hairs 3-4 cm long.

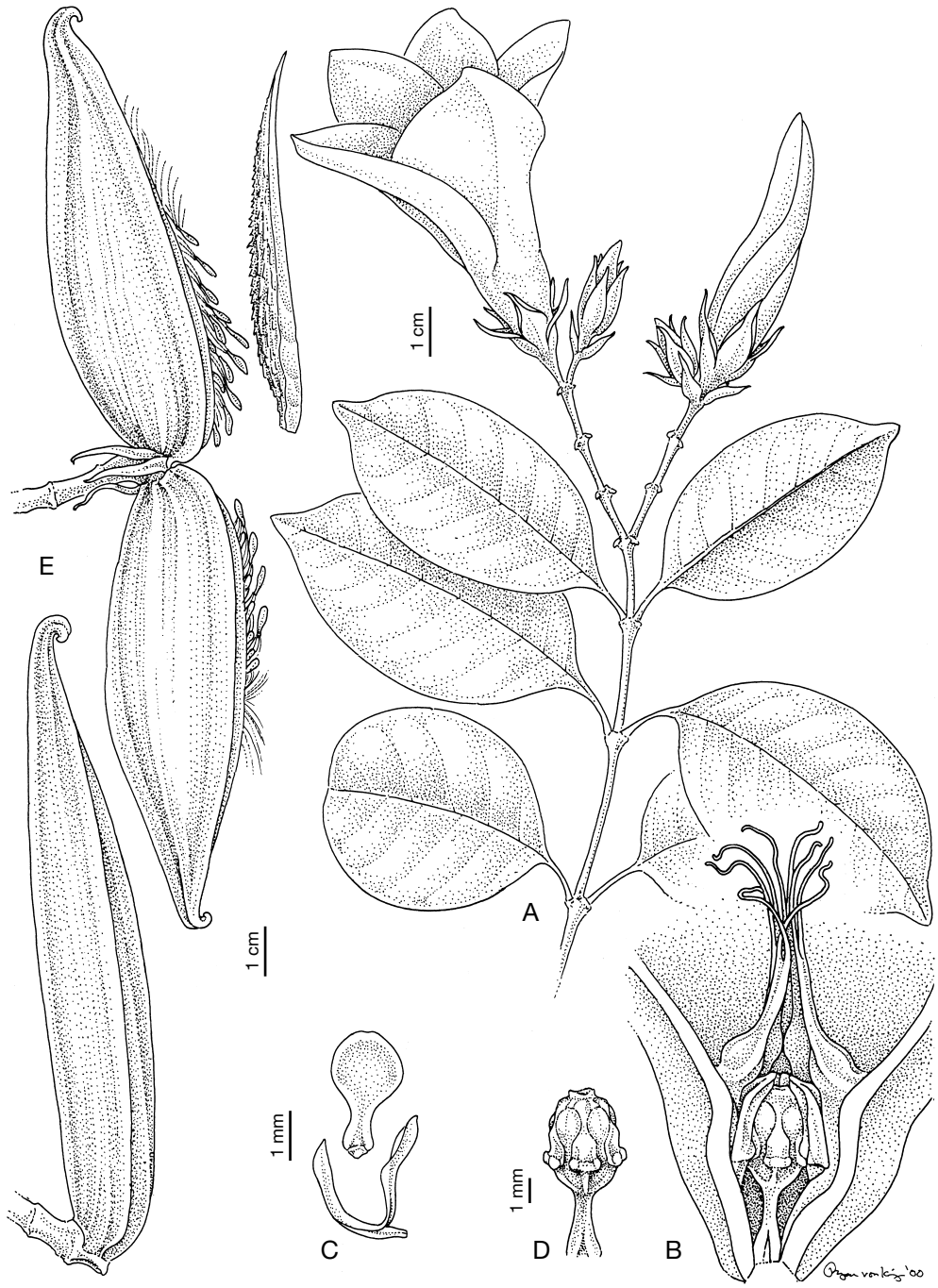

Fig. 3. — ***Cryptostegia grandiflora*** Roxb. ex R. Br.: **A**, habit (*Du Puy et al. MB32*); **B**, central part of flower with fraction of tube, one corona lobe and one anther removed; **C**, translator, lateral (below) and adaxial view; **D**, style and style head (*Civeyrel 1221*, from spirit material); **E**, follicles, long and short ones from same specimen. Shorter ones mature, showing seeds and a detached placenta (right) (*Allorge 658*). — Drawn by P. VON KNORRING.

