A TAXONOMIC REVISION OF THE MASCARENE *HIBISCUS* SECT. *LILIBISCUS* (MALVACEAE), WITH MORPHOMETRIC ANALYSIS AND DESCRIPTION OF TWO NEW SPECIES[1]

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Abstract

Hibiscus L. sect. *Lilibiscus* Hochr. comprises 31 species, the majority of which occur on volcanic islands in the Indian and Pacific Oceans. Four species are currently described in the Mascarene Archipelago: *H. boryanus* DC., *H. fragilis* DC., *H. genevei* Bojer, and *H. liliiflorus* Cav. Though they are a small group, the Mascarene species in section *Lilibiscus* have a complex taxonomic history. While type collections and species descriptions are sufficiently detailed to apply the existing names *H. liliiflorus* and *H. genevei* to species, the brief species descriptions and insubstantial type collections of *H. boryanus* and *H. fragilis* have complicated the application of these two names to the remaining two species. In addition, morphological variation within *H. boryanus* s.l. as it is currently delimited suggests that the name comprises three distinct species. Thus, the names *H. boryanus* and *H. fragilis* could each be applied to one of four species, leaving two species to be described. To determine the proper application of the names *H. boryanus* and *H. fragilis*, we conducted a thorough study of herbarium specimens and species descriptions combined with morphometric analyses of seven floral characters obtainable from the 220-year-old type specimens of *H. boryanus* and *H. fragilis* and 70 other flowering specimens. Although morphometric analyses were sufficient to determine that the name *H. fragilis* is best applied to the red-flowered species in Mauritius, additional lines of evidence inferred from the original description of *H. boryanus* were necessary to apply this name to the yellow-flowered species in Réunion. Consequently, we describe two new species formerly treated under *H. boryanus* s.l.: a magenta-flowered species endemic to Mauritius (*H. dargentii* Mashburn) and a red-and-yellow–flowered species endemic to Réunion (*H. igneus* Mashburn). We provide an identification key to differentiate the Mascarene *Hibiscus* sect. *Lilibiscus* species and new and updated species descriptions for all six species.

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Morphometric data and scripts for data analyses and production of figures are available on GitHub (<github.com/brockmashburn>).

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Résumé

Le genre *Hibiscus* L. sect. *Lilibiscus* Hochr. comprend 31 espèces, dont la majorité se trouve sur des îles volcaniques des océans Indien et Pacifique. Quatre espèces sont actuellement décrites dans l'archipel des Mascareignes : *H. boryanus* DC., *H. fragilis* DC., *H. genevei* Bojer et *H. liliiflorus* Cav. Bien que ce groupe soit restreint, les espèces de la section *Lilibiscus* des Mascareignes présentent une histoire taxonomique complexe. Alors que les collections types et les descriptions des espèces sont suffisamment détaillées pour permettre l'application correcte des noms *H. liliiflorus* et *H. genevei*, les descriptions succinctes et les collections types limitées pour *H. boryanus* et *H. fragilis* ne permettent pas une identification précise de ces deux noms aux espèces correspondantes. De plus, la variation morphologique observée au sein de *H. boryanus* s.l., tel qu'il est actuellement défini, suggère que ce nom comprend en réalité trois espèces distinctes. Ainsi, les noms *H. boryanus* et *H. fragilis* pourraient correspondre à deux des quatre espèces, laissant deux autres espèces encore non décrites. Pour déterminer l'application correcte des noms *H. boryanus* et *H. fragilis*, nous avons mené une étude approfondie des spécimens d'herbier et des descriptions d'espèces, complétée par des analyses morphométriques portant sur sept caractères floraux sur les spécimens types de *H. boryanus* et *H. fragilis*, âgés de 220 ans, ainsi que sur 70 autres spécimens fleuris. Alors que les analyses morphométriques étaient suffisantes pour établir que le nom *H. fragilis* s'applique à l'espèce à fleurs rouges de l'île Maurice, des preuves supplémentaires déduites de la description originale de *H. boryanus* étaient nécessaires pour attribuer ce nom à l'espèce à fleurs jaunes de La Réunion. Nous décrivons donc deux nouvelles espèces auparavant considérées sous *H. boryanus* s.l. : une espèce à fleurs magenta endémique de l'île Maurice (*H. dargentii* Mashburn) et une espèce à fleurs rouges et jaunes endémique de La Réunion (*H. igneus* Mashburn). Enfin, nous proposons une clé de détermination pour identifier les espèces d'*Hibiscus* sect. *Lilibiscus* des Mascareignes ainsi qu'une description actualisée des six espèces reconnues.

Key words: Biodiversity conservation, *Hibiscus*, Indian Ocean, *Lilibiscus*, Malvaceae, Mauritius, morphometrics, Réunion, Rodrigues.

The cosmopolitan genus *Hibiscus* L. contains over 200 species of herbs, woody shrubs, and large trees (Pfeil et al., 2002; Hanes et al., 2024; POWO, 2025; WFO, 2025). *Hibiscus* sect. *Lilibiscus* Hochr. (hereafter "*Lilibiscus*") consists of 31 species with a wide geographic distribution, occurring mostly on volcanic islands in the Indian and Pacific Oceans (Thomson & Braglia, 2019; Braglia et al., 2024). *Lilibiscus* has been shown by molecular studies to be monophyletic and is thought to have arisen in Madagascar (Koopman & Baum, 2008; Hanes et al., 2024). The nearby Mascarene Archipelago, consisting of the islands of Mauritius, Réunion, and Rodrigues, has been considered home to four described species within *Lilibiscus*: *H. boryanus* DC., *H. fragilis* DC., *H. genevei* Bojer, and *H. liliiflorus* Cav. (Friedmann, 1987). These four Mascarene *Lilibiscus* species have been of interest to the botanical community for hundreds of years because of their large, colorful flowers and interfertility. Horticultural hybrids initially produced over 150 years ago between Mascarene and South Pacific *Lilibiscus* species have led to thousands of cultivated varieties commonly treated as *H. rosa-sinensis* L. (Singh & Khoshoo, 1989; Braglia et al., 2010, 2024). In the wild, however, three of the four Mascarene species (*H. fragilis*, *H. genevei*, and *H. liliiflorus*) are highly threatened, requiring conservation actions to prevent their extinction (Walter & Gillett, 1998; Bachraz & Strahm, 2000; Tatayah et al., 2021). Consequently, these species are often featured in informational publications about endemic Mascarene plants (Cadet, 1984, 1989; Atkinson & Sevathian, 2005; Gurib-Fakim, 2022).

Despite the popular attention given to the Mascarene *Lilibiscus* species, the taxonomy and application of names to species in the section are unclear. This is particularly true for *Hibiscus boryanus* and *H. fragilis*, primarily because of limitations in the type specimens and the original species descriptions. The original material of both *H. boryanus* (G-DC [barcode] G00218968) and *H. fragilis* (G-DC [bc] G00218958) was collected by French botanist Jean-Baptiste Bory de Saint-Vincent (1778–1846) in 1801–1802. The specimens contain scant plant material and lack descriptions of any physical characters of the living plants from which they were taken (Fig. 1). The type specimens were also not annotated with locality information until 1821, when the Swiss botanist Augustin Pyramus de Candolle (1778–1841) received the specimens and suggested that they were collected in Réunion ("Bourbon") (de Candolle et al., 1794–1921). Other Bory collections annotated by de Candolle in his herbarium (G-DC) also indicate a lack of certainty about their origin (e.g., G-DC [bc] G00218973), which implies that the annotated locality information on these Bory collections is likely unreliable and corresponds to similar findings in other Mascarene taxa collected by him (Florens et al., 2008). Nevertheless, when de Candolle described *H. boryanus* and *H. fragilis* in the first volume of his *Prodromus* (de Candolle, 1824), he placed both species in Réunion. In addition, de Candolle's (1824) morphological descriptions were brief and did not clearly differentiate the species; in particular, when he described *H. fragilis*, de Candolle made no mention of the flower color or other characters to distinguish it from *H. boryanus* and *H. liliiflorus*. Consequently, authors treating the Mascarene *Hibiscus* over the last 200 years have applied these names to the extant Mascarene species in different and even contradictory ways. Bojer (1837) treated *H. fragilis* as occurring in Mauritius but did not note how it was distinct from *H. liliiflorus* (and made

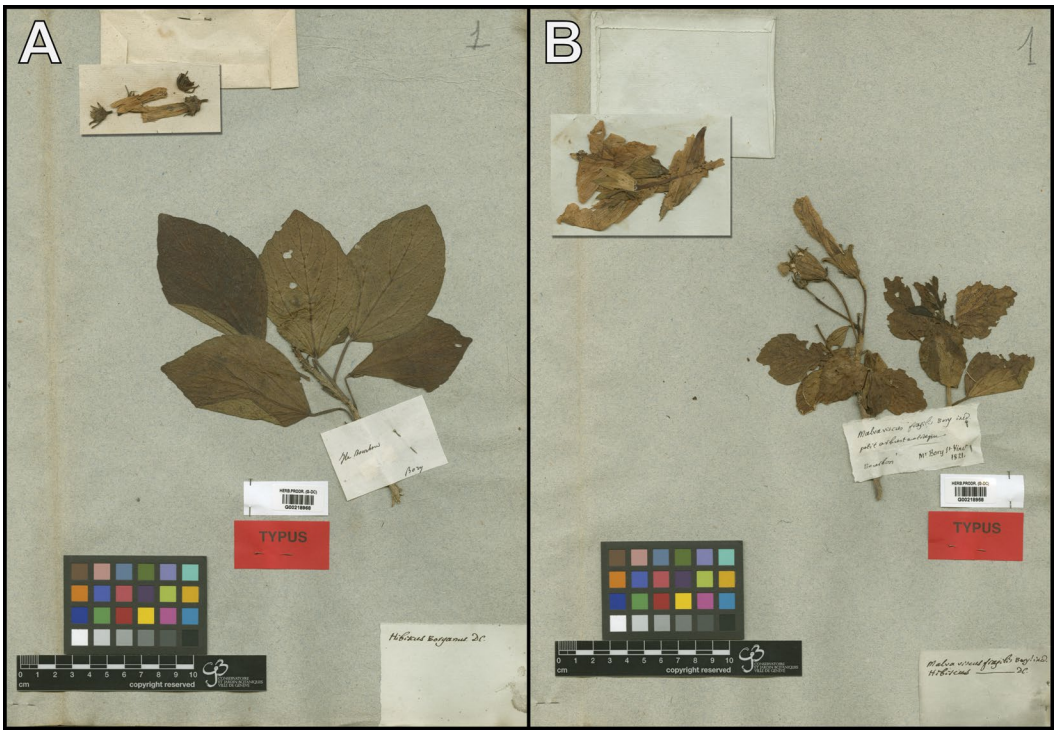

Figure 1. Type specimens of *Hibiscus boryanus* DC. and *H. fragilis* DC., both collected by the French botanist Jean-Baptiste Bory de Saint-Vincent in 1801–1802. —A. *Hibiscus boryanus* (G-DC [barcode] G00218968!). —B. *Hibiscus fragilis* (G-DC [bc] G00218958!). (© Conservatoire et Jardin de Genève)

no mention of *H. boryanus*). Baker (1877) then synonymized *H. fragilis* under *H. liliiflorus* and treated the latter as a species with red flowers found in Mauritius (and also did not mention *H. boryanus*). De Cordemoy (1895) recognized both *H. boryanus* and *H. fragilis* as distinct species, both with yellow flowers and occurring in Réunion. Hochreutiner (1900), in his revision of the genus, recognized *H. boryanus* in Réunion (without morphological description) but treated *H. fragilis* as a synonym of *H. rosa-sinensis*. Clearly each of these authors struggled to interpret de Candolle's original species description in a consistent way.

In the *Flore des Mascareignes*, Friedmann (1987) recognized four *Lilibiscus* species in the Mascarenes and established the taxonomic consensus used by botanists in the region today. Friedmann delimited *Hibiscus liliiflorus* to be the species with orange flowers that is extant in Rodrigues and presumed extinct in Réunion (Fig. 2A). He considered *H. genevei* to be the species occurring in Mauritius with pale pink flowers and a dark purple center (Fig. 2B). Friedmann differentiated *H. fragilis* and *H. boryanus* based primarily on plant habit, flower color, and the relative sizes of the epicalyx and calyx. Friedmann treated *H. fragilis* as a species occurring in Mauritius with a low, bushy habit and drooping branches, a long calyx (with the epicalyx roughly half as long as the calyx), and uniformly red flowers (Fig. 2C). Friedmann then treated *H. boryanus* as a species occurring in both Mauritius and Réunion with a shrubby habit, a short calyx (with the epicalyx roughly the same length as the calyx), and three distinct, geographically structured color morphs: (1) plants with carmine-red to pink flowers found in Mauritius (hereafter, "magenta morph") (Fig. 2D); (2) plants with yellow to reddish-orange flowers found at lower elevations in Réunion ("yellow morph") (Fig. 2E); and (3) plants with vermilion-red flowers with a yellow center found at higher elevations in Réunion ("red morph") (Fig. 2F). Despite their clear differences in geography and flower color, the three color morphs of *H. boryanus* s.l. have never been evaluated for recognition at the species level.

Though Friedmann's (1987) concepts of *Hibiscus boryanus* and *H. fragilis* were tractable, one unresolved issue remained: his conclusion that *H. fragilis* was endemic to Mauritius contrasted with the annotation on the type specimen as coming from Réunion ("Bourbon," Fig. 1B). In his treatment, Friedmann (1987) suggested that de Candolle's annotation was an error. This suggestion, however, did not reduce hopes that one day

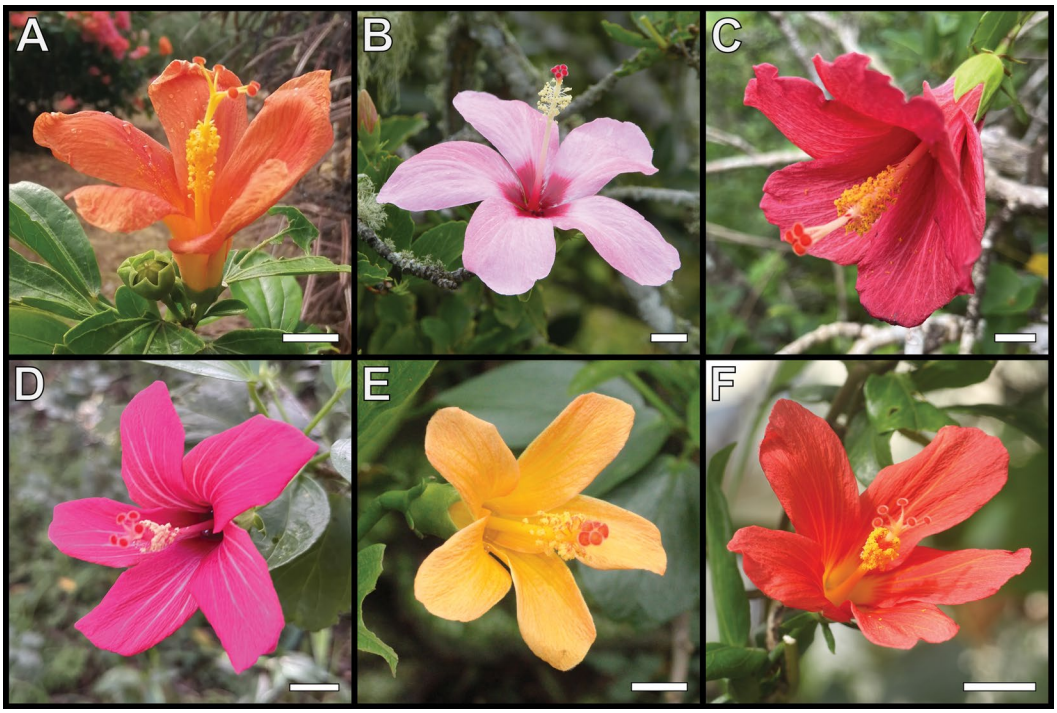

Figure 2. The six floral morphotypes found in the Mascarene species of *Hibiscus* L. sect. *Lilibiscus* Hochr., sorted according to the taxonomy of Friedmann (1987). —A. *Hibiscus liliiflorus* Cav. —B. *Hibiscus genevei* Bojer. —C. *Hibiscus fragilis* DC. —D. *Hibiscus dargentii* Mashburn, sp. nov. (*H. boryanus* s.l. magenta morph). —E. *Hibiscus boryanus* DC. (*H. boryanus* s.l. yellow morph). —F. *Hibiscus igneus* Mashburn, sp. nov. (*H. boryanus* s.l. red morph). Photo credits: A, Jean Alfred Bégué; B, Vikash Tatayah; C, D, F, Brock Mashburn; E, Jean-Maurice Tamon.

a population of *H. fragilis* might be rediscovered in Réunion. Indeed, Thomas et al. (2016) reported the discovery of a red-flowered population of *Hibiscus* in a remote and near-inaccessible area of Réunion, which they identified as *H. fragilis*. If true, this suggests that *H. fragilis* occurs in both Mauritius and Réunion. Resolving the taxonomic issues concerning *H. boryanus* and *H. fragilis* has important implications for their conservation. If *H. fragilis* truly occurs in Réunion, then the population discovered by Thomas et al. (2016) would need immediate protection, given that the species is listed as critically endangered and is currently thought to occur in only three sites in Mauritius (Bachraz & Strahm, 2000). In addition, if *H. boryanus* were to be divided into three species based on the three color morphs, these species would need to be described and individually assessed for their conservation status.

