TAXONOMIC REVISION OF THE NEOTROPICAL GENUS: *ERITHALIS* (RUBIACEAE: CHIOCOCCEAE)

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ABSTRACT

A taxonomic revision of *Erithalis*, genus of perennial trees and shrubs, is presented utilizing morphological data. Principal Component Analysis involving 14 vegetative and floral characters provided support for four morphologically distinct taxa (*E. angustifolia*, *E. harrisii*, *E. odorifera*, and *E. quadrangularis*) and a fifth poorly defined complex (*E. diffusa*, *E. fruticosa*, *E. salmeoides and E. vacciniifolia*). A few qualitative characters, as well as geographic distributions of the taxa, however, can distinguish the latter group. *Erithalis insularis* grouped within the fifth group, and is here placed in synonymy with *E. fruticosa*. Thus, in this study are recognized *E. angustifolia*, *E. diffusa*, *E. fruticosa*, *E. harrisii*, *E. odorifera*, *E. quadrangularis*, *E. salmeoides*, and *E. vacciniifolia* based on differences in inflorescence, flower, leaf, and growth habit characteristics. Phylogenetic relationships among the species, morphological description of their inflorescences and flowers, and the breeding system of *E. fruticosa* are presented. A key to the species, synonymies, typifications, descriptions, uses, and list of representative specimens is provided.

RESUMEN

Se presenta una revisión taxonómica de *Erithalis*, un género de árboles y arbustos de hoja perenne, utilizando análisis morfológicos. Análisis de Componentes Principales basados en 14 características vegetativas y florales confirman cuatro taxones (*E. angustifolia*, *E. harrisii*, *E. odorifera*, y *E. quadrangularis*) y un quinto complejo (*E. diffusa*, *E. fruticosa*, *E. salmeoides* y *E. vacciniifolia*). Este último grupo, sin embargo, puede distinguirse por varios caracteres cualitativos, además de la distribución geográfica de estos taxones. *Erithalis insularis* se agrupó con éste último grupo, y se coloca aquí como sinónimo de *E. fruticosa*. Por lo tanto, en este estudio son reconocidos *E. angustifolia*, *E. diffusa*, *E. fruticosa*, *E. harrisii*, *E. odorifera*, *E. quadrangularis*, *E. salmeoides*, y *E. vacciniifolia*, basándonos en diferencias de la inflorescencia, flor, hoja, y hábito de crecimiento. Se presentan las relaciones de filogenia entre las especies, descripción morfológica de sus inflorescencias y flores, y el sistema reproductor de *E. fruticosa*. Se provee una clave para las especies, sinónimos, tipificación, descripciones, usos y especímenes representativos.

INTRODUCTION TO *ERITHALIS*

Taxonomic History

Erithalis P. Browne (Rubiaceae: Chiococceae) is comprised of perennial trees or shrubs. It is distributed throughout the Caribbean Basin, Venezuela, and in the island of Fernando de Noronha, Brazil (Fig. 1). Twenty-six species, subspecies and varieties have been described in the genus (Andersson 1992; Candolle 1830; Correll & Correll 1982; Engler 1897; Lioger 1962, Lioger & Martorell 1982;

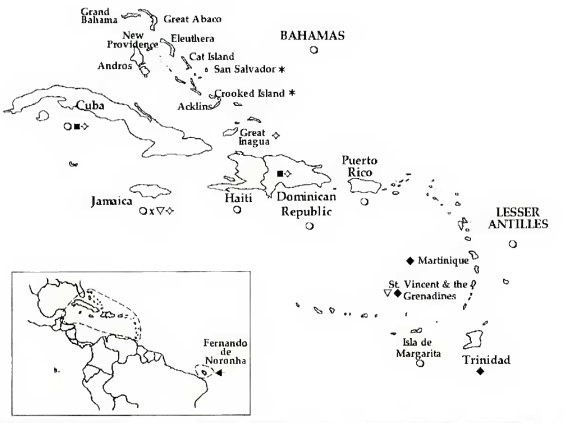

FIG. 1. Distribution of *Eritholis*. Symbols represent: ♦ = *E. angustifolia*, ✶ = *E. diffusa*, x = *E. harrisii*, ☽ = *E. dorifera*, ▽ = *E. quadrangularis*, ✧ = *E. salmeoides*, ■ *E. vacciniifolia*. Inset: disjunct distribution of *E. fruticosa*.

Grisebach 1864, 1866; Moore & Rendle 1936; Rafinesque 1838; Sauvalle 1869; Standley 1934; Steyermark 1974; Urban 1903, 1908; Zappi & Nunes 2000). In particular, the two widely distributed species—*E. fruticosa* L. and *E. odorifera* Jacq.—have been described under different names (Candolle 1830; Grisebach 1866; Rafinesque 1838; Urban 1903). For example, *E. odorifera* has been ranked as synonym, variety, or subspecies of *E. fruticosa* by many specialists on the Caribbean flora (Correll & Correll 1982; Grisebach 1864, 1866; Howard 1989; Lioger 1962) and on the neotropical Rubiaceae (Standley 1934; Steyermark 1974).

There has been little or no comprehensive examination of this genus across its entire range, and many species have been described on the basis of extremely limited material. Previous studies include the original species descriptions, which are mostly brief (Hooker 1873; Correll 1977; Candolle 1830; Engler 1897; Rafinesque 1838; Urban 1903, 1908; Zappi & Nunes 2000), taxonomic keys and/or species lists for particular regions (Adams 1972; Andersson 1992; Correll & Correll 1981; Lioger 1962; Lioger and Martorell 1982; Grisebach 1864, 1866; Moore and Rendle 1936; Sauvalle 1869; Steyermark 1974), and phylogenetic and biogeographical studies based on molecular data (Negrón-Ortiz & Watson 2002, 2003).

Among the regional floras, i.e., taxonomic keys and/or species lists for par-

ticular regions, the work done in Cuba (Grisebach 1866; Lioger 1962; Sauvalle 1869) is notable. In *Catalogus Plantarum Cubensium*, Grisebach (1866) lists for Cuba (without descriptions except when noted) four species of *Erithalis* and one variety: *E. angustifolia* DC., *E. fruticosa*, *E. fruticosa* var. *odorifera* Jacq., *E. parviflora* Griseb., and *E. rotundata* Griseb. He transferred *E. angustifolia* Rich. to *E. parviflora*, briefly describing it as follows: "corolla quam in ceteris minor, calycis limbo minutissime 5 dentato, antheris filamento brevioribus." Shortly thereafter, Sauvalle (1869) revised Grisebach's list, and reached similar conclusions. However, he treated *E. fruticosa* var. *odorifera* as a synonym of *E. rotundata*. In addition, he included *Chione* Griseb. in *E. vacciniifolia* (Griseb.) Wr., without any description except by listing the collection number, *2719*. By the mid-20th century, Liogier (1962) recognized only two species for this island, *E. fruticosa* and *E. vacciniifolia*, perhaps following Standley's treatment (see below for details).

The most complete treatment, but limited to species descriptions, is by Standley (1934), who recognized six species of *Erithalis*. He ranked *E. angustifolia* sensu Griseb. as synonym of *E. acuminata* Krug & Urb., and recognized the Puerto-Rican endemic *E. revoluta* Urb. as a distinct taxon. Liogier and Martorell (1982) then placed the latter species in synonymy with *E. fruticosa*. Standley (1934) was the first to proposed a broad delimitation for *E. fruticosa*: he considered *E. odorifera*, *E. inodora* Jacq., *E. elliptica* Raf., *E. odorata* Raf., *E. rotundata*, *E. parviflora*, *E. fruticosa* var. *inodora* DC. and *E. fruticosa* var. *odorifera* to be synonymous. In addition, Standley treated *E. angustifolia* DC., *E. pentagonia* DC., and *E. uniflora* Gaertn.f. as doubtful species. Subsequently, Liogier (1962) determined that *E. angustifolia* DC. is a synonym of *E. fruticosa*.

Moore and Rendle (1938) followed Standley's classification for their treatment in *Flora of Jamaica*, but with several modifications. In their classification, they maintained *E. fruticosa*, *E. harrisii* Urb. and *E. quadrangularis* Krug & Urb., which were also later sustained by Adams (1972). They ranked *E. odorifera* at the species level indicating that "this and *E. fruticosa* are very distinct," and that the leaves and calyx-tube are "much larger." They also added a new variety, *E. harrisii* var. *angusta* S. Moore ex Rendle. Adams (1972) placed the later two taxa in synonymy with *E. fruticosa*.

In his checklist of Neotropical Rubiaceae, Andersson (1992) listed 21 *Erithalis* taxa, including synonyms, varieties and subspecies. Of those, he tentatively accepted nine species, which represent merely Standley's six species with the addition of *E. salmcoides* Correll and *E. diffusa* Correll (Correll 1977), and *E. odorifera*, which he elevated to species rank separating it from *E. fruticosa* following Howard (1989). *Erithalis revoluta*, synonymized with *E. fruticosa* by Liogier and Martorell (1982), was maintained as a separate species by Andersson, who was perhaps not aware of Liogier and Martorell's work. Clearly, throughout these local floras and treatments, *E. fruticosa* ranked as a distinct species.

Species Concept

Various morphological characters have been used to delimit the species of *Erithalis*. I use the basic framework of Andersson who recognized nine species, and the recently transferred species, *E. insularis* (Ridl.) Zappi & T.S. Nunes (Zappi & Nunes 2000). Many of the morphological characters used historically display continuous variation among species, especially among taxa with overlapping distributions. *Erithalis fruticosa*, as traditionally recognized, exhibits considerable morphological diversity and a pan-Caribbean geographical distribution, and overlaps in distribution with many of the recognized taxa in the genus. *Erithalis odorifera* shares a similar distribution and habitat as *E. fruticosa*, occurring sympatrically on several islands, and intermediate forms between these two taxa appear to bridge the main differences between them (Moore & Rendle 1938; Negrón-Ortiz, pers. obs.; Steyermark 1974). Howard (1989) used characters such as size of the corolla tube, floral fragrance intensity, and leaf size to separate these two species.

Erithalis harrisii, *E. quadrangularis*, *E. revoluta*, and *E. vacciniifolia* are each considered endemic to one or several islands of the Greater Antilles (Fig. 1). Characters such as stipule length, the ratio of leaf length to width, petiole length and robustness, leaf apex, and calyx lobes shape have been used to separate these endemic species from *E. fruticosa* (Urban 1903). *Erithalis acuminata*, the only species reported endemic to the Lesser Antilles, is separated from *E. fruticosa* by the size of the corolla tube and height of the plant. *Erithalis diffusa* and *E. salmeoides*, currently considered endemic species to the Bahamian Archipelago (Correll & Correll 1982), differ from each other and *E. fruticosa* in growth habit, corolla, and anther length.

Erithalis insularis, a species collected from the island of Fernando de Noronha, Brazil, was recently transferred by Zappi and Nunes (2000) based on a type specimen originally described as *Palicourea insularis* Ridl. They claim it differs from the other *Erithalis* by "its poorly branched, few-flowered inflorescences, and leaves distributed along the new branches."