DISTRIBUTION AND HABITAT. — *Cryptostegia grandiflora* is distributed in the southern part of Madagascar, mostly in the drier southwestern and western domains. It grows from sea level up to 600 m alt., usually in full sun. It is found in dry forest (e.g. Didiereaceae), savannah, disturbed grazed grassland, on laterite soil often on river beds.

Flowering specimens seen from August, October, November and January to March.

SPECIMEN EXAMINED. — *Alluaud 53*, Mandrare inf., Ampasimpolaka, 1900 (P); *Allorge 658*, prov. de Toliara, Route Nationale 7, 1992 (P); *Boiteau 363B*, env. d'Isoanala, 1966 (P); *Bosser 10458*, bas Fiherenana, 1956 (P); *Civeyrel 1221*, nord de Toliara, route côtière de Toliara à Ifaty, P.K. 32, 5 m, 1994 (S); *Croat 30753*, prov. Toliara, along Route Nationale 7 in vicinity of Sakaraha, 700 m, 1975 (MO); *Croat 31115*, prov. Toliara, along Route Nationale 10 between Andranovory and Tongobory at PK 25, 1975 (MO); *Croat 31120*, prov. Toliara, along Route Nationale 10 between Andranovory and Tongobory at PK 25, 250 m, 1975 (MO); *Croat 31429*, prov. Toliara, along road between Ampanihy and Androka, 10 km W of Ampanihy and Etrobeke, 1975 (MO); *Croat 31239*, prov. Toliara, along Route Nationale 10 between Betioky and Ejeda, between 175-225 m, 1975 (MO); *Croat 31321*, prov. Toliara, along Route Nationale 10 S of Ejeda between second and third branches of Linta River, 200 m, 1975 (MO); *Croat 32024*, prov. Toliara, along Route Nationale 13, from Antanimora to Beraketa, 250-460 m, 1975 (MO); *Du Puy, Du Puy & Ravonjiarisoa MB32*, SW Madagascar of route national 10, south of Tranoroa, near village of Manova, 300 m, 1989 (MO, P); *Decary 9347*, Beteny, limite NE de l'Androy, 1931 (P); *Descoings 1465*, sud Ambovombe, 1956 (P); *Geay 4790*, plaines du Fiherenana, 1904 (BM, G, K); *Geay 4790bis*, *4793*, ibid. (P); *Humbert 6785*, bassin supérieur du Mandrare, vallée de la Manambolo, 300-400 m, 1928 (P); *Humbert & Swingle 5552*, env. d'Ampanihy, 200-300 m, 1928 (P); *Keraudren-Aymonin & Aymonin 24736*, route Toliara à Betioky, 1970 (P); *Leeuwenberg 14166*, Andohahela Res., NW corner near Ihazofotsy, 200 m, 1991 (K, MO, WAG); *Marohasy C1*, Miary, Toliara, 1987 (K); *Marohasy C3*, Amboasary, 1987 (K, MO); *Marohasy C4*, Ejeda, 1987 (MO); *Marohasy C5*, Tranoroa, 1987 (MO); *Marohasy C6*, Marolinta, Menarandra river, 1987 (K, MO); *Marohasy C7*, Beloha, 1987 (K, MO); *Marohasy C8*, 10 km S of Betioky, 1987 (MO); *Marohasy C9*, Tsiombe, 1987 (K, MO); *Marohasy C10*, Etrobeke, Ampanihy, 1987 (K, MO); *Marohasy C15*, Mangoky riv., Beroroha, 1987 (K, MO); *Marohasy C41*, 30 km E of Betioky, 1987 (K, MO); *Marohasy C63*, Ambohimahavelona, 1988 (K, MO); *Marohasy C75*, 20 km N of Sakaraha, 1988 (K, MO); *Perrier de la Bâthie 12859*, Mangoky, 1919 (P); *Perrier de la Bâthie 16660*, vallée du Fiherenana, 1924 (P); *Phillipson 1696*, prov. Toliara, Beza Mahafaly reserve Betioky, near Sakamena riv., 1987 (MO, P, WAG); *Phillipson 2532*, prov Toliara, near Beza Mahafaly reserve, near Betioky, hills east of Sakamena river, near Ambinda, 140 m, 1987 (K, MO, P, WAG); *Randriamampionona 515*, Andohahela, Réserve Intégrale 11, Esomony, 1993 (P, S); *Service Forestier*: *SF-4740*, distr. Ihosy, canton Sakalalina, forêt de Menarahaka, 1951 (P); *Sussman 327*, prov. Toliara, 40 km NE of Betioky, on path from Beza Mahafaly Reserve to village Ambinda, 1987 (MO); *Turnour 5*, prov. Toliara, Ankoronga, 1986 (K, MO, P).