To address these issues, we conducted field sampling of individuals from nearly all known extant *Lilibiscus* populations in Rodrigues and Mauritius and the majority of populations in Réunion (Fig. 3). We first investigated how to apply the four existing species names to the taxa currently occurring in the Mascarenes. Given the thorough descriptions of *Hibiscus liliiflorus* and *H. genevei*, the proper application of these names to taxa in the Mascarenes is incontrovertible. However, because of their inadequate type material and original descriptions, it is unclear how the names *H. boryanus* and *H. fragilis* should be applied. Thus, we conducted a thorough morphological study, including morphometric analyses, to determine the proper application of the names *H. boryanus* and *H. fragilis* to taxa in the Mascarenes. Second, we evaluated the morphological evidence for recognizing the three color morphs within *H. boryanus* s.l. as species. Finally, we produced a complete taxonomic treatment for section *Lilibiscus* in the Mascarenes with a dichotomous key, updated species descriptions, and extinction risk assessments.

Materials and Methods

Study System

Following the taxonomy of Friedmann (1987), five species of *Hibiscus* are native to the Mascarenes, with four placed in section *Lilibiscus* (Hochreutiner, 1900). The fifth species, *H. columnaris* Cav., is both morphologically and phylogenetically distinct from section

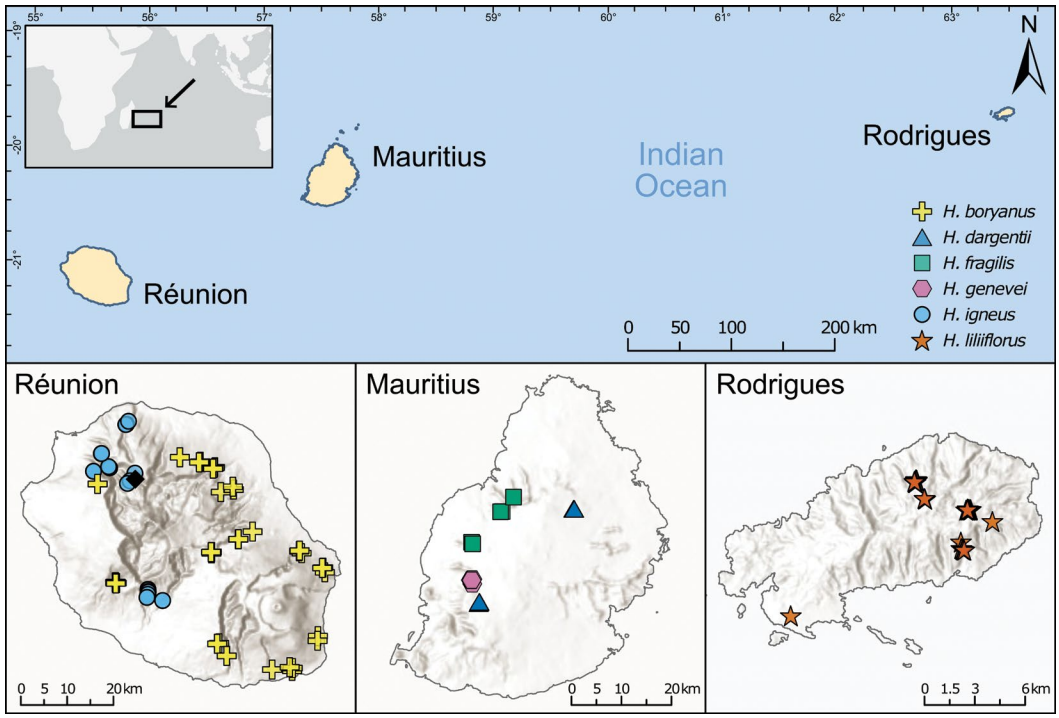

Figure 3. Distribution map of the six Mascarene species of *Hibiscus* L. sect. *Lilibiscus* Hochr. (including the two new species described in this study, *H. dargentii* Mashburn, sp. nov. and *H. igneus* Mashburn, sp. nov.). Locations of *H. boryanus* DC. and *H. igneus* in Réunion are wild populations visited during fieldwork in 2022. The black diamond indicates the location of the reported discovery of *H. fragilis* DC. in Réunion by Thomas et al. (2016). Locations of *H. dargentii*, *H. fragilis*, and *H. genevei* Bojer in Mauritius are extant wild populations verified during fieldwork in 2018 and 2022. Locations of *H. liliiflorus* Cav. in Rodrigues include reintroduced populations, all of which were visited in 2018.

Lilibiscus (Friedmann, 1987; Hanes et al., 2024). No single synapomorphy differentiates section *Lilibiscus* from other sections of *Hibiscus*, but the following combination of characters can be used to place species in the section: plants are tropical woody shrubs to trees; leaf lamina usually ovate to obovate, often heterophyllous, with a distinct, often deeply divided juvenile form; pedicels articulated near the apex; epicalyx with five to nine free, narrowly triangular to subulate lobes, usually shorter than the calyx, green; calyx with five partially connate sepals, green; corolla large and showy, many-colored; staminal column exserted; styles exserted from the staminal column and spreading with five capitate stigmas; fruits usually dry dehiscent capsules, brown, rarely indehiscent and green, with glabrous interior; seeds brown to black, more or less hairy.

MATERIALS

A total of 213 herbarium specimens of *Hibiscus* sect. *Lilibiscus* from the Mascarenes, including four type specimens, were examined from 10 herbaria: ANG, CBNM, G, K, MARS, MAU, MO, MPU, P, and REU (abbreviations follow Thiers, 2025). These included 61 specimens we collected during expeditions in Mauritius and Rodrigues from March 11 to 27, 2018, and in Mauritius and Réunion from April 5 to 17, 2022. In Rodrigues, we visited every known wild and cultivated individual of *H. liliiflorus*, including three sites where plants are being reintroduced on the island (Mashburn et al., 2023). In Mauritius, we visited every population of *H. fragilis* except Le Morne, which is inaccessible except by helicopter, and every population of *H. boryanus* s.l. In Réunion, where *H. boryanus* s.l. is more widespread and some populations are difficult to reach, we selectively targeted populations that represent both the breadth of the species' range across the island and the diverse environments it inhabits (Fig. 3). We visited 15 populations of the yellow morph of *H. boryanus* s.l., representing approximately half the sites where it is found. We visited eight populations of the red morph of *H. boryanus* s.l., representing approximately 75% of the sites where it is found. We also collected individuals only 1.25 km from the site where Thomas et al. (2016) reported their discovery of *H. fragilis*, as the original site was inaccessible in 2022 because of a land-

slide. Coordinates used in mapping (Fig. 3) were from our field collections in 2018 and 2022. Maps were produced in ArcGIS Pro 2.7 (Esri, 2020).

Morphometric analyses of *Hibiscus boryanus* s.l. and *H. fragilis*

To determine the proper application of the names *Hibiscus boryanus* and *H. fragilis*, we first conducted morphometric analyses of herbarium specimens to determine whether the type specimens grouped with one or more clusters of samples corresponding to existing species concepts in this group. Specimens of *H. genevei* and *H. liliiflorus* were not included, as these names are easily applied to species based on their type material and original species descriptions. Measurements were conducted on 72 specimens of *H. boryanus* s.l. and *H. fragilis* with complete flowers at anthesis. Of these, 68 were mounted herbarium specimens and four were unmounted collections from Réunion of the yellow morph of *H. boryanus* s.l. Following the taxonomy of Friedmann (1987), our 72 samples included the type specimens of both *H. boryanus* and *H. fragilis*, 13 yellow-morph *H. boryanus* s.l. from Réunion, 27 red-morph *H. boryanus* s.l. from Réunion, 10 magenta-morph *H. boryanus* s.l. from Mauritius, 19 *H. fragilis* from Mauritius, and one collection identified as *H. fragilis* from Réunion (*Thomas 358*, P [bc] P02290573).

Seven continuous quantitative floral characters were measured from mature parts of one flower on each specimen (Supplementary Fig. S1): (A) the length of the pedicel from the leaf axil to the base of the epicalyx; the length (B) and width (C) of the epicalyx lobes; (D) the length from the base of the calyx to the tip of the calyx lobes; (E) the length of the connate portion of the calyx from the base of the calyx to the sinus where the fused portion of the sepals separates; (F) the width of the sepals at the sinuses of the connate portion of the calyx; and (G) the length of the corolla from the base of the epicalyx to the farthest extent of the corolla. Because the type specimen of *Hibiscus boryanus* (G-DC [bc] G00218968) was missing a portion of the pedicel, only six characters could be used in multivariate analyses. All measurements were taken in millimeters to one tenth of a millimeter precision.

Morphometric analyses were performed in R (R Core Team, 2020). Univariate comparisons of morphological measurements between species were made with the package "FactoMineR" (Le et al., 2008), using a pairwise Wilcoxon rank sum test to test for significant differences between character distributions for each species. Multivariate analyses were performed using a model-based clustering approach with the function "Mclust" from the package "mclust" (Scrucca et al., 2016) implemented in "FactoMineR." Model-based clustering considers the data as coming from one or more Gaussian distributions, consistent with theoretical expectations for how continuous morphological traits should be distributed within populations of species assumed to have unimpeded gene flow (Zapata & Jiménez, 2012; Cadena et al., 2018). The "Mclust" function fits the data to models that vary in the shape, volume, and orientation of Gaussian distributions. Each model and number of clusters (k) is given a Bayesian information criterion (BIC) score, with the highest BIC score given to the model and value of k with the best fit to the data. The visualization of "Mclust" results are shown on a principal component analysis (PCA) of the data. We interpreted correspondence between species hypotheses and morphological clusters as a strong indicator that the morphological traits under consideration were useful in differentiating species. If a type specimen clustered with a group corresponding to a single proposed species, this indicated that the name given to the specimen should be applied to the corresponding species. If multiple species clustered together, we would infer that these species could not be differentiated based on the measured floral traits alone, and any type specimen placed in such a cluster could not be ascribed to a particular species with certainty.

Results

Morphometric analyses of *Hibiscus boryanus* s.l. and *H. fragilis*

Model-based clustering selected two clusters as optimal from the morphometric dataset, with the model VVE (ellipsoidal, equal orientation) as the best-fit model (BIC score: –923.12) (Supplementary Fig. S2A). Cluster 1 contained 52 samples and included the type specimen of *Hibiscus boryanus* and 50 samples currently treated as *H. boryanus* s.l. in both Mauritius and Réunion (Fig. 4A). Cluster 1 also included the collection that Thomas et al. (2016) reported as *H. fragilis* in Réunion (sample #63 in Supplementary Fig. S2B). Cluster 2 contained the type of *H. fragilis* and the 19 samples currently treated as *H. fragilis* in Mauritius (Fig. 4A).

Principal components 1 and 2 accounted for 75.1% of the variation in the morphometric dataset (PC1, 54.9%; PC2, 20.2%), with the two clusters identified by model-based clustering differentiated primarily on PC1 (Fig. 4A). Three morphological variables were highly correlated with PC1 (Supplementary Fig. S2C, D): calyx length (93.1% correlated), the length of the connate portion of the calyx (89.0%), and corolla length (88.7%). Univariate comparisons between the two groups showed that the *Hibiscus fragilis* group had significantly longer calyces (sepals) and corollas (pet-

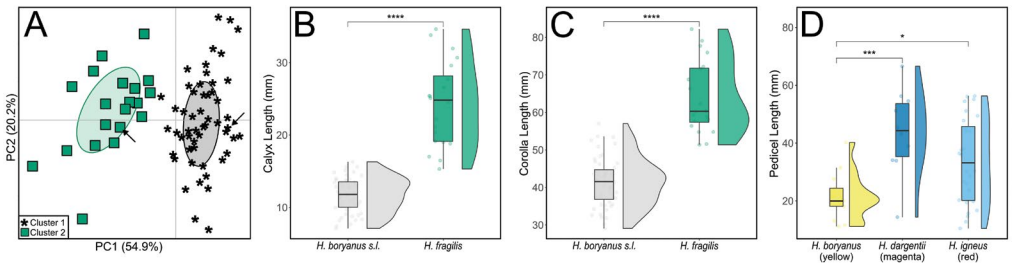

Figure 4. —A. Results of model-based clustering with 72 samples of *Hibiscus boryanus* DC. s.l. and *H. fragilis* DC. using six quantitative floral characters; cluster 1 corresponds to specimens ascribed to *H. boryanus* s.l., and cluster 2 corresponds to specimens ascribed to *H. fragilis*; arrows indicate the placement of types (*H. boryanus* in cluster 1 and *H. fragilis* in cluster 2). —B, C. Box and violin plots showing significant differences between *H. boryanus* s.l. and *H. fragilis* samples in calyx length (B) and corolla length (C), two floral characters that are highly correlated to PC1 and contribute to the differentiation between clusters in (A). —D. Box and violin plots of pedicel length between the three color morphs in *H. boryanus* s.l. (corresponding to the taxa we treat here as *H. boryanus*, *H. dargentii* Mashburn, sp. nov., and *H. igneus* Mashburn, sp. nov.), showing that *H. boryanus* s. str. has significantly shorter pedicels than both *H. dargentii* and *H. igneus*. Asterisks in B–D indicate significant differences between distribution medians using a pairwise Wilcoxon rank sum test; number of asterisks indicates level of statistical significance (one: $P \leq 0.05$; three: $P \leq 0.001$; four: $P \leq 0.0001$).

als) than the specimens corresponding to *H. boryanus* s.l. (Fig. 4B, C).

TAXONOMIC EVALUATION OF *HIBISCUS BORYANUS* S.L.

Model-based clustering did not identify unique clusters within *Hibiscus boryanus* s.l. when all 72 samples were included. When *H. fragilis* specimens were removed and clustering was performed only with samples of *H. boryanus* s.l., model-based clustering selected a single cluster as optimal (not shown), indicating that floral measurements alone did not distinguish the three color morphs of *H. boryanus* s.l. However, our review of herbarium specimens and field observations did identify multiple traits in addition to flower color that distinguished the three morphs of *H. boryanus* s.l., including distribution, ecology, leaf and floral morphology, and flower and fruit phenology.

Regarding distribution and ecology, our review of herbarium specimens and field observations confirmed Friedmann's (1987) observation that the magenta morph of *Hibiscus boryanus* s.l. was found only in Mauritius, whereas the yellow and red morphs were restricted to Réunion. In Mauritius, the magenta morph of *H. boryanus* s.l. occurred in transitional and wet forests near running water and in wet, boggy soils. In Réunion, though Friedmann (1987) observed that the yellow and red morphs were structured by elevation, we found both morphs from ca. 200 to 1200 m in elevation, although the yellow morph was found up to 1350 m. Instead, we observed that the yellow morph was found exclusively in wet forests, which occur primarily on the eastern (windward) side of the island and in wet calderas on the western side of the island, whereas the red morph was found only in seasonally dry forests, which are restricted to the western (leeward) side of the island.

Many morphological characters also distinguished the three color morphs of *Hibiscus boryanus* s.l. (Table 1). For example, we found that plants of the magenta morph were understory shrubs, reaching a maximum of 5 m in height, whereas individuals of the red and yellow morphs were often canopy trees that attained heights of 10 and 15 m, respectively. The shape of the heterophyllous juvenile leaves was also distinctive among the morphs, though imperfectly so: in brief, juvenile leaves were often simple in the red morph (though they could also be trilobed or 5-lobed), exclusively trilobed in the magenta morph, and initially trilobed but becoming 5-lobed in the yellow morph. Additional distinguishing characters primarily differentiated the yellow morph from the red and magenta morphs (Table 1), such as the presence of thickened, often succulent, glabrous epicalyx and calyx lobes (vs. foliaceous, sparsely or densely covered with stellate hairs), and fruits being green, hard-fleshy, indehiscent capsules (vs. brown, dry, dehiscent capsules). Unique flower and fruit phenological traits also distinguished the yellow morph, which rarely flowers in the dry season but produces a distinctive flush of flowers (and subsequently fruits) in the rainy season (vs. flowering and fruiting throughout the year in the other two morphs). Consequently, given the number of distinguishing environmental, morphological, and phenological traits discernible among the three *H. boryanus* s.l. color morphs, we concluded that each of the three morphs deserves recognition as a distinct species.

Table 1. Geographic, habitat, morphological, and phenological characters differentiating the six species of *Hibiscus* L. sect. *Lilibiscus* Hochr. in the Mascarene Archipelago.