PHYLOGENY AND EVOLUTION

Morphometrics

Taxonomy of island genera is often regarded as difficult because of their complexity, including widespread and variable species that contain several more or less distinct forms, joined to one another by intermediates, and by the lack of discrete characters to separate these forms (Henderson & Ferreira 2002). Infra- and inter-specific variability of island species and other groups of taxa have frequently been examined by multivariate statistical techniques (e.g., Fritsch & Lucas 2000; Henderson & Ferreira 2002; Janovec & Harrison 2002; Negrón-Ortiz & Hickey 1996; Thompson & Lammers 1997), thus, I used multivariate techniques to investigate morphological variation within *Erithalis*. This was

done as a precursor to determine the best characters for use in the phylogenetic analyses, and in the taxonomic treatment.

Morphological studies were based on specimens examined from herbaria BM, FTG, GH, LL, MO, MU, NY, Tex and US, and from field collections made in Jamaica, St. Vincent and the Grenadines (Lesser Antilles), Puerto Rico, Florida (USA), and Andros Island (Bahamas). Over 278 specimens were examined over the course of the study, representing the entire range of morphological and geographical variation within this genus. A total of 14 characters (leaf length, leaf width, corolla length, number of corolla lobes, style length, calyx length, anther length, filament length, inflorescence length, growth habit, petal type, stigma type, inflorescence type, position of anther relative to the stigma) were measured on 133 specimens. Specimens with complete data sets were selected for combined analyses of floral and vegetative data; these totaled 70 collections and represented ten species. The holotypes of *E. acuminata* (here after: *E. angustifolia*, see taxonomic treatment), *E. quadrangularis*, *E. salmeoides*, and *E. vacciniifolia*, isotypes of *E. angustifolia*, *E. diffusa*, *E. insularis*, *E. parviflora* and *E. salmeoides*, and syntypes of *E. angustifolia*, *E. harrisii* and *E. rotundata* were included in the study. The data matrix was subjected to standarized Principal Component Analyses (PCA) using JMP 3.1 (Statistical Discovery Software, SAS Institute Inc. 1995); scatter plots were generated using CA-Cricket Graph III 1.5.3 (Computer Assoc. International, Inc. 1992).

The results of the PCA indicate that the first three principal components for vegetative and floral characters accounted for 72% of the standardized variance. The first component explained 50% of the total variance, with the highest loading for the following characters: leaf length, leaf width, corolla length, style length, anther length, and filament length. The second component explained a further 12% of the variance, with the highest loading for calyx length and inflorescence type.

Five clusters were evident in the two dimensional PCA (Fig. 2). The type specimen of *E. angustifolia* is located in the upper part of the figure, separated from the other species by its narrow paniculate and racemose inflorescence-types, and larger acuminate leaf. *Erithalis harrisii* forms a single cluster, separated from the other clusters by its densely branched panicle inflorescence-type (sensu Delprete 1996) and recurved corolla lobes. A third cluster, separated from the rest by larger leaves, longer corolla and anthers, is comprised of *E. quadrangularis* and two specimens of *E. odorifera* from Dominica and St. Vincent, Lesser Antilles. In addition, these two *E. odorifera* specimens are small trees, similar in height and habit to *E. quadrangularis*. A fourth cluster grouped *E. odorifera* specimens, except for four individuals (Fig. 2), by characters of intermediate size between *E. quadrangularis* and *E. fruticosa* (Figs. 2, 3).

Erithalis diffusa, *E. fruticosa*, *E. salmeoides* and *E. vacciniifolia* formed a single cluster (Fig. 2), which also includes four individuals of *E. odorifera*. The

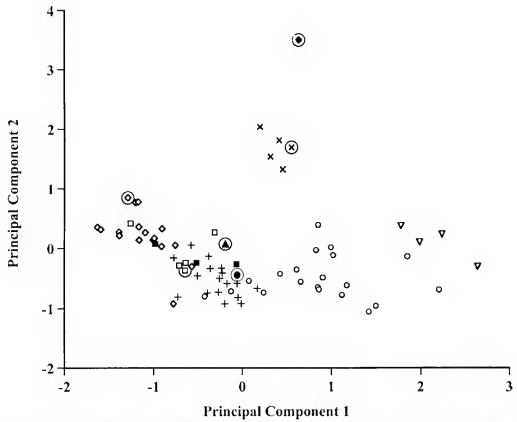

Fig. 2. Two dimensional PCA for floral and vegetative characters. The analyses involved 70 specimens. Symbols represent: ♦ = *E. angustifolia*, □ = *E. diffusa*, + = *E. fruticosa*, x = *E. harrisii*, ▲ = *E. insularis*, ○ = *E. odorifera*, ▽ = *E. quadrangularis*, ● = *E. rotundata*, ◇ = *E. salmeoides*, ■ = *E. vacciniifolia*. Circled symbols represent holotypes, isotypes or syntypes.

types of *E. insularis* and *E. rotundata* group within this cluster. Although overlap between *E. diffusa*, *E. fruticosa*, *E. salmeoides* and *E. vacciniifolia* was evident in this cluster (Fig. 2), the geographic distributions of *E. diffusa*, *E. salmeoides* and *E. vacciniifolia* are not continuous. Typical *E. salmeoides* is found on Great Inagua, Bahamas, northern Dominican Republic, Jamaica and Cuba, *E. diffusa* is found in San Salvador & Crooked Island, Bahamas, and *E. vacciniifolia* is found in Cuba and southern Dominican Republic. In addition to their geographic distribution, they differ in growth habit and stigma type. *Erithalis vacciniifolia* and *E. diffusa* are prostrate or sprawling shrubs, whereas *E. salmeoides* is an erect shrub. *Erithalis diffusa* and *E. salmeoides* possess a bilobed stigma (Fig. 4 A, B, E), whereas the stigma of *E. vacciniifolia* consists of 5–8 minute lobes, with papillae spreading along the style (Fig. 4, C, D, F). Also, the placement of the anthers above the stigma is distinctive in *E. salmeoides*.

Erithalis fruticosa overlaps in distribution with many of the species, and in these areas of sympatry there are individuals with intermediate characters, masking species delimitations. For instance, *E. fruticosa* and *E. odorifera* co-occur in the SW coast of Puerto Rico intergrading continuously in vegetative and

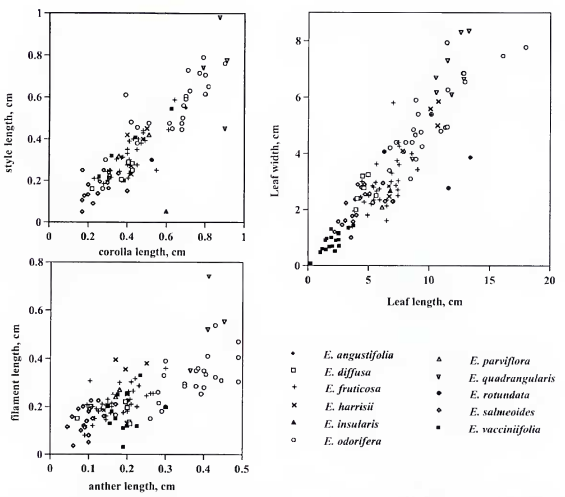

FIG. 3. Scattergrams of floral (A, B) and vegetative (C) characters. Symbols represent species, and each point represents an individual plant.

floral characters. Similarly, in Dominican Republic *E. vacciniifolia* and *E. fruticosa* occur together along the SE coast and intergrade continuously in stature and leaf size (McDowell, pers. obs.). In the Bahamas, *E. fruticosa* and *E. salmeoides* intergrade in their vegetative characters, but their floral traits are distinct. The presence of intermediates suggests hybridization. However, no experimental work has been done to investigate the potential for hybridization between the recognized species of *Erithalis*.

Most of the quantitative characters are not good discriminatory characters (Fig. 3). Nevertheless, it is obvious that specimens of *E. harrisii*, *E. quadrangularis*, and *E. odorifera* have distinctly larger flowers and leaves, compared to the other species of the genus (Fig. 3). *Erithalis vacciniifolia* has smaller and narrower leaves (Fig. 3C), whereas *E. salmeoides* has smaller flowers (Fig. 3A, B).

In summary, the PCA presented here provides support for recognition of four morphologically distinct groups, and a fifth poorly defined group. The distribution of individuals in the PCA ordination indicated the specimens of *E.*

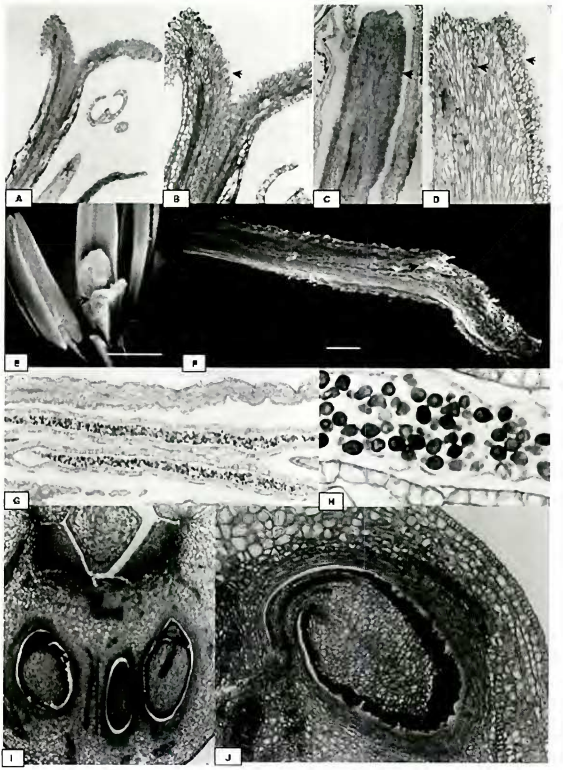

FIG. 4. Stigmas, anther, and ovules of *Erithalis*. **A–D, G–J.** Light micrographs of longitudinal sections. **E–F.** Scanning electron micrographs (SEM). A, B, E. Receptive bi-lobed stigma of *E. diffusa* (*Strittmatter s.n.*); Bar = 500μm. **C–D.** Stigma of *E. odorifera* (*Negrón-Ortiz 806*) from a flower bud showing the position of the stigmatic papillae (C), and detail of longitudinal slits of the middle lobes (D). F. Style of *E. vacciniifolia* (*Delprete 7551*) showing a minute and agglutinated lobe, and stigmatic papillae (arrow); Bar = 250μm. **G–H.** Basifixed anther (G, arrow) of *E. odorifera* (*Negrón-Ortiz 806*), and a close view of binucleated pollen grains (H). **I–J.** Pendulous ovules of *E. diffusa* (*Strittmatter s.n.*).

angustifolia, *E. harrisii*, *E. quadrangularis*, and *E. odorifera* were readily distinguishable from each other and from specimens of the other species. The remaining taxa, *E. diffusa*, *E. fruticosa*, *E. salmeoides* and *E. vacciniifolia*, do not show clear-cut taxonomic distinctions based on the two dimensional PCA. Although characters such as stigma type, placement of the anthers relative to the stigma, growth habit, as well as their geographic distribution (to some extent) can distinguish these four species, the lack of distinct groupings in the PCA could be a consequence of introgression between *E. fruticosa* and any of the other species.