2. **Cryptostegia madagascariensis** Bojer ex Decne.

In A. DC., Prodr. 8: 492 (1844); Bojer, Hortus Mauritianus: 212 (1837), nomen. — Type: *Bojer s.n.*, "*Cryptostegia madagascariensis*" (holo-, P!).

Cryptostegia glaberrima Hochr., Annuaire Conserv. Jard. Bot. Genève, 11 & 12: 89 (1908). — *Cryptostegia madagascariensis* Bojer ex Decne. var. *glaberrima* (Hochr.) Marohasy & P.I. Forst., Austral. Syst. Bot. 4: 576 (1991). — Type: *Guillot 43*, distr. Vatomandry, Sakarive, 1903 (holo-, G!).

Cryptostegia madagascariensis Bojer ex Decne. var. *septentrionalis* Marohasy & P.I. Forst., Austral. Syst. Bot. 4: 576 (1991). — Type: *Marohasy C52*, Antsiranana, 1987 (holo-, BRI; iso-, CANB, K!, L, MO!).

ILLUSTRATIONS: Figs. 2B (map), 4. — HEMSLEY 1904, pl. 7984; JUMELLE 1907: fig. 1; JUMELLE & PERRIER 1908, pl. 4; POLHAMUS et al. 1934, pl. 2B, C, 4C, 5C; SPELLMAN 1975, fig. 1; MAROHASY & FORSTER 1991, figs. 1, 2.

NOMENCLATURAL NOTE. — BOJER (1837) did not accompany his name with any diagnostic character distinguishing this species from *Cryptostegia grandiflora* and consequently did not validly publish this taxon.

When describing the new species *Cryptostegia glaberrima*, HOCHREUTINER (1908) also discussed possible type material of *C. madagascariensis*. Unfortunately, HOCHREUTINER ascribed this species to DE CANDOLLE and consequently lectotypified it, effectively although not formally, by a specimen in G-DC. The type specimen was

collected by BOJER and said to be from Malagasy material cultivated in Mauritius. This lectotypification was accepted and formalized by MAROHASY & FORSTER (1991), who however, corrected the author of this species from DE CANDOLLE to DECAISNE, who treated the family Asclepiadaceae in DE CANDOLLE's Prodromus. However, the selected G-DC specimen was collected in 1839, two years after the publication of BOJER's Hortus Mauritianus, and consequently could not be the type material. Collections and types of BOJER as well as of DECAISNE are usually deposited in the Natural History Museum in Paris. Furthermore, DECAISNE (1844) clearly stated in the protologue that the specimen studied by him came from Madagascar and was kept in Paris ("in insul. Madagascar cl. Bojer [v. s. h. M. p.]"). Consequently, the type material should correctly be sought in Paris and not in Geneva. There is a single corresponding BOJER specimen in the Paris herbarium identified by DECAISNE himself as *Cryptostegia madagascariensis*, that should be considered to be the holotype. This specimen has glabrous leaves. As DECAISNE in the protologue described this species as pubescent he might also have studied other material, e.g. the BOJER collection from Mauritius in the de Candolle herbarium, which is a mixed collection with both hairy and glabrous leaves present. There is no doubt, however, that the type is the Paris specimen. As a consequence, *C. madagascariensis*, *C. glaberrima* and *C. madagascariensis* var. *septentrionalis* are in fact all based on glabrous-leaved specimens. The type material of *Cryptostegia glaberrima* is most probably from a cultivated plant as it was collected at the Malagasy east coast, i.e. far outside the known distribution of *Cryptostegia* in drier western Madagascar.