	H. boryanus DC. (yellow *H. boryanus* s.l.)	*H. dargentii* Mashburn (magenta *H. boryanus* s.l.)	*H. fragilis* DC.	*H. genevei* Bojer	*H. igneus* Mashburn (red *H. boryanus* s.l.)	*H. liliiflorus* Cav.
Island of occurrence	Réunion	Mauritius	Mauritius	Mauritius	Réunion	Rodrigues
Habitat	wet forest, often along streambeds	rocky streambeds in transitional and wet forest	cliffs and rocky outcroppings on basaltic mountains	wet forest	semi-dry forests	forests on basaltic soils
Plant habit	canopy trees reaching 15 m	understory shrubs to trees reaching 5 m	sprawling shrubs reaching 1 m	understory shrubs to trees reaching 5 m	shrubs to canopy trees reaching 10 m	shrubs to canopy trees reaching 10 m
Juvenile leaf form	initially trilobed, lobes subulate to narrowly triangular, becoming 5-lobed with very irregular margins	trilobed, lobes subulate	simple, narrowly elliptic	trilobed or 5-lobed, lobes narrow and subulate	simple and narrowly elliptic, or trilobed (rarely 5-lobed) with narrow, subulate lobes	initially with a single lobe, quickly becoming trilobed with linear, subulate lobes
Mature leaf form	simple, elliptic to ovate	simple, elliptic to ovate	simple, elliptic to ovate	simple, elliptic to ovate	simple, narrowly elliptic	simple, obovate
Epicalyx and calyx form	epicalyx spreading or ascending; epicalyx and calyx somewhat thickened, often succulent, glabrous, the central ridge and connate portion of the sepal lobes often barely visible	epicalyx spreading or ascending; epicalyx and calyx foliaceous, sparsely covered with stellate hairs, the central ridge and connate portions of the sepal lobes often prominently raised	epicalyx spreading or ascending; epicalyx and calyx foliaceous, sparsely covered with stellate hairs, the central ridge and connate portions of the sepal lobes prominently raised	epicalyx spreading or ascending; epicalyx and calyx foliaceous, sparsely covered with stellate hairs, the central ridge and connate portions of the sepal lobes prominently raised	epicalyx spreading or ascending; epicalyx and calyx foliaceous, densely covered with rough, stellate hairs, the central ridge and connate portions of the sepal lobes not visibly raised	epicalyx lobes appressed to the calyx; epicalyx and calyx thickened, verrucose, densely covered with soft, stellate hairs forming a leathery texture, the central ridge and connate portions of the sepal lobes not visibly raised

Epicalyx lobe size	5 to 7(to 13) lobes, 5–17 × 1–2.5 mm, subulate, spreading or ascending	7 to 8 lobes, 8–10 × 1.5–2.5 mm, ensiform, spreading or ascending	6 to 9 lobes, 7–12 × 1.5–2 mm, ensiform, spreading or ascending	6 to 9 lobes, 8–12 × 0.5–1.5 mm, ensiform, spreading or ascending	5 to 8 lobes, 4–16 × 1.5–3 mm, ensiform, spreading or ascending	6 to 8 lobes, 2–8 × 1–2 mm, ensiform, appressed to the calyx
Calyx lobe (sepal) size	8–14 mm from base to apex, 4–10 mm wide, 6–10 mm from base to sinus of the connate portion	13–17 mm from base to apex, 6–7 mm wide, 9–10 mm from base to sinus of the connate portion	(15–)20–35 mm from base to apex, 6–7 mm wide, 15–17 mm from base to sinus of the connate portion	18–25 mm from base to apex, 5–8 mm wide, 11–12 mm from base to sinus of the connate portion	9–16 mm from base to apex, 5–6 mm wide, 6.5–10 mm from base to sinus of the connate portion	10–14 mm from base to apex, 6–8 mm wide, 9–12 mm from base to sinus of the connate portion
Corolla color	often pale yellow, rarely reddish orange, sometimes with distinct streaks of red	pink to magenta, sometimes fading with an orange tinge, the exterior sometimes pale pink with white streaks	entirely scarlet-red externally and internally, sometimes with pale red to white veins	pale pink with dark pink to purple-red internally at the center	red, the exterior tinged yellow basally and sometimes along the veins, the interior yellow at the center	orange, often tinged yellow basally
Petal size	30–45 × 9–14 mm	32–45 × 17–22 mm	50–82 × 14–25 mm	60–90 × 25–50 mm	33–50 × 12–21 mm	70–80 × 25–30 mm
Fruit type	indehiscent capsule with a green, hard, fleshy exterior, entire fruit falling from the plant	dry loculicidal capsule persistent on the plant while seeds are dispersed from the fruit	dry loculicidal capsule persistent on the plant while seeds are dispersed from the fruit	dry loculicidal capsule persistent on the plant while seeds are dispersed from the fruit	dry loculicidal capsule persistent on the plant while seeds are dispersed from the fruit	dry loculicidal capsule persistent on the plant while seeds are dispersed from the fruit
Phenology	flowers and fruits rarely in the dry season; a distinct flush of flowers during the rainy season (Dec.–Apr.), with fruits appearing soon after flowering	flowers and fruits regularly throughout the year	flowers and fruits regularly throughout the year	flowers and fruits regularly throughout the year	flowers and fruits throughout the year, slightly more profuse during the rainy season (Dec.–Apr.)	flowers and fruits regularly throughout the year

APPLICATION OF THE NAME *HIBISCUS BORYANUS*

Because model-based clustering was unable to differentiate the three proposed species in *Hibiscus boryanus* s.l. and therefore could not be used to place the type of *H. boryanus*, we returned to the protologue of *H. boryanus* (de Candolle, 1824) to determine whether other characters noted by de Candolle could be used. We identified three useful characters from de Candolle's (1824) brief species description of *H. boryanus*: 5-veined leaves ("Foliis [. . .] 5-nerviis"), short pedicels ("Flores [. . .] brevissimè pedicellati"), and whitish/pale flowers ("Flores albidi"). We found that all three of these characters were best applied to the yellow morph of *H. boryanus* s.l. For leaf venation, we found that 80.9% of yellow-morph *H. boryanus* s.l. specimens had leaves with five principal palmate veins, whereas only 43.8% and 27.8% of red- and magenta-morph specimens had 5-veined leaves, respectively. We also found that the yellow morph had significantly shorter pedicels than either the red morph ($P = 0.019$) or the magenta morph ($P = 0.00064$), whereas the pedicel lengths of the red and magenta morphs did not differ significantly (Fig. 4D). Finally, de Candolle's description of the flowers of *H. boryanus* as whitish/pale best fits the flowers of the yellow morph compared to the red and magenta morphs (Fig. 2; flowers of the yellow morph are sometimes paler yellow than those shown in E). It should be noted that de Candolle's (1824) observation of short pedicels in *H. boryanus* could result from the lack of an obvious pedicel on the type collection (Fig. 1A). Nevertheless, when taken in conjunction with the leaf venation and flower color observations, all three characters together indicate that the name *H. boryanus* should be applied to the yellow-flowered species in Réunion. As a result, we determined that both the red-flowered species in Réunion and the magenta-flowered species in Mauritius should be new species.

Discussion

Our taxonomic study of the Mascarene *Hibiscus* sect. *Lilibiscus* entailed thorough examinations of herbarium specimens and comprehensive collecting expeditions in 2018 and 2022. We now recognize six morphologically unique species occurring in the Mascarenes instead of the previously recognized four. The presence of six *Lilibiscus* species in the Mascarenes is also strongly supported by genetic data (Mashburn et al., 2025). However, the goals of the present study were to use a morphology-based approach to determine the proper application of the existing four names—*H. boryanus*, *H. fragilis*, *H. genevei*, and *H. liliiflorus*—which had been used in various and contradictory ways over the last 200 years, and to assess the morphological evidence for treating the three color morphs previously placed under *H. boryanus* s.l. as unique species.

Our revision of type specimens and species descriptions quickly revealed that the names *Hibiscus liliiflorus* and *H. genevei* were easy to apply to species because of distinctive morphological characters outlined in the species descriptions. *Hibiscus liliiflorus* is clearly the species occurring in Rodrigues and is distinguishable from the other Mascarene species based primarily on leaf shape, epicalyx and calyx morphology, and flower color and size (Table 1). *Hibiscus genevei* occurs in Mauritius and is distinguishable primarily based on flower color and size (Table 1). In contrast, the names *H. boryanus* and *H. fragilis* were more difficult to ascribe to species. Morphometric analyses of floral characters suggested the presence of two distinct morphological clusters corresponding to the species concepts of *H. boryanus* and *H. fragilis* proposed by Friedmann (1987). The type of *H. fragilis* was placed with the cluster of samples corresponding to the red-flowered species occurring in Mauritius (cluster 2 in Fig. 4A) and was differentiated from cluster 1 based on larger floral traits, including calyx length, the length of the fused portion of the calyx, and corolla length. No collections from Réunion were placed in this *H. fragilis* cluster, even though the type specimen of *H. fragilis*, collected by Bory without locality information, was annotated by de Candolle as coming from Réunion. Given the lack of collection information provided by Bory and the later date of specimen annotation by de Candolle, we conclude, along with Friedmann (1987), that de Candolle's annotation was an error, and that Bory collected the type of *H. fragilis* in Mauritius. Notably, the collection of *H. fragilis* in Réunion reported by Thomas et al. (2016) was placed in cluster 1 with other red- and yellow-morph *H. boryanus* s.l. specimens from Réunion. With this result, in conjunction with our placement of *H. fragilis* in Mauritius, we found no substantial evidence that *H. fragilis* has ever naturally occurred in Réunion.

Clustering analyses then grouped all collections associated with Friedmann's (1987) concept of *Hibiscus boryanus*, including the type collection of *H. boryanus*, into a single cluster (cluster 1 in Fig. 4A). Based on floral measurements alone, the three flower color morphs of *H. boryanus* s.l. did not differ significantly, which suggests the valid possibility of a unified concept of *H. boryanus* s.l. occurring in both Mauritius and Réunion. However, we identified many additional morphological characters that, together, indicated that each of the three flower color types is a unique species. Therefore, to properly apply the name *H. boryanus* to one of these three taxa, we returned to de Candolle's Latin diagnosis of the species (de Candolle, 1824) and identified three characters—leaf venation, pedicel length, and

flower color—that together link the name *H. boryanus* with the yellow morph occurring in humid forests in Réunion (*H. boryanus* s. str.). As a result, the red morph of *H. boryanus* s.l. from dry forests in Réunion and the magenta morph from humid forests in Mauritius remain hitherto undescribed.

Two exceptional characters displayed by *Hibiscus boryanus* s. str. are unique compared to other species in *Hibiscus* sect. *Lilibiscus* and are possibly unique in the genus as a whole. First, though *H. boryanus* is evergreen (not deciduous), individual plants often drop the majority of their leaves at the onset of the primary flush of flowers, especially those leaves at the apex of branches where flowers are borne. While many *Hibiscus* species occurring in seasonally dry habitats will lose leaves during the dry season, we are not aware of any other species that is evergreen throughout the year, only to drop leaves at the onset of flowering. In addition, unlike other Mascarene *Lilibiscus* species, which continue to flower throughout the year, *H. boryanus* rarely flowers outside of the rainy season in Réunion (typically December to April). A second unique character of *H. boryanus* is the presence of hard-fleshy fruits (Fig. 5J, K), which are produced throughout the rainy season and fall from the tree without dehiscing. To our knowledge, all other *Hibiscus* species produce dry dehiscent capsules, and fruits typically dehisce on the plant while seeds are dispersed from the persistent fruit. The hard-fleshy fruits of *H. boryanus* are possibly an adaptation to enhance seed dispersal by extinct terrestrial vertebrates (e.g., Réunion giant tortoises, *Cylindraspis indica*) in lowland humid forests on Réunion, where an estimated 80% of species are fleshy fruited (Albert et al., 2021).

Our findings result in a novel picture of *Hibiscus* sect. *Lilibiscus* in the Mascarenes, with six single-island endemic species. Rodrigues has only one species, *H. liliiflorus*. Mauritius harbors three endemic species, *H. fragilis*, *H. genevei*, and the magenta-flowered taxon previously treated under *H. boryanus*, described here as *H. dargentii*. Réunion is home to two endemic species, the yellow-flowered *H. boryanus* s. str. found in humid forests, and the red-flowered taxon previously treated under *H. boryanus* s.l. from dry forests, described here as *H. igneus*. Given these determinations, we provide a key to aid in the identification of the species of *Hibiscus* sect. *Lilibiscus* in the Mascarenes, as well as updated species descriptions for all six species.

Key to the Mascarene *Hibiscus* sect. *Lilibiscus*

1. Mature leaves obovate with a rounded or retuse apex, thickened and coriaceous; epicalyx lobes appressed to the calyx; calyx leathery, with a dense covering of soft, stellate hairs; corolla orange, fading to pale yellow basally (Rodrigues) . . . . . *Hibiscus liliiflorus* Cav.
1′. Mature leaves elliptic to ovate with an attenuate to acuminate apex, thin and membranous; epicalyx independent of the calyx, ascending or spreading; calyx foliaceous and sparsely to densely covered with typically rough, stellate hairs, or thickened, fleshy, and glabrous; corolla pale pink with a darker red-purple center, magenta, entirely red, red with a yellow center, entirely yellow, or pale orange with streaks of red. 2
2. Corolla pale pink with a darker red-purple center, opening broadly and spreading up to 165 mm in diameter (Mauritius) . . . . . *Hibiscus genevei* Bojer
2′. Corolla magenta, entirely red, red with a yellow center, entirely yellow, or pale orange with streaks of red, tubular basally and gradually widening distally to < 65 mm in diameter. 3
3. Sprawling woody shrubs reaching 1 m in height and spreading up to 1 m at maturity, the branches strongly ramified with short internodes; calyx (15–)20–35 mm from base to apex, 15–17 mm from base to sinus of the connate portion; corolla entirely red; petals 50–82 mm long (Mauritius) . . . . . *Hibiscus fragilis* DC.
3′. Upright shrubs to trees reaching 5–15 m in height, the internodes > 5 mm; calyx < 17 mm from base to apex, < 10 mm from base to sinus of the connate portion; corolla magenta, red with a yellow center, entirely yellow, or pale orange with streaks of red; petals < 50 mm long. 4
4. Understory trees reaching 5 m in height at maturity, with few branches; corolla magenta (dark pink); filaments white to pink with dark pink anthers; stigmas dark pink to reddish orange (Mauritius). . . . . *Hibiscus dargentii* Mashburn
4′. Typically canopy trees reaching 10–15 m in height at maturity, with many branches; corolla red with a yellow center, entirely yellow, or pale orange with streaks of red; filaments red, yellow, or orange; stigmas red orange to dark red. 5
5. Leaves partially deciduous during main flush of flowering, rarely flowering outside of the rainy season; corolla yellow to pale orange, rarely dark orange with a reddish hue and/or streaked with red; fruits hard-fleshy, green, falling from the plant while still green; seeds maturing inside the fruit (Réunion) . . . . . *Hibiscus boryanus* DC.
5′. Leaves persistent during flowering season, flowering throughout the year but slightly more profusely during the rainy season; corolla red with a yellow center; fruits dry dehiscent capsules, persistent; seeds maturing and dispersing from the fruit (Réunion) . . . . . *Hibiscus igneus* Mashburn

Taxonomic Treatment

1. Hibiscus boryanus DC., Prodr. 1: 446. 1824. TYPE: Réunion [France]. s. loc., s.d., *J.-B. Bory de Saint-Vincent s.n.* (holotype, G-DC [bc] G00218968!). Figure 5.

Trees reaching 15 m tall and 60 cm DBH. **Bark** striate, light gray to brown, often covered with mosses and

lichens; young stems green to gray-brown, lenticellate, glabrous to very sparsely covered with stiff, stellate hairs. **Leaves** alternate, stipules narrowly triangular, ca. 5 × 0.5 mm, caducous; petioles 8–75 mm, green, sometimes distally tinged maroon, sparsely covered with stiff, stellate hairs; lamina heterophyllous, with juvenile form present from ground level up to 1–2 m, transitional form in between, and mature form present above ca. 2 m; juvenile form initially trilobed with subulate to narrowly triangular lobes of variable size (central lobe reaching 130 × 4 mm, for example), often green suffused with maroon, hispid with simple hairs; transitional form often becoming 5-lobed and palmatifid to palmatisect, sometimes with irregular incised margins, central lobe up to 200 mm; adult form typically smaller than transitional form, 55–150 × (18–)30–90 mm, elliptic to ovate, green, base obtuse to rounded, apex acute to attenuate, glabrous to very sparsely pubescent with stiff, stellate hairs, margin basally entire, repand to serrate toward apex, palmately veined with 5 main veins sometimes tinged red to maroon below. **Flowers** solitary in upper leaf axils, leaves often deciduous during main flush of flowering; pedicels spreading to ascending, 8–55 mm, articulated 4–20 mm from apex, glabrous; epicalyx with 5 to 7(to 13) spreading or ascending, irregular lobes, individual lobes 5–17 × 1–2.5 mm, subulate to narrowly triangular, semi-erect, somewhat thickened, green, glabrous; calyx cupuliform, green, with 5 thickened, ± succulent, connate sepals, central ridge and connate portion of sepal lobes often barely visible, sepal lobes 8–14 mm from base to apex, 4–10 mm wide, 6–10 mm from base to sinus of connate portion, glabrous; corolla often pale yellow, rarely reddish orange, sometimes with distinct streaks of red, estivation contorted, opening to 30–60 mm in diam., petals 30–45 × 9–14 mm, asymmetrically obovate, margins repand, apex rounded; staminal column 26–41 mm, yellow to pale orange, ending in 5 triangular lobes sometimes tinged red; stamens many, appearing at ca. 1/2 the length of the staminal column and clustered at distal end, filaments 1.5–2.5 mm, yellow to reddish orange, anthers yellow to red, pollen yellow; styles 5, forming a tube emerging from the staminal column, straight or slightly curving upward, branching 3–4.5 mm, spreading and becoming umbelliform, yellow to pale orange; stigmas globose to oblate, ca. 2 mm in diam., orange-red. **Fruits** 5-carpellate, 14–28 × 13–20 mm, obovoid, size depending on number of fertilized ovules, hard-fleshy, green, indehiscent, falling from plant at articulation of pedicel while still green; seeds ca. 3.5 × 3 mm, ovoid, maturing dark brown inside fruit, covered with short, tan-colored, stellate hairs.

Phenology. *Hibiscus boryanus* plants produce a distinct flush of flowers and fruits during the rainy season (December–April), though flowers and fruits can occasionally be found throughout the year.

Distribution and habitat. *Hibiscus boryanus* is endemic to the island of Réunion, where it occurs in low- to high-elevation wet forests in the eastern (windward) and central mountainous sections of the island, as well as in wet calderas to the west (Fig. 3). The presence of extant populations at low elevations (ca. 200 m), particularly in the forests to the northeast and southeast of the active volcano Piton de la Fournaise on the eastern edge of the island, indicates that *H. boryanus* was probably once common in the low-elevation tropical humid forests that have almost entirely disappeared because of deforestation (Strasberg et al., 2005). Presently, individuals are found in mid- to high-elevation wet forests up to 1350 m, primarily in the eastern and central parts of the island, as well as in pockets of wet forest on the western side, such as Sans-Souci and Les Makes. Plants occur as canopy trees in good-quality remnant forests throughout the range of the species, where the lower bole can attain up to 60 cm in diameter. However, in degraded areas, plants reach smaller sizes (ca. 10–20 cm DBH and up to 8 m in height) and are often found along streambeds and riverbanks.