Phylogeny

Monophyly, phylogenetic relationships, and biogeography of *Erithalis* have been investigated by Negrón-Ortiz and Watson (2002, 2003) using DNA sequence data of the Internal and External Transcribed Spacers (ITS and ETS) of nuclear ribosomal DNA, and the chloroplast *trn*L-*trn*F intergenic spacer. These analyses involved seven species of *Erithalis*, including multiple populations of the widespread *E. fruticosa* and *E. odorifera*, but excluded *E. angustifolia* and *E. insularis*. I was unable to relocate *E. angustifolia*, and *E. insularis* is only known from the type specimen (Zappi & Nunes 2000). Negrón-Ortiz and Watson (2002) concluded that *Erithalis* is a well-supported monophyletic genus (Fig. 5); the evidence includes an eight base-pair indel in the *trn*L-*trn*F intergenic spacer, present in all species of this genus but in neither of the outgroup taxa. In addition, both molecular and morphological data support a close relationship of *Erithalis* to *Chiococca* P. Browne ex L. (Bremer & Jansen 1991; Delprete 1996; Negrón-Ortiz & Watson 2002). Biogeographic analyses suggest that a combination of vicariance and dispersal events appears to be involved in the historical and present distributions of *Erithalis*, and support a Greater Antillean origin for *Erithalis* (Negrón-Ortiz & Watson 2003).

To provide a more robust resolution of phylogenetic relationships within *Erithalis*, I carried out parsimony analyses of a combined data set of molecular characters (ITS, ETS & *trn*L-*trn*F sequences) and five morphological characters (corolla lobe: recurved, straight; growth habit: prostrate, erect; inflorescence type: corymbose, paniculate, racemose, others; position of anther relative to the stigma: above, below; stigma lobes: bi-lobed, 5–8) using PAUP* 4.0b8 (Swofford 2001), with gaps treated as missing data and polymorphic states as uncertain. The Branch and Bound Search Option was employed with MULTREES in effect and Furthest Addition Sequence. Bootstrap analysis was conducted for 500 replicates, with tree-bisection-reconnection (TBR) and STEEPEST DESCENT in effect (Felsenstein 1985), and branch support analyses (Bremer 1998) were performed using Autodecay 4.02 (Eriksson 1999). In addition, the molecular data set was analyzed using hierarchical likelihood ratio tests to estimate the best-fit model for the data set (MODELTEST v3.06; Posada & Crandall 1998). This procedure showed that the K80+G model best fit the data, then the heuristic

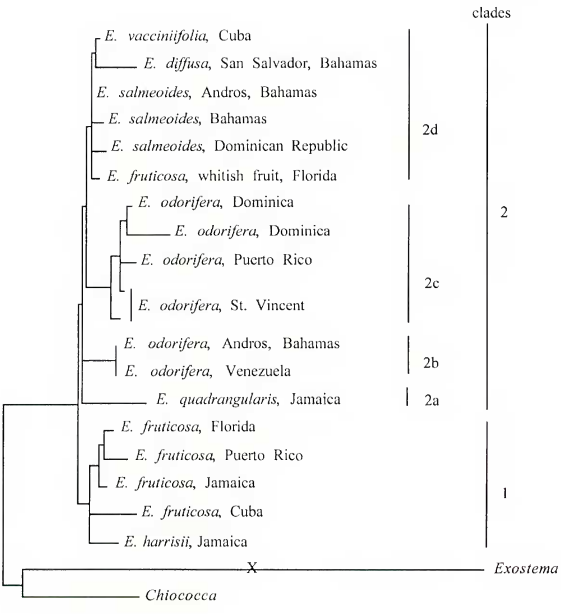

Fig. 5. The best maximum likelihood tree (–Ln = 4211.63789) inferred from analyses of molecular data. X = reduced 2.50 cm. Numbers represent clades.

ML analysis was done with random sequence addition for 100 replicates, MULTREES on and TBR branch swapping.

Analyses of the combined morphological and molecular data generated 13 most parsimonious trees of 101 steps (CI=0.561, RI=0.538, excluding constant and uninformative characters). Eight ML trees with a score of -Ln = 4211.63789 were recovered using the K80+G model of evolution (Fig. 5). The topology of the best ML tree is congruent with the 13 equally most parsimonious trees of

combined morphological and molecular data set, and to those obtained via the analysis of ITS, ETS, and *trn*L-*trn*F spacer (Negrón-Ortiz & Watson 2000). Therefore, a cladogram with the results of heuristic ML analysis is shown in Fig. 5.

The phylogenetic analyses consistently identified two weakly supported major clades (Fig. 5). Clade 1 weakly supports a sister group relationship of *E. harrisii* to multiple populations of *E. fruticosa* that occur in the Greater Antilles and Florida. These two shrubby species share corolla size (mean = 4.4 vs. 4.0 mm, respectively), a stigma of 5–8 minute lobes, but differ in leaf length (mean = 9.21 vs. 6.12 cm, respectively; Fig. 3C) and leaf width (mean = 4.61 vs. 2.83 cm, respectively; Fig. 3C), inflorescence type, corolla lobe curvature, and leaf texture. In *E. harrisii* the inflorescence is a densely branched panicle, the corolla lobes are strongly recurved, and the leaves are thick, glossy above and scabrous below. In *E. fruticosa*, the inflorescence is commonly cymose [some individuals have a sparsely branched panicle (sensu Delprete 1996), others a corymb inflorescence type], corolla lobes vary from somewhat reflexed to straight, and the leaves are usually leathery. *Erithalis harrisii* occurs in mid- to high elevations (~500–800 m) in the mountains of Jamaica, whereas *E. fruticosa* is mostly found at sea level throughout the Caribbean.

Clade 2 contains four subclades of five remaining species, but also includes one sample of the white-pinkish fruited *E. fruticosa* from Florida, suggesting that *E. fruticosa* is not monophyletic and/or that sample is of hybrid origin. Within clade 2, *E. odorifera* is largely monophyletic, with the exception of two samples from the Bahamas and Venezuela (subclade 2b), which fall outside the main *E. odorifera* subclade (2c). Perhaps, these populations lack sufficient molecular characters for supporting monophyly, or represent two cryptic lineages.

The Jamaican endemic *E. quadrangularis* is placed sister to the second major clade (2). *Erithalis odorifera* populations, morphologically resemble *E. quadrangularis*, sharing character states of floral morphology [linear anther shape and size (Fig. 3B), calyx length (mean = 0.13 cm), corolla length (Fig. 3A), stigma of 5–8 minute lobes (Fig. 4C, D, F), and upright growth habit]. *Erithalis quadrangularis* occurs at high elevations (600 - 800 m) in the mountains of Jamaica, at sea-level in the coast of St. Vincent (Lesser Antilles), and exhibits relatively larger (range = 8–21.7 vs. 6–13 cm in *E. odorifera*) and wider leaves (range = 3.5–10.1 vs. 3–7.7 cm in *E. odorifera*), axillary or terminal cymose-corymbose inflorescences (Fig. 6A), and recurved corolla lobes. *Erithalis odorifera* can be found from sea level to 300–500 m of elevation, exhibits axillary, cymose inflorescences (Fig. 6D), and straight corolla lobes.

The data weakly support a sister relationship of *E. odorifera* populations from the Lesser Antilles and Puerto Rico (subclade 2c) to subclade 2d which is composed of multiple species from the Bahamas, Florida, and the Greater Antilles. These two subclades exhibit more morphological differences than similarities. The *E. odorifera* subclade (2c) is comprised of shrubs or small trees with cymose

FIG. 6. Inflorescences of *Erithalis*. **A.** *E. quadrangularis* (*Harris* 12013). **B.** Solitary flower of *E. vacciniifolia* (*Pollard, Palmer & Palmer* 212). **C–D.** Axillary-cymose inflorescences of *E. fruticosa* (C, *Negrón-Ortiz* 795), and *E. odarifera* (D, *Negrón-Ortiz* 800). Bar = 1 cm.

inflorescences, larger corollas of 5–7 lobes, and long and wider leaves. The species of the Bahamas, Florida and Greater Antilles subclade (2d) are erect or prostrate shrubs, with corymbose inflorescences and/or solitary flowers or reduced cyme (sensu Delprete 1996), and small corollas (1.8–6.0 mm long; Figs. 3A, 6B).

The species of subclade 2d are morphologically distinct from each other, distinguished by differences in growth habit, leaf length and width, anther length, stigma type, and the placement of the anthers relative to the stigma. The taxa comprising this subclade vary from erect shrubs, such as *E. salmeoides*, to sprawling shrubs with prostrate branches, such as *E. diffusa* and *E. vacciniifolia*. *Erithalis vacciniifolia* displays smaller and narrower leaves, stigma of 5–8 minute lobes (Fig. 4F), and longer anthers (Fig. 3B). *Erithalis salmeoides* exhibits smaller anthers and styles (Fig. 3A, B), and the anthers extend above the stigma. *Erithalis salmeoides* and *E. diffusa* have a bi-lobed stigma (Fig. 4A, B, E).

In summary, the phylogenetic analyses presented here are in agreement with previous studies (Negrón-Ortiz & Watson 2002, 2003). The data confirm the monophyly of *Erithalis*, provide good resolution at the interspecific level, but do not support monophyly where more than one plant per species was sampled.

Geographic distribution and ecology

Erithalis is distributed from southern Florida throughout the West Indies, to Margarita and other Venezuelan islands, Quintana Roo (Mexico), the coast of Honduras, Colombia and the island of Fernando de Noronha, Brazil. The species occur in a wide variety of habitats, including coastal areas, open disturbed locales, rocky areas, montane areas, coppices, pinelands, sand dunes, limestone soils, and near coastal mangrove communities.

The species have bird-dispersed fruits (Bancroft & Bowman 1994; Negrón-Ortiz & Watson 2002, 2003), which helps explain the distribution of the genus across so many islands in the Caribbean, and the disjunct geographical distribution of *E. fruticosa* (Fig. 1).

FLORAL BIOLOGY

Inflorescence

The most common type of inflorescence is an axillary, many flowered compound cyme (Fig. 6); this varies greatly in length and number of flowers, and occurs either one or two per node. By various reductions or amplifications of development, these cymose inflorescences may appear paniculate, corymbose, or racemose. In other cases the inflorescence is reduced to a solitary, axillary flower (Fig. 6). In addition to these axillary inflorescence types, rarely terminal cymose-like inflorescences also occur in *Erithalis*.

The proximal portions of the inflorescences typically bear leaf-like bracts (pherophylls) of variable size and shape. In some cases the leaf-like bracts are similar in size and shape to leaves in the vegetative portion of the plant. The bracts decrease in size towards the distal parts, becoming small to minute.