Branches glabrous to hairy, usually with few conspicuous lenticels. Leaf blade usually oblong or elliptic to ovate, sometimes broadly ovate to rarely obovate or almost orbicular, 2-11 × 1.5-5.5 cm, almost truncate to usually tapering at base, usually acuminate at apex, glabrous to hairy below or on both sides or along veins only; petiole 3-10 mm long, glabrous to hairy.

Internodes of cymes 5-15 mm long; pedicels 3-7 mm long, usually hairy; bracts 2-7 mm long. Calyx lobes narrowly ovate to elliptic, 5.7-12.8 × 2.7-5.4 mm, with non-reflexed margins. Corolla tube (9-)15-25 mm long; lobes (20-)25-44 × (8-)14-26 mm. Corona lobes 6-9 mm high, entire. Staminal cone 3.2-5.2 mm high; anthers 2.7-4.5 mm. Translator spathe ovate, 1.3-1.8 mm long, acute at the apex. Style 1.3-3.4 mm long; style including style head 4.8-6.8 mm long.

Follicles (5-)7-9 × 1-3 cm, glabrous to finely pubescent. Seeds 5-8 mm long; hairs 2-3 cm long.

DISTRIBUTION AND HABITAT. — *Cryptostegia madagascariensis* is distributed along the whole of the western part of Madagascar, mostly in western phytogeographical domain but is also found in the Toliara region in southwestern domain. Habitat preferences are similar to those of *C. grandiflora*. It has been found from sea level up to 700 m alt., usually in full sun. It grows in dry forest (e.g. Didiereaceae, *Euphorbia*), savannah, tsingy, disturbed grazed grassland, on lateritic soil and sand, often on river beds.

Flowering specimens seen from July to May.

SPECIMEN EXAMINED. — *d'Alleizette s.n.*, env. de Mahajanga, nov. 1906 (P); *Baron 4578, 4636*, Central Madagascar (K); *Baron 5323, 5817*, NW Madagascar (K); *Bernardi 11240*, de Ihosy, 47-49 km ad SE per viam ad Ivohibe, 650-700 m, 1967 (G); *Bernier 172*, Nord de Madagascar, 1839 (G); *Bosser 3553*, Ambato Boeni distr., Anjiapia, 1952 (P); *Bosser 8395*, Marovoay, 1955 (P); *Bosser 9714*, Morondava, à 20 km sur la route de Belo sur mer, 1956 (P); *Civeyrel 1236*, 20-25 km à l'est de Toliara en direction de la rivière Onilahy, première route sur la droite de la Route Nationale 7 après la "Montagne de la Table", 20 m, 1994 (S); *Cours 3977*, station de Marovoay à Madirokely, 1951 (P); *Decary 8211*, Maintirano, 1930 (P); *Decary 14523*, massif de l'Ankara, 1939 (P); *Decary 15573*, Besalampy, 1940 (P); *Decary 15595*, distr. Maintirano, Antsingimavo, 1940 (P); *Decary 15747*, Soalala distr., Namoroka, 1940 (P); *Dequaire 27144*, Mahabo (P); *Descoings 765*, bas Mangoky, 1955 (P); *Edmonson 95-23*, Mahajanga, on road S of Katepsy, c. 100 m, 1995 (P); *Gentry 11472*, vicinity of Lac Ampijoroa, 30 km W of Tsaramandroso on highway to Mahajanga, 1974 (MO); *Gentry 11787*, prov. Mahajanga, 51 km N of Mampikony, c. 150 m, 1974 (K, MO, P); *Goudot s.n.*, baie d'Antsiranana, 1833 (G); *Grevé 64*, Morondava (K, P); *Harder et al. 1698*, Antsiranana prov., Vovo village distr., c. 6 km from Antsiranana on road to Vovo village, 85 m, 1993 (MO, P); *Hildebrandt 3053*, Beravi, 1879 (BM, K, P);