Conservation assessment. Approximately 70% of native vegetation in Réunion has been lost since human colonization began in the late 17th century; the vast majority of this occurred before the 20th century (Strasberg et al., 2005). In particular, 87% of lowland tropical forests, the primary habitat of *Hibiscus boryanus*, were lost by the year 1800. Increased awareness of conservation threats in Réunion in recent decades has resulted in programs targeted at reducing deforestation and the impact of invasive species; however, the remaining native vegetation is still at risk from threats such as fires and alien species invasions (Baret et al., 2013). Natural regeneration of *H. boryanus* is evident throughout its native habitat but is limited because of predation of fruits and seeds by invasive alien rats (J.-M. Tamon, pers. comm.). Seedlings are found primarily in the vicinity of mature individuals, indicating low seed dispersal, likely a result of lost interactions with extinct dispersers that are not compensated by introduced species (Heinen et al., 2023). The extent of occurrence (EOO) of *H. boryanus* is estimated to be ca. 1300 km^2, with an area of occupancy (AOO) of ca. 300 km^2, both of which would indicate an assessment as Endangered. However, more than 10 locations are known, and though we do not infer a significant continuing decline of habitat by deforestation, habitat degradation continues through the impacts of invasive species and past extinctions (Albert et al., 2020, 2021). Therefore, we suggest an assessment of *H. boryanus* as

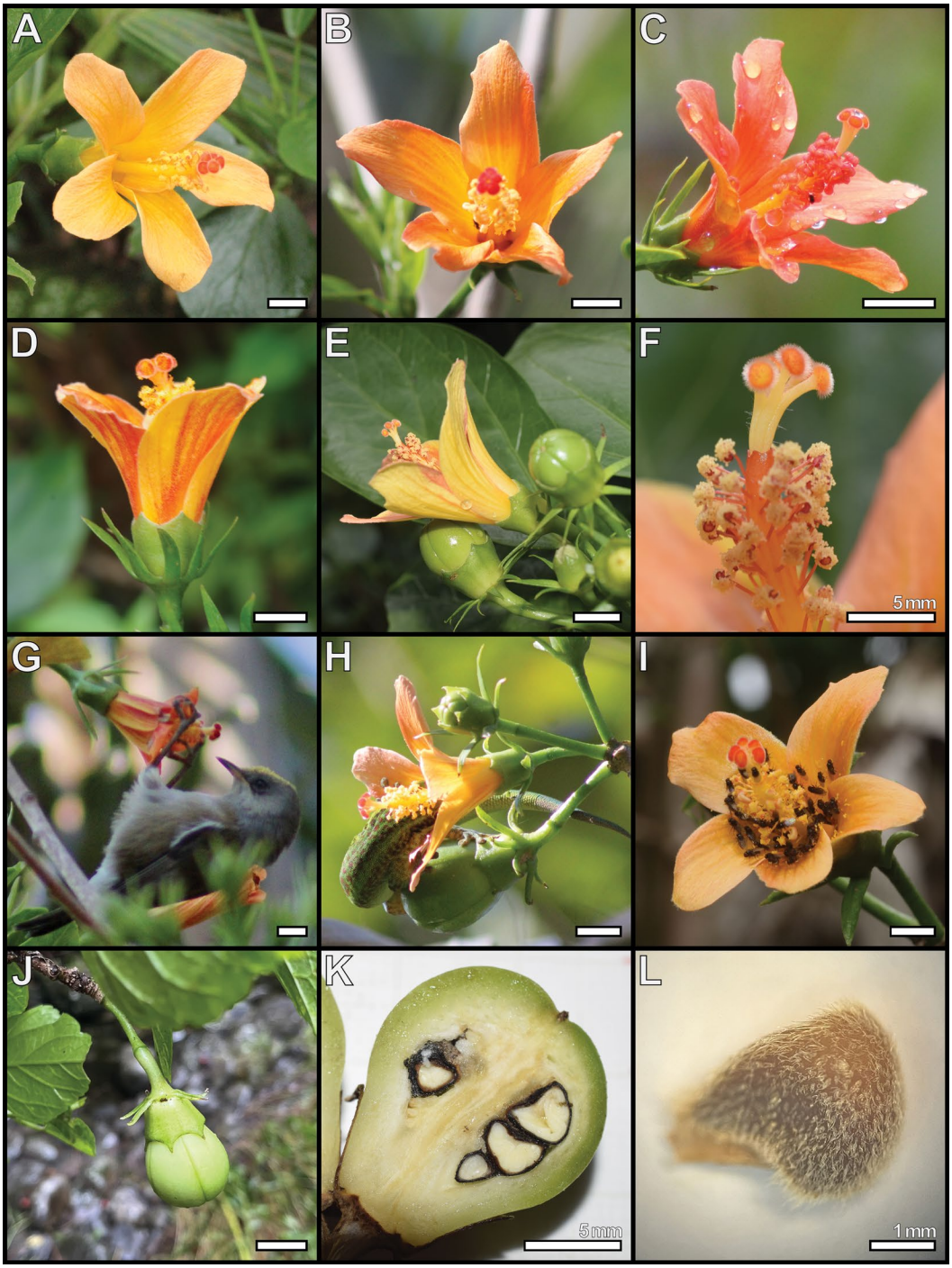

Figure 5. Flowers of *Hibiscus boryanus* DC. typically have entirely yellow corollas (A). Less often, the corollas may be orange-yellow (B), orange (C), or streaked with yellow and orange (D, E), especially on the exterior of the corolla. The staminal column and stigmas are light to dark orange (F). Flowers are visited by white-eyes (*Zosterops borbonicus* and *Z. olivaceus*) (G), the Réunion day gecko (*Phelsuma borbonica*) (H), gnats (I), and occasionally bees and wasps. Fruits of *H. boryanus* are unique in the genus, maturing green on the tree (J), then falling to the ground; seeds mature inside the fruit (K) and are less densely covered with hairs compared to those of other Mascarene species (L). Scale bars indicate 10 mm, except where noted. Photo credits: A–I, Jean-Maurice Tamon; J, L, Brock Mashburn; K, Alexis Gorissen.

Near Threatened (NT), with the real possibility of increased habitat loss through degradation by invasive species in the coming decades.

Notes. De Candolle's (1824) diagnosis of *Hibiscus boryanus* provided only a brief description and mentioned that it was collected by Bory in Réunion. It was described as having 5-nerved, ovate, undivided leaves with subdentate margins, an epicalyx with five to seven lobes, a calyx with five sepals a little longer than the epicalyx, and whitish/pale flowers on very short pedicels. Neither Bojer (1837) nor Baker (1877) mentioned the species in their treatments of Mauritius. De Cordemoy (1895) described *H. boryanus* as a tree with oval leaves, the margins deeply toothed, with medium-sized yellow flowers. He understood the species as somewhat rare, occurring in the forests of Grand-Tampon, Grand-Fond, and Saint-Benoît, on both the east and west sides of Réunion. De Cordemoy also noted that the wood was used to make boards for construction and indicated that the trees were likely tall and straight, with trunks of significant size. Hochreutiner (1900) recognized the species as occurring in Réunion but provided no description.

The *Flore des Mascareignes* (Friedmann, 1987) described *Hibiscus boryanus* as a species found in both Réunion and Mauritius, exhibiting young leaves with three to five lobes and an irregular shape (e.g., Fig. 6A), reaching 19 cm; elliptic to oval mature leaves with margins entire to slightly crenulate near the apex; an epicalyx with eight linear lobes, generally as long as or longer than the calyx; and a corolla of variable color (yellow, red-orange, vermilion-red, carmine-red, red with yellow-orange striations, or pink with a carmine-red or purple center). Friedmann (1987) recognized three main floral color morphs, each corresponding to a unique geographic range and habitat, but did not differentiate the three morphs as unique taxa. We recognize the same three flower color morphs as distinct species: yellow-orange = *H. boryanus*, red with yellow center = *H. igneus*, sp. nov., and pink/magenta = *H. dargentii*, sp. nov.

Some populations of *Hibiscus boryanus*, particularly those close to the dry forests where the red-flowered *H. igneus* occurs, exhibit flowers that are dark orange and/or streaked with red, possibly from limited introgression with *H. igneus* (Mashburn et al., 2025). These individuals of *H. boryanus* can be differentiated from *H. igneus* by a highly variable juvenile leaf form with five lobes (vs. typically narrow, simple or trilobed juvenile leaves in *H. igneus*) (Fig. 6); mature leaves with five main palmate veins (vs. typically three main veins); thickened and fleshy, succulent, glabrous epicalyx and calyx lobes (vs. foliar thickness, densely covered with stellate hairs); typically yellow corolla, but when red-dish orange the color encompassing the entire corolla interior and exterior, or occurring in streaks (vs. a red corolla with a distinct yellow center on the inside); and hard-fleshy fruits (vs. dry dehiscent capsules).

Hibiscus liliiflorus is the only other Mascarene *Lilibiscus* species to produce orange flowers similar to those of *H. boryanus*. *Hibiscus boryanus* is differentiated from *H. liliiflorus* by having elliptic to ovate adult leaves with repand or serrate margins in the distal half of the lamina (vs. obovate adult leaves with an entire margin); spreading or ascending epicalyx lobes (vs. appressed to the calyx); thickened, fleshy, succulent, glabrous sepals (vs. leathery, with a dense covering of stellate hairs); petals 30–45 mm (vs. 70–80 mm); and hard-fleshy, indehiscent fruits (vs. dry dehiscent capsules).

Additional specimens examined. RÉUNION [FRANCE]. **Saint-Benoît:** Commune Bras-Panon, Forêt Eden-Libéria, 793 m, –21.035°, 55.604°, 12 Apr. 2022, *Mashburn 253* (MO, P); ibid., 618 m, –21.031°, 55.628°, 12 Apr. 2022, *Mashburn 254* (MO, P); ibid., 656 m, –21.025°, 55.627°, 12 Apr. 2022, *Mashburn 255* (MO, P); Commune La Plaine-des-Palmistes, La Tanguière, 750 m, 26 May 2004, *Grondin 1251* (CBNM); Commune La Plaine-des-Palmistes, Petite Plaine, 1243 m, –21.143°, 55.586°, 7 Apr. 2023, *Mashburn 238* (MO, P); Commune Saint-André, Site du Diorée, 740 m, –20.990°, 55.592°, 5 Apr. 2022, *Mashburn 231* (MO, P); ibid., 754 m, –20.992°, 55.592°, 5 Apr. 2022, *Mashburn 232* (MO, P); ibid., 809 m, –20.993°, 55.589°, 5 Apr. 2022, *Mashburn 233* (MO, P); Commune Saint-Benoît, La Plaine des Palmistes, Ravine Biberon, 920 m, –21.120°, 55.638°, 7 Apr. 2023, *Mashburn 237* (MO, P); Commune Saint-Benoît, rive gauche du Grand Bras, 359 m, 14 Apr. 2016, *Ferard 4437*, *4438*, *4439* (CBNM); Commune Sainte-Rose, Chemin Touzet, 453 m, –21.180°, 55.806°, 13 Apr. 2022, *Mashburn 256* (MO, P); ibid., 463 m, –21.172°, 55.802°, 13 Apr. 2022, *Mashburn 257* (MO, P); ibid., 505 m, –21.141°, 55.756°, 13 Apr. 2022, *Mashburn 258* (MO, P); Forêt de Grand Fond, Oct. 1866, *de Cordemoy s.n.* (MARS); Plaine des Palmistes, s.d., *de Cordemoy s.n.* (MARS [3 sheets]). **Saint-Denis:** Commune Saint-Denis, Cascade du Chaudron, 1200 m, 9 Aug. 2007, *Ferard 2355*, *2869* (CBNM); Commune Sainte-Marie, public park below Forêt de Fougéres, 1141 m, –20.972°, 55.524°, 6 Apr. 2022, *Mashburn 236* (MO, P); Commune Sainte-Suzanne, Ravine Bras Laurent, 779 m, –20.980°, 55.564°, 6 Apr. 2022, *Mashburn 234* (MO, P); ibid., 776 m, –20.981°, 55.562°, 6 Apr. 2022, *Mashburn 235* (MO, P); La Montagne, crête dominant la Rivière Saint-Denis, 800 m, 20 July 1972, *Cadet 3667* (P). **Saint-Paul:** Commune Saint-Paul, Forêt Sans Soucis, 1350 m, –21.020°, 55.365°, 11 Apr. 2022, *Mashburn 250* (MO, P). **Saint-Pierre:** Brûlé de Baril, 300 m, 13 July 1979, *Lorence 2730* (K, MAU, MO, P); Commune Saint-Joseph, Plaine des Grègues, 1152 m, –21.308°, 55.601°, 14 Apr. 2022, *Mashburn 265* (MO, P); ibid., 1087 m, –21.309°, 55.597°, 14 Apr. 2022, *Mashburn 266* (MO, P); ibid., 670 m, –21.331°, 55.615°, 14 Apr. 2022, *Mashburn 267* (MO, P); Commune Saint-Joseph, Rivière des Remparts, 855 m, 1 Oct. 2014, *Ferard 4144*, *4214* (CBNM); Commune Saint-Louis, Forêt Les Makes, 959 m, –21.200°, 55.402°, 11 Apr. 2022, *Mashburn 252* (MO); Commune Saint-Philippe, Chemin de Takamaka, –21.304°, 55.792°, 15 Apr. 2022, *Mashburn 270* (MO, P); Commune Saint-Philippe, Forêt de Basse Vallée, 335 m, –21.356°, 55.703°, 14 Apr. 2022, *Mashburn 268*

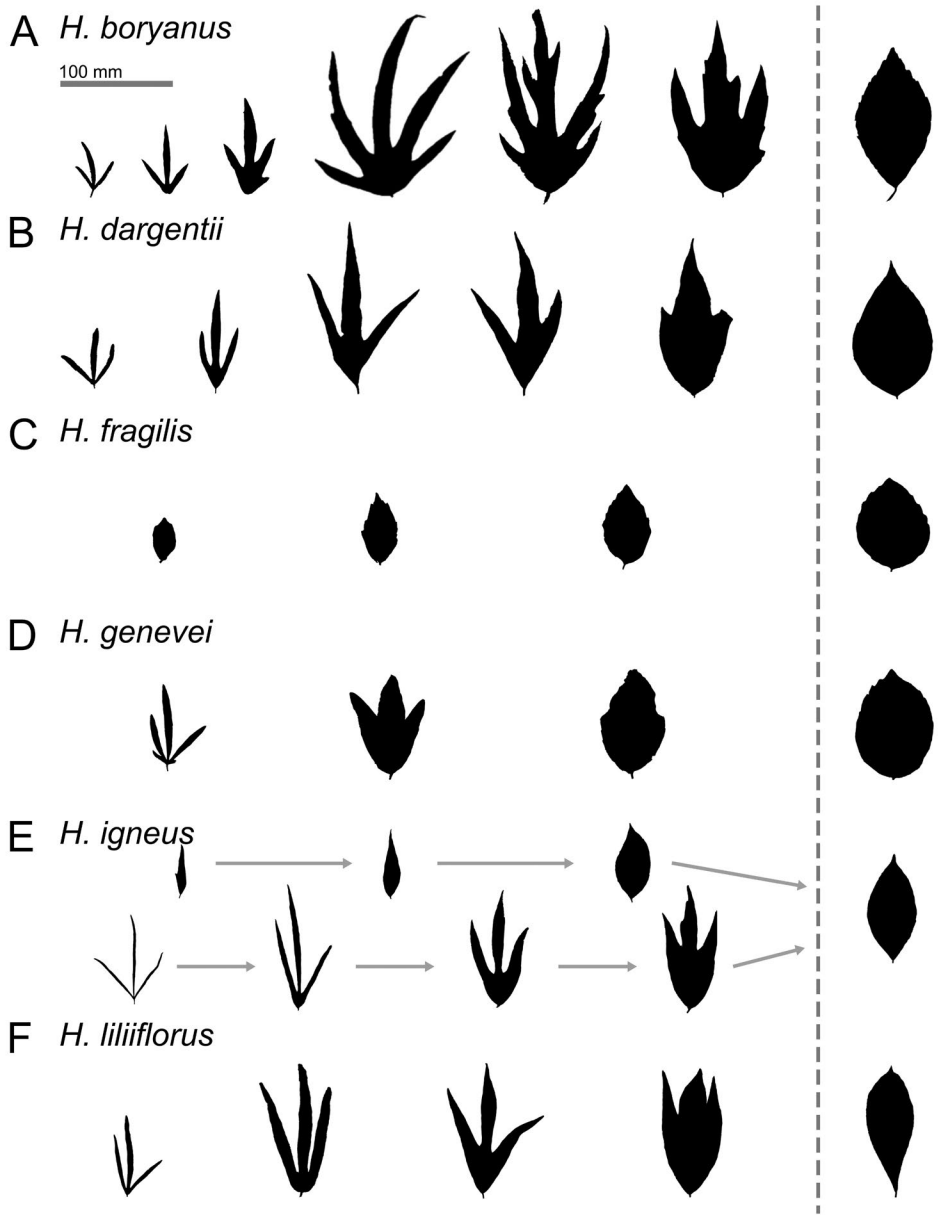

Figure 6. Variation in leaf forms across the six Mascarene *Lilibiscus* Hochr. species from the seedling through juvenile stages (left of the dashed line) to maturity (right of the dashed line). The scale bar at the top left applies to all images. *Hibiscus boryanus* DC. (A) shows the greatest variation in leaf form across developmental stages. *Hibiscus fragilis* DC. (C) is the only species not to exhibit pronounced heterophylly. Seedlings of *H. igneus* Mashburn (E) may or may not exhibit pronounced heterophylly; both forms can be found in the same population and even in seedlings of the same self-pollinated parent.