Flowers

The flowers are bisexual, mainly white, but pinkish-white (Delprete, pers. obs.) and creamy-white corollas are also reported. The latter color, however, could be indicative of flower senescence (pers. obs.). Pentamerous corollas are typical in most species, but plants with 4–8-merous corollas do occur, and the number can vary even within a single inflorescence. Corolla lobes are mostly straight, but recurved corolla lobes are also present and characteristic of the Jamaican species *E. harrisii*. Rarely, both straight and recurved lobes occur within the same plant of certain species. Generally, the outside and inside of the corolla are entirely glabrous. In *E. harrisii* and some plants of *E. quadrangularis* an external indumentum is present, comprised of short hairs.

Stamens are present in the same number as the corolla lobes and alternate with the latter. The anthers are yellow, basifixed (Fig. 4E, G), and can be situated above, below or at the same level as the stigma. The latter character can be useful for species delineation, i.e., *E. salmeoides*. The pollen grains are binucleate (Fig. 4H). The bases of the filaments are either glabrous, with scattered hairs, or densely pubescent, and are connate forming a minute tube.

Erithalis exhibits two types of stigmas, which are of taxonomic importance (Fig. 4A–F). In almost all species the stigma consists of 5–8 minute lobes (usually 5), with papillae spreading along the style forming grooves (Fig. 4C, D, F). In only two species, *E. salmeoides* and *E. diffusa*, a bi-lobed stigma is present with papillae confined to the inside of the lobes (Fig. 4A, B, E). In the field, the papillae consisting of the first type of stigma change color from white to purple, indicative of loss of receptivity and senescence.

Erithalis displays two ripe fruit colors, dark-purple and whitish-pink. Whitish-pink fruit color has been reported in the Bahamas (Andros, Great Abaco, Great Inagua and Cat Islands), Florida (Miami), Virgin Islands (St. John), Cuba, and Mexico. Unique to *Erithalis* is the presence of a multi-locular ovary, whereas a single pendulous ovule per locule occurs in all genera of the Chiococceae (Fig. 4I, J).

Breeding systems

All species of *Erithalis* are monomorphic and homostylous. The flowers are fragrant, and produce abundant nectar. Neither secondary pollen presentation nor heterostyly occurs in any of the species. In addition, neither protandry nor protogyny was observed in the field (pers. obs.), so stigma receptivity appears simultaneous with anthesis.

The breeding system of dark-purple and whitish-pink fruited morphs *E. fruticosa* was examined at Fairchild Tropical Garden (FTG), Coral Gables, FL. The garden hosts small, wild populations of *Erithalis* where both fruit color morphs grow sympatrically. Eleven plants (7 dark-purple, and 3 whitish-pink fruited *E. fruticosa*) were marked, and five pollination treatments were designed to test the type of mating system (Negrón-Ortiz 1996). Emasculated and bagged flowers were tested for apomixis. Unpollinated and bagged flowers provided a test for autogamy; hand pollinated and bagged flowers tested for selfing, and emasculated, bagged and hand-pollinated flowers tested for outcrossing. Control flowers were neither bagged, emasculated, nor hand pollinated. Abscised corollas with their styles attached were examined for pollen tube growth (for details of methods see Negrón-Ortiz 1996), and at the end of field season, fruits from monitored flowers were collected and inspected for seeds.

A total of 350 flowers were monitored (subjected to pollination treatments and controls). Germinated pollen tubes were observed on the stigma of virtually every replicate for each pollination treatment, i.e., self, outcross, autogamy and control (Fig. 7A–C). Additionally, a greater number of pollen tubes reached

the middle of the style than the base (Fig. 8A), suggesting intraspecific pollen tube competition. In 97% of outcrossed flowers (63 of 65 monitored flowers) the tubes successfully reached the base of the style (Fig. 7A), and seeds were produced (Fig. 8B). In the self- and unpollinated-bagged (autogamy) treatments, however, approximately 90% of the tubes were arrested in the stigma (Fig. 7B), and only a few reached the base of the style producing fruits (Fig. 8).

The results indicate that allogamy, i.e., outcrossing, is the main mating system occurring in *E. fruticosa*. However, self-sterility is incomplete because a few mature fruits were produced after self- (3%) and unpollinated-bagged (autogamy, 6%) treatments (Fig. 8B). There is no evidence for asexual seed production (Fig. 8B).

Fruit set was significantly greater for cross-pollinated flowers than for controls (97% vs. 26 %), suggesting that most fruits from the control treatment resulted from selfing and/or self-pollen deposition. In addition, comparisons between fruit set of manual cross-pollinated flowers and the control treatment of open-pollinated flowers reveals whether floral visitors are effective as pollinators. The results are consistent with an explanation of insufficient pollinator visits or limited pollination efficiency (e.g., if most visitors are acting as nectar robbers). Nectar was abundant at noon, and the only visitors observed at this site were bees and butterflies. Thus, it is possible that the study site at FTG lacks the natural pollinators.

USES

Erithalis, specifically *E. fruticosa*, has various economic and medicinal uses. The wood has been used for posts and torches (Kimber 1988; Little et al. 1974). The bark, fruits, and the resin have diuretic and astringent properties and are used to treat inflammation of the kidney and bladder, and blennorrhoea (any mucous discharge from the urethra or vagina; Liogier 1990). The leaves are used to treat skin sores (University of the Virgin Islands 2002). Other uses include treatment of hemorrhoids and measles, use as a styptic, drink ('spirit'), and as charms against spirits/witches.

The leaves and fruits of *E. fruticosa* are used as a source of food by the rock iguanas of British Virgin Islands, the Florida Key Deer and by the threatened white-crowned pigeon. The plant is used as a larval host by the coleoptera *Plocctes bahamensis* Casey (Anderson 1991).

SYSTEMATIC TREATMENT

Erithalis

Erithalis P. Browne, Civ. Nat. Hist. Jamaica. 165, t. 17, fig. 3. 1756. TYPE SPECIES: *Erithalis fruticosa* L.

Herrera Adanson, Fam. des plantes 2:158. 1763. TYPE: based on P. Browne, Civ. Nat. Hist. Jamaica. 165, t. 17, fig. 3. 1756.

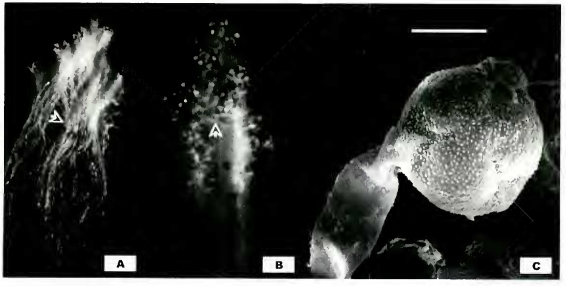

Fig. 7. Pollen grains and pollen tubes of ***Erithalis*. A–B.** Epifluorescent micrographs of *E. fruticosa* (*Negrón-Ortiz 795*). Pollen tubes following outcross (A) and self (B) pollinations. **C.** SEM pollen grain and tube of *E. vacciniifolia* (*Delprete 7551*), Bar = 10μm.

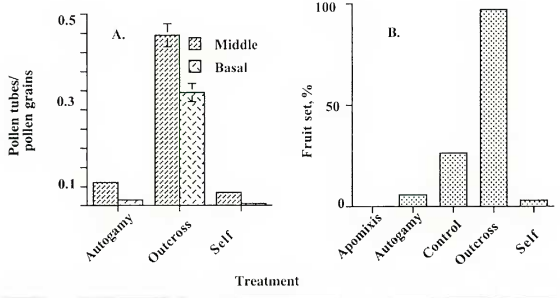

Fig. 8. Pollen tubes and fruit set per treatment. **A.** Ratio of pollen tubes in the style to pollen grains on the stigma; bars represent SE. **B.** Percent of fruit set per treatment.

Shrubs or **small trees**; raphides absent. Stipules interpetiolar, connate at base into cup-shaped sheath, truncate, deltoid to broadly triangular, apiculate, rarely acuminate, persistent. **Leaves** opposite, entire, long- to short-petiolate or sessile; blades acuminate, ovate, broadly ovate, broadly elliptic, narrowly obovate, obovate, oblong or oblanceolate, thinly to thickly coriaceous; domatia absent. **Inflorescence** axillary, paniculate and sparsely branched, corymbose, racemose,

uniflorous, cymose-paniculate, cymose-corymbose, glabrous or puberulent; middle bracts long or minute. **Flowers** bisexual, fragrant, pedicellate. **Hypanthium** ovoid, obovoid or globose. **Calyx** cup-shaped, lobes small, 5 to 10, broadly triangular, broadly ovate or rounded, absent or minute, persistent. **Corolla** hypocrateriform or narrowly infundibuliform or rotate, actinomorphic, white to cream-white, rarely pinkish-white; tube internally glabrous, some with an external indumentum of short hairs; lobes 4–8, slightly imbricate, oblong or linear, margin entire, rounded at apex, recurved or somewhat straight. **Stamens** alternate to the corolla lobes, 4–8; **filaments** attached at base of the corolla tube, basally connate, filiform, smaller, equal or longer than corolla tube, puberulent or pubescent at basal portion (glabrous above) or with a tuft of hairs at base; **anthers** situated above, below or at the same level of the stigma; narrowly elliptic, narrowly oblong, or linear, round at base, round or acute at apex, dehiscing by longitudinal slits, basifixed. **Pollen** tricolpate, exine surface echinate-perforate, released as monads, binucleate. **Style** exserted just beyond the corolla, terete, glabrous. **Stigma** bilobed or 5–8 lobed, minute and agglutinated, ovate or oblong. **Ovary** inferior, 2–5 locules, 5–20 celled; placentation axile, placenta reduced, ovules pendulous. **Fruit** drupaceous, with woody pyrenes; pericarp fleshy, dark purple or whitish-pink. **Seeds** laterally compressed; **embryo** small.

KEY TO THE SPECIES

1. Prostrate or sprawling shrubs, with decumbent branches.
   2. Leaves sub-orbicular, rounded at the apex, 3.8–5.9 cm × 1.8–3.4 cm, pedunculate; stigma bi-lobed, anthers 1.9–2.1 mm long, longer than the filament; inflorescence a cyme, or cymose-paniculate (Bahamas) ____ **E. diffusa**
   2. Leaves ovate, elliptic, obovate, rounded to obtuse at the apex, 1.3–4.7 cm × 0.8–1.9 cm; sessile or short pedunculate; stigma with 5–8 small lobes; anthers approximately 1.2–2.8 mm long, shorter than the filament; inflorescence either a cyme, a solitary flower, a raceme, or found in any combination within the same plant (Cuba and Dominican Republic) ____ **E. vacciniifolia**
1. Erect shrubs or trees, with upright branches.
   3. Leaves narrowly elliptic with blade tip acuminate; inflorescence narrowly paniculate with long stalks and/or racemose (Martinique, St. Vincent and Trinidad) ____ **E. angustifolia**
   3. Leaf blades ovate, elliptic, or obovate.
      4. Leaf leathery, glossy above and scabrous beneath; inflorescence densely paniculate; corolla lobes recurved (Jamaica) ____ **E. harrisii**
      4. Leaves leathery or papery, glabrous above and predominantly smooth beneath; inflorescences primarily cymose, some racemose, narrowly paniculate, or found in any combination within the same plant; corolla lobes typically straight, or somewhat recurved.
         5. Anthers positioned above the style; stigma bi-lobed; inflorescence usually less than 4 cm long, rarely longer (Bahamas, Dominican Republic, Cuba and Jamaica) ____ **E. salmeoides**
         5. Anthers positioned below or equal to the style, rarely above the style or in any combination; stigma with 5–8 small lobes; inflorescences 5–9.7 cm long.