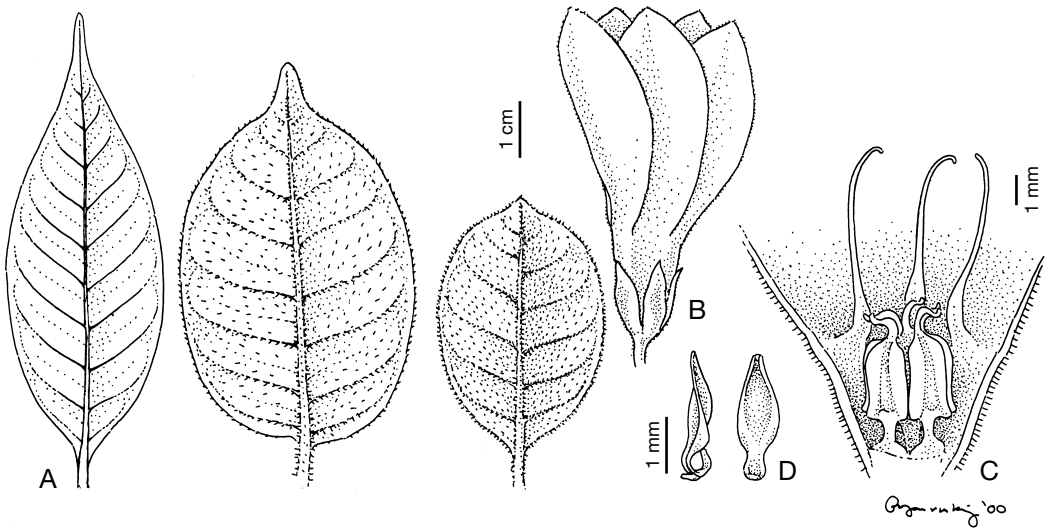

Fig. 4. — ***Cryptostegia madagascariensis*** Bojer ex Decne.: **A**, leaves (from left to right: *Villiers et al. 4960, Bosser 3553, Bernardi 11240*); **B**, flower; **C**, central part of flower with fraction of tube and with two corolla lobes removed; **D**, translators (*Bernardi 11240*). — Drawn by P. VON KNORRING.