(MO, P); Commune Saint-Philippe, Forêt de Mare Longue, 126 m, –21.358°, 55.742°, 15 Apr. 2022, *Mashburn 271* (MO, P); Commune Saint-Philippe, Forêt de Mare-Longue, 201 m, 6 Nov. 2019, *Ferard 5350* (CBNM); Commune Saint-Philippe, Sentier du Tremblet, 273 m, –21.295°, 55.792°, 15 Apr. 2022, *Mashburn 269* (MO, P); Forêt de Mare Longue, 2 Feb. 1968, *Capuron 28189-SF* (K, P [3 sheets]); Forêt de Mare Longue, Oct. 1985, *Figier s.n.* (REU); Mare Longue, [305 m], 19 Nov. 1967, *Barclay 635* (K [2 sheets], MAU [4 sheets]); Mare Longue, 19 Oct. 1972, *Bosser 21275* (K); Mare Longue, 23 Nov. 1973, *Coode 4178* (K [2 sheets]); Mare Longue, 300 m, Nov. 1972, *Friedmann 1991* (K, MAU, P, REU); Mare Longue, Dec. 1971, *Bosser 20807* (G, MAU); Mare Longue, 10 Dec. 1977, *Friedmann 3069* (K, P [2 sheets],

REU); Plaine d'Affouches, s.d., *Friedmann 936* (K); Takamaka, 700 m, 25 Oct. 1970, *Cadet 2832* (P).

2. Hibiscus dargentii Mashburn, sp. nov. TYPE: Mauritius. Gaulettes Serrées, S of Nouvelle Découverte, 15 Jan. 1976, *D. Lorence 1595* (holotype, MAU [bc] MAU0016119!; isotype, K!). Figures 7, 8.

Diagnosis. *Hibiscus dargentii* Mashburn is distinguished from other Mascarene *Hibiscus* L. sect. *Lilibiscus* Hochr. species by being small trees (reaching 5 m) and having an entirely pink to magenta corolla opening to 48–62 mm in diameter, with 32–45 mm petals and reddish-orange stigma lobes.

Understory trees reaching 5 m tall and 15 cm DBH. **Bark** light gray to brown, often covered with mosses and lichens; young stems green to gray-brown, glabrous to very sparsely covered with clear stellate hairs. **Leaves** alternate, stipules narrowly triangular, ca. 3.5 × 0.5 mm, caducous; petioles 10–30 mm, green, sometimes tinged maroon at apex, sparsely covered with stellate hairs; lamina heterophyllous, with juvenile and transitional form present from ground level up to ca. 1.5 m, mature form present higher; juvenile form initially trilobed with narrow, subulate lobes, transitional form filling in and becoming 3-lobed palmatipartite, central lobe up to 140 × 12 mm, often green suffused with maroon, hispid with simple hairs; adult form 50–120 × 30–65 mm, elliptic to ovate, green, base obtuse to rounded, apex acute to attenuate, glabrous to sparsely pubescent with stiff, stellate hairs, margin basally entire, repand to shallowly serrate toward apex, palmately veined, typically with 3 main veins. **Flowers** solitary in upper leaf axils; pedicels spreading to ascending, 55–65 mm, articulated 10–15 mm from apex, sparsely covered with stellate hairs; epicalyx with 7 to 8 spreading or ascending lobes, individual lobes 8–10 × 1.5–2.5 mm, ensiform, green, sparsely covered with stellate hairs; calyx cupuliform, green, with 5 foliaceous, connate sepals, central ridge and connate portion of sepal lobes often prominently raised, sepal lobes 13–17 mm from base to apex, 6–7 mm wide, 9–10 mm from base to sinus of connate portion, sparsely covered with stellate hairs; corolla pink to magenta, sometimes fading with an orange tinge in low light, veins somewhat lighter in color, exterior sometimes pale pink with white streaks, estivation contorted, opening to 48–62 mm in diam., petals 32–45 × 17–22 mm, asymmetrically obovate, margins repand, apex rounded; staminal column 38–40 mm, white to pink, ending in 5 triangular lobes tinged pink; stamens many, appearing at ca. 1/2 the length of staminal column and clustered at distal end, filaments 1.5–2.5 mm, white to pink, anthers dark pink, pollen yellow; styles 5, forming tube emerging from staminal column, branching 3–4.5 mm, spreading like flattened umbel, white; stigmas globose to oblate, ca. 2 mm in diam., reddish orange with white simple hairs. **Fruits** 5-carpellate, 18–22 × 13–16 mm, obovoid, maturing to dry loculicidal capsule persistent on plant while seeds are dispersed from fruit, exterior brown, covered with small, tan, stellate hairs, interior tan, glabrous; seeds ca. 3.5 × 3 mm, ovoid, dark brown, thickly covered with long, soft, light tan, stellate hairs.

Phenology. *Hibiscus dargentii* plants produce flowers and fruits regularly throughout the year.

Distribution and habitat. *Hibiscus dargentii* is endemic to Mauritius and known from only two extant wild populations, one in remnant forests near the Tamarind [Tamarin] Falls Reservoir (north of Black River Gorges National Park), and the second in a private reserve known as Gaulettes Serrées (north-central plateau) (Fig. 3). These populations are in transitional and wet forests, respectively, particularly in streambeds and adjacent to running water. The existence of two disjunct populations suggests that *H. dargentii* may have once occupied mid-elevation transitional and wet forests across the central plateau of Mauritius, where most of the natural vegetation has disappeared (Vaughan & Wiehe, 1937). Indeed, Bojer's (1837) *H. "liliflorus"* is possibly *H. dargentii*, which he mentioned was growing in many different mountains across the island. Thus, the existence of extant *H. dargentii* populations near water might simply reflect a restriction of the species' range by competition with invasive species, which may be less competitive in very wet conditions. For example, the Mauritian endemic shrub *Chassalia capitata* DC. (Rubiaceae) reached a density of 240 plants per 0.1 ha in 1939 at Macchabée (Vaughan & Wiehe, 1941), but surveys in 1986 found no individuals at the same site (Strahm, 1993).

Conservation status. Extant populations of *Hibiscus dargentii* occur on privately owned land. The Tamarind Falls population consists today of a single wild individual and planted propagated individuals; the planted individuals are thought to be clones of three wild individuals that once occurred at the site but died within the last 20 years. In recent decades, almost no natural regeneration has been noted at the Tamarind Falls population (one sapling was located near the Tamarind Falls population in 2006 by C. B. and F. B. V. Florens). The Gaulettes Serrées population consisted of 37 plants in 2012 (K. Pynee, unpubl. data), with a mix of adult plants (N = 15, 41%), juvenile plants (N = 4, 11%), and seedlings (N = 18, 49%). At both sites, small-scale deforestation and invasive species are the main threats. For example, forest was cut near the Tamarind Falls population for the construction of a cable

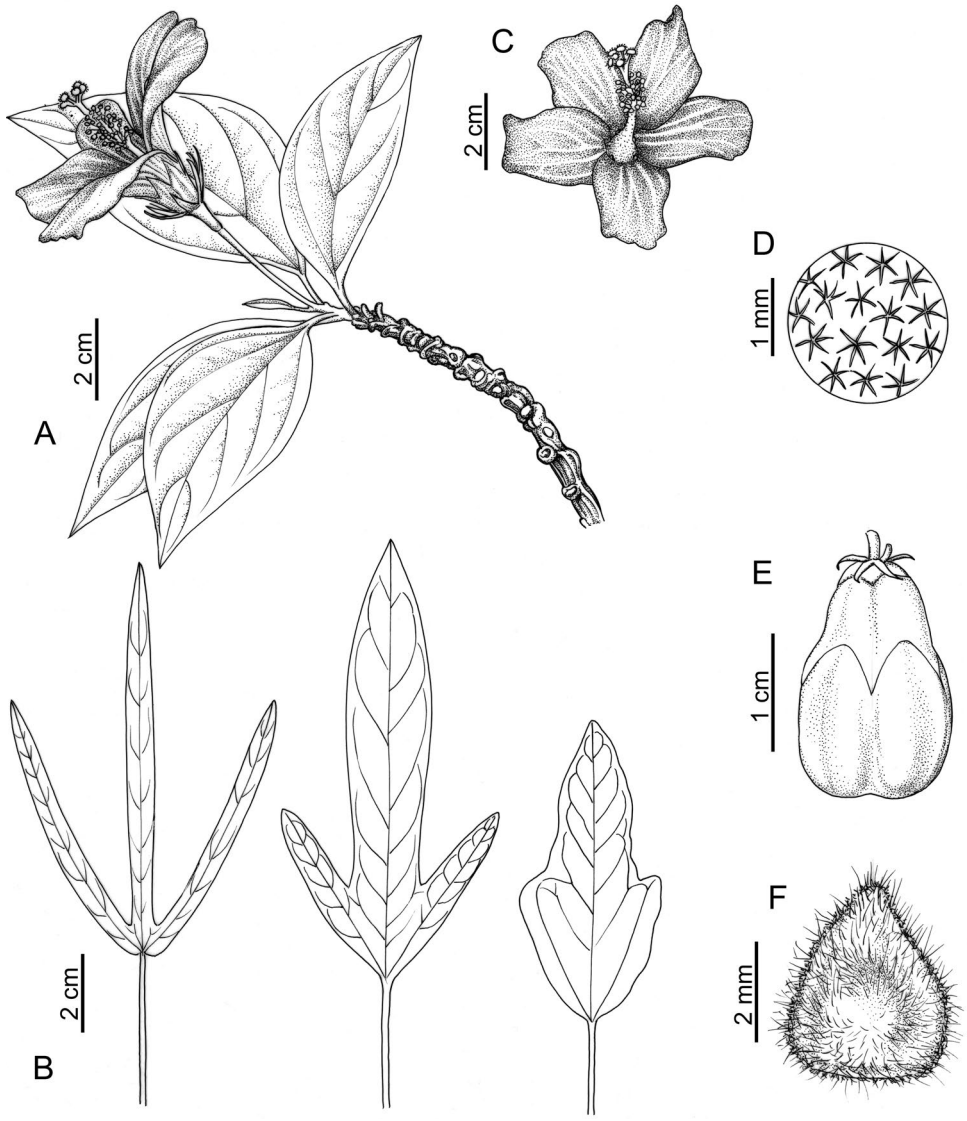

Figure 7. Illustration of *Hibiscus dargentii* Mashburn. —A. Flowering branch. —B. Shapes of juvenile leaf forms. —C. Frontal view of a flower. —D. Stellate hairs on leaves and flowers. —E. Fruit before dehiscence. —F. Seed. Illustration by Barbara Alongi.

car as a local tourism project. At the Gaulettes Serrées population, alien invasive animals (Java deer [*Rusa timorensis*], wild boar [*Sus scrofa*], long-tailed macaques [*Macaca fascicularis*], and rats [*Rattus rattus* and *R. norvegicus*]) prey upon leaves, flowers, and fruits and prevent regeneration by overturning soil or predating on seedlings. Strawberry guava (*Psidium cattleyanum* Sabine) is the main alien plant species at both sites and can attain high densities (up to 80% of all stems > 1.3 m tall) even in the best-preserved Mauritian forests (Florens et al., 2016). More than 50 clones from the Tamarind Falls population have been planted in at least three different localities by governmental and nongovernmental agencies (J. C. S., K. P., V. T., pers. comm.). As only two small populations are known, the EOO for *H. dargentii* is less than 2.5 km^2 and the AOO is 4 km^2. Therefore, because of the declines in the number of mature individuals in the last 20 years, severely fragmented populations, a population size estimate of fewer than 30 individuals, and an inferred

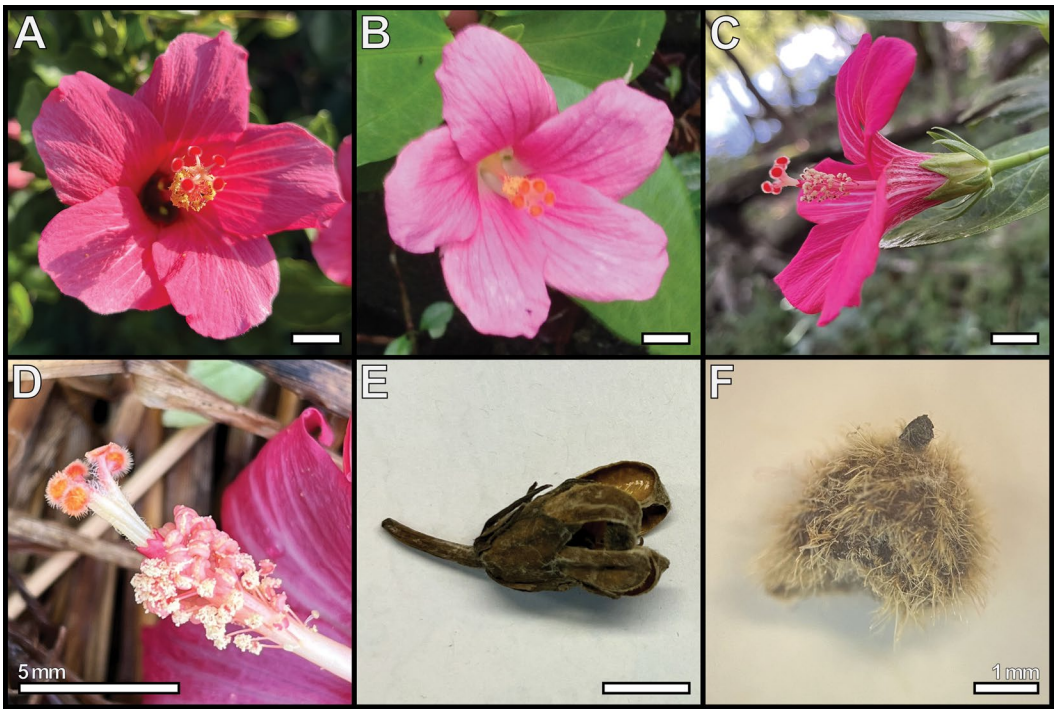

Figure 8. Photos of *Hibiscus dargentii* Mashburn. —A, B. Frontal view of flowers showing dark pink/magenta and pink corolla coloration. —C. Side view of a flower showing white streaks on the exterior of the corolla. —D. Anthers and stigmas. —E. A mature dehisced fruit. —F. Seed. Scale bars indicate 10 mm, except where noted. All images by Brock Mashburn.

continued decline because of invasive species and low natural regeneration, we recommend a conservation assessment for *H. dargentii* of Critically Endangered (CR A2ac, B1+2ab[ii]c[iv], D).

Etymology. *Hibiscus dargentii* is named in honor of Gabriel D'Argent (1924–2019), who devoted his life to the plants and forests of Mauritius. D'Argent joined the Mauritius Forestry Service in 1941 at the age of 17. He spent his career working with the native plants of the island and made an impact on many generations of both Mauritian and international scientists. D'Argent retired from the Forestry Service in 1984 at the age of 60 and then joined the Mauritian Wildlife Foundation. For the next 34 years, he was primarily involved in the restoration of the Mondrain Reserve, the site where, in 1968, the Mauritian botanist Joseph Guého, along with Luigi Bernardi, relocated *H. genevei*. D'Argent's dedication to protecting and propagating *H. genevei* was integral in preventing its extinction, and we hope to honor his work by naming this new endemic Mauritian *Hibiscus* species for him. Gabriel D'Argent retired from his second career at the Mauritian Wildlife Foundation in 2018 at the age of 94 and passed away in January 2019.

Notes. *Hibiscus dargentii* is described from material formerly treated as *H. boryanus*. The species grows as an understory treelet in remnant forests of Mauritius, although individuals planted in open areas become small, multibranched trees and produce copious flowers throughout the year. Flowers are unscented but produce abundant nectar that attracts honeybees and beetles, though often gnats and alien ants are the main nectar feeders. Given the amount of nectar and the bright corolla color, the flowers were probably visited by one or more species of native nectarivorous birds or reptiles; we are not aware of any observations of extant bird or reptile species pollinating *H. dargentii* flowers, leading us to hypothesize that the original pollinating species are now extinct. *Hibiscus dargentii* plants are self-fertile and produce fruits throughout the year (B. M., pers. obs.), though cross-pollination could increase seed production as seen in other endemic species (Bissessur et al., 2019).

The flowers of *Hibiscus dargentii* are comparable in size to those of the Réunion endemics *H. boryanus* and *H. igneus*, sp. nov. *Hibiscus dargentii* is distinguished from these species by its habit (small branching trees reaching 5 m vs. canopy trees reaching 15 m in *H. boryanus* and 10 m in *H. igneus*) and flower color, with its

dark pink to magenta corolla and reddish-orange stigma lobes (vs. yellow to reddish-orange corolla and yellow to orange stigma lobes in *H. boryanus*, and red corolla with a yellow center and red stigma lobes in *H. igneus*). The pink-magenta color of *H. dargentii*'s corolla is much darker than the flowers of *H. genevei* (also endemic to Mauritius), which are light pink with a dark pink center; in addition, the flowers of *H. dargentii* are 35%–50% smaller than those of *H. genevei* (opening to 62 mm in diam., petals 32–45 mm, vs. opening to 165 mm in diam., petals 70–90 mm in *H. genevei*). In cultivation, *H. dargentii* and *H. fragilis* can be crossed, but wild individuals are distinguished by the dark pink–magenta corollas of *H. dargentii* (vs. scarlet-red in *H. fragilis*), and smaller sepals 13–17 mm (vs. [15–]20–35 mm), and the two species do not naturally co-occur (Fig. 3).