6. Anthers linear, 1.4–5.0 mm long; inflorescence 8 cm long or longer; middle bracts large; leaf papery or coriaceous, 7.7–21.6 cm long; corolla lobes straight or recurved.
   7. Inflorescences axillary or terminal, cymose-corymbose; middle bracts 3.4–10.4 cm long; corolla lobes recurved in anthesis; leaf coriaceous, 8–21.6 × 3.6–10.1 cm (mountains of Jamaica and St. Vincent). _____ **E. quadrangularis**
   7. Inflorescence axillary, mainly cymose; middle bracts minute to 2.4 cm long; corolla lobes straight in anthesis, rarely recurved; leaf papery or coriaceous, 6–12.9 × 3–7.7 cm (Bahamas, Greater and Lesser Antilles, Venezuelan islands) _____ **E. odorifera**
6. Anthers ellipsoid, oblong, subglobose, in some cases somewhat linear, 0.7–3.5 mm long; inflorescence less than 8 cm long; middle bracts primarily minute; leaf coriaceous, 3.4–10.7 × 1.4–5.7 cm; corolla straight 4–6 lobes (throughout the Caribbean, Fernando de Noronha Island) _____ **E. fruticosa**

Erithalis angustifolia DC., Prodr. 4:465. 1830. TYPE: CUBA: without locality, 1825, *de la Ossa* (HOLOTYPE: G; IDC herbarium geneovense, microfiche!).

Erithalis acuminata Krug & Urb., Notizbl. Königl. Bot. Gart. Berlin. 1:319–320. 1897. TYPE: LESSER ANTILLES: Martinique, Guilding, 1877, *Duss 206* (HOLOTYPE: B, destroyed; LECTOTYPE: NY!, here designated).

Chiococca pulcherrima Wernh., J. Bot. 51:322. 1913. TYPE: LESSER ANTILLES: St. Vincent, without date, *Anderson 308* (HOLOTYPE: BM, ISOTYPE: K!).

Shrub 1–2 m high, the branches glabrous. **Leaves** coriaceaous; blades acuminate, gradually narrowed to the base, 6.2–13.8, 2.6–4.1; petioles 1.9–2.3 cm long. **Inflorescences** axillary, narrowly paniculate with long stalks and a few flowers, racemose, 9–10.5 cm long; glabrous; bracts minute. **Flower** pedicels 1–1.5 cm long. **Calyx** and hypanthium glabrate, calyx 0.9 mm long, denticulate. **Corolla** white, 1.7 cm long; **lobes** 5; **style** 5.5 mm long; stigmatic papillae 5 small lobes. **Stamens** 5; filaments white, 2 mm long, placed below the style; anther 3 mm long. **Fruit** a drupe, globose.

The name *E. angustifolia* is based on Candolle's description. The type is probably at G, while the photo is in the IDC microfiche, without number.

Distribution and ecology.—Found between 900–1100 m height in Montagne Pelée, Martinique, and St. Vincent and the Grenadines (Lesser Antilles). In addition, it was documented in the mountains of Trinidad.

Anderson collected *E. angustifolia* (as '*Chiococca pulcherrima*,' Fig. 9) in Trinidad, and described it as a scarce "beautiful shrub that grows on the summits of the highest mountains" (Wernham 1913). However, personal communication with Mr. Winston Johnson from the National Herbarium of Trinidad & Tobago indicates that *E. angustifolia* no longer occurs on the island.

Kimber (1988) listed this species (among others), and mentioned that all the species in the list were collected in 1962, 1963 and 1975. However, the species is not listed for the island in the document "Arbres de la Martinique-Les arbres

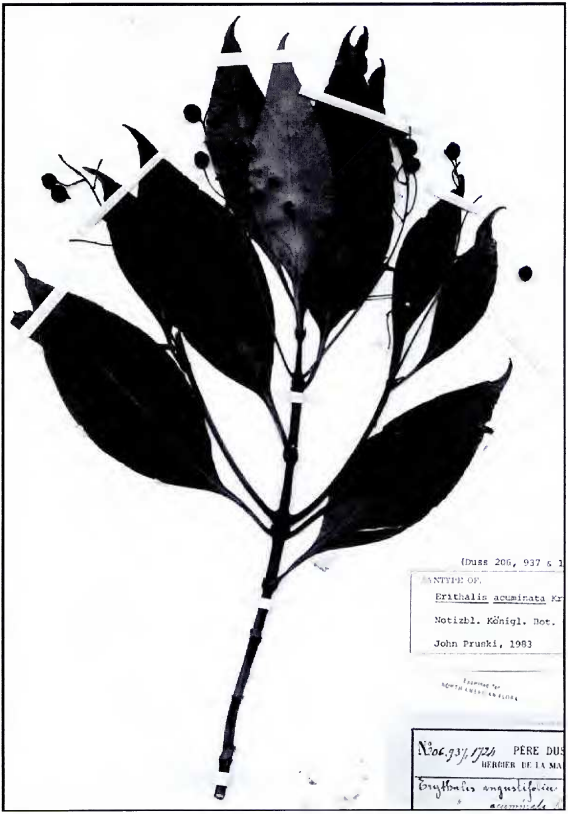

FIG. 9. *Erithalis angustifolia* (*Duss* 206) from Martinique, Lesser Antilles.

de la forêt martiniquaise–répertoire complet" written by F. Palli (www.palli.ch/"kapeskreyol/divers/arbres.html); only *E. odorifera* is documented.

Specimens examined: **TRINIDAD:** without locality, s.d., *Anderson 308* (Type of *Chiococca pulcherrima*, BM). **LESSER ANTILLES:** Martinique, Montagne Pelée, 1877, *Duss 206* (NY); Montagne Pelée, 1877, 1879, 1883, *Duss 206, 937, 1724* (SYNTYPE: NY; all numbers and dates on one label).

Common name.—Bois flambeau montagne.

Conservation status.—I was unable to locate *E. angustifolia* in St. Vincent and the Grenadines. According to Howard (1989), the Guilding collection cited by Urban may have been from St. Vincent Botanical Garden. However, I searched the collection at this institution, and found neither the plant nor records of its existence. I recommend searching for this species in Martinique and Trinidad to determine whether this taxon, is extinct. Certainly, it should be among the taxa in highly endangered of extinction.

Erithalis diffusa Correll., J. Arnold Arbor. 58:47. 1977. TYPE: BAHAMAS: San Salvador, N of airport, 21 Nov 1974, *Correll 43840* (HOLOTYPE: A; ISOTYPES: FTG!, NY!)

Sprawling shrubs to 1 m high, the branches prostrate on ground to low-arching. **Leaves** glossy above; the blades leathery and thick, sub-orbicular to broadly oval, rounded at apex, 3.8–5.9, 1.8–3.4 cm; the petioles 0.8–1.0 mm long; young leaves slightly sticky. **Inflorescences** axillary, cymose, cymose-paniculate, 4.7–7 cm long; middle bracts minute; or solitary flowers. **Flowers** fragrant, pedicellate. Calyx and hypanthium glabrate, calyx 5-denticulate, 0.4–0.5 mm long; hypanthium about 1.5 mm long. **Corolla** white, 2.2–4.5 mm long; tube 1.5 mm long; lobes 4 or 5, somewhat straight. **Stamens** 5; filaments white, 1–2.5 mm long; **anther** yellow, linear, 0.19–0.21 cm long; situated below or at the same level with the stigma; longer or as long as the filaments. **Style** 1.6–3.3 mm long; stigma bilobed. **Fruit** a drupe, orbicular, about 5 mm in dm, dark purple when ripe.

Distribution and ecology.—*Erithalis diffusa* (Fig. 10) is endemic to the Bahamas: San Salvador and Crooked Islands. It grows in rocky shore locations; common in beach strand, scrub-land, coppices and coastal thickets. This species is a component of the coastal vegetation of San Salvador, which is defined as the sea strand/sea oats community, consisting of sea oats (*Uniola paniculata* L.), sea grapes (*Coccoloba uvifera* L.), and railroad vine (*Ipomea pes-caprae* (L.) R. Br.), all of which assist in stabilization of the dunes.

Specimens examined: **BAHAMAS. Crooked Island:** 20 Feb 1975, *Correll* (FTG); 18 Feb 1975, *Correll 44380* (FTG). **SAN SALVADOR:** N of airport, 21 Nov 1974, *Correll 43840* (Type FTG, NY); *Strittmatter* s.n. 2000 (MU); along Snow Bay, 2 May 2000, *Vincent et al. 8955* (MU); N of Polaris, 7 Feb 1973, *Van Eenwyk et al. 4-2* (FTG); E of Field Station, 28 Dec 1980, *Thieret 52532* (MU).

Erithalis fruticosa L., Syst. Nat., ed. 10, 930. 1759. TYPE: JAMAICA: without locality, s.d. (HOLOTYPE: P, Browne, Civ Nat. Hist. Jamaica 1, t. 17, fig. 3, 1756).

Erithalis odorata Pers, Syn. Pl. 1:200. 1805, nom. Alt.

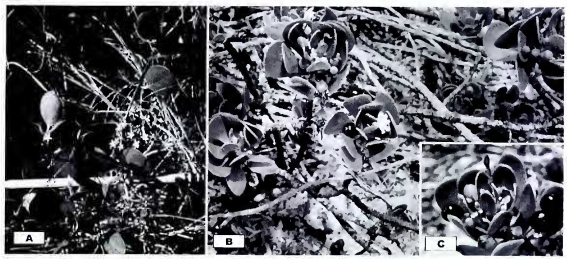

FIG. 10. *Erithalis diffusa* from San Salvador, Bahamas. **A.** Growth habit. **B.** Detail of the globose, dark-purple drupaceous fruit (Photographs by Eric J. Tepe and Michael Vincent).

Erithalis elliptica Raf., Sylva Tellur. 123. 1838. TYPE: JAMAICA: based on Swartz' description of *E. fruticosa*.

Erithalis harrisii Urb. var. *angusta* S. Moore ex Rendle, Fl. Jam. J. Bot. 73:279. 1935. TYPE: JAMAICA. Luana Point, Harris 9821 (HOLOTYPE: BM!).