Hildebrandt 3053a, Nosi-Andiana, 1880 (BM, G, K); *Hladik 17*, 50 km N de Morondava, forêt de Marosalaza, 1973 (P); *Humbert & Perrier de la Bâthie 2018*, env. de Mahajanga, 2-15 m, 1924 (P); *Hure s.n.*, secteur de Miandrivazo (P); *Klackenberg 93.03.10-1*, 7 km E Antsalova along trail to Tsingy of Bemaraha, 1993 (S); *Klackenberg 93.03.11-25*, 11 km E Antsalova, at dry tsingy near the edge of the Tsingy de Bemaraha (S); *Lam & Meeuse 6070*, Antsiranana, montagne des Français, 50 m, 1938 (P, WAG); *Leandri 114*, Tsingy du Bemaraha, 1932-33 (P); *Leandri 533*, Maroarivo, Ambato, 1932 (K); *Mabberley 737*, near Ambohibe between Morondava and Antananarivo, 240 m, 1971 (MO); *Marohasy C17*, Morondava, Ankilizato, 1987 (K, P); *Marohasy C18*, Belo Tsiribihina, 1987 (K, MO); *Marohasy C19*, Ambatolahy, 1987 (K, MO); *Marohasy C20*, Mahajanga, Boanamary, 1987 (K, MO); *Marohasy C21*, Mahajanga, 1987 (K, MO); *Marohasy C29*, Maromandia, 1987 (K, MO); *Marohasy C51*, Antsiranana, Ramena, 1987 (MO); *Marohasy C52*, Antsiranana, 1987 (K, MO); *Marohasy C53*, Sadjoavato, 1987 (K, MO); *Marohasy C54*, 20 km N of Ambilobe, 1987 (K, MO); *Marohasy C55*, Ambilobe, 1987 (K, MO); *Marohasy C61*, Ambohimahavelona, 1988 (MO); *Marohasy C62*, ibid., 1988 (K, MO); *Marohasy C67*, Ankaraobato, Manombo river, 1988 (K, MO); *Marohasy C68*, ibid., (MO); *Marohasy C69*, Analamisampy, 1988 (K, MO); *Marohasy C70*, *C71*, Bevoay, 1988 (K, MO); *Marohasy C72*, *C73*, Morondava, 1988 (K, MO); *Marohasy C74*, Andrevo, Manombo river (MO); *Marohasy C76*, Ambohimahavelona, 1988 (K, MO); *Marohasy C81*, 5 km N of Maromandia, 1988 (K, MO); *Marohasy C83*, 10 km S of Maromandia, 1988 (K, MO); *Marohasy C84*, 33 km S of Maromandia, 1988 (K, MO); *Marohasy C85*, *C86*, Maintirano, 1988 (MO); *Marohasy C87*, 22 km S of Maintirano, 1988 (K, MO); *Mathuen s.n.*, Toliara, 9 Sep. 1911 (K); *Morat 964*, Rés. Nat. 8, 1964 (P); *Omlor 12*, Concession forestière du C.F.P.F. 55 km north of Morondava, river Kirindy, 50 m, 1992 (MO); *Omlor 17*, Belo sur Mer, 70 km south of Morondava, 0-50 m, 1992 (MO); *Peltier 5301*, Amborovy, 1965 (P); *Perrier de la Bâthie 73*, Boina, bords de Bemarivo, 1906 (P); *Perrier de la Bâthie 4584*, bords du Iabohazo, à Ankirihitra, 1902 (P); *Perrier de la Bâthie s.n.*, env. de Marovoay, 1910 (G); *Perrier de la Bâthie s.n.*, Toliara, 1910 (P); *Pervillé 172*, Antsiranana, 1841 (P); *Pervillé? 694*, Ambongo, 1841 (P); *Phillipson 2622*, prov Toliara, near Beza Mahafaly reserve, near Betioky, ridge east of Sakamena river, valley of Analafahy, 1987 (K, MO, P, WAG); *Rahantamalala 105*, Morondava, 1990 (P); *Villiers, Klackenberg & Badré 4857*, 10 km E Antsalova, 1993 (S); *Villiers, Klackenberg & Badré 4864*, 10 km E Antsalova, 1993 (S); *Villiers, Klackenberg & Badré 4959*, *4960*, 15 km E Ankiliromotsy, 27 km SE Antsalova, 1993 (S); *Villiers, Klackenberg & Badré 5005*, piste de Bekopaka, 10 km SSE Antsalova, 1993 (S); *Réserves Naturelles*: *RN-1108*, *RN-1109 Ratoto*, distr. Ambato Boeni, canton Tsaramandroso,

Ampombilava, 1947 (P); *Réserves Naturelles*: *RN-2131 Sajy*, distr. Mandritsara, canton Antsirabe, 1950 (P); *Réserves Naturelles*: *RN-s.n. Rakoto*, Mahajanga distr., canton d'Ambalakida, Marohogo, 1947 (P); *Service Forestier*: *SF-16*, Tsingy de Namoroka (BM, P); *Service Forestier*: *SF-179 Capuron*, Marohogo, SE de Mahajanga, 1949 (P); *Service Forestier*: *SF-1287*, Antsiranana, montagne des Français, 1950 (P); *Turnour 4*, *6*, Toliara, Maroamalona, lower Onilahy riv., 1986 (K, MO, P).

Specimens intermediate between *Cryptostegia grandiflora* and *C. madagascariensis* :

Marohasy C2, Tongobory, Betioky, 1987 (K, MO); *Marohasy C64*, Toliara, Tongobory, 1988 (K, MO); *Marohasy C65*, ibid. (MO); *Perrier de la Bâthie 16584*, versant W de l'Isalo, 1926 (P); *Phillipson 2594*, prov. Toliara, near Beza Mahafaly reserve, near Betioky, 1987 (K, MO, P, WAG).

TAXON OF UNCERTAIN POSITION

Cryptostegia grandiflora Roxb. ex R. Br. var. *tulearensis* Costantin & Gallaud, Bull. Mus. Hist. Nat. (Paris) 12: 417 (1906). — Type: *Geay s.n.,*"Lombiri-Voharoto"(not seen). — Although characterized by having smaller follicles, this is probably *C. grandiflora*.

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