Paratypes. MAURITIUS. **Moka:** Gaulettes Serrées, 27 Mar. 1978, *Bosser 22423* (P); Gaulettes Serrées, 400–450 m, 19 May 1979, *Lorence 2640* (K, MO); Gaulettes Serrées, 11 June 1997, *Page s.n.* (MAU); Gaulettes Serrées, 350 m, –20.204°, 57.637°, 16 Mar. 2018, *Mashburn 81*, *82*, *83* (MAU, MO). **Plaines Wilhems:** just S of Tamarin Reservoir on banks of Rivière des Aigrettes, 30 Nov. 1968, *Barclay 1379* (K [2 sheets], MAU); on left bank of Tamarind River above dam diverting water to Tamarind Falls reservoir, 21 Dec. 1968, *Wiehe s.n.* (MAU [2 duplicates]); Tamarin Falls, 5 Apr. 1972, *Edgerley s.n.* (MAU); Tamarind Falls, [–20.363°, 57.466°], 523 m, 12 May 2011, *Pynee s.n.* (MAU); Tamarind Falls, [–20.360°, 57.468°], 511 m, 12 May 2011, *Pynee s.n.* (MAU); Tamarind Falls, 27 Mar. 1978, *Bosser 22422* (G, P); Tamarind Falls Reservoir, 514 m, –20.360°, 57.468°, 14 Mar. 2018, *Mashburn 78, 79* (MAU, MO).

3. Hibiscus fragilis DC., Prodr. 1: 446. 1824. TYPE: Mauritius. s. loc., s.d., *J.-B. Bory de Saint-Vincent s.n.* (holotype, G-DC [bc] G00218958!). Figure 9A–D.

Sprawling woody shrubs, reaching 0.5–1 m tall and 0.5–1 m wide, strongly ramified with short, horizontal or pendent branches. **Bark** fissured, mottled light gray, often covered with mosses and lichens; stems often with very short internodes, gray-brown, lenticellate, glabrous to very sparsely covered with stiff, simple or stellate hairs. **Leaves** alternate, often grouped at apex of branches, stipules narrowly triangular, 1–5 × 0.5 mm, caducous, green to red; petioles 10–28 mm, tinged red, sparsely covered with stellate hairs; lamina narrowly elliptic at seedling stage, very sparsely covered with simple or stellate hairs, maturing to 40–55 × 30–45 mm, elliptic to ovate, dark green, base obtuse to rounded, apex acute, glabrous with small stellate hairs sparsely occurring along veins, margin basally entire, becoming shallowly serrate toward apex, palmately veined with 3 or 5 main veins. **Flowers** solitary in upper leaf axils; pedicels spreading to ascending, 55–60 mm, articulated 15–20 mm from apex, sparsely covered with stellate hairs, green to red; epicalyx with 6 to 9 spreading or ascending lobes, variable in size on same flower, 7–12 × 1.5–2 mm, ensiform, exterior green, interior tinged red, sparsely covered with stellate hairs; calyx tubular, green, with 5 foliaceous, connate sepals, central ridge and connate portion of sepal lobes prominently raised, sepal lobes (15–)20–35 mm from base to apex, 6–7 mm wide, 15–17 mm from base to sinus of connate portion, sparsely covered with stellate hairs; corolla entirely scarlet-red externally and internally, sometimes with pale red to white veins, estivation contorted, opening to 65 mm in diam., petals 50–82 × 14–25 mm, asymmetrically narrow-obovate, margins repand, apex rounded, exterior sparsely covered with stellate hairs, interior glabrous; staminal column 40–53 mm, basally pale red, becoming white distally, ending in 5 triangular lobes with red tips; stamens many, appearing at ca. 1/2 the length of staminal column and clustered at distal end, filaments ca. 1.5 mm, white to pale red, anthers yellow to reddish brown, pollen yellow; styles 5, forming tube emerging 5–10 mm from staminal column, straight or slightly curving upward, branching 4–7 mm, spreading and becoming umbelliform, white to pale red, villose where branching; stigmas capitate, ca. 2 mm in diam., orange-red to dark red. **Fruits** 5-carpellate, ca. 20 × 15 mm, obovoid, brown, maturing to dry loculicidal capsule persistent on plant while seeds are dispersed from fruit; seeds ca. 4 × 3.5 mm, ovoid, dark brown, covered with stellate hairs.

Phenology. *Hibiscus fragilis* plants produce flowers and fruits regularly throughout the year.

Distribution and habitat. *Hibiscus fragilis* occurs on basalt cliffs and rocky outcroppings on mountaintops in Mauritius along the western side of the island. Collections and reported populations come from the mountains of Letard, Snail Rock, Le Pouce, Junction Peak, Ory, Corps de Garde, Trois Mamelles, and Le Morne. These sites, ranging from roughly 300 to 665 m in elevation, are often subjected to heavy winds and driving rain throughout the year, which, in combination with poor, rocky soils, results in an unusual type of dwarf forest with small windswept plants. *Hibiscus fragilis* occurs today only at the very tops of a few of these mountains in exposed areas or as a sprawling understory plant.

Conservation status. *Hibiscus fragilis* is listed as Critically Endangered (Bachraz & Strahm, 2000). Our surveys in 2018 and 2022 verified small populations on Corps de Garde and Letard, with an additional individual occurring on Mount Ory/Junction Peak. However, although the Mount Ory individual was observed

Figure 9. A–D. Photos of *Hibiscus fragilis* DC. —A. Frontal view of a flower showing the entirely red corolla. —B. Side view of a flower. —C. A dissected flower just before anthesis. —D. Characteristic ramified branches with short internodes. E–H. *Hibiscus genevei* Bojer. —E. Flowering branches. —F, G. Frontal views of a flower. —H. Seed. I–L. *Hibiscus liliiflorus* Cav. —I. Frontal view of a flower. —J, K. Side views of flowers and flower buds. —L. Immature fruits. Scale bars indicate 10 mm, except where noted. Photo credits: A–D, H, Brock Mashburn; E–G, J, K, Vikash Tatayah; I, L, Jean Alfred Bégué.

in 2018, it could not be found in 2022. Historic collections from Le Pouce Mountain (*Bojer s.n.*, ca. 1821–1856), Snail Rock (*Staub 11423*, 1964), and Trois Mamelles (*Chapelier s.n.*, ca. 1800) have not been located since they were collected, and much of the native forest in these areas has been lost or is heavily degraded. For example, the dry forest in the region called Le Pouce by Bojer (1837) has all been deforested. Up to 26 individuals of *H. fragilis* have been reported to be growing on the top of Le Morne Mountain (Bachraz & Strahm, 2000; photo of a flower included in Owadally, 2009: 92), which today is accessible only via helicopter. Eight adult plants were counted in a 2012 survey of Le Morne (Forestry Service officer R. Ramjaun, pers. comm., 2024), when cuttings were taken for propagation, though it is uncertain how many of these cuttings survived. Based on our field observations, we estimate that fewer than 30 wild *H. fragilis* individuals remain. An updated IUCN Red List assessment would be similar to the one performed by Bachraz and Strahm (2000): severely fragmented populations with a continuing decline in the number of mature individuals, largely because of the impact of invasive species (Florens et al., 2016), and no natural regeneration. Because *H. fragilis* has not been assessed in 25 years (Bachraz & Strahm, 2000), we recommend an updated assessment as Critically Endangered (CR A2ac, B1ab[v]+2ab[v], D).

Notes. De Candolle (1824) described *Hibiscus fragilis* as having ovate, slightly trilobed leaves with dentate margins, solitary flowers as long as the leaf, and an epicalyx with five lobes. He understood the species as occurring in Réunion, based on Bory's collection ascribed to the island, and credited Bory with an unpublished name, "Malvaviscus fragilis Bory ined." In de Candolle's herbarium (G-DC), this is the specimen with barcode G00218958, which is clearly the holotype. De Candolle annotated this specimen as coming from Réunion ("Bourbon"), but, along with Friedmann (1987),

we suggest that this annotation was an error and the collection was made in Mauritius.

Bojer (1837) applied the name *Hibiscus fragilis* to a shrubby species from the northern slopes of Le Pouce Mountain (southeast of Port Louis) and the nearby Nouvelle Découverte but otherwise gave no additional descriptive features. No population of *Hibiscus* is known to persist on Le Pouce Mountain; *H. fragilis* has been collected in the last five years on surrounding peaks of the same mountain range, all with long, dark red flowers. Plants from Nouvelle Découverte mentioned by Bojer, if collected, cannot be traced to any herbaria. Baker (1877) considered *H. fragilis* to be a synonym of *H. liliiflorus*, which, in his conception, included a large, funnel-shaped corolla with bright red petals. In Réunion, de Cordemoy (1895) considered *H. fragilis* to be a shrub that had longer leaves than *H. liliiflorus*, medium-sized flowers, and a yellow corolla barely longer than the calyx. It is difficult to tell from de Cordemoy's brief descriptions how he differentiated his yellow-flowered *H. fragilis* from his understanding of *H. boryanus*, which he also described as having medium-sized yellow flowers. Hochreutiner (1900) treated *H. fragilis* as a synonym of *H. rosa-sinensis*. Friedmann (1987) described *H. fragilis* as a species known to occur only in Mauritius, on the mountains near Port Louis and Corps de Garde Mountain. Notable characters outlined by Friedmann include short stature (< 1.5 m tall) with highly ramified branching; calyx 2.5(–3) cm with lobes ("teeth") 0.5–1.5 cm; and a uniformly carmine-red corolla with white striations on the exterior, reaching 5–6 cm.

Hibiscus fragilis is unique among other Mascarene *Lilibiscus* species with its sprawling habit (not reaching more than 1 m in height), ramified branches, long sepals ([15–]20–35 mm from base to apex), and entirely deep red corollas. The sprawling habit of the species is possibly the result of evolving on mountaintops exposed to high winds, and plants growing in cultivation sometimes grow taller, though they continue to exhibit the ramified branches with short shoots.

Additional specimens examined. MAURITIUS. **Moka/ Port Louis:** in monte Pollicis [Le Pouce Mtn.], s.d., *Bojer s.n.* (K); Junction Peak, close to summit, in betw. Mount Ory & Guiby Peak, 532 m, [–20.210°, 57.509°], 19 Apr. 2018, *Pynee s.n.* (MAU); Mont Ory, edge of cliff, 511 m, –20.211°, 57.506°, 15 Mar. 2018, *Mashburn 80* (MAU, MO); Mt. Ory, escarpment facing Moka, July 1982, *Lecordier s.n.* (MAU [3 sheets]). **Plaines Wilhems:** below N-facing cliffs of Corps de Garde, 300 m, 24 Apr. 1976, *Richardson 4026* (K); Corps de Garde Mtn., 661 m, –20.261°, 57.453°, 24 Mar. 2018, *Mashburn 95* (MAU, MO); ibid., 665 m, –20.262°, 57.454°, 24 Mar. 2018, *Mashburn 96* (MAU, MO); Corps de Garde Mtn., Dec. 1971, *Guého s.n.* (MAU [2 sheets]); Mt. Corps de Garde, June 1976, *Friedmann 2870* (P); N slope of Corps de Garde Mtn., 14 June 1975, *Lorence 1307* (MAU). **Port Louis:** Anse Courtois, Mt. Snail Rock, 10 Oct. 1964, *Staub s.n.* (MAU [2 sheets]); La Montagne de "Fort" Louis, Sep. 1849, *Boivin s.n.* (P); Letard Mtn., E of Port Louis, 543 m, –20.186°, 57.529°, 27 Mar. 2018, *Mashburn 100* (MAU, MO). **Rivière Noire/ Plaines Wilhems:** La Montagne des Trois Mamelles, s.d., *Chapelier s.n.* (MPU [bc] 764437). **S. loc.:** s.d., *Ayres s.n.* (K-18037); s.d., *Bojer s.n.* (K); 1847–1852, *Boivin s.n.* (P [bc] P030960, P [bc] P6624248, P [bc] P6624249); 1854, *Boivin s.n.* (K [bc] K006377917); s.d., *Sieber 1825* (G); 29 Nov. 1845, *s. coll., s.n.* (P [bc] P06701693).

4. Hibiscus genevei Bojer, Bot. Mag. 59: t. 3144 (as "*Genevii*"). 1832. *Abelmoschus genevei* (Bojer) Walp., Repert. Bot. Syst. 1(2): 310. 1842. TYPE: Mauritius. s. loc., s.d., *W. Bojer s.n.* (lectotype [as "holo[type]"], designated by Friedmann, 1987: 32, K [bc] K000240598!). Figure 9E–H.

Multistemmed shrubs to small single-stemmed trees reaching 3–5 m tall and 8 cm DBH. **Bark** smooth to fissured, light gray to brown; young stems green to gray-brown, lenticellate, glabrous. **Leaves** alternate, stipules subulate, ca. 3 × 0.25 mm, caducous, green; petioles 10–28 mm, tinged red, sparsely covered with soft, stellate hairs; lamina heterophyllous, with juvenile form present up to ca. 1.5 m and mature form present above; juvenile form with 3 or 5 lobes of variable size, initially narrow and subulate but quickly widening (central lobe reaching 85 × 23 mm, for example), green, very sparsely covered with simple or stellate hairs; adult form 40–90 × 25–65 mm, elliptic to ovate, green, base obtuse to rounded, apex acute, glabrous with small stellate hairs sparsely occurring along veins, margin basally entire, becoming shallowly serrate toward apex, palmately veined with 3 or 5 main veins. **Flowers** solitary in upper leaf axils; pedicels ascending, 40–55 mm, articulated 7–14 mm from apex, green to red, glabrous; epicalyx with 6 to 9 spreading or ascending lobes, 8–12 × 0.5–1.5 mm, ensiform, exterior green, interior green to tinged red, sparsely covered with stellate hairs; calyx cupuliform, green, with 5 foliaceous, connate sepals, central ridge and connate portion of sepal lobes prominently raised, sepal lobes 18–25 mm from base to apex, 5–8 mm wide, 11–12 mm from base to sinus of connate portion, sparsely covered with stellate hairs; corolla pale pink, interior dark pink to purple-red at center, estivation contorted, opening to 165 mm in diam., petals 60–90 × 25–50 mm, asymmetrically narrow-obovate, margins repand, apex rounded, sparsely covered with stellate hairs; staminal column 75–90 mm, basally dark pink, becoming white distally, ending in 5 triangular lobes with pink tips; stamens many, clustered in distal 1/3 of staminal column, filaments ca. 6.5 mm, white to pale pink, anthers yellow, pollen globose, pale yellow; styles 5, forming white tube emerging from staminal column, branching and becoming umbelliform, turning pink after branching; stigmas globose to oblate, ca. 2.5 mm in diam., orange to red. **Fruits**

5-carpellate, ca. 20 × 15 mm, obovoid, brown, maturing to a dry loculicidal capsule persistent on plant while seeds are dispersed from fruit, exterior and interior both glabrous; seeds ca. 4 × 3 mm, ovoid to reniform, dark brown, densely covered with ca. 0.5 mm tan hairs.

Phenology. *Hibiscus genevei* plants produce flowers and fruits regularly throughout the year.

Distribution and habitat. Wild individuals of *Hibiscus genevei* are currently known only from Mondrain Reserve, which is at ca. 500 m elevation at the north end of the Black River Mountain Range in Mauritius. Five plants were recorded on nearby Mount Simonet (Page & D'Argent, 1997) but have not been relocated since (F. B. V. Florens & C. B., pers. obs., 2006). Little is known about the historical distribution and ecology of the species. Bojer mentioned it was growing in the lower Rivière Noire Gorges (Hooker, 1832), implying the species could have once been more widespread, though this name could also include the present location of Mondrain. Individual plants are canopy trees reaching ca. 5 m in height in forest with a densely interwoven canopy, suggesting adaptation to cyclones and heavy winds.

Conservation status. *Hibiscus genevei* was assessed as Endangered (E) in the *1997 IUCN Red List of Threatened Plants* (Walter & Gillett, 1998). Mondrain was declared a private reserve following the rediscovery of the species in 1968 (Guého & Staub, 1979). A total of 179 adults were found inside and around Mondrain in a recent survey, indicating strong natural regeneration in this heavily managed and fenced reserve (K. P., unpubl. data). One sapling was recorded in 2024 in the Cabinet Nature Reserve ca. 2.8 km south of the Mondrain Reserve and 1.8 km southeast of Simonet (F. B. V. Florens & C. B., pers. obs.). If only the population at Mondrain is considered, *H. genevei* has an EOO and AOO of < 1 km^2. As is the case with most native Mauritian plants, the long-term survival of the species is dependent on the control of alien species. Management of alien species, especially invasive plants, is known to improve the status of highly threatened endemic species (Baider & Florens, 2011). Therefore, we suggest an assessment of *H. genevei* as Critically Endangered (CR A2ac, B1ab[iii]+2ab[iii]).

Notes. *Hibiscus genevei* is the only Mascarene *Lilibiscus* species that has not been the subject of significant confusion since its description in 1832, though some clarification concerning both the spelling of the specific epithet and the authorship of the species is necessary here. Though it was originally known only in cultivation in Mauritius, a wild population of *H. genevei* near Rivière Noire was presented to the botanist Wenceslas Bojer by Auguste Genève, an avid horticulturist who lived nearby (Hooker, 1832). Bojer described and illustrated the species, then presented the finding to the Société d'Histoire Naturelle de l'Île Maurice in a public reading in 1830 (RSASM, 1872: 188). Bojer also communicated his description and illustration to Joseph Hooker, who published both under the name "*Hibiscus Genevii* Bojer" (Hooker, 1832), and subsequent authors followed this spelling (Bojer, 1837; Baker, 1877; Hochreutiner, 1900; Friedmann, 1987). Regarding orthography, under Article 60.8 of the International Code of Nomenclature (Turland et al., 2018), the spelling of the specific epithet as "genevii" is correctable to "genevei." Regarding authorship, Hooker (1832) clearly attributed the Latin diagnosis, the species name, the species description, and the illustration all directly to Bojer by placing Bojer's name at the end of each pertinent section of the text and at the bottom of the illustration. In addition, Hooker (1832) cited a letter from Bojer as the source of the species' name, description, and illustration. Subsequent authors followed Hooker (1832) in ascribing authorship to Bojer alone (Bojer, 1837; Baker, 1877; Hochreutiner, 1900) until Friedmann (1987) treated the species as "*H. genevii* Bojer ex Hook." Following Article 46.2 of the International Code of Nomenclature, the name should be cited as "*H. genevei* Bojer," as Hooker (1832) unequivocally ascribed the name, diagnosis, and description to Bojer alone.