Erithalis inodora Jacq., Select. Stirp. Amer. 73. 1763. *Erithalis fruticosa* var. *inodora* (Jacq.) Persoon, Syn. Pl. 1:200. 1805. TYPE: CURAÇAO: (no Jacq. specimen located).

Erithalis parviflora Griseb., Cat. Pl. Cub. 134. 1866. TYPE: CUBA: 1860–64, *Wright 2721* (HOLOTYPE: GOET!; ISOTYPES: K!, MO!, NY!, US!).

Erithalis revoluta Urb., Symb. Ant. 3:379. 1903. TYPE: PUERTO RICO: Guánica, Caña Gorda, *Sintenis 3796* (no type located). One set of Sintenis' West Indian collection was placed at B (now destroyed).

Erithalis insularis (Ridl.) Zappi & T.S. Nunes, Kew Bull. 55:655–656. 2000. Syn. nov. *Palicourea insularis* Ridl., J. Linn. Soc. Bot. 27:41. 1890. TYPE: BRAZIL: Pernambuco, Fernando de Noronha Island, 1887, *Ridley, Lea & Ramage 86* (HOLOTYPE: BM-n.v., not at BM per BM staff., LECTOTYPE: K!, here designated; ISOTYPE: B-destroyed, photo NY!).

Shrubs or **small trees** 0.6–8 m high, the branches mainly glabrous, some puberulent. **Leaves** glossy, leathery and thick; the blades dark-green above, obovate, oblong, elliptic-oblong, orbicular, oblanceolate, rounded or obtuse at the apex, 3.4–10.7, 1.4–5.7 cm; the petioles 0.4–5 mm long. **Inflorescences** cymose, cymose-paniculate, axillary or terminal, 5.8–6.8 cm long, the branches glabrous; bracts variable in length to minute. **Flowers** white, fragrant, pedicellate. Calyx and hypanthium glabrate, green, calyx 0.2–01.5 mm long. **Corolla** white, 2–6.5 mm long; **lobes** 4–6, straight. **Stamens** 4–6; **filaments** white, 0.8–3.8 mm long, the base with scattered hairs; **anther** yellow, 0.7–3.5 mm long, situated below or above the stigma. **Style** 1.1–6.0 mm long. **Stigma** with 5–8 minute lobes. **Fruit** a drupe, 3 to 5 mm in diameter, globose, dark-purple or whitish-pink; five to 14-celled.

Erithalis was established in 1756 (Browne 1756) based on *E. fruticosa* L. from Jamaica. In 1786, Forster, not aware of P. Browne's description, illegitimately used

the name *Erithalis* for a description of an entirely different genus, *Timonius* DC. (= *Timonius* Rumph., originally described in 1743).

Erithalis fruticosa (Fig. 11) is morphologically a highly variable species (Long & Lakela 1976). It is a slow growing, evergreen shrub that typically is 1 to 2 m in height, and can occasionally reach 8 m in height. Commonly, the species has multiple stems arising near the ground. The branches root when they come in contact with the ground. The bark is gray, and smooth to warty. The resinous wood is brown, hard, fine-textured, and heavy. The foliage may be dense or sparse depending on whether the shrubs grow in full sun or partial shade (pers. obs.).

The species flowers and fruits throughout the year (Little et al. 1974; Nelson 1996) with peaks during the dry months of January, February and March. The fruits can be either dark- purple or whitish-pink, and both color fruits occur sympatrically in populations of Andros Island (Bahamas) and Coral Gables, Florida. Acevedo-Rodriguez (1996) observed the whitish-pink fruited form in St. John, U.S. Virgin Islands. Correll reported it in Cat Island (FTG # 46194) and Great Abaco (NY # 45561), and Shafer in Cuba (NY # 2803). The dark-purple fruits have a bittersweet flavor and are dispersed by birds (Bancroft & Bowman 1994; Howard 1989; Liogier 1997; Little et al. 1974; Nelson 1996). Fruits collected in Puerto Rico averaged 0.1087 + 0.0071 g/fruit, and air-dried seeds separated from them averaged 0.00092 g/seed or 1,080,000 seeds/kg (Francis, JK).

Distribution and ecology.—Erithalis fruticosa occurs in Florida, the Bahamas, the Greater and Lesser Antilles, Trinidad, Quintana Roo (Mexico), Belize (Howard 1989; Little et al. 1974), Parque Nacional Morocoy and Venezuelan Caribbean islands (Liogier 1962), San Andrés, Providencia and Santa Catalina (Colombia; Jiménez-B. 2002), and the island of Fernando de Noronha (Brazil, Pernambuco). Although the species is reported for the Lesser Antilles, I did not see evidence of E. fruticosa during two recent collecting trips to St. Vincent and the Grenadines (Lesser Antilles).

Erithalis insularis is here placed as synonym of *E. fruticosa*, thus extending the range of *Erithalis*' distribution to the Atlantic Ocean. The fruits of *E. fruticosa* are dispersed by the threatened white-crowned pigeon in the Florida Keys and the Bahamas (Bancroft & Bowman 1994). Therefore, it is plausible that the disjunct geographical distribution exhibited by this species (Fig. 1) is a consequence of avian dispersal.

Erithalis fruticosa grows from near sea level to 120 m in elevation in Puerto Rico in areas that receive from 750 mm to about 1800 mm of annual precipitation (Little et al. 1974). The species is drought tolerant, and can grow in open areas and under the canopy of low-density forest. It is most common near beaches, on rock outcroppings and bluffs near the shoreline, especially in moist limestone areas, and on limestone hills in the interior. In Florida, it is found in beach strand vegetation, on sand dunes, and coastal hammocks (Nelson 1996).

FIG. 11. *Erithalis fruticosa*. **A.** Growth habit. **B.** Detail of the flower. **C–D.** White-pinkish (C; *Negrón-Ortiz* 794) and dark-purple (D; *Negrón-Ortiz* 795) fruits. (Photos A, B taken at Discovery Bay, Jamaica, and C, D at Fairchild Tropical Garden, Coral Gable, Florida).

In Martinique, it is reported as a component of the community of the littoral hedge, "a dense thicket at the seaward margin of the littoral woodland" (Kimber 1988).

Representative specimens examined. **U.S.A. FLORIDA. Dade Co.:** Coral Gables, Fairchild Tropical Garden, 1 Jan 1999, *Negrón-Ortiz* 794, 795, 798, (MU); Key Biscayne, Cape Florida State Park, 19 Jun 1970, *Gillis* 9439 (FTG). **Monroe Co.:** Big Pine Cay, 30 Apr 1958, *Travers* 710 (LL); 17 Feb 1991, *Orzell & Bridges* 15996 (LL). **Cuba:** without locality, 1860–1864, *Wright* 2722 (MO). **Camaguey:** 28 Oct 1909, *Shafer* 2803 (NY); **Matanzas:** Puerto Escondido, 16 Apr 1994, *Acevedo et al.* 6525 (NY). **Santiago:** rd. to El Morro, Jun 1943, *Bro. Clemente* 2830 (NY); without locality, Sep 1859-Jan 1860, *Wright* (s.n. MO); 17 Nov 1915, *Ekman* 6611 (MO). **Dominican Republic:** about 20 m W of Santiago, 19 May 1969, *Liogier* 15251 (NY). **Laguna Oviedo:** 18 Sep 1981, *Zanoni & Mejia* 16786 (MO). **La Altagracia:** 21 km SE Playa El Macao, 13 May 1980, *Mejia & Zanoni* 6527 (FTG). **Isla Catalinita:** 8 Oct 1981, *Zanoni & Mejia* 17126

(FTG, NY). **Haiti:** vicinity of Jean Rabel, 27 Jan–9 Feb 1929, *Leonard & Leonard* 12856 (MO). **JAMAICA. St. Mary Parish:** 5 m [mi] from Port Maria, 10 Jan 1960, *Adams* 6132 (MO); around Green Castle, 5 Jul 1963, *Crosby et al.* 509 (NY). **Puerto Rico Cabo Rojo:** Faro, 24 Dec 1998, *Negrón-Ortiz* 725, 726 (MU). **Guanica:** Dry Forest, 1 Jan 1998, *Negrón-Ortiz* 569 (MU). **Isla de Mona:** camino de Sardinera a Uvero, 28 May 1991, *Acevedo & Staca* 4359 (FTG). **Virgin Islands. St. John:** 21 Jun 1989, *Acevedo Rodriguez* 002731 (NY). **LESSER ANTILLES. Anguilla:** near beach, W end of the island, 5 Feb 1985, *Howard & Kellog* 19004 (NY) **BAHAMAS. Ackling Island:** about 4 m N of Pinefield, 21 Feb 1975, *Correll* 44462 (NY). **Andros:** May 1998, *Negrón-Ortiz* 655 (MU) **Anegada:** NW part of the island, 8 Jul 1990, *Smith* s.n. (FTG). **Cat Island:** between Dolphin Head and Zonicle Hill, 22 Nov 1975, *Correll* 46194 (FTG). **Crooked Island:** W of Colonel Hill, 20 Apr 1971, *Willis* 10609 (FTG). **Bimini Island:** about 0.5 m S of Ferry landing, 12 Jun 1964, *Stimson* 709 (LL); near middle of Cat Cay, 10 Jul 1975, *Correll & Correll* 45583 (FTG). **Great Abaco:** E end of Well's Cay, 25 Jun 1975, *Correll* 45561 (NY). **Grand Bahama:** 9 m ESE of W end, 23 Dec 1968, *Lewis* 7153 (FTG). **Grand Cayman:** 11 Nov 1979, *Correll & Correll* 51034 (FTG); 16 Aug 1938, *Kings* G.C. 335 (NY). **Great Exuma:** in marshland near Steventone, 7 Dec 1973, *Correll* 40770 (FTG); E of Stuart Manor, 9 Dec 1973, *Correll* 40862 (FTG), in coppice near George Town airport, 9 Jul 1978, *Correll* 49996 (FTG); Far Bay, 16 May 1989, *Houghton* 1098 (MO); Fartz 4003 (FTG). **Great Inagua:** 18 Oct 1904, *Nash & Taylor* 1149 (NY); Union Creek, 7 May 1970, *Hill* 479 (FTG). **SAN SALVADOR:** SE end, 27–28 Nov 1907, *Wilson* 7280 (NY). **Belize: Cayo Caulker**, 25 Jun 1981, *Whitefoord* 3320 (MO). **Turneffe Island:** 28 Feb 1942, *Egler* 42-6 (LL). **Gallows Point:** N end, 13 Oct 1977, *Janzen & Ives* 1117 (MO). **Water Cay:** 25 Mar 1967, *Dwyer et al.* 678 (MO). **Mexico. Quintana Roo:** W of Puerto Morelos, 4 May 1982, *Davidse et al.* 20049 (LL); Playa Puerto Morelos, *Tellez & Cabrera* 10794 (MO). **Venezuela. Parque Nacional Morrocoy:** ca. 5 km NE of Chichiriviche, 19 May 1984, *Ramirez* 925 (MO). **BRAZIL. Pernambuco:** Fernando de Noronha, 1887, *Ridley, Lea & Ramage* 86 (K).

Common names and uses.—'Black torch' (Bahamas, Belize, Florida, Puerto Rico & Virgin Islands); 'Black candlewood' (Cayman Islands); 'Cubra prieta' or 'Rompe machete' or 'Víbona' or Jayajabico' or 'Yayajabico' (Cuba); 'Candlewood' (Lesser Antilles); 'Tea' or 'Manglillo' (Puerto Rico & Virgin Islands).

The wood is resistant to rot and has been used for posts and torches (Kimber 1988; Little et al. 1974; University of the Virgin Islands 2002). Native people from Martinique used boughs of *E. fruticosa* for torches during late 1600s, and by 1930s the natives were still using it, thus contributing to the species decline in that island (Kimber 1988). The bark, fruits, and the resin have diuretic and astringent properties and are used to treat inflammation of the kidney and bladder, and blennorrhoea (Liogier 1990). The leaves are parched and ground for treating skin sores (University of the Virgin Islands 2002). Other uses include treatment of hemorrhoids and measles, and use as a styptic.

The leaves and fruits of *E. fruticosa* are used as a source of food by a few animals. The leaves represent 3.5% of the rock iguanas' diet on Anegada, British Virgin Islands (Mitchell 1999). The fruits are consumed by the Florida Key Deer (Dooley 1975), a Federal Endangered mammal, and by the threatened white-crowned pigeon during nestling (Bancroft & Bowman 1994).

Conservation status.—Threatened in Florida (www.plantatlas.usf.edu/browse2.asp?family=RUBIACEAE).

Erithalis harrisii Urban, Symb. Ant. 5:514. 1908. TYPE. JAMAICA: near Troy, 30 June 1904 (H), *Harris* 8743 (LECTOTYPE: NY 00115115, here designated).

Shrubs or **small tree** to 3–7.5 m tall, the branches puberulent. **Leaves** glossy above, scabrous below, thick; the blades obovate-oblong to elliptic-oblong, 4–10.9, 1.7–6 cm; the petioles 1–1.9 cm long. **Inflorescences** panicle, axillary or terminal, the branches puberulent; bracts 1–2, 0.9–2.8 mm. **Flowers** fragrant, pedicellate. **Hypanthium** globose. Calyx and hypanthium glabrate, calyx 5-denticulate, 0.5 mm long. **Corolla** white, 4–4.8 mm long; lobes 5, recurved. **Stamens** 5; filaments white, the base densely puberulent, 1.3–4 mm long, as long as or 3/4 as high as the style; **anther** yellow, linear, 1.5–2.5 mm long. **Style** 2.3–4.5 mm long. **Stigma** of 5–8minute lobes. **Fruit** globose, green when immature, turning red to dark-red when mature or pink.

Distribution and ecology.—This species (Fig. 12) is endemic to the mountains of Jamaica. It is found in a few localities of woodland margins on rough limestone. It grows on rocky banks, at 500–800 m elevations.

Conservation status.—This taxon is listed under the 2003 IUCN Red List of Threatened Species and considered a low risk species, subcategory: nt (WCMC 1997).

Specimens examined. **JAMAICA:** near Troy, 30 Jun 1904 (fl), *Harris* 8743 (NY); syntypes: [NY (00115114), US]. **Trelawny Parish:** 1 Jan 1999 (fl), *Negrón-Ortiz* 789 (MU); 791 (MU); 14 Aug 1963, *Crosby & Anderson* 1196 (LL); Ramgoat cave, N of Albert Town, 29 Jul 1962, *Fosberg* 42935 (NY). **St. Ann Parish:** Mount Diablo, 12 Jul 1989, *Nesbeth & Scott* 078 (MO); road to Hollymount, 21 Sep 1962, *Adams* 11680 (MO). **Clarendon:** 30 Sep 1912, *Harris* 11227 (MO).

Erithalis odorifera Jacq., Select. Stirp. Amer. Hist. 72, pl. 173 (fig. 23: flower & fruit). 1763. *Erithalis fruticosa* L. var. *odorifera* (Jacq.) Grisebach, Fl. Brit. WI. 336. 1861. *Erithalis fruticosa* L. subsp. *odorifera* (Jacq.) Steyermark, Fl. Venez. 9:869. 1974. *Erithalis odorata* Raf., Sylva Tellur. 123. 1838. (LECTOTYPE: Jacquin, Martinique. Plum. ic. 249, f. 2, here selected).

Erithalis rotundata Griseb., Mem. Amer. Acad. Arts 2, 8:507. 1862. TYPE: CUBA. Monte Verde, Jan–Jul 1859, *Wright 1268* (LECTOTYPE: GOET!, here designated), ibid, *Wright 1267* (SYNTYPES: GOET!, MO!); ibid, *Wright 1268* [SYNTYPES: MO! (2 copies), NY! (2 copies)].

Large shrubs or **small trees** to 1–8 m tall, the branches glabrous. **Leaves** glossy, leathery and thick or papery; the blades obovate-oblong to elliptic-oblong, 6–13, 3–7.7 cm; the petioles 0.05–3.2 cm long. **Inflorescences** cymose, axillary, 9–9.7 cm long, the branches glabrous; bracts minute to 2.2 cm long. **Flowers** sweet fragrant, pedicellate. Calyx and hypanthium glabrate, calyx 0.5–1.1 mm long. **Corolla** white, 3.9–9 mm long; lobes 5–7, straight, rarely recurved. **Stamens** 5–7; filaments white, the base glabrous or with scattered hairs, 1.5–5 mm long; **anther** yellow, linear, 2–5 mm long. **Style** 1.2–8 mm long. **Stigma** of 5–8 minute lobes, rarely bi-lobed. **Fruit** a drupe, globose, dark-purple when mature.

Distribution and ecology.—The Bahamas, Greater and Lesser Antilles, and Caribbean coast of Venezuela.

Erithalis odorifera (Fig. 13) grows near the beach, on sandy coastal thickets, coppice, along the road, and from sea level to ~300 m in elevation; occurring solitary to abundant. This species is very distinctive in the Lesser Antilles, and according to Sandwith (1938), "it appears to replace *E. fruticosa*" in most of these

FIG. 12. *Erithalis harrisii*. **A.** Portion of a small tree with glossy leaves (arrows). **B.** SEM of the style and stamens. Bar = 1000µm. **C.** Inflorescences with immature fruits, flowers in anthesis, and flower buds; note the recurved corolla lobes. (Photos A & C taken in Trelawny Parish, Jamaica).

islands. When it overlaps in distribution with *E. fruticosa*, individuals with intermediate characters are formed, bridging the taxonomic-diagnostic character between these two species.

Specimens examined. **BAHAMAS. Andros:** S of Maidenhair Coppice, 24 May 1997, *Vincent* et al. 7784 (MU); May 1998, *Negrón-Ortiz* 654 (MU). **Great Abaco:** Lubbers Quarters Cay, 4 Jul 74, *Correll et al.* 42568 (FTG). **New Providence:** Lake Cunningham, 25 Sep 1963, *Popenoe* (bar code 000162, FTG). **St. Kitts:** 18 Jun 1944, *Beard* 289 (MO) **CUBA:** 1865, *Wright* 1869 (NY), 26 Aug 1893, *Combs* 538 (NY). **DOMINICAN REPUBLIC. Barahona:** Boca de Maniel, 20 May 1981, *Zanoni et al.* 13514 (MO, NY). **El Seibo:** Los Haitises, 29 Jun 1982, *Zanoni* et al. 21105 (NY). **La Altagracia:** Laguna Bávaro, 29 Apr 1981, *Zanoni et al.* (FTG). **HAITI:** without locality, 14 Aug 1903, *Nash* 431 (NY); W of Jeremie, 28 Dec 1941, *Holdridge* 923 (NY); vicinity of St. Louis du Nord, 7 Apr 1929, *Leonard* & *Leonard* 14398 (NY). **Puerto Rico. Arecibo:** Barrio Río Arriba, Río Abajo Forest Reserve, 6 Jul 1994, *Axelrod* et al. 7928. **Cabo Rojo:** Guanquilla, La Mela, near the ocean, Jan 1999, *Negrón-Ortiz* 700 (MU). **Río Grande:** Barrio Zarzal, Punta Picúa, 2 Jun 1992, *Proctor & Rivera* 47972 (FTG) **Isla Vieques:** Sun Bat, Half Moon Beach, 26 Nov 1981, *Hansen et al.* 9461 (FTG) **US VIRGIN ISLANDS. St. John:** 21 Jan 1991, *Acevedo* et al. 3988 (NY); Jumbie Beach, 17 Jun 1984, *Mori* et al. 16594 (NY). **LESSER ANTILLES. Dominica:** Bataka area, 10 Jan 1994, *Higgins* 102 (NY). Grand Bay, near point Carib, 27 Jul 1964, *Wilbur et al.* 8020 (MO); near

FIG. 13. *Erithalis odorifera*. **A.** Habit of an immature shrub. **B.** Flowers in anthesis; note the variation of corolla lobe number. **C.** SEM of the style and stamens. Bar = 1000µm. (Photos A & B taken on Bequia island, St. Vincent and the Grenadines, Lesser Antilles).

Ansedume on the northern coast, 11 Aug 1964, *Wilbur* et al. 8304 (MO, LL); Bluffs leading down to L'Anse Noire, 16 Jul 1964, *Wilbur et al.* 7517 (LL, MO); St. Andrew Parish, 28 Aug 1992, *Lee* 57 (NY); St. David Parish, 12 Mar 24751, *Hill* 24751 (NY). **Guadaloupe:** without locality, 1894, *Lee* 2557 (NY); 6 Aug 1973, *Sastre & Jeremie* 1861 (MO). **Martinique:** without locality, 1879, *Duss* 945 (NY). **St. Vincent and the Grenadines:** along the road, Jan 2000, *Negrón-Ortiz* 800 (MU); *Negrón-Ortiz* 807 (MU).

Common names and uses.—'Scented blacktorch' (Bahamas, Puerto Rico); 'Bwa flanbo' or 'Bwa chandèl' or 'Flambeau noir' or 'Bois chandelle' or 'Bois flambeau' (Dominica, Martinique); 'Parrot apple' (Tobago). In Dominica, the plant (part not specified) is used as a drink ('spirits'), and the twigs as charms against spirits/witches [label data, *Higgins* 102 (NY)].

Erithalis quadrangularis Krug & Urb., Notizbl. Königl. Bot. Gart. Berlin. 1:320. 1897. TYPE: JAMAICA: Manchester, 29 Apr 1896, *Harris 6318* (HOLOTYPE: B-destroyed; LECTOTYPE: NY!, here designated).