Hooker's (1832) publication of *Hibiscus genevei* did not note any herbarium specimens. However, a Bojer collection (K [bc] K000240598) is presumably uncited original material sent to Hooker along with Bojer's description and illustration. Given that Hooker (1832) did not indicate a type, both the illustration and the Bojer collection had equal standing as potential lectotypes until Friedmann (1987) treated the K specimen as the holotype.

Bojer's original description of *Hibiscus genevei* provided in Hooker (1832) is quite detailed and, combined with the illustration, makes the species easy to differentiate from others in the Mascarenes based on the pale pink petals with deep purple at the base, yellow anthers, purple style, and purple stigmas. Bojer's *Hortus Mauritianus* (1837) treated the species likewise. Baker (1877), however, saw *H. genevei* as a synonym of *H. liliiflorus*, without mention of the unique floral features described by Hooker (1832). De Cordemoy (1895), concerned with species in Réunion, made no mention of *H. genevei*. Hochreutiner (1900) considered *H. genevei* to be a synonym of his broadly perceived *H. rosa-sinensis.* In the *Flore des Mascareignes*, Friedmann (1987) described *H. genevei* in considerable de-

tail, including the comparatively large flowers. Indeed, *H. genevei* is unique among the other Mascarene *Lilibiscus* with its large flowers (opening to 165 mm in diameter) with a light pink corolla and a dark pink to purple-red center.

Additional specimens examined. MAURITIUS. **Plaines Wilhems:** Henrietta, outside Mondrain Nature Reserve, close to fence, 580 m, [–20.332°, 57.455°], 18 Sep. 2012, *Pynee s.n.* (MAU); Mondrain Reserve, 508 m, –20.326°, 57.454°, 17 Mar. 2018, *Mashburn 84* (MAU, MO); ibid., 519 m, –20.325°, 57.453°, 17 Mar. 2018, *Mashburn 85* (MAU, MO); ibid., 519 m, –20.326°, 57.453°, 17 Mar. 2018, *Mashburn 86* (MAU, MO); ibid., 508 m, –20.324°, 57.455°, 17 Mar. 2018, *Mashburn 87* (MAU, MO); Vacoas Ridges, 21 Jan. 1968, *Guého s.n.* (MAU); Vacoas Ridges, W of central plateau, 600 m, 5 May 1979, *Lorence 2614* (MO); Vacoas Ridges, 550 m, 21 Aug. 1979, *Lorence 2916* (K, MO, P); Vacoas Ridges, Réserve Privée Le Mondrain, 9 Feb. 1978, *Friedmann 3348* (P). **Rivière Noire:** Dans les Gorges de la Montagne de la Rivière Noire, 1864, *Bouton s.n.* (K). **S. loc.:** s.d., *Bojer s.n.* (K [bc] K000240598).

5. Hibiscus igneus Mashburn, sp. nov. TYPE: Réunion [France]. Dos d'Âne, 1250 m, July 1972, *F. Friedmann 1716* (holotype, P [bc] P06624160!; isotypes, K!, MAU [bc] MAU0016124!, REU [bc] REU016757!). Figures 10, 11.

Diagnosis. *Hibiscus igneus* Mashburn is distinguished from other Mascarene *Hibiscus* L. in section *Lilibiscus* Hochr. by its erect, shrubby to arborescent habit reaching 10 m in height; typically narrowly elliptic leaves, often with 3 main palmate veins; sepals 9–16 mm from base to apex; and red corolla with a yellow center.

Shrubs to canopy trees reaching ca. 10 m tall and 20 cm DBH. **Bark** slightly fissured, light gray to brown, often covered with gray, green, and pink lichens; young stems green to gray-brown, lenticellate, glabrous to very sparsely covered with stiff, simple or stellate hairs. **Leaves** alternate, stipules subulate, ca. 3 × 0.25 mm, caducous, green to tan; petioles 3–20 mm, green, adaxial surface covered with soft, stellate hairs; lamina heterophyllous, with juvenile form occurring from ground level up to 0.5–1.5 m and mature form present above ca. 1.5 m; juvenile form simple, elliptic, or trilobed (rarely 5-lobed), with narrow, subulate lobes of variable size (central lobe reaching 130 × 10 mm, for example), green, very sparsely covered with simple or stellate hairs; adult form 35–95 × 12–50 mm, elliptic, often narrowly so, green, base attenuate to obtuse, apex attenuate to acuminate, glabrous to sparsely pubescent with simple and stellate hairs, margin basally entire, repand toward apex, palmately veined with 3 (less often 5) main veins. **Flowers** solitary in upper leaf axils; pedicels spreading to ascending, 25–52 mm, articulated 18–40 mm from apex, glabrous; epicalyx with 5 to 8 spreading or ascending lobes, individual lobes 4–16 × 1.5–3 mm, ensiform, green, glabrous; calyx cupuliform, green, with 5 foliaceous, connate sepals, central ridge and connate portion of sepal lobes not visibly raised, sepal lobes 9–16 mm from base to apex, 5–6 mm wide, 6.5–10 mm from base to sinus of connate portion, densely covered with rough, stellate hairs; corolla red, the exterior tinged yellow basally and sometimes along veins, interior yellow at center, estivation contorted, opening to 26–55 mm in diam., petals 33–50 × 12–21 mm, asymmetrically narrow-obovate, margins repand, apex rounded, exterior covered with small stellate hairs; staminal column 22–45 mm, basally yellow-orange, becoming orange-red distally, ending in 5 red triangular lobes; stamens many, appearing at ca. 1/2 the length of staminal column and clustered at distal end, filaments ca. 1.5 mm, orange to red, anthers orange to red, pollen globose, yellow; styles 5, forming a pale green tube emerging from staminal column, straight or slightly curving upward, branching and becoming umbelliform; stigmas globose to oblate, 1–2 mm in diam., dark red. **Fruits** 5-carpellate, 15–25 × 14–20 mm, obovoid, brown, maturing to dry loculicidal capsule persistent on plant while seeds are dispersed from fruit, exterior densely covered with small stellate hairs, interior glabrous; seeds ca. 4 × 3 mm, ovoid, dark brown, densely covered with ca. 1 mm tan hairs.

Phenology. *Hibiscus igneus* plants produce flowers and fruits regularly throughout the year, though flowering is slightly more profuse during the rainy season (December–April).

Distribution and habitat. *Hibiscus igneus* occurs in Réunion in semi-dry forests (annual rainfall 1000–1500 mm) that experience a pronounced dry season, and in dry portions of the leeward submontane rainforest (annual rainfall 1500–6000 mm); both forest types are found on the western (leeward) side of the island of Réunion. Semi-dry forests occur from 200 to 750 m in elevation, and less than 2% of this forest type remains intact, whereas leeward submontane rainforests occur from 750 to 1100 m elevation, and less than 15% remains intact (Strasberg et al., 2005). *Hibiscus igneus* is a canopy tree in the shorter semi-dry forests and with increasing altitude becomes an understory tree in increasingly wetter forests with a higher canopy.

Conservation status. In Réunion, less than 2% of the semi-dry forest and less than 15% of the leeward submontane rainforest where *Hibiscus igneus* occurs remains; in addition, much of this remaining forest is heavily invaded by alien invasive species (Strasberg et al., 2005; Barbé et al., 2015). We estimate the EOO of *H. igneus* to be approximately 205 km^2 and the AOO to be 128 km^2. Given the fragmentation in the forests where *H. igneus* occurs, combined with the continued

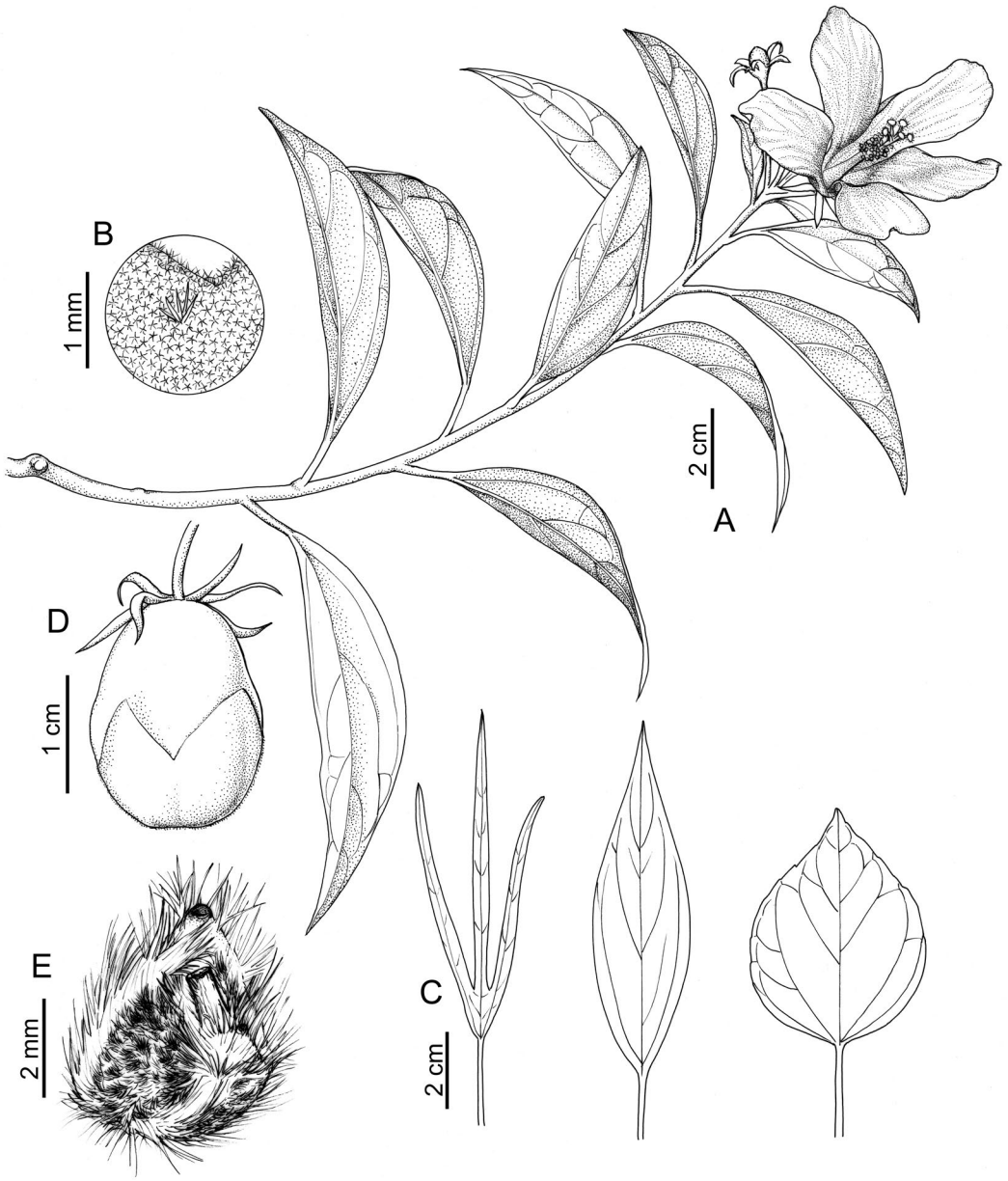

Figure 10. Illustration of *Hibiscus igneus* Mashburn. —A. Flowering branch. —B. Stellate hairs on leaves and flowers. —C. Shapes of juvenile and adult leaf forms. —D. Fruit before dehiscence. —E. Seed. Illustration by Barbara Alongi.

advancement of invasive species (Barbé et al., 2015), we propose a risk assessment of Endangered (EN B1ab[iii]+2ab[iii]).

Etymology. The specific epithet *igneus* comes from Latin, meaning "fiery" or "hot." The name refers both to the ecology of *Hibiscus igneus*, as it occurs in the hot, seasonally dry forests of Réunion, and to the color of the flowers, which are red with a yellow interior, reminiscent of a flame.

Notes. *Hibiscus igneus* is described from material formerly treated as *H. boryanus*. It is the only Mascarene species exhibiting a red corolla with a yellow center (Fig. 11). The other red-flowered Mascarene species, *H. fragilis* (occurring in Mauritius), has an

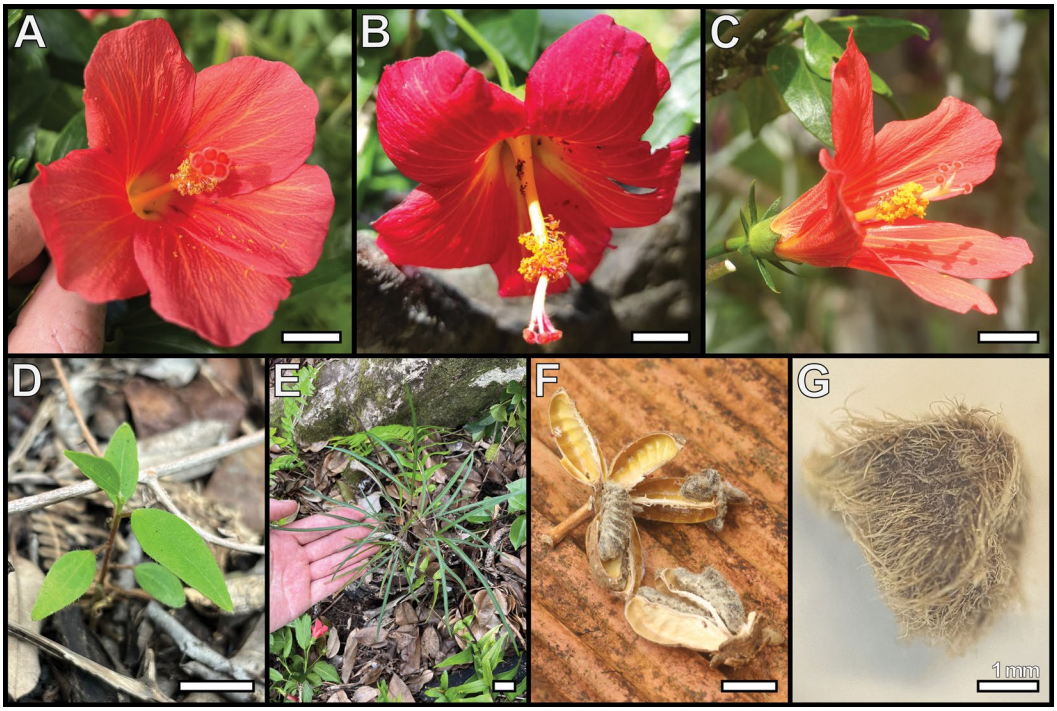

Figure 11. Images of *Hibiscus igneus* Mashburn. —A, B. Frontal view of flowers showing the red corolla with a yellow center. —C. Side view of a flower. —D, E. Two juvenile leaf forms in seedlings. —F. A mature dehisced fruit with seeds. —G. Seed. Photo credits: A, D, E, G, Brock Mashburn; B, Lucille Jourdain Fievet; C, F, Jean-Maurice Tamon.

entirely red corolla. The two species can be further differentiated by habit (*H. igneus* are erect shrubs and trees reaching 10 m, vs. sprawling shrubs reaching only 1 m in *H. fragilis*) and sepal size (9–16 mm from base to apex, 6.5–10 mm from base to sinus of the connate portion, vs. [15–]20–35 mm from base to apex, 15–17 mm from base to sinus of the connate portion). Populations of *H. igneus* can occur in proximity to populations of the other Réunion endemic species, *H. boryanus*, particularly in areas with sharp transition zones between dry and wet portions of the leeward submontane rainforest. The two species have flowers of similar size, and some *H. boryanus* flowers can exhibit yellow, orange, and red streaks (Fig. 5), though these flowers never have the red corolla with a yellow center seen in *H. igneus*. *Hibiscus igneus* is further differentiated from *H. boryanus* by narrow, simple or trilobed, rarely 5-lobed, juvenile leaves (vs. highly variable and 3- to 5-lobed in *H. boryanus*) (Fig. 6); mature leaves often with three main palmate veins (vs. five main palmate veins); epicalyx and calyx lobes with foliar thickness and texture, covered with stellate hairs (vs. thickened and fleshy, glabrous); and fruits maturing as dry, brown, dehiscent capsules (vs. hard-fleshy, green, indehiscent capsules).