Large shrub or **small tree** to 3.5–9 m tall, the branches glabrous. **Leaves** leathery and thick; the blades oval, ovate-elliptic, 8–21.6, 3.5–9.2 cm; the petioles 1–1.9 cm long. **Inflorescences** cymose-corymbose, axillary or terminal, 5.25–11.5 cm long; bracts 3.5–10.4 cm long. **Flowers** fragrant, pedicellate. Calyx and hypanthium glabrate or puberulent, calyx denticulate, 1–2.1 mm long. **Corolla** white, turning yellow, 6.8–12 mm long; lobes 6–8, recurved. **Stamens** 6–8; filaments white, 3–7.8 mm long, the base with scattered hairs; **anther** yellow, linear, 3.5–4.8 mm long. **Style** 4.5–10 mm long. **Stigma** of 5–8 minute lobes. **Fruit** subglobose.

Distribution and ecology.—*Erithalis quadrangularis* (Fig. 14) is endemic to Jamaica and to St. Vincent and the Grenadines. Known from a few Jamaican parishes: St. Ann, Clarendon, Manchester, and from Unity Valley district. It grows in woodlands on limestone, on rocky slopes, along roads, from sea level to 457 m elevation, and is not common. Although in many cases morphologically similar to *E. odorifera*, *E. quadrangularis* could be distinguished by longer, wider and thicker leaves, longer inflorescences, and recurved corolla lobes.

Conservation status.—This taxon is listed under the 2003 IUCN Red List of Threatened Species and represents a vulnerable species, criteria: B1, 2c (WCMC 1997).

Specimens examined. **JAMAICA. Unity Valley District:** between Moneague and Mt. Diablo, 2 Jul 1965, *Proctor* (I.U.). **St. Ann Parish:** 23 May 1965, *Proctor* 26422 (I.U.); Douglas Castle District, 11 Jun 1976, *Thorne & Proctor* 48167 (NY); Albion Pen, 12 May 1915, *Harris* 12013 (NY). **Clarendon Parish:** 22 May 1912, *Harris* (NY); Peckham Woods, May 1955, *Robertson* 2005 (NY); **Manchester Parish:** Maudeville, 21–23 Sep 1908, *Britton* 3748 (NY); New Yveeu, 21–23 Sep 1908, *Britton* 3756 (NY); Marshall's Penn, 30 May 1959, *Proctor* 19678 (NY); vicinity of Marshalls Penn Est., 23 Apr 1961, *Kramer & Proctor* 1682 (NY); 25 Jul 1997, *Barcelona et al.* 1196 (MU). **Near Manchester:** New Green, 29 Apr 1896, *Harris* 6318 (NY). **LESSER ANTILLES. St. Vincent and the Grenadines:** along the road, Jan 2000, *Negrón-Ortiz* 806 (MU).

Erithalis salmeoides Correll, J. Arnold Arbor. 58:49. 1977. TYPE: BAHAMAS. GREAT INAGUA: between Conch Shell Point and Lanter Head, 3 Aug 1975, *Correll* 45897 (HOLOTYPE: AU; ISOTYPE: FTG!).

Shrubs 3–7.5 m tall, the branches glabrous. **Leaves** leathery and thick; the blades obovate to broadly oval, rounded at the apex, 1.9–4.7, 1.2–3.8 cm; the petioles 0.4–0.9 cm long. **Inflorescences** cymose, cymose-paniculate, axillary, 4.5–5.4 cm long, glabrous; bracts variable to minute. **Flowers** fragrant, pedicellate. **Calyx** and hypanthium glabrate, calyx denticulate, 0.1–0.6 mm long. **Corolla** white, 1.7–4 mm long; lobes 4–5, straight. **Stamens** 4–5, longer than the style; filaments white, 0.3–2.5 mm long, the base with scattered hairs; **anthers** ellipsoid, 0.2–1.9 mm long. **Style** 0.5–2 mm long. **Stigma** bi-lobed. **Fruit** orbicular, dark-purple or whitish-pink.

Distribution and ecology.—Bahamas (Fig. 15): Great Inagua, Little Inagua, Mayaguana; Turks & Caicos; Dominican Republic, Jamaica, and Cuba.

This species is morphologically variable. In the southern Bahamian islands,

FIG. 14. *Erithalis quadrangularis* (*Proctor* 26422) from St. Ann Parish, Jamaica.

the species is reported as a low shrub, but in other areas it is taller in habit and morphologically (e.g., leaf size and shape, inflorescence length) indistinguishable from *E. fruticosa*, except for the position of the anthers with respect to the stigma height and the bi-lobed stigma (vs. stigma of 5–8 minute lobes, stamens positioned ≤ than the style, in *E. fruticosa*). In the molecular data phylogeny several specimens of *E. salmeoides* are placed in a polytomy with *E. fruticosa*, suggesting a close relationship or hybridization between these species.

Representative specimens examined. **BAHAMAS. Great Inagua:** Nov 1890, *Hitchcock* s.n. (MO), Salt Point Hill, 15 Dec 1997, *Freid* 97-093 (MU); 12 Oct 1904, *Nash & Taylor* 949 (NY); between Conch Shell Point and Lanter Head, 3 Aug 1975, *Correll* 45897 (Isotype FTG), near Smith's Thach Pond, between Conch Shell Point and Lanter Head, 23 Jul 1976, *Correll* 47475 (FTG, MO); near entrance to Flamigo Reserve, 27 Jul 1976, *Correll* 47565 (FTG). **Little Inagua:** Moujean Harbor, 17 Jul 1976, *Correll* 47351 (FTG). **Mayaguana:** S of Low Point Bay, 8 Feb 1973, *Proctor & Gillis* 33173 (MO). **Turks & Caicos:** Pine Cay, 24 Jan 1993, *Raven* 28205 (FTG, MO, NY); Salt Cay, Long Bay Point, 13 Jun 1979, *Buden* 23 (FTG); Providenciales, 16 Dec 1975, *Correll* 46406 (FTG, NY); 17 Dec 1975, *Correll* 46445 (FTG, NY). **Grand Turk:** Mount Wisdom, 20 Dec 1975, *Correll* 46558-A (FTG, NY). **CUBA. Southern Baracoa:** 17 Jul–4 Aug 1924, *Fre. Leon* 12413 (NY). **DOMINICAN REPUBLIC. Monte Cristo Prov.:** El Morro de Monte Cristo, 19 Jul 1981, *Judd et al.* 2992 (FTG, NY). **Jamaica. Pedro Bluff:** honey-combed limestone, 9 Jul 1907, *Harris* 9718 (NY).

Erithalis vacciniifolia (Griseb.) Wright, Anal. Acad. Ci. Habana 6:126. 1869. *Chione vacciniifolia* Griseb., Cat. Pl. Cub. 133. 1866. *Erithalis fruticosa* L. subsp. *vacciniifolia* (Griseb.) Borhidi, Bot. Közlem. 58:177. 1971. TYPE: CUBA: Baracoa, 1860–64, *Wright 2719* (HOLOTYPE: GOET!; SYNTYPE: K!).

FIG. 15. *Erithalis salmeoides* (*Raven* 28205) from Pine Cay, Bahamas.

Prostrate or **creeping shrub** to 2 m tall, the branches glabrous or puberulent. **Leaves** glossy, leathery and thick; the blades obovate or broadly oval, 1.1–4.7, 0.8–1.9 cm; sessile or short-petiolate, the petioles to 0.3 cm long. **Inflorescences** cymose, or cymose-paniculate or solitary flowers, axillary; bracts minute up to 2 mm long. **Flowers** fragrant, pedicellate. Calyx and hypanthium glabrate, calyx denticulate, 0.5–0.8 mm long. **Corolla** white, 2.5–6.5 mm long; lobes 4–6, straight. **Stamens** 4–6; filaments white, 0.3–3.6 mm long, the base with scattered hairs; **anther** yellow, linear to ellipsoid or oblong, 1.2–2.8 mm long. **Style** 1.2–5.2 mm long. **Stigma** of 5–8 minute lobes. **Fruit** globose, dark purple to blackish.

Distribution and ecology.—Cuba and Dominican Republic (Fig. 16) (Isla Beata, collected in 1950, but not re-collected since then). Found growing on

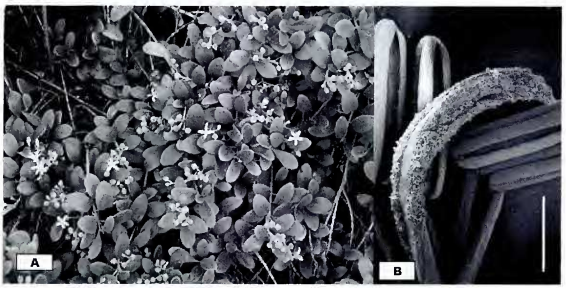

FIG. 16. *Erithalis vacciniifolia* from Dominican Republic, Greater Antilles. **A.** Habit. **B.** SEM of the style and stamens (*Delprete* 7551 NY). Bar = 1000μm. (Photo A was taken by Piero Delprete).

coastal thickets, on limestone hills or coastal cliffs, sandy beach, and in depressions in limestone rock. Common.

Specimens examined. **BAHAMAS. Andros:** 18 Aug – 10 Sep 1906, *Brace* 5152 (NY). **CUBA. Santiago:** 10 Mar 1938, *Bro. Clemente* 2352 (GH); oeste de la playa de Zuragúa, Oct 1950, *Hno. Clemente & Chrysogone* 7434 (GH); 7 Nov 1917, *Ekman* 8711 (GH); El Morro, 10 Mar 1938, *Bro. Clemente* 2351 (GH); Siboney, 18 Jul 1953, *Bro. Alain & López Figueira* 3056 (GH); near Siboney, Apr 1949, *Bro. Clemente* 6557 (GH, NY); El Dudosa, Pilón, Jul 1949, *Bro. Alain* 1099 (GH); May 1947, *Bro. León* 22794 (GH); vicinity of Baracoa, 1–7 Feb 1902, *Pollard* et al. 212 (GH); near Santiago, 13 Apr 1902, *Hamilton* 233 (NY). **DOMINICAN REPUBLIC:** E of ciudad Trujillo, on road to Boca Chica, Cancedo beach, Dec 1962, *Bro. Augusto* 455 (NY); 1 Apr 1958, *Moore* 7578 (GH). **Barahona:** N end of Beatu Island, 9 Aug 1950, *Howard* 12416 (GH); Caucedo, 15 Feb 1964, *Bro. Augusto* 1362 (NY).

EXCLUDED TAXA

Illegitimate names include: *Erithalis obovata* Forst., *Erithalis timon* Spreng., and *Erithalis polygama* Forst. var. *timonius* Willd., all of which are synonyms of *Timonius timon* (Spreng.) Merr. var. *timon* (Darwin 1993). *Erithalis uniflora* Gaertn. is *Polyphragmon minus* A. Rich. ex DC., a description based upon a fruit of unknown origin (Standley 1934), and *Erithalis cymosa* Forst. is *Timonius forsteri* DC (Candolle 1830; Lioger 1962). *Erithalis pentagonia* DC is synonym of *Dendropanax arboreous* (L.) Dec. & Planch; Araliaceae), described from Cuba (Liogier 1962; Standley 1934).

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