Paratypes. RÉUNION [FRANCE]. **Saint-Denis:** sur les montagnes qui avoisinan la rivière de St-Denis, 1834, *Goudot s.n.* (G, P); Plaine d'Affouches, 3 Feb. 1971, *Friedmann 920* (MO, P); Plaine d'Affouches, 1000 m, 2 Mar. 1975, *Friedmann 2676* (P). **Saint-Paul:** Commune de La Possession, Mon Îlet, 876 m, –20.965°, 55.372°, 17 Apr. 2022, *Mashburn 273* (MO); Commune de La Possession, Rivière des Galets Bras de Sainte Suzanne, 550 m, [–21.006°, 55.432°], 2 Aug. 2016, *Thomas 358* (P); Dos d'Âne, Sentier du Cap Noir, 800 m, 7 Apr. 1968, *Cadet 1327* (P); Dos d'Âne, 6 Dec. 1970, *Friedmann 864* (K, P); Dos d'Âne, 20 Mar. 1974, *Bosser 21664* (P); Dos d'Âne, 1200 m, May 1974, *Friedmann 2295* (P); Edden Farm, trail toward Sans Soucis/Orangers from the upper Bois de Sans Soucis, 909 m, –20.997°, 55.357°, 11 Apr. 2022, *Mashburn 251* (MO); La Possession, Aurère, Mafate, Sentier Augustave, 1012 m, –21.015°, 55.428°, 13 Apr. 2022, *Mashburn 259*, *260*, *261*, *262*, *263*, *264* (MO); Parc Colorado, 737 m, –20.912°, 55.421°, 10 Apr. 2022, *Mashburn 248* (MO); ibid., 662 m, –20.907°, 55.425°, 10 Apr. 2022, *Mashburn 249* (MO); Sentier Cap Noir, W of the Cap Noir viewpoint, 1138 m, –20.991°, 55.388°, 9 Apr. 2022, *Mashburn 245* (MO); ibid., 1164 m, –20.989°, 55.386°, 9 Apr. 2022, *Mashburn 246* (MO); ibid., 1164 m, –20.989°, 55.386°, 9 Apr. 2022, *Mashburn 247* (MO); Saint-Leu, Les Colimaçons JBR, 29 June 2018, *Anxionnaz 4993* (CBNM). **Saint-Pierre:** Commune Entre-Deux, Ravine des Citrons, along Sentier des Trophées Mondiaux, 595 m, –21.231°, 55.491°, 15 Apr. 2022, *Mashburn 272* (MO); Sentier Bayonne, à Entre-Deux, 800–950 m, Sep. 1993, *Girard s.n.* (P); Sentier Bayonne, from Grand-Font Exterieur toward Sentier de la Grande Jument, 1018 m, –21.211°, 55.463°, 8 Apr.

2022, *Mashburn 239* (MO); ibid., 983 m, –21.212°, 55.462°, 8 Apr. 2022, *Mashburn 240* (MO); ibid., Sentier Bayonne, from Grand-Font Exterieur toward Sentier de la Grande Jument, 969 m, –21.215°, 55.463°, 8 Apr. 2022, *Mashburn 241* (MO); ibid., 964 m, –21.216°, 55.463°, 8 Apr. 2022, *Mashburn 242* (MO); ibid., 930 m, –21.220°, 55.462°, 8 Apr. 2022, *Mashburn 243* (MO).

6. Hibiscus liliiflorus Cav., Diss. 3: 154, pl. 57, f. 1. 1787. TYPE: Réunion [France]. "Ile du Bourbon," s.d., *P. Commerson 27* (lectotype [as "holo[type]"], designated by Friedmann, 1987: 29, P-JU n° 12354!; isolectotypes, ANG digital image!, G [bc] G00416976!, LINN-HS n° 1164.44, MPU [bc] MPU016688 digital image!, MPU [bc] MPU016689 digital image!, MPU [bc] MPU764436 digital image!, P [bc] P06624318!). Figure 9I–L.

Trees reaching 10 m tall and 20 cm DBH. **Bark** smooth to striate, light gray to brown; young stems green to light brown, smooth to lenticellate, glabrous to very sparsely covered with stellate hairs. **Leaves** alternate, often tightly bunched at ends of stems, stipules triangular, ca. 0.5 × 0.2 mm, caducous; petioles 10–50 mm, green, sparsely covered with short stellate hairs; lamina heterophyllous, with juvenile form present from ground level up to ca. 1.5 m and mature form present above ca. 1.5 m; juvenile form initially with single lobe, quickly becoming trilobed with linear, subulate lobes of variable size (central lobe reaching 120 × 5 mm, for example), green, very sparsely covered with simple or stellate hairs; adult form 50–115 × 25–46 mm, obovate, green, thick and coriaceous, base cuneate to obtuse, apex rounded, sometimes either slightly apiculate or retuse, glabrous to very sparsely covered with short stellate hairs along veins below, margin basally entire, repand toward apex, palmately veined with 3 or 5 main veins. **Flowers** solitary in upper leaf axils; pedicels spreading to ascending, 31–40 mm, articulated 4–7 mm from apex, sparsely pubescent below articulation, densely so above with small (ca. 0.2 mm wide) stellate hairs; epicalyx with 6 to 8 lobes appressed to calyx, individual lobes 2–8 × 1–2 mm, ensiform, green, sparsely covered with small stellate hairs; calyx cupuliform, green, with 5 thickened connate sepals, verrucose, densely covered with pale yellow, soft, stellate hairs producing leathery texture, central ridge and connate portion of sepal lobes not visibly raised, sepal lobes 10–14 mm from base to apex, 6–8 mm wide, 9–12 mm from base to sinus of connate portion; corolla orange, often tinged yellow basally, estivation contorted, opening to 90 mm in diam., petals 70–80 × 25–30 mm, asymmetrically narrow-obovate, margins repand, apex rounded, exterior densely covered with pale yellow stellate hairs, interior glabrous or very sparsely covered with same hairs; staminal column 58–61 mm, yellow, ending in 5 yellow triangular lobes; stamens many, appearing at ca. 1/2 the length of staminal column and clustered at distal end, filaments 1.5–2 mm, yellow, anthers yellow, pollen yellow; styles 5, forming pale orange tube emerging 5–6.5 mm from staminal column before branching and becoming umbelliform, individual style branches 7–8 mm, yellow, sparsely covered with long, simple or stellate hairs; stigmas capitate, globose to oblate, 1.7–2.5 mm in diam., orange, villose with simple hairs. **Fruits** 5-carpellate, ca. 20 × 20 mm, obovoid, brown, maturing to dry loculicidal capsule persistent on plant while seeds are dispersed from fruit; seeds ca. 4.5 × 3.5 mm, ovoid to reniform, brownish black, pubescent with simple white hairs.

Phenology. *Hibiscus liliiflorus* plants produce flowers and fruits regularly throughout the year.

Distribution and habitat. *Hibiscus liliiflorus* is currently found only on the island of Rodrigues, with two wild individuals extant in the southeastern part of the island. Wild individuals were once known from Grande Montagne, also in the east, and Oyster Bay in the north-central part of Rodrigues (e.g., MAU [bc] MAU0016186, MAU0016189, MAU0016190, MAU0016193). All of these sites exhibit basaltic soils with clay loam texture, suggesting that the species once occurred across the island where these types of soil are found. Though the species is now known only from Rodrigues, the first collections of *H. liliiflorus* come from Réunion (e.g., *Commerson s.n.*, June 1771 and Aug.–Sep. 1771; *Bory s.n.*, 1801–1802; *Thouars s.n.*, s.d.; none of the collectors visited Rodrigues). Of these, Commerson was the only collector to indicate the locality of his collections in Réunion, in the vicinity of the modern-day villages of Saint Louis and Saint Pierre in the southwest of the island. The fact that these collections were made near early settlements suggests that the *H. liliiflorus* collections could have been from plants originating in Rodrigues that escaped cultivation. However, Friedmann (1987: 30) doubted this possibility, saying that "the wild origin of these plants in Réunion is almost certain." In either case, wild plants of *H. liliiflorus* have not been collected in Réunion since Bory's collections in 1802, despite over a century of botanical surveys, and the species is likely extirpated from the island.

Conservation status. *Hibiscus liliiflorus* has recently been assessed as Critically Endangered (CR C2a(i); D) (Tatayah et al., 2021). Four wild adult plants were known in the early 1990s, but only two remain alive today (Mashburn et al., 2023). Concern about the long-term survival of the species began in the 1940s, when

the first cuttings from Rodrigues were taken to Mauritius for propagation (Strahm, 1989). Ex situ and in situ conservation measures, including propagation and replanting in protected areas of Rodrigues, have increased the number of individuals, but the species remains at high risk of extinction (Tatayah et al., 2021). A detailed genetic study of the remaining wild and propagated plants in Rodrigues has already led to improved actions to conserve the existing genetic diversity of the species (Mashburn et al., 2023).

Notes. The original description of *Hibiscus liliiflorus* by Cavanilles (1787) noted specimens from Philibert Commerson's herbarium and indicated communication with "D. de Jussieu." Many, if not all, of Commerson's collections were initially in the custody of Antoine-Laurent de Jussieu (1748–1836), which were then incorporated along with much of de Jussieu's collection into the Paris herbarium as P-JU (Stafleu & Cowan, 1976). Before this, however, some of Commerson's specimens were sent to Jean-Baptiste de Lamarck (1744–1829) (now at P-LA) and Charles Louis L'Héritier de Brutelle (now at G), and a large portion was sent to André Thouin (1747–1824), who then shared specimens with Carl Linnaeus filius (eventually deposited in LINN-HS) (Callmander et al., 2019). The remainder of Thouin's herbarium was purchased by Jacques Cambessèdes (1799–1863) and then was left to the Faculté des Sciences de Montpellier (MPU) (Planchon, 1863; Callmander et al., 2019). All of these herbaria hold Commerson's collections of *H. liliiflorus*, with additional Commerson collections of *H. liliiflorus* at ANG, B, K, MA, and MAU, amounting to ca. 25 specimens in total.

The Commerson collection in de Jussieu's herbarium (P-JU n° 12354) was annotated "Cremontia columnaris Commers., La Fleur de St. Louis, Isle de Bourbon, Herb. De Commerson" and numbered "No. 27 C," all in the hand of Thouin. This is the only specimen numbered "27 C," so it may be a numbering system organized by Thouin and not Commerson. The specimen was annotated as the type of *Hibiscus liliiflorus* by J. van Borssum Waalkes in 1959 and treated as the holotype by Friedmann (1987). We accept Friedmann's (1987) typification here after correction of the term "holotype" to "lectotype" (Turland et al., 2018: Art. 9.10). In order to determine isolectotypes, we followed Callmander et al. (2019) in recognizing as original material any specimens with annotations in Thouin's hand, many of which include identifiable notations such as "Isle de Bourbon," "C^{om}," or "Cremontia Com." Two of these specimens (LINN-HS n° 1164.44, MPU016688) bear the number 614 in Thouin's hand, possibly indicating a list number provided by Thouin when he shared specimens with Linnaeus filius (Callmander et al., 2019).

In total, Commerson collected over two dozen individual sheets of *Hibiscus liliiflorus* in Réunion. A few of these collections were annotated with one of two dates (June and August/September 1771), indicating two independent collection events (though most collections are not annotated with dates). All Commerson collections specifically annotated as being taken in June are sterile (e.g., K, P [bc] P06624317, P [bc] P06624320, P [bc] P06624321), which accounts for four of the five sterile specimens. In contrast, four specimens that are annotated as collected in "August/September" (MAU [bc] MAU0000036, MPU [bc] MPU764436, P [bc] P06624315, P [bc] P06624318) contain fertile material. Therefore, it is possible that Commerson collected the species in June when sterile, then returned to the plant in August or September and collected additional fertile material.

The detailed description of *Hibiscus liliiflorus* by Cavanilles (1787), coupled with the provided illustration, make *H. liliiflorus* relatively easy to differentiate from the other Mascarene *Lilibiscus* species. Characters particular to the species found in Cavanilles's description include trinerved, oblong, ovate-lanceolate leaves with entire margins; a large, leathery, hemispherical to cupular calyx; and a large corolla with petals forming a tube and opening (reflexing) distally, forming a bell shape. Cavanilles described the color of the petals using the Latin term *phoenicea*, which can be interpreted variously as bright red, scarlet, or purple-red but has also been used to describe the color orange (Stearn, 1973; Brown, 2000); this is perhaps the source of confusion leading later authors to apply the name *H. liliiflorus* to other Mascarene species. Cavanilles (1787) noted that the new species "occurs in Réunion, in the mountains and forests where it was first discovered, described, and illustrated by D. Commerson."

Later treatments of *Hibiscus liliiflorus* vary widely in their understanding of the morphology and distribution of the species. De Candolle's (1824) treatment referenced Cavanilles's description and noted the trinerved, oblong-lanceolate leaves typical of the species. He also associated the species with Réunion, and with an unpublished name given by Bory, "*Malvaviscus puniceus*." In 1829, Joseph Hooker published a hybrid variety, purportedly a horticultural cross between *H. liliiflorus* and *H. rosa-sinensis*, as *H. liliiflorus* var. *hybridus* Hook. (Hooker, 1829); this name is considered a synonym of the nothospecies *H.* ×*telfairiae* Maund (Maund, 1841; POWO, 2025). In Bojer's (1837) *Hortus Mauritianus*, de Candolle is cited as the author of *H. liliiflorus* instead of Cavanilles, possibly indicating that Bojer did not examine Cavanilles's species description and illustration. He recognized *H. liliiflorus* as a species occurring in Mauritius with no reference to Réunion, noting that it "grows in forests, on mountains in different sections of the island" (Bojer, 1837: 27). Notably, Bojer

(1837) recognized only one of the two species described by de Candolle (1824), *H. fragilis*, with no mention of *H. boryanus*. Thus, Bojer may have considered *H. liliiflorus* to apply to the species in Mauritius with dark pink to magenta flowers (*H. dargentii*, sp. nov.). Later, Baker (1877) treated *H. liliiflorus* as a species with a large, funnel-shaped, bright red corolla, occurring in Mauritius, Rodrigues, and Réunion. He treated both *H. fragilis* and *H. genevei* as synonyms of *H. liliiflorus* and, like Bojer (1837), made no mention of the name *H. boryanus*. Clearly, Baker (1877) considered all previously described entities as one species spread across all three islands. De Cordemoy (1895), focused on Réunion, described *H. liliiflorus* as a tree with polymorphic leaves and large flowers with variable colors (light red, pink, pale pink, orange-yellow, "aurore" [light yellowish orange], or "chamois" [pale yellow-brown]). He described it as occurring only rarely in the wild in Réunion, in ravines or other low areas, but commonly cultivated around the island. Given that de Cordemoy (1895) differentiated *H. liliiflorus* from *H. boryanus* and *H. fragilis* and mentioned its continued, albeit rare, presence on Réunion, we consider this the latest known date that the species may have persisted on the island. Hochreutiner (1900: 131) recognized many of the distinctive features of *H. liliiflorus*, noting that "this species is quite distinct from all the others in the section [*Lilibiscus*]." The *Flore des Mascareignes* (Friedmann, 1987) treated *H. liliiflorus* as a species extant on Rodrigues and extirpated from Réunion. Important characters noted by Friedmann (1987) included obovate or elliptic adult leaves, quite thick and almost fleshy, with an entire margin; calyx covered with a dense layer of small stellate hairs; corolla dark orange, with a brighter central zone appearing varnished, and densely covered on the exterior with yellowish stellate hairs.

Hibiscus liliiflorus is unique among all other Mascarene *Lilibiscus* species in having obovate leaves that are dark green, thickened, and somewhat coriaceous (vs. ovate to elliptic, thinner, and membranous in all other species). Another unique character of *H. liliiflorus* is its thickened calyx with a leathery texture formed by a dense covering of soft, stellate hairs (vs. thickened and glabrous, or foliaceous and sparsely to densely covered with stellate hairs). The orange flowers of *H. liliiflorus* also set it apart from the group; though the flowers of *H. boryanus* can sometimes be tinged orange, the orange in *H. boryanus* flowers tends to occur in streaks with yellow or red. The flowers of *H. liliiflorus*, however, are much larger than those of *H. boryanus* (e.g., petals 70–80 mm vs. 30–45 mm).

Additional specimens examined. RÉUNION [FRANCE]. **Saint-Pierre:** environs du Gol, June 1771, *Commerson s.n.* (K, P [bc] P06624317, P [bc] P06624320, P [bc] P06624321); St. Paul, du Gol, du quartier St. Louis, de la rivière d'abord, Aug.–Sep. 1771, *Commerson s.n.* (MAU [bc] 0000036, P [bc] P06621318). **S. loc.:** s.d., *Bory s.n.* (G); s.d., *Commerson s.n.* (B [bc] W12879-010, MA [bc] 475806, MPU [bc] 016690, P [bc] P00287550, P [bc] P00842617, P [bc] P06624319, P [bc] P06624332, P-LA [bc] P00287551, P-LA [bc] P00287552, P-LA [bc] P00287553); s.d., *Cosson 18* (P [bc] P06624316); s.d., *du Petit-Thouars s.n.* (P [bc] P06624314, P [bc] P06624315). RODRIGUES [MAURITIUS]. **Coromandel-Graviers:** Décidé, Saponaire, Montagne Ursule, 173 m, –19.712°, 63.476°, 27 Mar. 2018, *Mashburn 91* (MAU, MO). **Lataniers-Mont Lubin:** Grande Montagne, 3 Aug. 1976, *Guého 18215* (MAU); Grande Montagne, next to entrance stairway to the Nature Reserve, 320 m, –19.706°, 63.462°, 24 Mar. 2018, *Mashburn 88* (MAU, MO); Grande Montagne, sommet, Aug. 1976, *Friedmann 2910* (P). **Oyster Bay:** upper part of Oyster Bay Valley, 7 June 1957, *Julien s.n.* (MAU [3 sheets]); valley of Oyster Bay, July 1960, *Jauffret R/92* (MAU [2 sheets]); vic. of Oyster Bay, 20 Sep. 1938, *Wiehe R/55* (MAU). **Plaine Corail-La Fouche Corail:** Plaine Corail, Rivière Anse Quittor, –19.759°, 63.368°, 29 Mar. 2018, *Mashburn 93* (MAU, MO). **Port Mathurin:** Solitude Nursery, –19.691°, 63.436°, 25 Mar. 2018, *Mashburn 89* (MAU, MO). **Port Sud-Est:** Cascade Mourouge [Mourouk], 19 Nov. 1956, *Remy 4* (MAU); Mourouk, 119 m, 28 Mar. 2018, –19.722°, 63.460°, *Mashburn 92* (MAU, MO). **S. loc.:** 1864, *Bouton s.n.* (K); 1874–1875, *Balfour s.n.* (K, P).

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